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FIELDIANA

Geology

NEW SERIES, NO. 24

The Ear Region in Xenarthrans (= Edentata: Mammalia) Part II. Pilosa (Sloths, Anteaters), Palaeanodonts, and a Miscellany

†Bryan Patterson

†Walter Segall

William D. Turnbull

Timothy J. Gaudin

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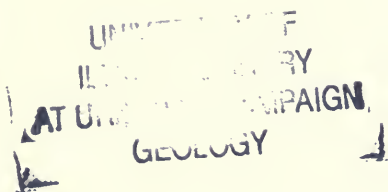
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NEW SERIES, NO. 24



The Ear Region in Xenarthrans (= Edentata: Mammalia) Part II. Pilosa (Sloths, Anteaters), Palaeonodonts, and a Miscellany

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Preface

This paper represents the second and final portion of Bryan Patterson and Walter Segall's study of the bony anatomy of the xenarthran ear region. The history of this project was outlined by Turnbull in the preface to Part I—Cingulates (Patterson et al., 1989). To review it briefly, it was the result of a decade of collaboration, starting some time in the late 1940s, between Patterson, who was at that time Curator of Fossil Mammals at the Field Museum, and Segall, a research associate with the museum and a Chicago area physician specializing in eye, ear, nose, and throat. Patterson took the only copy of the manuscript with him to Harvard when he left the museum in 1955, and he worked on the study sporadically in the ensuing years. Much to Segall's regret, Patterson never completed it.

As was detailed in Part I, after Patterson's and Segall's deaths, one of us, William Turnbull, pulled together what could be found of the original manuscript and figures and began work on revising them for publication. The figures were photographed on high contrast negatives to eliminate some of the accumulated damage. The figures lacked labels, except for a few of Patterson's penciled-in notations. The labels those figures now bear are thus attributable almost entirely to the work of the latter two authors, Turnbull and Gaudin. We decided on the features to be labeled according to our interpretation of what was needed by or intended in the original manuscript.

This second part of the original study, detailing the anatomy of the auditory region in sloths, anteaters, and palaeonodonts, and the morphology of the ear ossicles for the order as a whole, was far less complete than the first half of the study, and far less straightforward in its organization. We have therefore made much more substantial additions and revisions of this manuscript than was needed in Part I. A fair amount of new material has become available for these groups since Patterson and Segall completed the bulk of the work on this study. We have examined some of this new material, and have included notes on new specimens for several of the described genera, including *Glossotherium*, *Lestodon*, *Nothrotheriops*, *Hapalops*, *Palaeonodon*, and *Metacheiromys*. As in Part I, any additions or revisions made to the paper by the latter two authors are set off in square brackets [] so that they can be distinguished from the original work. Other taxa that were not discussed in the original manuscript, but for which good spec-

imens are now available, are not covered here. For further information on the auditory region in these forms, the reader is referred to the works of Hirschfeld and Webb (1968, *Pliometanastes*), Fischer (1971, *Mesocnus* and *Neocnus*), Hirschfeld (1985, *Pseudopreotherium*), Frailey (1986, *Stenodon* and *Nothropus*), and Webb (1989, *Thi-nobadistes*). In addition, as mentioned in Part I, the works of Guth (1956ab, 1957, 1961, 1962) on the temporal region of xenarthrans in many ways parallel this study, but they are based on a completely different set of specimens and come to somewhat different conclusions. Guth's 1961 paper, a monograph which synthesizes all the earlier work, is an essential companion to this study but is difficult to obtain.

In Part I, Turnbull discussed how difficult a task it is for any outside party to join in an effort of this sort, not knowing why the original study was never finished, or whether or not the first two authors would have wished others to meddle with their work. We have weighed the pros and cons of the situation carefully and have concluded that Patterson and Segall would want the time, effort, and insight invested in this study to be made available to present and future students of mammalian evolution, and that they would approve of our decision to publish their manuscript. We hope that in our various additions and revisions we have done the two senior authors no disservice, and that the information contained in the figures and descriptions of this monograph proves valuable to those interested in xenarthran evolution and the structure and evolution of the mammalian auditory region in general.—W.D.T. & T.J.G.

The fortuitous arrival of Tim Gaudin on the scene at the University of Chicago in the Department of Organismal Biology and Anatomy at the precise time for this project has meant that this portion of the Patterson-Segall study is being readied at least two or three years ahead of the time it would have taken me to complete the work. Furthermore, with his focus so directed on the Xenarthra, it is an ideal collaboration. Most important, it has permitted a more extensive expansion of the original manuscript than I could have managed alone. Hence, this has been a true collaboration, which has made it possible to maximize the updating that was needed. And for me personally, it is great to gain such a diligent and enthusiastic young colleague to work with.—W.D.T.

The Ear Region in Xenarthrans (= Edentata: Mammalia) Part II. Pilosa (Sloths, Anteaters), Palaeanodonts, and a Miscellany

†Bryan Patterson †Walter Segall
William D. Turnbull Timothy J. Gaudin

Abstract

This paper is the second in a series of two works detailing the descriptive and comparative anatomy of the xenarthran ear region (basicranium and its immediate surrounds, including the middle but not the inner ear). The study was begun by Patterson and Segall in 1945 and continued until Patterson's departure from the Field Museum in 1955, but was never completed. Part I (Patterson et al., 1989) covers the anatomy of the auditory region in cingulates, i.e., armadillos, pampatheres, and glyptodonts. This paper examines the auditory anatomy of the Pilosa, i.e., sloths and anteaters, and the Palaeanodonta. Descriptions are provided for 20 extinct and extant sloth genera, four living and extinct genera of anteaters, and three genera of the extinct suborder Palaeanodonta. In addition, a section detailing the morphology of the auditory ossicles of all groups of living and extinct xenarthrans, both cingulates and pilosans, is included. The comparative anatomy of this region of the xenarthran skull provides new evidence in support of a monophyletic grouping of palaeanodonts and xenarthrans exclusive of pangolins, and a diphyletic origin of the living tree sloths, with *Choloepus* being linked to the extinct family Megalonychidae and *Bradypus* to the extinct family Megatheriidae. The suggestion is also put forward (although somewhat weakly supported) that the Megatheriidae and Megalonychidae form a monophyletic clade, with the family Mylodontidae as the sister group to this clade.

Introduction

William D. Turnbull and Timothy Gaudin

This work (Pilosa) constitutes Part II of the original Patterson and Segall manuscript on the ear region of the Xenarthra. As was discussed in Part I (Cingulates), the original outline of the study called for an introduction with a general discussion of the anatomy of the auditory region, a main systematics section, and a conclusion. Unfortunately, no text has been found for either the first or last section, although undoubtedly such text existed at some time in the past. We have thus written a brief introduction and conclusion ourselves. The introduction, as in Part I, is an attempt to provide a framework for the study as a whole, taking into account the probable thinking of the two original authors. The conclusions, which are discussed in a separate section at the end of the work, were drawn solely by Turnbull and Gaudin.

We have tried to stress the implied and stated conclusions of the first two authors while taking into account our current understanding of pilosan phylogeny and palaeanodont relationships. The systematic portion of the manuscript (Descriptive Anatomy) contains entirely new descriptions of 27 fossil and Recent taxa, as well as an additional section on xenarthran auditory ossicles. More substantial changes have been made to this part of the study than was the case in Part I. These changes were made necessary by the incompleteness of the manuscript, and by the fact that in places the original authors' intended organization of the manuscript was unclear. Several descriptions had to be written for specimens that had been figured by Patterson and Segall but lacked an accompanying text. Other descriptions were written for specimens that were unavailable to the first two authors. In addition to these major changes, minor changes have been included to expand upon certain points, to correct inconsistencies, to account

for taxonomic changes, and, in a few instances, to provide contrasting interpretations.

As stated in Part I, Patterson and Segall had several goals in mind when they began their work. First, they were interested in expanding upon the knowledge gained by earlier students of the mammalian auditory region, especially as contained in the works of van Kampen (1905) and van der Klaauw (1931b). The two were also interested in reinterpreting xenarthran phylogeny, considering both fossil and Recent taxa, and using what they obviously felt was a somewhat neglected anatomical source. Being rather conservative men in their approach to systematics, Patterson and Segall would certainly have been cautious in their interpretation of this single character complex, but nevertheless they hoped for some insight into what was at that time (and in some ways remains today) the uncertain state of xenarthran systematics. It seems likely that this attempt, primarily on the part of Patterson, to sort out the phylogenetic implications of the study accounted in large part for the long delays in preparation of the study for final publication, delays necessitated by repeated revision attempts.

Several of the ideas generated by Patterson's early collaboration with Segall appeared in published form in the later works of Patterson and Pascual (1968, 1972), including the suggested diphyletic origin of the two extant tree sloth genera. The phylogeny presented in these works gives us some idea of Patterson's ultimate systematic conclusions. As was mentioned in Part I, Patterson and Pascual divided the Xenarthra into three infraorders—the Cingulata, Vermilingua, and Pilosa. Such a trichotomous split of xenarthrans has been challenged recently by Engelmann (1978, 1985), who has presented strong morphological evidence linking the Pilosa and Vermilingua into a single monophyletic lineage to which Engelmann applies the term Pilosa (he created the term "Phyllophaga" to refer to the sloths). This alliance of sloths and anteaters has been supported by one of us on the basis of a phylogenetic analysis of auditory region characters based in part on this study (Gaudin, 1990). We will discuss this matter further in the Conclusions, but for introductory and organizational purposes we will follow the arrangement of Patterson and Pascual (1968, 1972), who subdivided the sloths and anteaters as follows (note: Patterson and Pascual's phylogeny only covered subfamilial groups and higher taxonomic units—the generic contents of these subfamilies are based on de Paula Couto, 1979, except where noted):

Infraorder Pilosa

Superfamily †Mylodontoidea

Family †Mylodontidae

Subfamily †Octomyodontinae

†*Octomyodon* (Scillato-Yané, 1977)

Subfamily †Mylodontinae¹

†*Octodontotherium*

†*Orophodon*

†*Analcitherium*

†*Nematherium*

†*Pseudopreotherium* (Hirschfeld, 1985)

†*Promylodon*

†*Sphenotherus*

†*Stenodon* (Frailey, 1986)

†*Ranculus*

†*Thinobadistes* (Webb, 1989)

†*Pleurolestodon*

†*Lestodon*

†*Glossotherium*

†*Paramylodon* (Engelmann, 1985)

†*Myodon*

Subfamily †Scelidotheriinae

†*Neonematherium*

†*Chubutherium*

†*Elassotherium*

†*Proscelidodon* (McDonald, 1987)

†*Catonyx* (= †*Scelidodon*) (McDonald, 1987)

†*Scelidotherium*

Superfamily Megatherioidea

Family Megatheriidae

Subfamily Bradypodinae

Bradypus

Subfamily †Planopsinae

†*Preotherium*

†*Planops*

Subfamily †Nothrotheriinae

¹ [The contents of this subfamily are somewhat controversial. Engelmann (1985) would restrict the term to the terminal Plio-Pleistocene genera *Myodon*, *Paramylodon*, *Glossotherium*, *Lestodon*, and *Thinobadistes*, which he places as the sister group to the subfamily Scelidotheriinae. Furthermore, he excludes all Miocene and Oligocene mylodonts from both of the aforementioned subfamilies, except for the Santacrucian genus *Nematherium*, which he includes with scelidotheres. Webb (1989) follows Engelmann in placing the scelidotheres as a sister group to Engelmann's Mylodontinae, but he takes two genera, *Lestodon* and *Thinobadistes*, from Engelmann's group and places them in the separate subfamily Lestodontinae. Moreover, he places the genera *Ranculus* and *Pleurolestodon* in the Mylodontinae, and he considers two Miocene forms, *Octomyodon* and *Pseudopreotherium*, to be more closely related to the mylodontines than are the scelidotheres.]

†*Schismotherium*²
 †*Pelecycodon*²
 †*Proschismotherium*
 †*Hapaloides*
 †*Hapalops*
 †*Eucholoeops*
 †*Hyperleptus*
 †*Analcimorphus*
 †*Megalonychotherium*
 †*Neohapalops*
 †*Senetia*
 †*Pronothrotherium*
 †*Nothropus*
 †*Diheterocnus*
 †*Synhapalops*
 †*Nothrotherium*
 †*Nothrotheriops*
 Subfamily †Megatheriinae
 †*Promegatherium*
 †*Plesiomegatherium*
 †*Paramegatherium* (Hoffstetter, 1958)
 †*Megathericulus*
 †*Megatheriops* (Rovereto, 1914)
 †*Megatheridium*
 †*Pyramiodontherium*
 †*Eremotherium*
 †*Megatherium*
 Family Megalonychidae
 Subfamily Choloepinae
Choloepus
 Subfamily †Ocnopinae
 †*Ocnopus*
 Subfamily †Ortotheriinae
 †*Ortotherium*
 †*Pliomorphus*
 †*Neocnus*
 †*Acratocnus*
 †*Miocnus*
 †*Synocnus*
 †*Paulocnus*³

Subfamily †Megalocninae
 †*Mesocnus*
 †*Megalocnus*
 Subfamily †Megalonychinae
 †*Protomegalonyx*
 †*Pliometanastes*
 †*Meizonyx* (Webb and Perrigo, 1985)
 †*Megalonyx*
 Infraorder Vermilingua
 Family Myrmecophagidae
Myrmecophaga (= †*Neotamandua*)
Tamandua
Cyclopes
 †*Protamandua*
 †*Palaeomyrmidon*

In the original manuscript, Patterson and Segall appear strongly in favor of a relationship between palaeonodons and xenarthrans, and deny any special resemblances between the former group and pangolins. With the publication of Emry's 1970 monograph on the Oligocene genus *Patriomanis*, in which Emry relegates the palaeonodons to the order Pholidota, Patterson seemed to have softened his stand somewhat. In Patterson and Pascual's 1972 paper, the two authors refuse to endorse Emry's placement of the palaeonodons, nor do they clearly favor xenarthran affinities for this group. They state rather that, with the accumulation of further evidence, the relationship of palaeonodons to other extant and extinct orders of mammals will become clearer. We discuss the phylogenetic implications of the palaeonodont auditory region below. For the purposes of providing a preliminary taxonomic framework, we follow Rose et al. (1991) in placing palaeonodons in the suborder Palaeonodonta, order Incertae Sedis. The suborder is divided as follows:

Family †Metacheiromyidae
 †*Propalaeonodon*
 †*Palaeonodon*
 †*Metacheiromys*
 Family †Epoicotheriidae
 †*Amelotabes*
 †*Dipassulus*
 †*Tetrapassulus*
 †*Pentapassulus*
 †*Xenocranium*
 †*Epoicotherium*
 †*Tubulodon*

The abbreviations used in the figures are for the most part standard; a detailed listing is provided

² [Note that Patterson and Segall have placed these two taxa in a "group" unto themselves in the systematics section of this study, implying subfamilial distinction. We have found no other suggestion for a subfamily "Schismotheriinae" elsewhere in the literature, and because it seems clear from the Patterson and Pascual phylogeny that such a subfamily would have to have some close relationship with nothrotheres, we prefer to leave the two genera in the Nothrotheriinae for the time being, rather than designate an entirely new subfamily.]

³ [This genus was placed in the Megalonychinae by Webb and Perrigo (1985).]

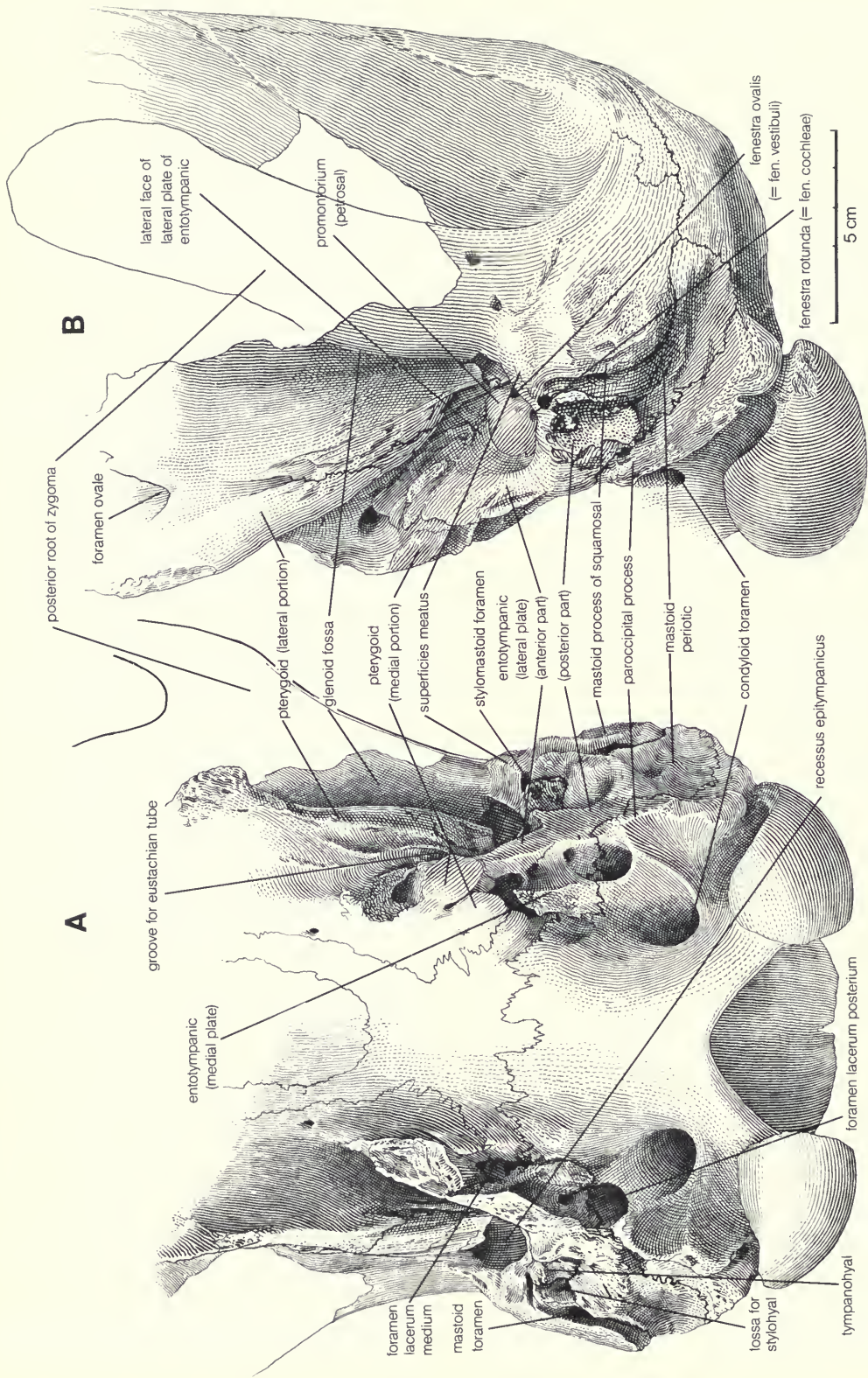


FIG. 1. *Mylodon darwini*, FMNH P14288: A-B, posterior portion of skull shown in ventral and left lateral views.

in the Appendix. The systematic section of the original manuscript is written in a style that combines discussion with description, and sometimes even includes conclusions. The overall conclusions, however, were drawn by Turnbull and Gaudin, and appear in the Conclusions section at the end of the work.

Descriptive Anatomy

Sloths

The Mylodont Division

The Mylodontines

Mylodon darwini,⁴ FMNH P14288, Pampean Formation, Pleistocene, Buenos Aires, Argentina. Figure 1.

The tympanic is missing. It was evidently small and ringlike, essentially similar in position and relation to that of *Choloepus*. [Patterson and Segall use the terms “ringlike” and “horseshoe-shaped” tympanic somewhat interchangeably. As a general rule, however, they refer to a nearly closed horseshoe-shaped tympanic as “ringlike,” and reserve the term “horseshoe-shaped” for a more dorsally open structure.] The superficial meatus [the groove on the ventral surface of the squamosal lateral and dorsal to the tympanum] is merely a small ridge that forms a sharp angle with the vertical zygomatic root. The glenoid fossa is situated well anterior to, and has no relation with, the external canal. The fossa is rounded-triangular with the apex directed posteriorly, and is gently concave transversely. The posterior root of the zygoma is directed anterolaterally, a contrast to *Megalocnus*, in which the direction is lateral.

⁴ [Patterson and Segall noted that several of the animals that were referred to as *Mylodon* by van der Klaauw, 1931a (*M. robustus*, *M. lettsoni*), actually belong to the genus *Glossotherium* (Kraglievich, 1928). The genus *Mylodon* can be distinguished from *Glossotherium* by, among other things, the loss of the anteriormost upper tooth (Kraglievich, 1928; Engelmann, 1985; Webb, 1989). Owen's “*Glossotherium darwini*” has but four upper teeth, and thus is properly placed in the genus *Mylodon* (as above and in van der Klaauw, 1931a). It should be noted here as well that the name *Neomylodon*, used by van der Klaauw (1931a), was synonymized with *Mylodon* by Kraglievich (1928).]

The entotympanic consists of two plates united dorsally beneath the petiotic to form a sagittal groove for the internal carotid; two small foramina leading to the tympanic cavity pierce the roof of the groove. The medial plate lies in the parasagittal plane. It is considerably shorter than the lateral and is suturally united with the basioccipital posteriorly and medially. The thickened posterior part of its ventral margin participates in the basicranial area [more specifically, it forms a portion of the flat basicranial plate located between the auditory regions of either side of the skull, this plate normally being formed exclusively by the basioccipital and basisphenoid]. Anteriorly this margin is sharp, recedes dorsally, and forms the lateral border of the foramen lacerum medium. In the specimen studied by van der Klaauw (1931a, pp. 638–639, fig. 2) the medial plate is smaller than in our [specimen], and shows no posterior thickening, differences that may be due to breakage.

The lateral plate consists of two portions, a thickened posterior part and a deep, narrow anterior part. The posterior portion is united by suture with the exoccipital posteriorly and with the mastoid posteriorly and laterally; it is in contact with the tympanohyal laterally. It forms the mediostral part of the fossa for the stylohyal. [The fossa for the stylohyal is a large oval articular facet for the stylohyal element of the hyoid arch. It is formed by several bones of the auditory region, usually but not always including the tympanohyal, mastoid, exoccipital, and entotympanic. It is a feature unique to sloths.] The sutures in the specimen studied by van der Klaauw (1931a, pp. 638–639) were not sufficiently distinct for him to be certain on this point or on the relations of petiotic and entotympanic within the foramen lacerum posterium. The specimen at hand shows that the entotympanic extended dorsally within the foramen for a short distance only. This posterior portion of the entotympanic continues without interruption into the ventral margin of the paroccipital process, which is feebly developed and inclined anteriorly. The anterior portion of the lateral plate is directed anteriorly and very slightly medially. The lateral face of this plate has a triangular shape, with the apex interposed dorsally between the promontorium and pterygoid. The dorsal margin of this portion of the bone thus curves around the promontorium, contrary to van der Klaauw's statement. This discrepancy is doubtless due to imperfect preservation of his specimen, in which, to judge from his account, the anterior extremity of this portion of the bone was missing. The an-

terior margin is suturally connected with the pterygoid. The lateral wall is rather deeply concave immediately ventral to the promontorium. Below this concavity, the wall is thickened and bent somewhat laterally, participating to a slight extent in the formation of the tympanic cavity. The ventral margin is thin and sharp. Anterior and posterior portions of the lateral plate of the entotympanic meet laterally at a right angle, the posterior portion swinging out to extend to the tympanohyal. Dorsally, this outswung portion recedes sharply posteriorly beneath the periotic, thus participating also in the floor of the tympanic cavity.

Posteriorly the pterygoid diverges into two portions, both of which are inflated. The inflation of the lateral portion involves also a small part of the squamosal; the foramen rotundum [lapsus: ovale is what was intended] runs through this area. The medial portion forms a protuberance on the ventral side of the cranial floor, in which the basi-sphenoid is involved to a slight extent. The lateral plate of the entotympanic extends forward to this structure. Between the two portions of the pterygoid there is a long and rather well-defined groove that evidently housed the Eustachian tube.

The tympanohyal is particularly well shown in this specimen. It is directed ventrally and slightly posterolaterally, whereas that of *Megalocnus* is directed almost directly ventrally. [We were able to detect little difference in the direction of the tympanohyal in *Myiodon* and *Megalocnus*.] It constitutes a minor portion of the fossa for the stylohyal; the fossa has a slight but definite lateral inclination. The epitympanic recess is large and nearly circular; there is no indication of a connection with a sinus in the surrounding elements. [Note: The epitympanic recess is a dorsal extension of the middle ear cavity above the level of the tympanum that contains the incudo-malleolar articulation (MacPhee, 1981). The epitympanic sinus is an accessory air space that connects to this recess (van der Klaauw, 1931b).] The mastoid process of the periotic is large and well exposed on the [lateral] surface of the skull. [The process that Patterson and Segall refer to as the mastoid process in this work and in Part I is typically a compound structure, formed in part by the mastoid and in part by the posttympanic portion of the squamosal.] Its width [i.e., the width of the mastoid] is approximately the same throughout its course, and the sutures between it and the squamosal and supra- and exoccipital are very clear in this specimen. It [the mastoid] forms the major part of the fossa for the stylohyal.

The internal carotid ran, as already stated, in the large groove between the lateral and medial plates of the entotympanic. Two small vascular foramina leave this groove and enter the cavum tympani. At the anterior end of the groove is the elongate foramen lacerum medium. There is no postglenoid foramen and no major venous foramina along the squamoso-parietal suture. The mastoid foramen is small, slitlike, and situated lateral to the fossa for the stylohyal.⁵ In correlation with these conditions, the foramen lacerum posterium is large, and a major sinus left the cranial cavity via the foramen magnum. [Patterson and Segall claim that the very large groove running from the inside of the foramen lacerum posterium to the foramen magnum carried a venous sinus. No such sinus is present in living sloths, or in any other extant xenarthran of which we are aware. The only justification that we can see for assuming that this groove carried a venous sinus is its large size.] The jugular canal [i.e., foramen lacerum posterium] is directed anteroventrally. The foramen is bordered anteriorly by the entotympanic, medially by the basioccipital, posteriorly and laterally by the ex-

⁵ [Patterson and Segall's use of the term "mastoid foramen" for this opening in *Myiodon* and other pilosans is somewhat problematic. The mastoid foramen is typically defined as an opening for a mastoid emissary vein, and is usually situated on or near the suture between the mastoid and occipital bones (Wahlert, 1974; Kielan-Jaworowska et al., 1986). In Part I of this work (Patterson et al., 1989), Patterson and Segall use this term to describe a ventrally situated foramen found in cingulates at or near the suture between the mastoid and squamosal. This foramen opens into a vertical canal that courses along the posterior margin of the occipital crest before opening onto the occiput again more dorsally. According to the work of Tandler (1899), this canal transmits the occipital artery, and not the mastoid emissary vein. Within the dorsal portion of this canal is a second foramen, again lying on the petrosquamous suture, and leading into a canal that runs anteriorly into the braincase. This foramen is the opening into the braincase for the arteria diploetica magna (Wible, 1984).

Within the Pilosa, the term "mastoid foramen" is used to describe two different foramina. In *Myiodon*, other mylodonts, and the genera *Megalonyx* and *Megalocnus*, the "mastoid foramen" is like that of the cingulates—a ventral opening leading into a vertical canal behind the occipital crest, presumably carrying the occipital artery. In other pilosans, including *Acratocnus* and the genera of the *Bradypus/Megatherium* division, the ventral foramen and canal are absent. In their place we find a groove running behind the occipital crest for the occipital artery, and a more dorsal foramen opening into an anteriorly directed canal. This second "mastoid foramen" is presumably the opening for the arteria diploetica magna.]

occipital. The groove within the tympanic cavity for the facial nerve is especially deep due to the well-developed crista facialis. After leaving the cavity, the nerve enters a ventrolaterally directed canal formed by the tympanohyal, mastoid, and squamosal. The orifice of this canal is bounded by the same elements and is therefore a foramen primitivum;⁶ it is situated squarely in front of the fossa for the stylohyal,⁷ a peculiarity of *Megatherium*. [Patterson and Segall had written *Meg.* here. From our comparisons it is evident that they intended *Megatherium* with the abbreviation.]

At the anterior end of the crista facialis there is

⁶ [Patterson and Segall's use of the terms "foramen primitivum" and "foramen definitivum" are somewhat different from common usage today. MacPhee (1981) defines the foramen primitivum as the membranous opening for the exit of the facial nerve in fetal and some adult mammals, and the foramen definitivum as an osseous opening that often appears later in development and is formed by various bony elements, including the tympanohyal, petrosal, entotympanic, and tympanic. Patterson and Segall follow van der Klaauw's (1931b) usage of the two terms, wherein the foramen primitivum is a primitive condition of MacPhee's foramen definitivum, an opening for the facial nerve with ossified walls formed by the tympanohyal and mastoid only. Van der Klaauw's foramen definitivum is a derived feature in which a secondary foramen forms lateral to the "foramen primitivum." The borders of this second foramen are variably composed of tympanic, squamosal, mastoid, tympanohyal, and exoccipital elements.]

⁷ [This is a modification of a more typical xenarthran condition in which the stylomastoid foramen is situated lateral or slightly anterolateral to the tip of the tympanohyal. This xenarthran condition is itself fairly unusual, for the primitive eutherian condition is to have a foramen located posterior to the tympanohyal. The lateral position of the foramen in xenarthrans appears to be due to an enlargement of the tympanohyal in the ventral direction, so that it forms a floor to the canal for the facial nerve, and the posterior direction, so that it continues on posterior to the canal and fuses to the mastoid at its distal extremity. In some genera, the facial nerve may then wrap around the base of the tympanohyal laterally and anteriorly. The xenarthran condition is unusual for eutherian mammals, but similar morphologies do occur in other eutherians and in monotremes. Van Kampen (1905) described the fusion of the tympanohyal to the mastoid in the echidna and pangolin (although in the latter the stylomastoid foramen remains posterior to the tympanohyal), and he figured a laterally placed stylomastoid foramen in the Proboscidea. Van der Klaauw (1931b) mentions several families of eutherians in which the tympanohyal participates in the border of the "foramen definitivum" (*sensu* Patterson and Segall), and of these the Sirenia, Felidae, and Viverridae appear to show a condition similar to that found in xenarthrans. The condition also appears to be present in the Soricidae (McDowell, 1958), *Potamogale* (McDowell, 1958), and *Hemicentetes* (MacPhee, 1981).]

the usual enlargement, which is here a relatively small, transversely enlarged plate that is apparently not in contact with other elements except, possibly, the anterior crus of the tympanic.

Myodontidae, gen. et sp. indet.

An isolated left tympanic collected by Dr. Robert T. Hatt from a Pleistocene deposit in Yucatan may be referred with confidence to some member of this family, tentatively referred to *Paramylodon* by Hatt (1953).⁸ We are indebted to Dr. Hatt for the opportunity to describe this specimen.

The bone as a whole is primitive, being little advanced beyond the simple arcuate type. Both crura are incomplete, the posterior less so than the anterior. As in *Choloepus* and the generalized Santa Cruz megalonychids, the posterior crus is more slender and curved than the anterior and has a gently rounded posterior face. The anterior crus is in comparison somewhat expanded anteroposteriorly, the anterior margin is straight, and the anterior face flat below and very slightly concave above, the concave part possibly marking the ventral extremity of a sulcus malleolaris. The ventral portion of the bone thickens toward a blunt styliform process, which is very slightly concave medially. The process lies in the same plane as the crura, and there is no indication whatever of lateral or medial expansion of the bone. The sulcus tympanicus and crista tympanica are prominent, the latter especially being better defined than in *Choloepus*; the crista terminates halfway up the posterior crus.

Length across crura 21.4 mm.

"Myloodon" garmani, MCZ 8429, Pleistocene of Nebraska (Allen, 1913).

The specimen is a little crushed laterally and this, as van der Klaauw suspected, has squashed the entotympanic a bit.

The tympanic is essentially as he has described it; the most striking thing about it is the greater depth as compared to the length (depth 26.6, length 19.1). It lies against the entotympanic at the junc-

⁸ [This description has already been published, word for word, in Hatt (1953). Hatt's paper also includes a drawing of the tympanic. We republish here the description and associated drawing (fig. 21A) for the convenience of the reader.]

tion of the hollow dorsal part and the vertical ventral plate of the latter (see description of *Scelidothorium*). The two bones are in contact only; they are not suturally united.

The entotympanic lateral ridge is very thin ventrally, and there is a visible suture between it and the large paroccipital process. Behind the tympanic the entotympanic expands laterally to form the medial part of the stylohyal fossa, as in *Myiodon darwini*. The tympanohyal is in the usual place lateral to this expanded part and forming the anterior portion of the stylohyal fossa. Its anterior rim is so thoroughly confluent with the rim of the mastoid portion of the fossa that its identity is largely obliterated. Van der Klaauw has mistaken the lateral enlargement of the entotympanic for the tympanohyal. The medial portion of the tympanic, so far as preserved, shows nothing unusual.

The stylohyal is very wide proximally, extending posteroventrally below and behind the articular surface. Its distal end is irregular and stocky and much more robust than in *Nothrotheriops*.⁹

Lestodon myloides, juv. AMNH 11270, Pampean Formation, Pleistocene of Argentina (van der Klaauw, 1931b).

Notes on van der Klaauw's description (1931b, p. 309):

The sulcus tympanicus is very close to the outside of the ring, thus all the expansion is medial. His element x is merely an anterior part of the entotympanic that is partially separated ventrally from the larger, more ventrally projecting ventral part by a groove. Apart from the groove, the two parts are continuous; this can very clearly be seen within the tympanic cavity, where the two form a smoothly flowing curve under the periotic.

Many of the peculiarities pointed out by van der Klaauw are no doubt due to the extreme youth of this specimen.

The recessus epitympanicus is small in comparison with those of the megalonychids and megatheres.

Paramyiodon and Glossotherium

Paramyiodon.—The entotympanic is probably shorter, especially posteriorly, than in *Myiodon*

and scelidothers; the caudal end has an expansion medial to the fossa for the stylohyal as in *Myiodon*. The paroccipital and mastoid [processes] are low as in *Myiodon*. The fossa for the stylohyal extends farther back than in *Myiodon*, reaching to the level of the anterior border of the condylar foramen. The foramen lacerum posterium is more lateral in relation to the condylar foramen than in *Myiodon* and the scelidothers. (The periotic may extend ventrally closer to the basis cranii than in other forms.)

Glossotherium (fide Owen's figures (Owen, 1842)) appears to agree closely with *Paramyiodon*. The fossa for the stylohyal may not extend as far posteriorly. [Guth (1961) describes and figures specimens of *Glossotherium* that have a *Myiodon*-style entotympanic extending from the pterygoid to the paroccipital process and bearing a medial sulcus for the internal carotid artery. This morphology is in strong contrast to the short, blocky entotympanic described for this taxon by van der Klaauw (1931b) and figured by Owen (1842). The Field Museum collections also contain a specimen of this genus (P12519), from the Pleistocene La Brea tar pits of California, that compares favorably with the descriptions of van der Klaauw and the figures of Owen. It is possible that the entotympanic is simply highly variable in its morphology in this genus. It is also possible that the specimens examined by Guth are misidentified specimens of *Myiodon*. Having not had the opportunity to examine Guth's specimens firsthand, we cannot say which is the more likely of the two alternatives.]

Octodontotherium grandae, FMNH P13616. Figure 2.

[One of the Field Museum specimens of this early mylodont was figured by Patterson and Segall, but a description was not included in the manuscript. Given the presence of the figure, and the fact that this genus, from the Desecadan of South America (Hoffstetter, 1954), represents one of the earliest pilosans known from reasonably well-preserved cranial material, we felt it important to include a description of its anatomy in the paper.

The specimen is quite incomplete. The tympanic is absent. Most of the entotympanic is missing, as is much of the lateral portion of the basi-cranium. The squamosal bears two small facets for the tympanic. These facets indicate that the tympanic was a small, almost complete ring, with

⁹ [See footnote 14, p. 27.]

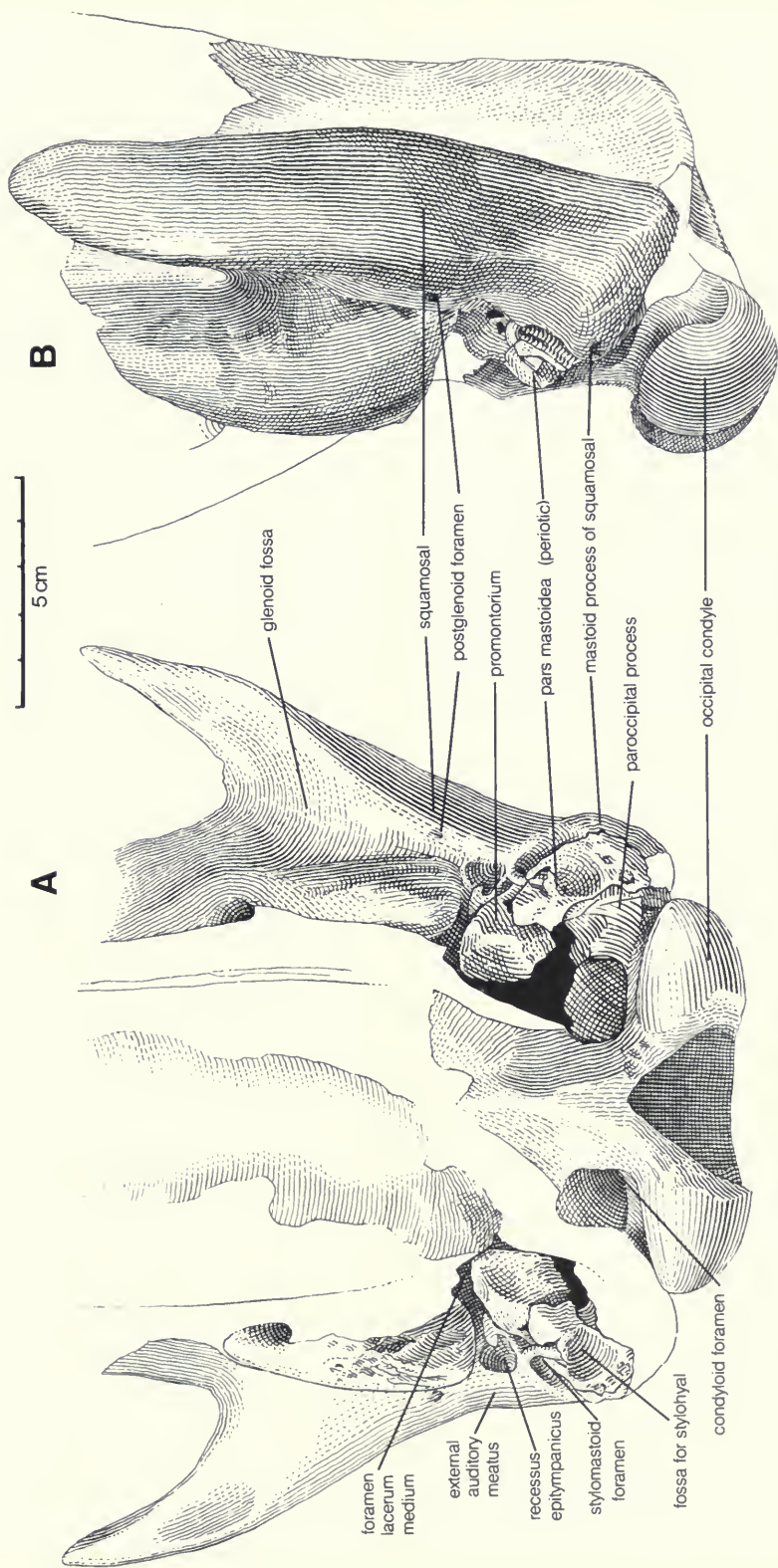


FIG. 2. *Octodontotherium grandae*, FMNH P 13616: A-B, posterior portion of skull shown in ventral and left lateral views.

a very small incisura tympanica. The superficies meatus of the squamosal is larger than that of *Mylodon*. It is located posterior and ventral to the root of the zygoma and forms a wide, shallow embayment that tapers medially. The glenoid fossa, as in all mylodonts, is well forward of the auditory meatus. It faces anterolaterally, is concave transversely, and is roughly triangular in shape.

The only portion of the entotympanic preserved is the lateral spur of the middle portion of the entotympanic plate. This spur, which contacts the tympanohyal laterally, can be seen rostromedial to the fossa for the stylohyal. This portion of the entotympanic does not participate in formation of the stylohyal fossa. The remainder of the entotympanic has been broken away. The petrosal, however, bears a large, deep facet on its ventral surface that presumably was the site of attachment for the entotympanic. This facet is oval and slopes anterodorsomedially. It bears a sharp dorsal "step" at its anterior extremity. The facet would seem to indicate that, as in *Mylodon* and the scelidotheres, the entotympanic was attached but not fused to the petrosal, and that the dorsal margin of the entotympanic curved around the ventral surface of the petrosal.

The petrosal itself is flattened anteriorly, becoming more globose posteriorly, as in most sloths. The fenestra ovalis is an elongate oval with a deeply recessed rim for the annular ligament of the stapedial footplate. The fenestra cochlea is situated ventral to the middle of the fenestra ovalis and is directed laterally and slightly posteriorly. Both the position and orientation of this opening are unusual in *Octodontotherium*. In other sloth genera the round window is more posteriorly situated relative to the oval window; only in *Glossotherium* is the round window so laterally directed. In other forms, it faces more posteriorly. The shape of the fenestra cochlea in *Octodontotherium* is fairly typical for sloths. It is slightly ovate but has a medially directed point formed by a small groove that may lead either to a foramen in the ventral surface of the petrosal itself, as in *Glossotherium*, or to a foramen between the entotympanic and petrosal, as in the Santacrucian genera, *Megalocnus* and the living species.

Little can be discerned of the internal surface of the petrosal in *Octodontotherium*. As in other sloths, there is a shallow subarcuate fossa located posterior and dorsal to the internal auditory meatus. The internal auditory meatus is obscured by matrix in *Octodontotherium*, but in most other sloths (with the exception of *Hapalops* and the

extant genera) it is very deep, without a discernible division into separate foramina for the auditory and facial nerves, and is directed posteriorly. The cochlear aqueduct is also posteriorly directed in most sloths. Typically it lies posterior and slightly ventral to the internal auditory meatus, in the walls of the foramen lacerum posterium, and is hidden from view medially by a small bony flange of the petrosal.

The pterygoids are poorly preserved, with the posterior sections of the bone absent on both sides. It would appear, however, that the pterygoids, like those of *Mylodon*, were greatly inflated posteriorly. This is indicated by the well-preserved portions of the squamosal medial to the glenoid, which, as in *Mylodon*, are quite well inflated.

The alisphenoid bone does not appear to have been preserved at all, though it is difficult to say for sure whether or not it formed part of the ventral eminence medial to the glenoid, which we have included as part of the squamosal bone. On the left side of the skull, however, the anteriormost part of this eminence bears clear corrugations on its flattened, dorsally sloping ventral surface. We interpret these corrugations as remnants of the suture between the squamosal and alisphenoid. The corrugations lie anterior to a groove, whose counterpart is especially clear on the opposite side of the skull, and which lies also on the ventral surface of the aforementioned eminence. We believe this groove to represent the dorsal surface of the foramen ovale.

The tympanohyal is well preserved, especially on the right side of the skull. It is directed ventrally and slightly posterolaterally, as in *Mylodon*, and forms the rostral portion of the fossa for the stylohyal. The epitympanic recess is not so large as in other mylodontids, but as in these forms and unlike megalonychids and megatheriids, it lacks any trace of an epitympanic sinus. The recess is walled medially and posteriorly by the crista facialis and tympanohyal, respectively, the remaining walls being formed by the squamosal. The shallow, circular fossa incudis lies in the posterointernal corner of the epitympanic recess. This fossa is typically deeper in other sloths, with the exception of *Bradypus* and *Choloepus*, and in all megatheriids and megalonychids (the living forms included) it occupies the entire back wall of the epitympanic recess.

The mastoid process forms the major part of the stylohyal fossa. The fossa itself is oval, with its long axis running anteromedial to posterolateral. In most mylodonts, the facet is more circular.

The oval facet of *Octodontotherium* may be an artifact of not having a well-preserved entotympanic, which in *Mylodon* contributes much to the mediocaudal portion of the stylohyal fossa. The mastoid is covered laterally by a large mastoid process of the squamosal, and the posterolateral corner of the skull is badly damaged, so that the extent of mastoid exposure is difficult to determine.

Because of damage to the entotympanic and basicranium, there is no information on the opening for the Eustachian tube, the foramen lacerum medium, or the course of the internal carotid artery. Posteriorly, the condyloid foramen and foramen lacerum posterium are confluent, again due to damage to the skull in this area, and the true extent of the two foramina cannot be determined accurately. All that remains of the paroccipital process is a low, dorsally situated projection that was evidently once part of a much more extensive process. This projection bears on its anteromedial surface a groove for the nerves and vessels of the foramen lacerum posterium. The sulcus for the facial nerve is deep, bounded laterally by a strong crista facialis. At its posterior extremity the sulcus opens medially into a large fossa for the stapedius muscle. In *Octodontotherium*, as in all sloths, this fossa is a deep, somewhat dorsoventrally elongate hollow situated directly posterior to the fenestra ovalis and dorsal to the fenestra rotunda. The facial nerve continues lateral and ventral to the stapedius fossa, opening externally at a stylomastoid foramen located well dorsal to the stylohyal fossa. Because of this dorsal position, the foramen opens directly anterior to the fossa. It is a foramen primitivum, exiting between the tympanohyal, mastoid, and squamosal. The skull has on either side a small postglenoid foramen situated posterior to the medial portion of the glenoid fossa.

At the anterior end of the crista facialis is a small, hooklike processus cristae facialis. The process appears to have been well separated from all other bony elements, including the anterior crus of the tympanic.]

The *Scelidotheriines*

Catonyx (Lund) (= *Scelidodon*) *chapadmalense* and *Scelidothorium leptocephalum*,¹⁰ Pampean Formation, Pleistocene, Buenos Aires, Argentina.

¹⁰ [We have checked the following description with the

The auditory region of these very closely related forms may most conveniently be described together. In general they are very similar to *Mylodon*. The tympanic is not preserved in any specimen we have seen; as in *Mylodon*, it must have been small, ringlike and almost surely not in contact with the entotympanic. The superficies meatus of the squamosal is remarkably wide in *Catonyx*. The entotympanic of both forms resembles that of *Mylodon*, differing in that the lateral ventral ridge is narrower laterally, the medial abuts against the side of the basicranium rather than being inset into it, and there is no appreciable lateral expansion medial to the fossa for the stylohyal. The lateral ventral ridge in *Scelidothorium* is longer than in *Catonyx* and appears to extend somewhat farther ventrally. The tympanohyal is more ventral in direction in both genera than in *Mylodon*. The fossa for the stylohyal is smaller in both, particularly in *Scelidothorium*, and deeper, particularly in *Catonyx*.

The recessus epitympanicus is well developed in both, but, like that of *Mylodon*, does not continue into an epitympanic recess. [Lapsus: They must be referring to the epitympanic sinus.] The mastoid is narrower than in *Mylodon* and extends in a rather deep groove, between the paroccipital and mastoid processes, which are much better developed in these genera than in others of the family. The paroccipital in *Scelidothorium* is especially prominent, being a thin, somewhat posteriorly covered projection. The foramina do not differ appreciably from those of *Mylodon*.

Scelidothorium leptocephalum, MCZ 8812, Pampean Formation, Pleistocene of Argentina (van der Klaauw, 1931b).

Van der Klaauw's description is accurate, but he makes too much fuss over everything. The lateral surface of the vertical entotympanic plate is not "very peculiar" but quite normal. The hollow dorsal part of this surface is the medial wall of the tympanic cavity, and the tympanic was in contact with or connected to the entotympanic at the junction of the hollow part and the ventral vertical portion. The structure of the entotympanic is revealed by several of our specimens almost as well

specimens available to us (FMNH P14267 and P14274), and find that they differ very little in the parts preserved. Their generally poor state of preservation, however, prevents us from checking much of this.]

as in his. The cleft between the basioccipital and the medial descending process of the entotympanic is possibly due to age. The concave ventral surface of the entotympanic is probably natural.

The basioccipital is very long in this form and in "*Mylodon garmani*."

The "ossiculum accessorium malleoli," figured but not discussed by van der Klaauw, is not an ossiculum accessorium malleoli but the usual process from the anterior extension of the crista facialis. Its outline and character are as in the figure, but this does not show its connection with the anterior extension or how closely it rests upon the rough postglenoid surface.

The basisphenoid extends laterally onto the side of the skull at the anterior extension of the entotympanic, as shown in the figure.

The attachments of the [tympanic] crura are visible on both sides. The anterior is immediately lateral to the posterior part of the "ossiculum accessorium malleoli" and the posterior is anteroexternal to the base of the tympanohyal. The epitympanic recess is moderate in size and is hardly a sinus. Van der Klaauw's figure does not show these last details.

The Mylodont Auditory Region

[Patterson and Segall included a point-by-point critique of van der Klaauw's description of the mylodont ear region (1931a) in their original manuscript. On many of the points discussed by van der Klaauw, Patterson and Segall either agreed with him or could not derive sufficient information from the specimens at hand to comment. Furthermore, many of their points of disagreement were discussed in the descriptions of individual specimens. However, some of these criticisms are not discussed elsewhere in the text. We felt that many of these criticisms were important, and that they should be included in the text in some form, as was apparently intended by Patterson and Segall. Thus, we have included the following paragraphs, heavily edited and condensed, which cover those criticisms not discussed elsewhere.]

The inclination of the tympanic means little or nothing: [it is apparently controlled by] an age factor (cf. *Choloepus*). In our *Paramylodon*, what we believe to be a remnant of the tympanic suggests that in this specimen there was an angle of about 75 degrees with the horizontal. The mylodont glenoid articulation is situated far anterior to the porus and slightly above it. Its surface is only

slightly concave and very poorly demarcated from the surrounding bone; [it extends] out well onto the zygomatic process of the squamosal, [and its] internal descending portion is slight.

The entotympanic [is not loosely attached, but is on the contrary] probably always well fused [to the surrounding elements. It is] fused or suturally connected with the tympanohyal. [It] is in contact with the [paroccipital process and] exoccipital proper, [although] it may or may not be united by suture with the paroccipital process as van der Klaauw [(pp. 616–618)] states. [The entotympanic] is closely attached but not fused [with the petrosal. In *Mylodon*], a suture between the entotympanic and petrosal can plainly be seen in the foramen lacerum posterium (not shown in van der Klaauw's specimen, fig. 2). The entotympanic does reach the pterygoid in our *Mylodon darwini* [(contra van der Klaauw, p. 620), but this feature is] evidently variable in mylodonts. In our *Mylodon* the suture between the entotympanic [and] mastoid [is] clearly visible. Our *Mylodon* shows a prominent medial portion of the entotympanic medial to the carotid groove that is in sutural contact with the basioccipital; anteriorly it reaches to the foramen lacerum posterium [lapsus: foramen lacerum medium] (van der Klaauw's fig. 2 of this form does not show the medial portion). There is considerable variation between scelidothers, mylodont[ines], and glossothers in this region. *Paramylodon* has a short, blocklike entotympanic that agrees with van der Klaauw's description of *Glossotherium* [(= *Mylodon*)].

The course of the [Eustachian tube] differs in megatheres/*Bradypus* and others. In the former group [it is] much more vertical, in the latter, especially the mylodonts, it is directed cranioventrally and slightly medially.

There is a ventrally flat, small prominence projecting laterally from the anterior extremity of the crista facialis. Van der Klaauw describes similar structures in his specimens of *Glossotherium* and *Mylodon* [(pp. 633–634)], and we have observed similar structures in other ground sloths (*Megatherium*, *Megalocnus*, etc.). It is homologous with a similar, often complicated prominence that appears to be characteristic of the Xenarthra generally. It has been claimed (e.g., by van Kampen, 1905) that this element is the ossiculum accessorium malleoli. Van der Klaauw denies this [p. 634]; Patterson agrees; Segall believes that it is the ossiculum, [although] he has no real evidence for this. [This process was discussed at length in Patterson et al. (1989), with the authors apparently

deciding that the process was a neomorph characteristic of xenarthrans. They gave the process the name *processus cristae facialis*.]

[Finally, in discussing the various mylodont ear "types" of van der Klaauw (pp. 646–651), Patterson and Segall note that in the *Glossotherium/Paramylodon* type] the entotympanic does extend slightly in front of the process for the stylohyal, [and bears] a lateral extension toward the tympanohyal. [Moreover,] in *Paramylodon* the entotympanic does form a prolongation of the paroccipital process.

The Megalonychoids

The *Choloepus-Megalonyx* Division

The *Choloepus* Group

Choloepus Illiger; *C. didactylus* and *C. hoffmani*.¹¹
Figures 3–4.

Twenty-two skulls of *Choloepus* have been examined. Pending an adequate revision of the tree sloths that will take into account the great variability in skull form shown by both of the living genera, we refer the material to *C. didactylus* Linnaeus. [Revision of the genus *Choloepus* has subsequently been undertaken by Wetzel (1985) and Wetzel and de Avila-Pires (1980). Specimens were assigned to one of the two species that constitute the genus *Choloepus*, *C. hoffmani* and *C. didactylus*, according to cranial characters given by Wetzel, the most consistently useful of these being a posterior pair of interpterygoid foramina that open into the pterygoid sinuses. These foramina are present in *C. hoffmani* but lacking in *C. didactylus*. Of the 22 original specimens examined by B.P. and W.S. (see footnote 11 for specimen numbers), 14 belong to *C. hoffmani*, including the two figured specimens, whereas the other eight can be placed in *C. didactylus*. We examined an additional 31 specimens, including 11 *C. didactylus* and 20 *C. hoffmani* (see footnote 11 for specimen

numbers). Specific differences in the ear region of the two species will be noted in the text.]

The tympanic is an incomplete, slender ring, irregular in outline. The incisura tympanica is large. The bone is small in comparison with the size of the skull and does not enlarge with advancing age. The anterior crus, the most expanded portion of the bone, is extensively attached to the squamosal and to the lateral side of the *processus cristae facialis*. The posterior crus is in contact with the tympanohyal, its dorsal extremity reaching to the mastoid and squamosal. The medial border of the ventral portion is free in the great majority of specimens. In a few individuals, spicules of bone connect it to the entotympanic, but only in two is there any very close connection between the two bones. [FMNH 123021 (*C. didactylus*) and 84552 (*C. hoffmani*), two juvenile specimens unavailable to B.P. and W.S., also show a bilaterally close association between tympanic and entotympanic along the whole ventral length of the two bones.] One of these is an asymmetrical skull in which the connection occurs on one side; in the other the condition is bilateral and there is a large opening anteriorly, through which the Eustachian canal passes. Half of the specimens in which the tympanic is present exhibit a connection between the two bones posteriorly. [Only 10 of the entire 35 available specimens in which tympanics were preserved show this posterior contact.] Sulcus tympanicus and crista tympanica are poorly developed and there is no recessus meatus. A sulcus malleolaris is present. All in all, the tympanic of *Choloepus* is of an extremely primitive type; among other edentates so primitive a bone is formed only in the mylodonts and in some of the smaller Santa Cruz ground sloths.

The glenoid articulation differs notably from those of the mylodonts. It is well defined, wide transversely, and narrow anteroposteriorly (Sicher, 1944, p. 163), and extends forward onto the zygomatic process of the squamosal. In adults the very short inflated postglenoid portion of the squamosal extends in the form of a buttress ventrolaterally from the junction with the anterior crus of the tympanic; in juveniles the buttress is not present.

The entotympanic is a thin, laterally compressed plate, tapering ventrally, that runs parallel to the ventral portion of the tympanic. Projections from either the ventral margin or the medial side, or both, occur in some individuals. It extends from the tympanohyal forward to the basioccipital-basisphenoid suture, but only very exceptionally does

¹¹ [Specimens examined include:

C. didactylus—B.P. & W.S.: FMNH 21730, 34326, 34711, 36099, 41207–8, 41503–4. W.T. & T.G.: FMNH 60058, 60068, 86893, 86895, 87905, 88892, 93177, 95447, 95449, 95450, 123021.

C. hoffmani—B.P. & W.S.: FMNH 14183–88, 30739 (illus. in fig. 3), 34706, 35738, 41206, 44053 (illus. in fig. 4), 44054, 65796, 68933. W.T. & T.G.: FMNH 60108, 60455, 60549, 60585–86, 69574–77, 84552, 89510–11, 90058, 121521, 123995, 127420–22, 128409–10.]

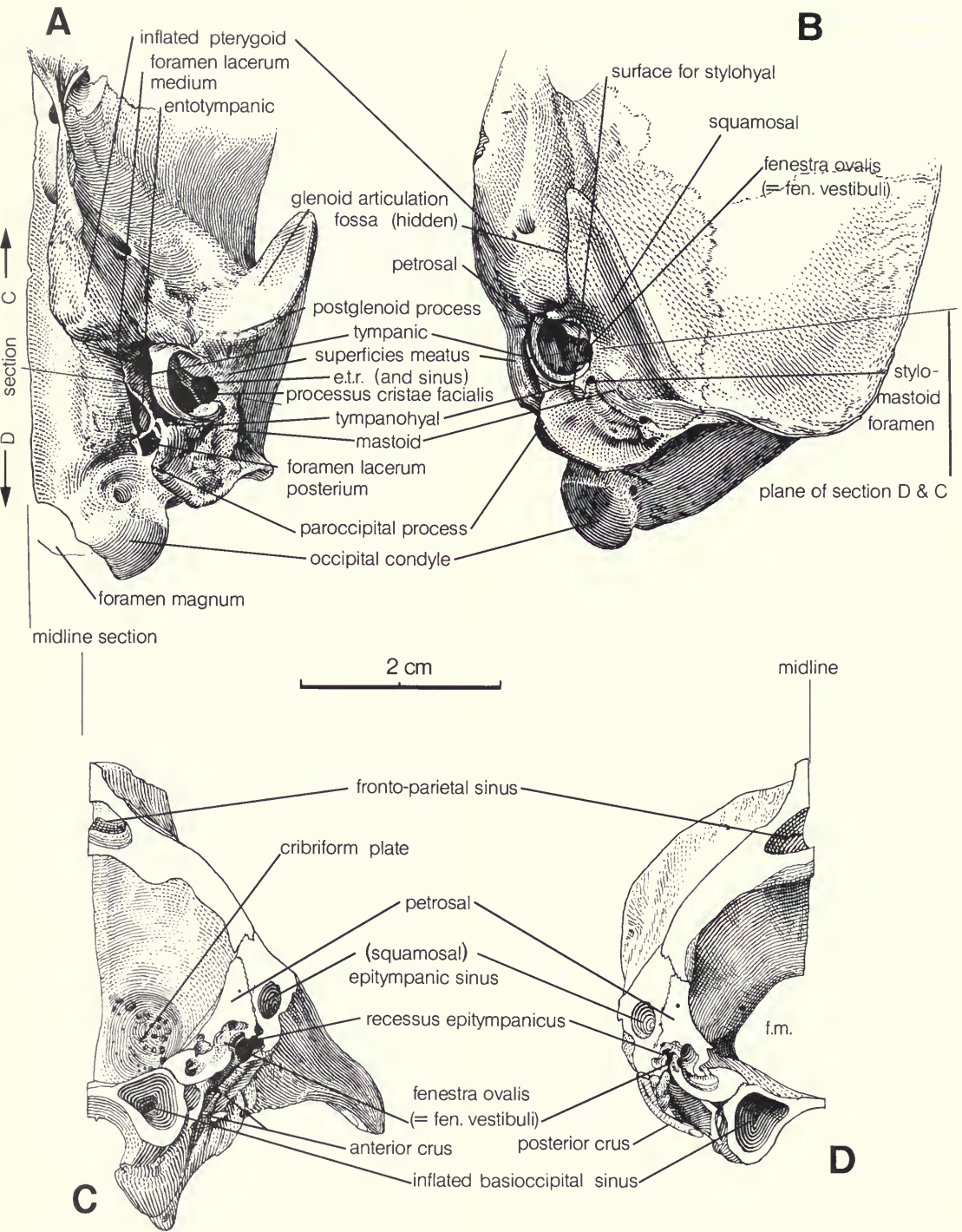


FIG. 3. *Choloepus hoffmani*, FMNH 30739: A-B, posterior portion of skull shown in ventral and left lateral views; C-D, sectioned skull, with cut running through tympanic ring, entotympanic, petrosal, and braincase, shown in views toward anterior and posterior sides of cut.

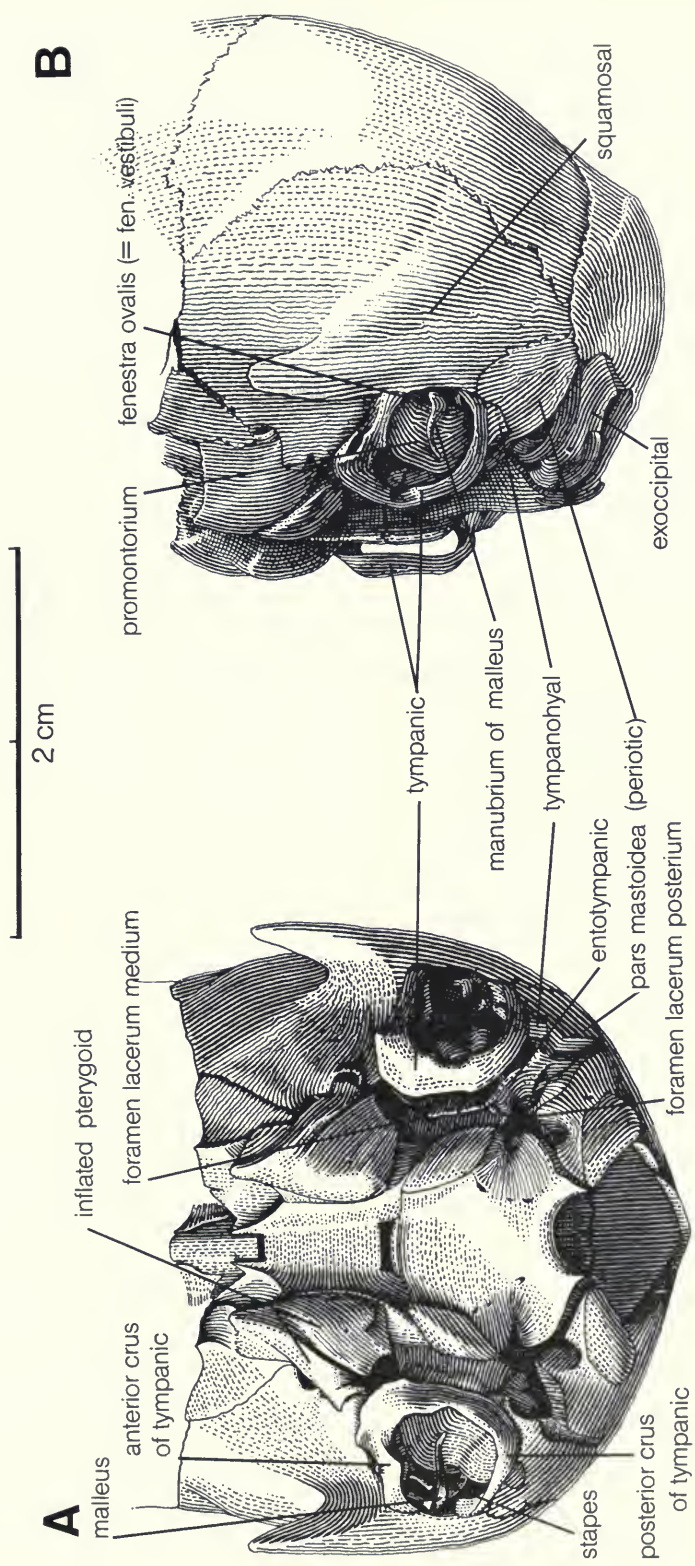


FIG. 4. *Choloepus hoffmani*, FMNH 44053: A-B, posterior portion of juvenile skull shown in ventral and left lateral views.

it turn laterally to extend above part of the anterior crus of the tympanic, as occurs in many armadillos, *Bradypus*, and the nothrotheriines. [In over half of the *C. didactylus* specimens examined, the entotympanic was observed to contact the pterygoid at its anterior extremity. Such a contact between entotympanic and pterygoid is much less common in *C. hoffmani*, where the entotympanic is frequently poorly ossified, especially anteriorly.] Tympanic-entotympanic relations have already been discussed. Dorsally, the entotympanic is attached to the medial part of the ventral portion of the pars petrosa, posterolaterally to the tympanohyal, and posteriorly to the paroccipital process, which in adults forms a crest that continues forward into the entotympanic. On the medial side, its relations to the basicranial elements are variable, depending upon the size of the projections and upon the angle of inclination of the bone as a whole. The youngest specimen in our series suggests that, as in many other edentates, the entotympanic is a compound bone formed from anterior and posterior centers of ossification; the posterior part, or caudal entotympanic, is considerably the larger of the two. [The specimen to which Patterson and Segall are referring, FMNH 44053 (see fig. 4), definitely has two separate centers of ossification in the medial and posterior wall of the bulla, as does our youngest specimen of *Bradypus*, FMNH 25315 (see fig. 8), and we have no clear reason for doubting the original authors' claim that these represent the rostral and caudal entotympanic. Schneider (1955) found only a single ossification center for the entotympanic in his study of skull development in *Bradypus*, but Wible (1984), in reexamining Schneider's specimens, noted a sizable gap between the youngest specimen with an entotympanic and the oldest without one. Wible (1984) has suggested that the entotympanic of *Tamandua* (almost certainly homologous with the caudal portion of the entotympanic in other xenarthrans) is in fact a caudal process of the petrosal, and it is possible that the so-called "caudal entotympanics" of *Choloepus* and *Bradypus* are likewise outgrowths of the petrosal. The caudal center of ossification in *Choloepus* does not appear to be separated dorsally from the petrosal, whereas in the juvenile *Bradypus*, the caudal ossification appears separate from the petrosal on the left side of the skull but not the right. Our evidence in this matter is equivocal.]

As is well known, the pterygoid, basisphenoid, and basioccipital are inflated in *Choloepus*, forming a connecting series of sinuses that also extends

laterally into the squamosal above the medial part of the glenoid surface, the whole opening to the nasal passage near the pterygoid-palatine suture. [As was mentioned earlier, an opening from the pterygoid sinus into the nasal passage is present only in *C. hoffmani*.] These sinuses, and the very extensive frontal sinus system, render the skull of *Choloepus* the most highly pneumatized of any living edentate. Among extinct forms, *Megalocnus* has a skull that is even more pneumatic. The basicranial sinuses, which are variable in degree of inflation, result in descending processes of the basioccipital and basisphenoid. These, together with the inflated pterygoid, impart a vaguely myrmecophagid-like appearance to the base of the skull. The resemblance is purely superficial, however. In anteaters, the pterygoid, its sinus, and the descending process of the basioccipital are integral parts of the middle ear; in *Choloepus* the pterygoid sinus is not in communication with the middle ear, and the bone itself and the basioccipital play only the usual minor role in the boundary of the same.

The tympanohyal is a conspicuous element that, as in other sloths, increases in size distally; the surface for the stylohyal varies from flat to cup-shaped. In some [most] specimens, the paroccipital process, pars mastoidea, and entotympanic combine with the tympanohyal to form a small fossa for the stylohyal, similar to but smaller than that [which is] almost universal in ground sloths.

The ventral surface of the pars petrosa is globular in shape. The processus cristae facialis begins as a very thin lamina of bone that passes ventrally between promontorium and squamosal and then expands to a long-oval plate that is gently concave on its distal surface and forms a part of the anterior wall of the cavum tympani. The plate forms the medial portion of the anterior wall of the middle ear and is in contact with the squamosal and pterygoid, and also with the entotympanic in those individuals in which the anterior extremity of this element turns laterally. As already noted, the medial surface of the anterior crus of the tympanic is in contact with the lateral margin of the plate for the greater part of its length. The plate fuses with the squamosal in old individuals. The large recessus epitympanicus passes into the sinus epitympanicus without any sharp demarcation. The sinus is smooth walled—in sharp contrast to *Bradypus*, in which the walls are rugose—and extends anteriorly well into the root of the zygoma. Its lateral wall is formed by the squamosal, its medial by the squamosal above and by the periotic below. Posteriorly, it does not extend beyond the tympanic

cavity and it does not connect with the pterygoid sinus system. The cerebellar face of the periotic lacks a fossa subarcuata.

The pars mastoidea unites completely with the surrounding elements in adult individuals. In very young specimens [see fig. 4] the exposed portion is approximately triangular in shape, with the apex pointing ventromedially, and is confined almost exclusively to the side of the skull.

There is only a vestigial mastoid process composed of squamosal and mastoid, which in adults but not in juveniles forms a slight protuberance on the side of the skull above and behind the stylomastoid foramen. [Although it is true that most *C. hoffmani* specimens have a small to rudimentary mastoid process, in almost half of the *C. didactylus* specimens examined the mastoid process was much larger, more comparable in relative size to mastoid processes of other sloths.] The exoccipital in adults forms a crest that is continuous above with the occipital crest, runs downward to the conspicuous, laterally compressed paroccipital process, which extends down to or below the level of the ventral margin of the tympanic, and is continuous anteriorly with the entotympanic. The pars mastoidea partly overlaps the external face of the exoccipital but does not extend to the edge of the crest. Between the crest and the rudimentary mastoid process there is a rather wide, shallow, and irregular groove.

The internal carotid runs forward between the entotympanic and the basioccipital and basisphenoid, entering the cranial cavity by the large foramen (apparently no "second artery")¹² lacerum medium. [In *C. hoffmani*, the entotympanic tends to be much more closely associated medially with the lateral basioccipital than in *C. didactylus*, often forming a medial connection to it posteriorly or ventrally, in one case actually suturing to the basioccipital ventrally. Because of this close association, it is quite common in *C. hoffmani* for the internal carotid to pass through a carotid foramen between the entotympanic and basioccipital before entering the median lacerate foramen. Such a carotid foramen is rare in *C. didactylus*.] There is no postglenoid foramen, and only minute, rather variable openings in the positions occupied by the subsquamosal and mastoid foramina in other xenarthrans. A large venous sinus runs posteriorly

in a shallow groove that begins above the internal orifice of the foramen lacerum posterium and ends at the side of the foramen magnum. In some specimens venous foramina, clearly parts of the transverse sinus drainage, open on the occiput just above the condyles. [These occipital venous foramina are found only in *C. didactylus*, and then only in about half of the specimens.] The foramen lacerum posterium is bounded anteroexternally by the entotympanic and posterointernally by the exoccipital. The stylomastoid foramen opens very slightly below the level of the superficies meatus and is bounded dorsally and posteriorly by the mastoid [and squamosal], anteriorly and ventrally by the tympanohyal; it is a foramen primitivum. The chorda tympani, after leaving the tympanic cavity anteriorly, runs in a groove in the posterior face of the adjacent portion of the squamosal. This groove is bordered posterolaterally by the tympanic and posteromedially by the processus cristae facialis.

The *Megalonyx* Group

Acratocnus Anthony

We have been able to examine the fine series of skulls of the Pleistocene Puerto Rican form in the American Museum. The following account is based largely on AMNH 17722, *A. odontrigonus* Anthony, in which the auditory region is almost perfectly preserved.

Acratocnus odontrigonus, AMNH 17722, 17715, 17720–21 (skulls), 17717 (mandibles), described and figured by Anthony, 1918, 1926.

A wonderful animal! So similar in many respects to *Choloepus* and yet indicating how such forms as *Megalonyx* and *Megalocnus* may be tied in to the living form. The remarks here [in these four paragraphs] are confined to such characters as vary or are not well shown in the borrowed skull.

The caniniformes [are similar to those of] *Choloepus* but relatively larger. The pits on the side of the face are variable in depth; [they are] very shallow in 17715. The jugal union is about as in *Choloepus*. The frontal sinuses are moderate in 17720–21 [and] enormous and arched in 17715, an old individual. The sinuses do not extend back into the parietals, [and the] sagittal crest is very

¹² [Patterson and Segall are presumably referring to Matthew's (1909) and others' concept of a medial and lateral internal carotid artery by their use of the term "second artery."]

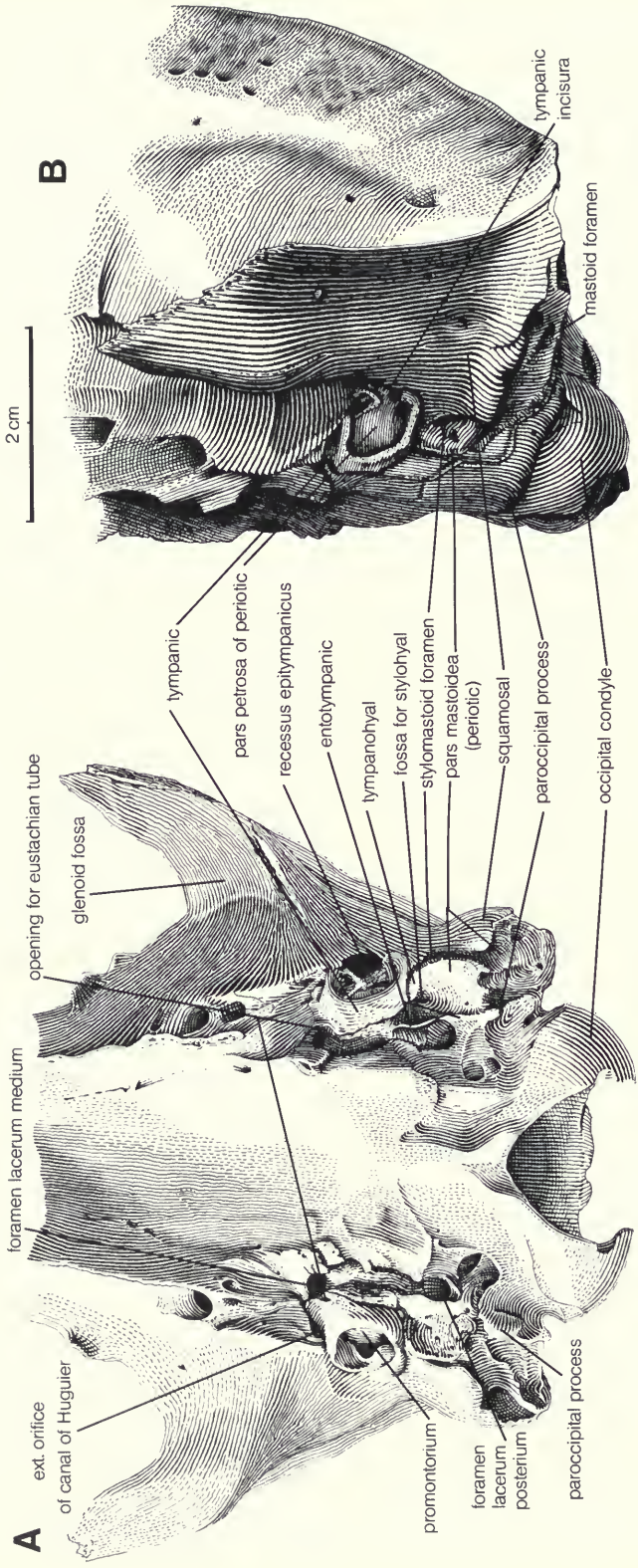


FIG. 5. *Acratocnus odonirigonus*, AMNH 17722. A-B, posterior portion of skull shown in ventral and left lateral views.

high and well developed. The dorsal contour of the skull is as in *Choloepus* and *Megalocnus*. [Some specimens (esp. 17715) show a small indentation in the normally smooth, unbroken curvature of the dorsal contour. This indentation is located just anterior to the bulging frontal sinus.] No inflation of pterygoids or basicranium [is present]. The occiput [has a] moderate forward slope. The glenoid fossa is of *Choloepus* type. The epitympanic recess is large, confined to the squamosal, and extends farther anteriorly than posteriorly. It is apparently rather variable in size. The tympanohyal is rather large, moderately tapering upward, and forms nearly all of the stylohyal fossa; the mastoid sends down a process that bounds the fossa laterally and extends far below it. [The above description of the tympanohyal is in contradiction to that of the tympanohyal in AMNH 17722, given below, in which the tympanohyal is said to form "only the anterior extremity" of the stylohyal fossa. Upon examination of the relevant specimens, it appears that the latter description is the correct one.]

The entotympanic is essentially a thin antero-posterior plate connected with the paroccipital process posteriorly and tympanohyal laterally. The periotic is bulbous, as in *Choloepus*.

The mandibular symphysis [has a] moderate spout; the angle is produced far posteriorly; the condyle is very wide [and] sinuous.

Acratocnus odontrigonus, AMNH 17722. Figure 5.

The tympanic agrees closely in relative size, shape, and direction [orientation] with that of *Choloepus*, differing only in being broader ventrally, the width of this portion increasing anteriorly as far as the opening for the Eustachian tube. The crista tympanica and sulcus tympanicus are very slight, essentially as in *Choloepus*. The sulcus malleolaris is well developed, again as in *Choloepus*. Due to lack of inflation of the squamosal, contact of squamosal and anterior crus is less extensive than in *Choloepus*, being limited to the superior two-thirds of the crus. The anterior crus extends slightly higher on the skull than the posterior. The two crura approach each other closely, being separated only by a small incisura. The spinae are identical with those of *Choloepus*. The porus is oval in outline with the long axis dorso-ventral, and presents laterally and ventrally, less ventrally than in *Choloepus*, however. It is situated a short distance behind the glenoid articulation, being almost exactly intermediate in this respect

between *Choloepus* and *Megalonyx*. The glenoid is similar in structure to that of *Choloepus* but is situated farther forward relative to the position of the tympanic.

The entotympanic is a thin plate directed anteriorly and slightly medially. In shape and direction it is very similar to that of *Choloepus*, but is in contact for much of its length with the tympanic, due to the medial expansion of the latter. Posteriorly it fuses with the paroccipital process, as in old individuals of *Choloepus*. Medially, the entotympanic is in contact with the basisphenoid [and the basioccipital, as evidenced by a clear suture on the right side of the skull]. The Eustachian tube is in the usual position and clearly defined. The tympanic margin is slightly raised but a definite styliform process is not developed.

In strong contrast to *Choloepus*, *Megalonyx*, and *Megalocnus*, there is little inflation of the pterygoids and basisphenoid.

The tympanohyal is very little larger than that of *Choloepus*, but in contrast to this form, and in common with all ground sloths, there is a large fossa for the stylohyal, of which the tympanohyal forms only the anterior extremity. The rest of the fossa is formed by the mastoid posteriorly and laterally and by the entotympanic and exoccipital medially. The articular surface is on a level halfway between that of the incisura tympanica and that of the ventral margin of the tympanic.

The promontorium is rather deep dorsoventrally. The recessus epitympanicus does not differ from that of *Choloepus*. The extent of the sinus cannot be determined. The pars mastoidea is basically similar to that of the living form but differs in detail. The mastoid process is better developed, projects laterally, forming a decided angle with the postglenoid surface in ventral view, extends down well below the level of the incisura tympanica, and has a sharp posterior edge that reaches to the occipital crest dorsally. The exoccipital crest is essentially as in *Choloepus*. The groove between crest and mastoid process is much deeper and better defined in *Acratocnus*, due to the larger mastoid process, and abruptly terminates anteriorly at the large stylohyal fossa. [We see a narrow extension of this groove that passes anterior to the stylohyal fossa to connect with the stylomastoid foramen.]

The carotid foramen is very small and situated between basioccipital and entotympanic. [There is a groove on the ventromedial surface of the entotympanic that extends anteriorly to reach the median lacerate foramen. This groove would seem to indicate that the internal carotid traveled ven-

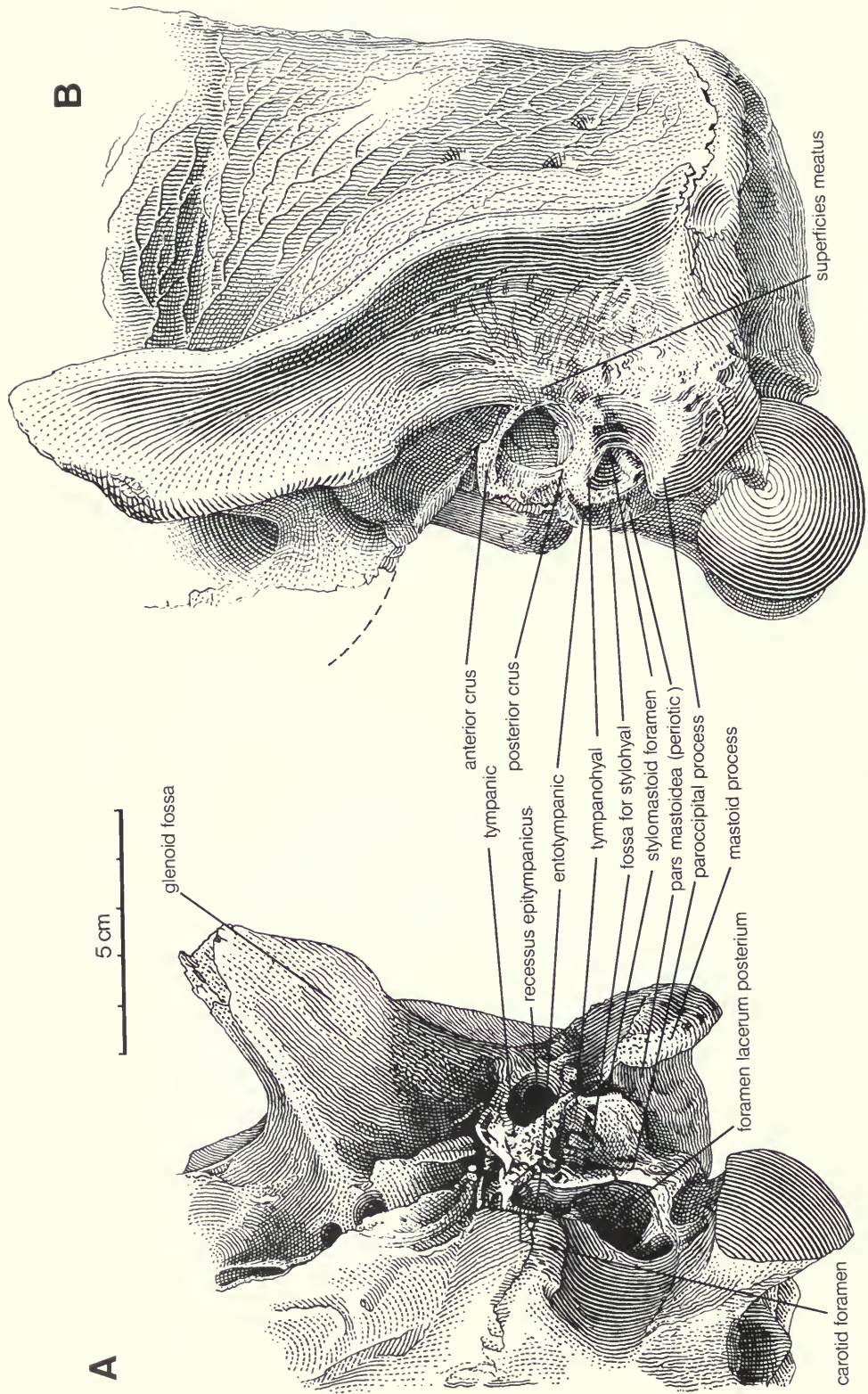


FIG. 6. *Megalonyx jeffersonii*, IMNH 38001/87 (= ISC 6377-87): A-B, posterior portion of skull shown in ventral and left lateral views.

tral to the entotympanic until it reached the median lacerate foramen, and did not pass through a carotid foramen. The foramen that B.P. and W.S. describe as the carotid foramen may be similar in function to the foramen that passes through the medial entotympanic in *Myiodon*.] The foramen lacerum medium is large and widely open below. There is no postglenoid foramen as in *Choloepus*. The mastoid foramen opens in the dorsal portion of the deep excavation between the exoccipital and the mastoid process. The foramen lacerum posterium is large and nearly circular in outline, essentially as in *Choloepus* and *Megalocnus*. The stylomastoid foramen is situated on the lateral side of the skull immediately behind the tympanohyal and hence well posterior to the tympanic; it is thus a foramen primitivum, as in *Choloepus*. The external orifice of the canal of Huguier [i.e., fissura Glaseri] is situated between squamosal and anterior crus, at a point near the dorsal extremity of the latter.

Megalonyx Harlan; *M. jeffersonii* and *M. brachycephalus*. Figure 6.

Two skulls have been available for study: an excellent, nearly complete specimen of *M. jeffersonii* Harlan, Idaho State College 6377-87, and the fine type of *M. brachycephalus* Stovall and McAnulty, Texas Memorial Museum -30907-60 (original G-333) [from the Pleistocene of Texas (Stovall & McAnulty, 1950)]. Previous accounts of the auditory region of this form have been based on inadequate material, and we therefore give a full description here.

The tympanic is small in comparison to the size of the skull, as in *Acratocnus* and *Choloepus*, and is inclined ventromedially. The ventral portion is enlarged, both dorsoventrally and transversely, more so than in *Acratocnus*, and has a decidedly rugose surface. The crura are slender. The dorsal portion of the anterior crus is fused, in adults, with the squamosal, which forms a broad superficial meatus. The limits of the incisura tympanica cannot be seen but it was probably as short as in *Megalocnus*. In *Megalonyx brachycephalus*, but not in *M. jeffersonii*, the posterior crus is separated from the stylohyal fossa by a conspicuous groove. The porus is oval, with the long diameter dorsoventral. *Choloepus*, *Acratocnus*, and *Megalonyx* form a structural series as regards enlargement and rugosity of the tympanic.

The glenoid articulation is basically similar to that of *Choloepus* but is lower and situated farther

forward relative to the tympanic than in that form, the postglenoid surface of the squamosal sloping gently upward and backward toward the squamoso-tympanic junction. *Acratocnus* is intermediate between the two, the three genera forming a structural series in the character also.

The large entotympanic consists of two vertical plates united above—much as in the mylodonts and other large ground sloths—and also anteriorly just behind the opening for the Eustachian tube. The lateral plate, which corresponds to the single one of *Choloepus* and *Acratocnus*, extends ventrally below the level of the tympanic and is continuous posteriorly with the paroccipital process. The medial plate is in sutural contact with the basioccipital, basisphenoid, and petiotic. The opening for the Eustachian tube is large. A small but sharp styliform process of the tympanic is present in the specimen of *M. jeffersonii*, and an even smaller blunter one is in *M. brachycephalus*.

The basicranium is inflated in the region of the basioccipital-basisphenoid suture and the inflation probably extends to the base of the pterygoid and possibly to the squamosal as well. In the type of *M. brachycephalus* there is a pair of large, posteriorly facing fossae in the basioccipital.

The tympanohyal is large, and forms the antero-external portion of the extensive stylohyal fossa, the rest of which is composed of the mastoid, exoccipital, and entotympanic. The fossa is on a level with the ventral margin of the tympanic, lower than in *Acratocnus*, in which in turn the articulation is lower than in *Choloepus*. A peculiar feature of the type of *M. brachycephalus* [lapsus: *M. jeffersonii*, as indicated above] is that the articular area for the stylohyal extends to the tympanic, which bears a facet on the ventral portion of the posterior surface.

Nothing can be seen of the ventral surface of the pars petrosa. [From the portion of the petrosal now exposed, it can be seen that the anterolateral surface of the bone forms a relatively flat surface, and that this surface extends anteromedially toward the basicranium.] The recessus epitympanicus is large and a definite foramen pneumaticus is present. The size of the epitympanic sinus cannot be determined. The position and extent of the pars mastoidea on the external surface of the skull appears to be comparable to the exposed portion in *Choloepus* and *Acratocnus*, but the surrounding region is quite different. The mastoid process is large, strongly projecting, continuous above with the occipital crest and descending to the level of the ventral border of the tympanic. It differs somewhat in the two available specimens, being later-

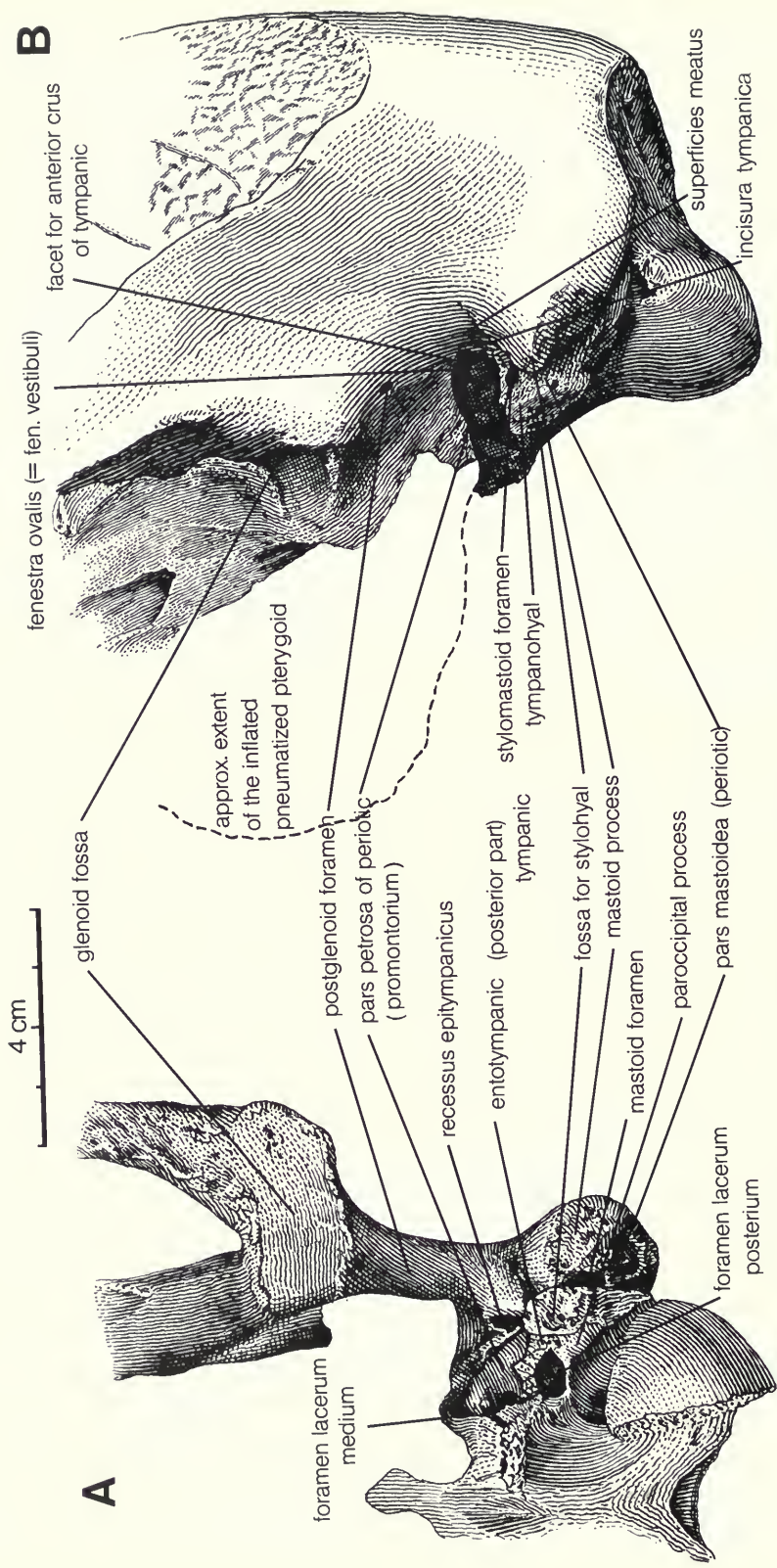


FIG. 7. *Megalocnus rodens*, FMNH P15104: A-B, posterior portion of skull shown in ventral and left lateral views.

ally compressed in *M. jeffersonii*, anteroposteriorly compressed in *M. brachycephalus*. The paroccipital process is greatly reduced in comparison with either *Acratocnus* or *Choloepus*; it does not project freely but is incorporated in the posterointernal portion of the fossa for the stylohyal. [This process is still large relative to those found in other sloths.] The exoccipital crest is short, not continuous with the occipital crest, and is concealed in lateral aspect by the mastoid process. The groove between these is wide and short and, as in *Acratocnus*, terminates abruptly at the fossa for the stylohyal. [Like *Acratocnus*, this groove continues lateral to the stylohyal fossa to terminate at the stylomastoid foramen.] As in several other characters, *Choloepus*, *Acratocnus*, and *Megalonyx* form a series in the structure of the mastoid area, the Puerto Rican form connecting the two extremes.

The structure of the Santacruzian megalonychid *Eucholoepus* (q.v. below) suggests that *Acratocnus* is in many respects a rather generalized form, and that *Choloepus* on one hand, *Megalonyx* and *Megalocnus* on the other, represent divergent specializations from a primitive megalonychid stem.

The carotid foramen opens posteriorly in the saddle between the two plates of the entotympanic. In the specimen of *M. brachycephalus*, but not in that of *M. jeffersonii*, there is a minute venous opening in the postglenoid surface. The mastoid foramen opens ventrally between the distal part of the mastoid process and the fossa for the stylohyal, the termination of a canal that runs down within the occiput from the squamoso-mastoid-supraoccipital junction. [This foramen is the equivalent of foramen "x" in Hirschfeld and Webb (1968). Their mastoid foramen is either a dorsal opening of the canal for the occipital artery or the foramen for the arteria diploetica magna—we cannot say which it is without examining the specimens personally.] The stylomastoid foramen is as in *Acratocnus*. The foramen lacerum posterium opens into an extensive fossa bounded by the basioccipital, exoccipital, and entotympanic.

Megalocnus Leidy; **M. rodens**. Figure 7.

A skull of *M. rodens* Leidy, FMNH P15104, from the Pleistocene of Cuba, has been available to us. Tympanic and entotympanic are unfortunately incomplete, but the remainder of the region is well preserved.

The posterior crus of the tympanic, all that is

preserved of this bone, is small and slender, as in *Acratocnus* and *Choloepus*. Much of the superficies meatus anterior to the attachment of the posterior crus is occupied by a facet evidently for the dorsal end of the anterior crus, leaving only a very short incisura tympanica. The space that was occupied by the tympanic is very short anteroposteriorly. Attachment of the anterior crus to the squamosal was apparently as extensive as in *Choloepus*. The position of the glenoid articulation relative to the tympanic, and the extent and degree of slope of the postglenoid surface, are essentially as in *Megalonyx*. The articular surface itself is very well defined, transverse, and does not extend forward onto the zygomatic process.

The posterior portion of the entotympanic is the only part preserved. It participates in the formation of the stylohyal fossa, forms the anterior border of the foramen lacerum posterium, and has a sutural contact with the basioccipital.

As already noted, *Megalocnus* has an extraordinarily pneumatized skull, the extreme in this respect among known edentates, nearly every bone being involved to some degree. In the auditory region, the squamosal, pterygoid, basisphenoid, basioccipital, exoccipital, and pars mastoidea are all invaded by an interconnecting sinus system.

The tympanohyal does not differ from that of other megalonychids except in position, the proximal portion being more anterior relative to the posterior crus of the tympanic.

The ventral portion of the pars petrosa is deep, being produced ventrally into a blunt, slightly rugose process that projects downward along the side of the basisphenoid. Due to this prolongation, the ventral aspect of the bone differs considerably from that of *Choloepus*, in which the promontorium is globular in shape. The rugosity on the prolongation is presumably the attachment surface for the entotympanic. The processus cristae facialis is largely broken away. What remains, together with the adjacent part of the squamosal, suggests that it was similar in general to the process in *Choloepus*. As in the living form, the recessus epitympanicus passes without sharp demarcation into the sinus epitympanicus. The latter is very small in the specimen at hand, much smaller absolutely than in *Choloepus*, being limited to the area immediately above the superficies meatus and not extending into the root of the zygoma, the sinus there communicating with the pterygoid system [of cranial sinuses]. The pars mastoidea and the adjacent area are much as in *Megalonyx*, the principal differences being that the mastoid process,

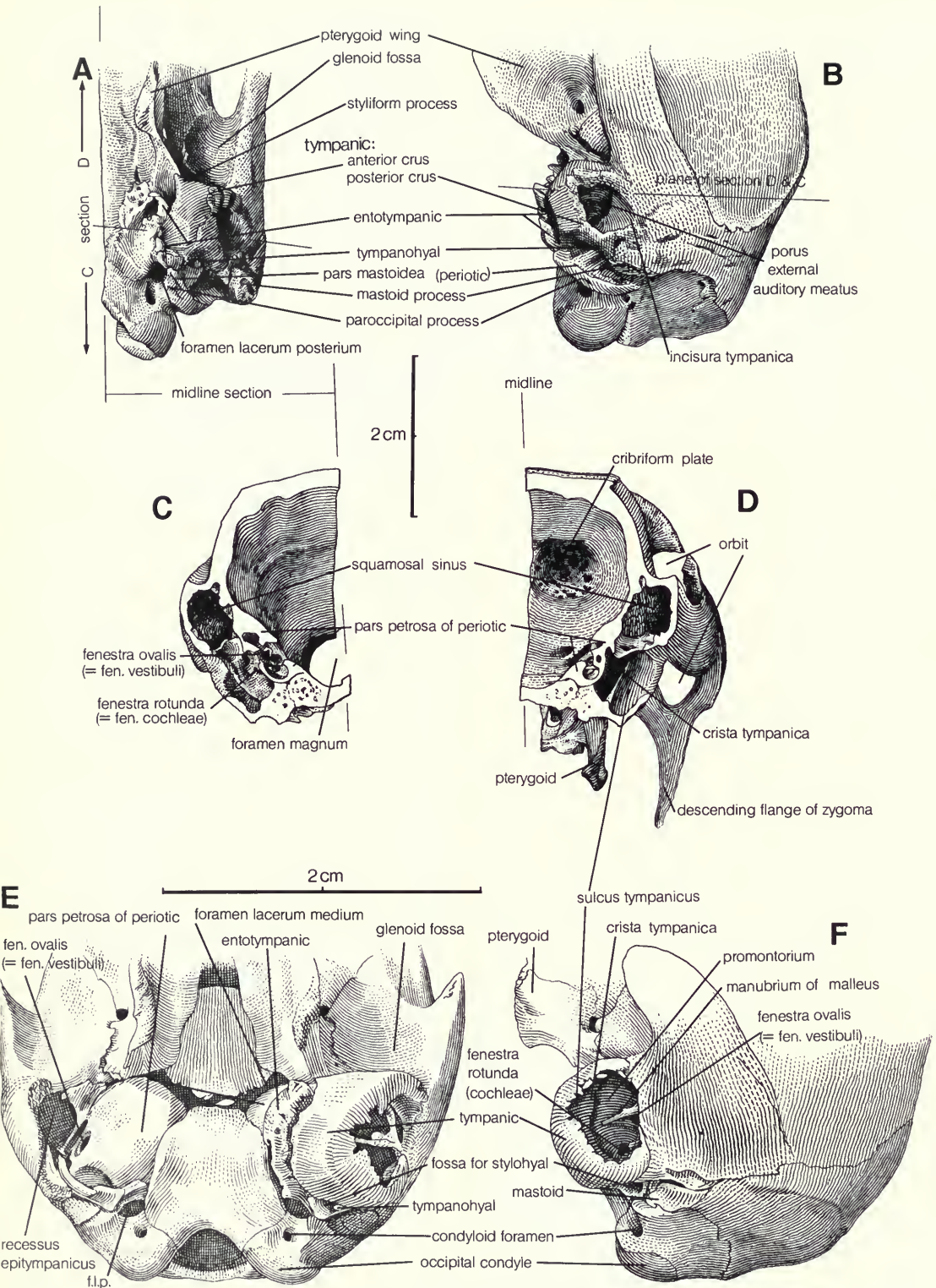


FIG. 8. *Bradypus tridactylus*, FMNH 16557: A-B, posterior portion of skull shown in ventral and left lateral views; C-D, sectioned skull, with cut running through meatus, bulla, petrosal, and braincase, shown in views toward anterior

although equally prominent, scarcely descends farther ventrally than the vestigial process of *Choloepus*; the groove between the occipital-mastoid crest and the exoccipital crest is narrower and is not blocked anteriorly by the very prominent, almost pedunculate fossa for the stylohyal but passes forward external to it; and the paroccipital process is even less prominent, being almost completely subordinated in the fossa for the stylohyal.

Concerning the relation of the internal carotid artery to the entotympanic, nothing definite can be said in the absence of the anterior portion of the entotympanic, although in all probability they were about as in *Acratocnus* and *Megalonyx*. The foramen lacerum medium is large and in the usual position immediately anterior to the medial portion of the pars petrosa. A small postglenoid foramen, an unusual feature in megalonychids, is present. As in *Megalonyx*, the mastoid foramen is the termination of a canal that runs down within the occiput; it opens in the rather narrow groove between the mastoid process and the exoccipital crest. The venous sinus running posteriorly from the internal orifice of the foramen lacerum posterium and leaving the skull via the foramen magnum ran in a large, very well-defined channel in the side of the medullar surface of the exoccipital. The foramen lacerum posterium is small in comparison with the size of the skull. The fossa into which it opens ventrally is much smaller than in *Megalonyx*. Due to the forward position of the proximal portion of the tympanohyal, the stylo-mastoid foramen is bounded anteriorly by the tympanic and is hence a foramen definitivum. In *Choloepus* and the megalonychids described above, it is bounded anteriorly by the tympanohyal and is therefore by definition a foramen primitivum. The difference is a trivial one.

The *Bradypus-Megatherium* Division

The *Bradypus* Group

Bradypus Linnaeus; **B. tridactylus** and **B. variegatus**. Figure 8.

Eighteen skulls have been available to us.¹³ The situation with regard to species is as confused as

¹³ [The following specimens of *Bradypus* were examined:

it is in *Choloepus*; numerous specific names having been proposed without consideration for the great variability that exists. Pending revision, the material is referred to *B. tridactylus* Linnaeus. [As with *Choloepus*, revision of the genus *Bradypus* has since been published by Wetzel (1985), and Wetzel and de Avila-Pires (1980). Wetzel splits the genus into three species: *Bradypus torquatus*, *B. tridactylus*, and *B. variegatus*. We did not have access to any skulls of the first species, *B. torquatus*. Skulls were assigned to either of the latter two species on the basis of cranial characters provided by Wetzel, the most consistently useful of these being the presence or absence of large foramina in the anterior nasopharynx (the foramina are present in *B. tridactylus*, lacking in *B. variegatus*). Two of the original 18 specimens examined by B.P. and W.S. (see footnote for specimen numbers) could be placed in the species *B. tridactylus*, including the figured adult. The remaining 16, including the figured juvenile, belonged to *B. variegatus*. We examined an additional 29 specimens, including five specimens of *B. tridactylus* and 24 of *B. variegatus*. No consistent differences were identified in the bony ear anatomy of the two species. Such small differences as did occur were undoubtedly attributable to our small sample size for *B. tridactylus* and to the fact that the skulls of this species that we did have were taken mostly from older individuals.] The structure of the auditory region, and indeed of the skull in general, is entirely different in the two genera of living tree sloths.

The tympanic in newborn specimens is relatively larger than in newborn *Choloepus*. In contrast to this and to all other sloths thus far described, the bone increases in size during life, being about one-third longer in adults than in very young specimens. The increase is especially notable in the lateral direction, where bone growth proceeds outward in varying degree from the original tympanic ring, a striking characteristic of the *Bradypus-Megatherium* division. The variability in this

Bradypus tridactylus—B.P. & W.S.: FMNH 16556, 16557 (illus. in fig. 8). W.T. & T.G.: FMNH 92079, 93297, 95444–45.

B. variegatus—B.P. & W.S.: FMNH 20132, 21393–94, 21430, 21551, 25315 (illus. in fig. 8), 25316–19, 30738, 31119, 34401, 50906, 51871, 57112. W.T. & T.G.: FMNH 60164, 68916–17, 68919–21, 69587–90, 70812–13, 86760–62, 86879, 86896, 88489, 88893, 90060–61, 94296, 94551.]

← and posterior sides of cut. *Bradypus variegatus*, FMNH 50906: E–F, posterior portion of juvenile skull shown in ventral and left lateral views.

feature results in striking differences in the length of the ventral wall of the meatus. With advancing age there is a tendency toward development of a rugose external surface, in some cases leading to the formation of a distinct lip of bone around the lower margin of the porus. This is not universal; a few old specimens retained a smooth surface. In newborn individuals the crura are seen to approach each other closely, with only a small incisura tympanica between them. The porus is very large and irregularly V-shaped, the apex of the V extending nearly to the sulcus tympanicus. Later on, with the lateral enlargement of the tympanic below and lateral growth of the squamosal above, a definite cylindrical auditory meatus, which ascends at a very steep angle, forms in most individuals. [It should be noted that the porus changes shape with lateral growth of the tympanic, becoming more oval, or even circular, in most adults.] The crista tympanica and sulcus tympanicus are well developed, the sulcus being very broad. In contrast to *Choloepus*, there is no sulcus malleolaris. The anterior process of the malleus extends forward to the fissura Glaseri.

Anterointernally, the tympanic sends forward a short styliform process, which may or may not unite with the base of the pterygoid process. Along its entire medial border, the tympanic is in close contact with the entotympanic; the two may become fused in adults. [In fact, in the large majority of specimens examined, the tympanic and entotympanic were solidly fused to one another.] Posteriorly the bone is in contact with the mastoid and the tympanohyal.

The stylohyal, as is well known, turns sharply forward to attach along a rugose surface at the medial border of the tympanic. In some individuals this surface forms a prominent crest.

The entotympanic is a relatively massive bone; in many specimens the surface is very rough and perforated by numerous minute foramina. It is long and narrow, almost parallel-sided, extending from the pterygoid posteriorly to the paroccipital process and then turning laterally to contact the squamosal posteroexternal to the vagina processus hyoidei. [Although B.P. and W.S.'s figured juvenile specimen of *B. variegatus* shows a contact between the entotympanic and squamosal dorsal to the vagina processus hyoidei, several of the juveniles that we examined (incl. FMNH 21430 (one of B.P. & W.S.'s specimens), 68917, and 70813) showed a clear exclusion of entotympanic/squamosal contact by the intervening mastoid. In these cases, the mastoid forms much of the posterodor-

sal portion of the vagina processus hyoidei. In most older individuals, the bones in this region fuse up, making it impossible to determine whether the entotympanic forms the entire posterior vagina or if there is mastoid participation.] In old individuals it fuses with the tympanic. Anterointernally a small process runs toward the inner side of the root of the pterygoid process with which it may fuse. In some individuals [indeed, most individuals that we examined] a crest develops near the lateral border of the bone parallel to the crest on the tympanic for attachment of the stylohyal; when present this also serves for attachment. A division between rostral and caudal portions midway between the carotid foramen and the vagina processus hyoidei is visible in FMNH 25315, a very young individual. Van der Klaauw (1931b, p. 313) has called attention to an opening in the posterior wall of the bulla in a young specimen: "... the tympanic bears a large aperture between the tympanohyal and the bulla, opening into the cavity of the bulla." Van Kampen (1905, p. 478) has described similar conditions. This is a variable feature. Only one of our young individuals, FMNH 50906, showed a small opening in this area between tympanic and entotympanic; other and younger skulls show no trace of it. In 50906 the opening was certainly due to delayed ossification of the caudal entotympanic in this area, and was closed by cartilage during life. [We found two additional specimens, one from each species (*B. tridactylus*, FMNH 93297, and *B. variegatus*, FMNH 94296) that showed the same condition as that described in 50906. Both of our specimens are young adults, substantially older than 50906, but with the cranial sutures still unfused.]

In decided contrast to *Choloepus* and some of the later megalonychids, sinuses other than the frontal and epitympanic are extremely rare. A small sinus in the pterygoid may occur, as is well known, and this has been used for taxonomic purposes, probably without justification.

The small tympanohyal occupies the bottom of the vagina processus hyoidei. The vagina is variable in size and shape and is formed by the tympanic anteriorly and the entotympanic posteriorly; the mastoid participates only slightly or not at all in its formation. [As discussed above, several of our juvenile specimens showed a large posterodorsal contribution of the mastoid to the vagina processus hyoidei. In addition, several young adults (FMNH 68919, 68920, and 70812) had incompletely fused sutures in this region, and appeared to show a substantial mastoid participation in the

vagina.] Van Kampen (1905, p. 478) stated that the vagina is formed exclusively by the tympanic, but this is clearly not the case. In its possession of a definite although small vagina processus hyoidei, *Bradypus* differs notably from the ground sloths and from *Choloepus*. [It is interesting to note that a juvenile specimen of *Glossotherium* (LACMHC 12230), an isolated temporal region loaned to us by the Page Museum, also possesses a definite vagina processus hyoidei, lacking in adult specimens of this genus. This opens up the possibility that the vagina of *Bradypus* is a neotenic retention of a more widespread juvenile morphology, although juveniles of *Choloepus* lack this morphology.]

The *Megatherium* Group

The Nothrotheriines

Nothrotheriops (*Nothrotherium*) *shastense*,¹⁴ YPM 13198, Pleistocene of New Mexico (Lull, 1929).

[We did not have access to YPM 13198, but the following description was checked against a Field Museum specimen (P15185) from Rancho La Brea (Pleistocene, California). The Field Museum specimen was well preserved and almost complete, except for the missing tympanic rings.] The tympanic crura approach each other very closely with only a small incisura; the anterior crus is much stouter than the posterior. The anterior crus touches but is separate from the pterygoid. The tympanic is expanded anteriorly and ventrally (medially), the ventral expansion being pointed, much as in *Megatherium* and, especially, *Pronothrotherium*. The length of the tympanic on the external side is 16.3 mm. The Eustachian opening is con-

cealed by dried soft parts, but is apparently about as in *Pronothrotherium*. The sulcus tympanicus lies somewhat in from the lip of the porus, so that a slight meatus is present. The lip of the porus is thickened anteriorly and ventrally; the porus is irregularly circular in outline. The tympanic is relatively small for the size of the skull; it is about the same absolute size as in *Pronothrotherium*.

The entotympanic is concealed entirely by stylohyal and dried soft parts.

The squamosal has a large epitympanic sinus. Its glenoid fossa is well forward of the tympanic, concealed largely by dried, soft parts and the dentary condyle, but is seemingly as in *Pronothrotherium*. The posttympanic portion is prominent and moderately expanded.

The stylohyal sits in the stylohyal fossa and articulates by means of a well-formed convex, oval articular area (as figured by Lull, 1929). There would appear to be a long process, broken into two parts, behind the stylohyal. Actually I [B.P.] think that these are parts of it that were either broken off or, and more probably, not yet ankylosed—the left side shows no trace of such a process, which would be wholly unslothlike in any event). The proximal portion of the stylohyal is expanded and has a triangular-shaped ventral process that is slightly expanded distally and posteriorly. Beyond the entotympanic-tympanic the bone tapers to a rodlike form only slightly deeper than wide and then expands slightly at the distal articulation. It projects forward to a point beneath the anterior extremity of the glenoid fossa, and is on the whole very similar to that of *Bradypus*.

So far as can be seen the mastoid is comparatively narrow transversely and forms the posterior part of the stylohyal fossa; there appears to be a rather deep cleft between it and the exoccipital.

The tympanohyal is barely visible; the stylo-mastoid foramen is immediately lateral to the tympanohyal and forms a groove on its lateral surface.

The basioccipital is short, with a pair of prominent tuberosities laterally at the junction with the basisphenoid.

The basisphenoid tapers rapidly anteriorly and is overlain by the vomer.

The vomer is an extraordinary bone. As described by Lull (1929), it bears a ventral median ridge, which is thin and jagged-edged. This begins to the left of the midline where its edge leans over below the ensheathing mesethmoid, then curves widely to the right, and finally turns directly posterior to run between the pterygoid sinuses for

¹⁴ [This specimen was listed as belonging to the species *Nothrotherium shastense*, the North American Shasta ground sloth, in the original manuscript. *Nothrotherium shastense*, however, was removed from the genus *Nothrotherium* by de Paula Couto (1971) and placed in its own genus *Nothrotheriops*. *Nothrotheriops* can be distinguished cranially from its South American relative *Nothrotherium* by, e.g., the shape of the jugal and zygomatic process of the squamosal, the morphology of its lower jaw, and the dorsal contour of the skull roof (de Paula Couto, 1971). All three specimens discussed in this section (YPM 13198, Lull, 1929; AMNH 30061, Simpson, 1933; and FMNH P15185 from Rancho La Brea) belong to the North American genus.]

about half their length. Posterior to the choanae the sides of the vomer spread abruptly and then gradually narrow as they approach the pterygoid anterior to the widened part of the pterygoid sinuses. Extending back beneath it is a bone (possibly the presphenoid) that is strongly convex ventrally as though inflated on either side of the vomer.

The curve of the median ridge of the vomer is duplicated, as Lull notes in the specimen described by Stock (1917, 1925), and an approach to this condition may be seen in the FMNH specimen of *Pronothrotherium*.

Anteriorly the palatine bones behave in the normal sloth manner [see e.g., Stock, 1925]. Posteriorly, however, they accompany the enlarged area of the vomer as thin strips that separate this bone from the pterygoids until it narrows down between the anterior ends of the pterygoid sinuses.

The pterygoid is the usual thin, large, descending plate, somewhat bowed out anteriorly, but posteriorly it is expanded by the enormous sinus that occupies half its length and extends back to the tympanic. Its shape and the elongate-oval orifice on its ventral surface have been well described by Stock (1917, 1925). The damage suffered by the right side of this skull permits a good view of the interior and makes possible a few additional statements as to the bones forming it. The anterior portion, sides, and most of the posterior portion are formed by the pterygoid. The basisphenoid shows through over a small area in the posterior portion. As Stock (1917, 1925) has pointed out, the alisphenoid forms most of the roof, but the squamosal also participates posterioexternally (no doubt conditions vary between skulls). There is one well-defined fossa posteriointernally where the basisphenoid participates and another in that part of the roof formed by the squamosal and a large concavity in the medial portion. The great degree of inflation that the posterior half of the pterygoid has undergone appears to have forced apart and spread the upper portion of the bone. There is, unlike conditions in *Choloepus*, no connection between this sinus and the frontal and no extension of the sinus posteriorly into the basioccipital tuberosities in this specimen. Neither Stock (1913, 1917, 1925) nor Reinhardt (1878) mentions any such connection or extension in the specimens described by them. It would seem that the pterygoid expansion has stood in the way of further growth of the tympanic beyond the size reached in *Pronothrotherium*. A large venous sinus left via the foramen magnum. [This sinus presumably ran in

a large groove connecting the posterior lacerate foramen to the foramen magnum on either side of the skull.]

Nothrotheriops sp., AMNH 30061, incomplete cranium, lacking squamosals and tympanic, briefly described by Simpson (1933), from a Nevada fauna of Pleistocene type.

The entotympanic on the left side is apparently complete. It is a relatively simple bone with an external portion projecting downward like a *Laevua* tooth [from the Latin *laevus*, meaning "smooth"?], and a broad medial groove concave transversely, convex anteroposteriorly with a raised medial rim, obviously for the carotid; the foramen lacerum medium is large. The external portion is rather like that of *Megatherium* and especially *Pronothrotherium* in having a shallow [vertical] groove anteriorly for the Eustachian tube. [The ventral surface of the] periotic is bulbous behind, flattened anteriorly, with an anterointernal ridge.

The tympanohyal is large and rapidly tapering within the tympanic cavity, forming the anterior half of the fossa for the stylohyal. The foramen lacerum posterium is large and oval; the stylo-mastoid foramen is on the external side of the tympanohyal.

The basioccipital [bears] large processes on either side just anterointernal to the foramen lacerum posterium. A large frontal sinus has deformed the anterior portion of the cerebrum. The sphenoidal region of the left side has two deep pits, the anterior considerably the deeper of the two, just above the basicranii [i.e., just lateral and dorsal to the platelike floor of the interpterygoid region]; the right side has the anterior [pit] but not the posterior, shallower depression—odd! There is little if any inflation around the basicranium.

Eucholoeps frontis, AMNH 9241.

[In addition to examining AMNH 9241, we have also compared the description given below with a Field Museum specimen of *Eucholoeps ingens* (P13139). Both specimens are taken from the early Miocene Santa Cruz Formation of southern Argentina.]

The tympanics are gone, the entotympanics largely so, but traces of the latter extending antero-internally from the tympanohyal appear to have been rather simple and ridgelike. [There appears to be a small fragment of the posterior crus of the tympanic still attached to the squamosal in FMNH P13139. The fragment is located anterolateral to the stylohyal fossa, directly in front of the stylo-mastoid foramen, making this a foramen definitivum. The entotympanic is a little better preserved in P13139, and rests dorsally on the rather globose promontorium. (AMNH 9241 bears a groove on the ventral surface of the promontorium in this position, much like the groove described above in *Octodontotherium*.) The preserved posterior portion of the entotympanic forms the anterior border of the posterior lacerate foramen, then runs medially to reach the stylohyal fossa and tympanohyal. The basioccipital bears lateral corrugations that appear to be the remains of a suture with the entotympanic. This would seem to suggest that the entotympanic was not simple and ridgelike but rather was expanded medially, and may very well have borne a sulcus for the internal carotid artery as seen in other sloth genera (cf. *Bradypus*, *Nothotheriops*, and *Megatherium*.)] The tympanohyal is small, tapering hardly at all within the tympanic cavity. The stylomastoid foramen is on the lateral side of it.

The mastoid exposure is large and deeply grooved, forming most of the stylohyal fossa. [The stylohyal fossa is small and circular. It is formed not only by the tympanohyal and mastoid, but also by the entotympanic medially.] The paroccipital process is moderately large, the mastoid descending with and joining it almost to its apex laterally. [There is a distinct mastoid foramen present, with a deep groove running ventrally from this foramen to the tip of the mastoid process. The groove becomes shallower here, then turns and runs anteriorly, becoming deeper once more, terminating finally at the stylomastoid foramen.] The foramen lacerum posterium is large and round. [The foramen is smaller in P13139, due to the presence of the entotympanic. The foramen is also more oval in appearance, with its long axis oriented posterolateral to anteromedial.] There is a large epitympanic sinus [extending anteriorly into the squamosal]. The glenoid fossa is transverse, similar to that of *Acratocnus*. [A clear postglenoid foramen is present on both sides of the skull in AMNH 9241.]

Pronothrotherium typicum, FMNH P14467, Pliocene Araucanense Formation of Argentina. Figure 9A–B.

The tympanic is well developed, aligned anteroposteriorly, and broadened in the medial direction, much more so anteriorly than posteriorly, as in *Megatherium*. The anterior crus sends forward a small process that indents the squamosal posterior to the glenoid fossa. [A similar process has been described by Guth (1961, pp. 120–121, fig. 103) in *Scelidotherium leptocephalum*, where it forms the anterior border to the fissura Glaseri.] Posteriorly the tympanic forms the greater part of the anterior boundary of the fossa for the stylohyal. It is not expanded laterally, in contrast to *Megatherium*. Anteriorly, save for the dorsal extremity, it is not in contact with the squamosal or pterygoid, but projects freely forward toward the glenoid fossa. In this it resembles *Megatherium* and *Bradypus*, the condition being less pronounced than in the former, more than in the latter. The bony meatus is very short; a ventral component is practically absent. The superficial meatus extends laterally and a little posteriorly; it continues dorsally in a smooth curve into the lateral surface of the squamosal. The porus [acousticus of the tympanic] is oval with the bony diameter running posterodorsally-anteroventrally. The relations of the crura to the squamosal are very similar to the conditions in *Bradypus*.

The entotympanic runs forward in an anterior and slightly medial direction. It is divided roughly into two portions, an anterolateral and a posteromedial. The anterolateral is united suturally with the tympanic, forming an osseous bulla as in *Bradypus* and *Megatherium*. It is produced anteromedially into a prominent blunt process, resembling the corresponding structure in *Megatherium*, which abuts against the pterygoid for the greater part of its depth. The tip projects freely. The posteromedial portion does not reach as far ventrally as the anterolateral; the two are closely connected and are separated ventrally only by a shallow groove into which minor foramina open. This portion of the entotympanic is better developed than in *Megatherium*. Its caudal extremity forms the medial part of the fossa for the stylohyoid and participates to a slight extent in the anterolateral portion of the foramen lacerum posterium.

The opening for the Eustachian tube occupies the same position as in *Bradypus* and *Megatheri-*

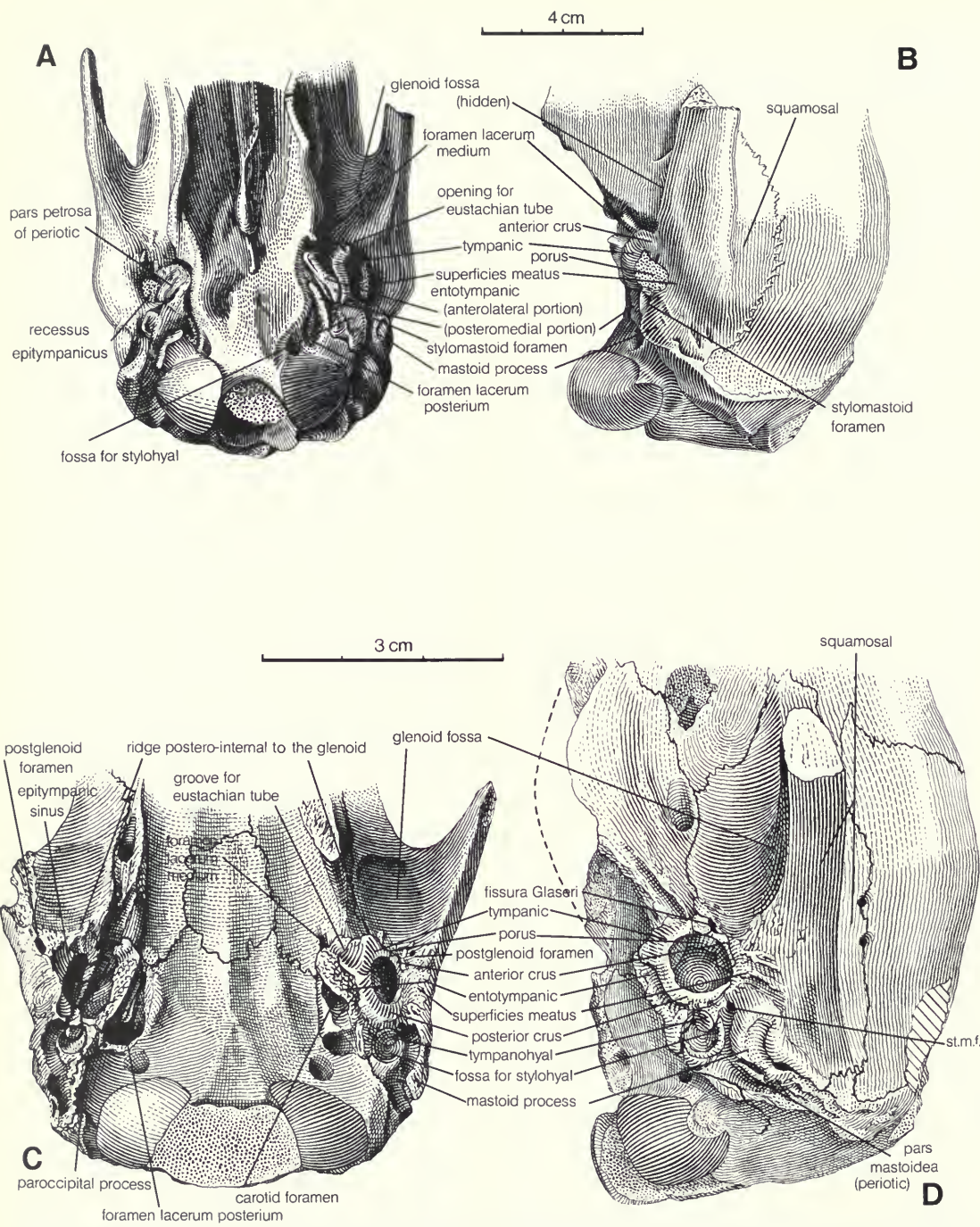


FIG. 9. *Pronothrotherium typicum*, FMNH P14467: A-B, posterior portion of skull shown in ventral and left lateral views. *Hapalops elongatus*, FMNH P13138: C-D, posterior portion of skull shown in ventral and left lateral views.

um. The styloform process is broken in the available material.
 The tympanohyal is almost identical to that of *Megatherium*, but participates to a greater extent

in the formation of the fossa for the stylohyal. The fossa is similar in the two forms, the only appreciable difference being that in *Pronothrotherium* it is posterior rather than posteromedial to the tym-

panic due to the enlargement, particularly in the caudal direction, of the tympanic in the Pleistocene form.

The cavum tympani [i.e., tympanic or middle ear cavity] is filled with very hard matrix so that no details can be determined. [The right side of the skull has now been prepared to such an extent that details of the composition of the tympanic cavity walls can be made out. The cavity is floored by the tympanic and entotympanic, the latter being hollowed out dorsally as in the mylodontoids. The posterior wall is formed largely by the tympanohyal, although there is a small entotympanic contribution via the usual process extending laterally from the entotympanic to the tympanohyal. The anterior and lateral walls are formed by the tympanic and squamosal, along with a small anteromedioventral participation of the pterygoid. The medial wall is composed of entotympanic and petrosal. The processus cristae facialis is clearly present but damaged, and a large epitympanic recess and sinus are present.]

The pars petrosa of the petiotic descends laterally and lies against the side of the basis cranii. Its anteroventral face is rather wide and flat, and forms a conspicuous angle with the slightly concave lateral face. [This anteroventral face appears to us, upon further preparation, to be a broken portion of the entotympanic.] The limits of the mastoid are not clear. This element evidently formed the posterior portion of the fossa for the stylohyal and appears to have contributed little, if at all, to the mastoid process, which is as well developed as in *Bradypus*.

The internal carotid ran forward beneath the medial portion of the entotympanic. The foramen lacerum medium is situated above the tip of the projecting process of the entotympanic. A few small vascular openings occur in the posterior portion of the glenoid fossa, as in *Megatherium*, and along the squamoso-parietal suture. The mastoid foramen is in the usual position. The foramen lacerum posterium is large, elongate anteroposteriorly, and continues forward into the groove for the internal carotid [i.e., it opens up into this groove], as in *Bradypus* and *Megatherium*. [In *Bradypus*, this groove is formed entirely by the entotympanic and is wholly ventral to the basicranium, whereas in *Pronothrotherium*, as well as in *Megatherium/Ermootherium*, the sulcus is walled medially by the basioccipital. *Nothrotheriops* is intermediate between these two conditions, with the anterior portion of the sulcus walled medially by the entotympanic and the posterior portion walled medially

by the basioccipital.] Also, as in these forms, the venous drainage through the foramen magnum was limited. [*Pronothrotherium* does not possess a distinct groove that exits the skull through the foramen magnum.] The stylomastoid foramen opens immediately behind the descending portion of the posterior crus of the tympanic and between the anterior extremities of the tympanohyal and the mastoid process. Since the posterior part of the facial canal is floored by the tympanic, its orifice is a foramen definitivum. As in the other bradypodids, the foramen faces more ventrally than in the mylodontids. [What Patterson and Segall mean by "other bradypodids" is not clear, because they clearly do not support a monophyletic Bradypodidae, *sensu* Simpson, 1945. However, both *Nothrotheriops* and *Megatherium/Ermootherium* have a ventrally directed stylomastoid foramen, much like that of *Pronothrotherium*.]

Hapalops (based in large part on FMNH P13138).
Figure 9C–D.

[We have also compared the description given below with Field Museum specimens P13133, P13135, and P13278, which Patterson and Segall certainly studied also. All specimens are taken from the Miocene Santa Cruz Formation of Argentina.]

The tympanic is exceptionally well preserved in FMNH P13138, somewhat less so in P13135. It is larger, relative to the size of the skull, and has a rougher surface than in either *Pelecycodon* or *Schismotherium*, and again unlike these forms, the anterior crus continues upward in a smooth curve and does not show a tendency to diverge laterally; both of these characters are points of resemblance to *Bradypus*. The bone is expanded medially far beyond the primitive ringlike condition. The anterior surface is not obscured, as it is in *Pelecycodon*, by the ridge on the squamosal posteroinferior to the glenoid surface. This ridge is very low in *Hapalops*. The medial surface approaches the entotympanic very closely along its entire length, not deviating from it posteriorly, as occurs in *Schismotherium* and *Choleopus*. Posteriorly it is in contact with the fossa for the stylohyal. The crura rest in a small, rugose excavation on the underside of the superficialis meatus of the squamosal; the [small] incisura tympanica is 2–3 mm in width. Van der Klaauw (1931b, p. 294) states that the tympanic is fused with the skull at the two extremities; this may happen in old individuals

but we have not detected any trace of it in specimens examined by us. He also remarks that the tympanic is narrow and without a distinct medial expansion. The bone is of course narrow in comparison with those of *Bradypus* and *Megatherium* or even *Pronothrotherium*, but is clearly wider and expanded medially in comparison with such forms as *Choloepus* or *Schismotherium*. The porus is round-oval with the longer diameter dorsoventral and distinctly smaller, as van der Klaauw notes [(1931b, p. 294)], than the medial opening. There is a very short recessus meatus. [The recessus meatus is "the most proximal part of the bony external auditory meatus, set off from the meatus proper by its broader diameter," as defined by McDowell, 1958, p. 128.] The sulcus tympanicus and crista tympanica are well defined, the crista continuing dorsally [two-thirds of the way up the anterior crus, and about half the way up the posterior crus]. Medial to the crista the tympanic continues for a short distance to form a rudimentary floor of the cavum tympani. The sulcus malleolaris is exceedingly broad.

Seen from below, the entotympanic has the usual irregularly triangular appearance with a long, lateral, vertical plate and a medial extension that bears a shorter medial plate. The lateral plate runs parallel with and in close proximity to the tympanic; it extends anteriorly to the pterygoid, where it curves laterally for a short distance. Posteriorly it forms the medial part of the fossa for the stylohyal and continues with hardly an interruption into the paroccipital process. [The latter is weakly developed and] appears to be lower than the mastoid and tympanohyal in our material, *contra* van der Klaauw (1931b, p. 295). It does not participate in the fossa for the stylohyal. The entotympanic is broadest, not narrower (cf. van der Klaauw, 1931b, p. 296), medial to the tympanohyal; it narrows immediately anterior to the [stylohyal] fossa and then widens again but never becomes as wide anteriorly as posteriorly. The medial extension of the entotympanic begins abruptly at the level of the anterior end of the fossa for the stylohyal, forming the anterior border for the foramen lacerum posterium, and runs forward in close contact with the straight lateral border of the basioccipital. This extension supports a short, ventrally directed eminence that forms the medial border of the sulcus caroticus. Between this medial extension and the basioccipital there is a well-defined anteroposteriorly directed groove. [Rostrally, the] entotympanic is connected with the basisphenoid, not the basioccipital [as suggested by van der Klaauw

(1931b, p. 298)]. The whole rostral part of the entotympanic is more ventral than the unswollen basicranium. Anteroexternally the bone bears a groove for the Eustachian tube. Tympanic and entotympanic are in contact behind the groove but are separate anterior to it.

The tympanohyal is inclined posteriorly to a conspicuous degree [especially in FMNH P13138 and P13278, but much less marked in P13135]. Within the fossa for the tympanohyal [lapsus: stylohyal—which, as Patterson and Segall noted, is smaller than in later forms], the boundaries between the various elements—tympanohyal, entotympanic, and mastoid—are very clearly shown in FMNH P13138 (fig. 9C–D).

The mastoid, so far as can be seen, forms the usual rather narrow strip between exoccipital and squamosal; anteriorly it is indistinguishably fused with the squamosal in all specimens that we have seen. The mastoid process is large and forms a rather conspicuous posteroexternal eminence in the ventral view of the skull. [The epitympanic recess is large and elongate anteroposteriorly. The recess is quite deep, apparently opening into an epitympanic sinus, the extent of which cannot be determined in the material at hand.]

The carotid foramen is, as usual, enclosed by the entotympanic and is situated at the anterior end of a groove running between the medial and lateral vertical plates of the entotympanic. The sulcus is situated entirely in the entotympanic and not between this bone and the basioccipital as van der Klaauw reported (1931b, p. 298). The postglenoid foramen is very small, sometimes absent, and frequently variable in development on the two sides of a specimen; it is situated immediately anteroexternal to the point of attachment of the anterior crus of the tympanic. There is no definite subsquamosal foramen, but a number of small, variable vascular openings are present in the squamosal and some larger ones along the squamosoparietal suture. The foramen lacerum medium is a minute opening situated at the anterior extremity of the entotympanic between this element and the pterygoid [very much resembling the condition in *Bradypus*]. The foramen lacerum posterium is large and transversely oval in outline; it is bounded anteriorly and laterally by the entotympanic, medially by the basioccipital, posteriorly by the exoccipital. The stylomastoid foramen is a foramen primitivum, but the tympanic is on the verge of forming a third part to the canal.¹⁵ The chorda

¹⁵ [Patterson and Segall are referring here to van der Klaauw's (1931b, following van Kampen, 1905) division

tympani left the tympanic cavity through a minute canal in the lateral extremity of the fissura Glaseri, medioventral to the attachment of the anterior crus of the tympanic. [The fissura Glaseri itself lies between the broad sulcus malleolaris and the squamosal, and opens externally near the squamosal/pterygoid suture. The fissura lies just above a much larger opening that serves to connect the tympanic cavity to a prominent groove running along the posterolateral edge of the pterygoid. The function of this groove is unknown, though it may have served as a site of origin for the tensor veli palatini muscle.]

The Megatherines

Eremotherium (*Megatherium*) *mirabile*. Figures 10–11.¹⁶

The tympanic is a stout, very rugose bone with a triangular enlargement that extends medially from the floor of the meatus and slightly overlaps the entotympanic ventrally. The short external auditory meatus is directed laterally; the dorsal and ventral walls are approximately equal in length. [The dorsal wall appears to us slightly longer.] The porus is roughly circular and lies in a nearly sagittal plane, being inclined about 10 degrees from the vertical in a ventromedial direction. In *Bradypus* the inclination from the vertical is much greater. The tympanic ring is open above, the squamosal participates to a slight extent in the dorsal wall

of the course of the facial nerve through the ear region (i.e., the “canalis facialis”) into as many as three parts. The first part is the facial canal proper, passing through the petrosal from the internal auditory meatus to the facial foramen. The second part is the facial sulcus, running medial to the crista facialis from the facial foramen to the stylomastoid foramen primitivum. The third part, when present, is a canal extending from the foramen primitivum to the foramen definitivum.]

¹⁶ [The specimen referred to by Patterson and Segall as *Megatherium americanum*, FMNH P26970 from the Pleistocene of Honduras, belongs rather to the genus *Eremotherium*, according to both its geographic distribution and the diagnosis provided by Hoffstetter (1952). Its specific designation, *E. mirabile*, was provided to us through the courtesy of a personal communication from Gerry Delulis of the University of Toronto. Following this description is a brief discussion of a specimen Patterson and Segall refer to as *Megatherium* (*Pseudomegatherium*) *lundi*, FMNH P14216, from the Pleistocene Tarija Formation of Bolivia. It would appear that this animal indeed belongs to the genus *Megatherium*, and that the differences noted between it and the above specimen constitute generic level differences.]

of the meatus. A recessus meatus can hardly be distinguished. The crista tympanica is moderately developed and sharp in FMNH P26970, running well up on each side, evidently to the limits of the [tympanic] spinae, where the two extremities approach each other. The spinae, especially the anterior, are well developed. Between and above them is the large incisura tympanica, whose presence imparts a pear-shaped outline to the hole opening into the middle ear. The sulcus tympanicus is moderately developed, being most clearly defined anteroventrally. Lateral to the crista [and sulcus], the wall to the meatus is ridged and grooved, especially anteriorly, and perforated by several small vascular canals, one of which runs back to open lateral to the stylomastoid foramen.

In the adult skull, the tympanic is for the most part fused with the surrounding elements. This is true of the squamosal and of the mastoid posteriorly. Between the tympanic and the large process for the stylohyal (formed mainly by the mastoid) there is a deep, rather sinuous groove that is closed anteriorly at the junction of the entotympanic and the apex of the medial, triangular enlargement of the tympanic.

The foramen stylomastoideum definitivum opens at the posterior end of this groove; three additional foramina also open into it [i.e., the groove] (see below). Tympanic and entotympanic are in contact only at the junction of the medial enlargement of the latter. There is no postglenoid process of the squamosal; the anterior portion of the tympanic in this region is very thick, rugose, and directed ventrally. The fissura Glaseri is obliterated, but the opening for the chorda tympani is visible above [i.e., anterodorsolateral to] the orificium tubae (see below).

The entotympanic is essentially an irregular, anteroposteriorly directed vertical plate of bone. It extends from the lateral margin of the foramen lacerum posterium to a point medial to the center of the external auditory meatus. Here its extremity turns medially to spread over and fuse with the basisphenoid. The anterior portion forms a conspicuous, ventrally directed process that unites with the medial enlargement of the tympanic. Posterolaterally it is fused with the process for the stylohyal; anterolaterally it forms the medial wall of the anterior portion of the groove between tympanic and stylohyal process described above. A broad and deep cleft, running between the foramen lacerum posterium and the carotid foramen, separates the greater part of it from the basioccipital and basisphenoid. In the upper part of this cleft

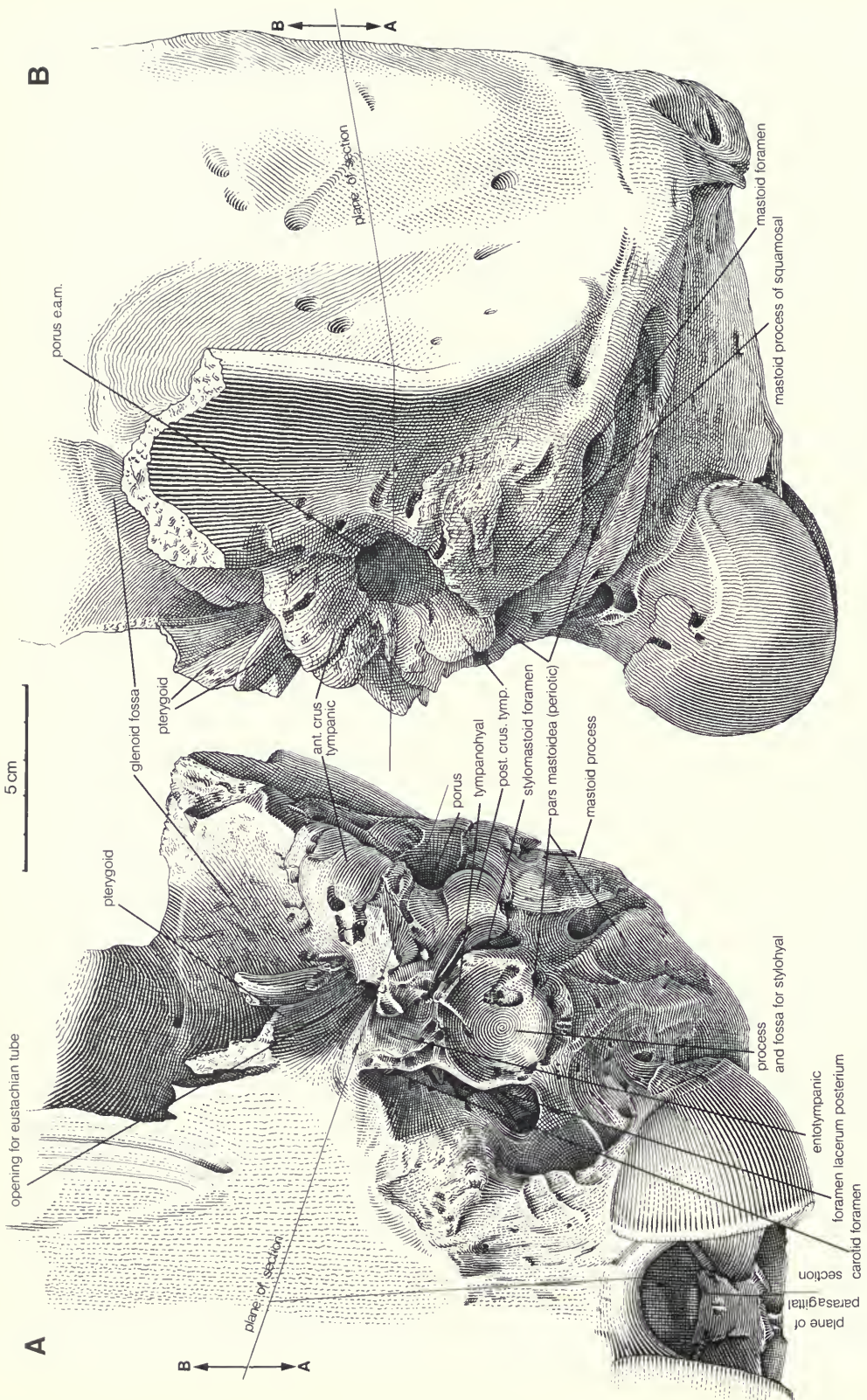


FIG. 10. *Eremotherium mirabile*, FMNH P26970: A-B, posterior portion of skull shown in ventral and left lateral views.



FIG. 11. *Eremotherium mirabile*, FMNH P26970: A-B, sectioned skull, with cut running through meatus, bulla, petrosal, and braincase, shown in views toward anterior and posterior sides of cut.

three processes from the medial surface of the entotympanic extend downward and medially along the side of the basisphenoid. Between and behind these processes are two foramina that lead dorsally into the tympanic cavity. Similar processes have been described at length by van der Klaauw (1930a). The cleft was occupied in life by the internal carotid artery (see below).

The opening to the Eustachian tube is large; it is bordered anteriorly by the pterygoid and posteriorly by the entotympanic and tympanic. After leaving the middle ear, the tube continues in a groove formed by the anterior extremity of the entotympanic and the posterior face of the pterygoid. This groove is directed ventrally and, to a slight extent, craniomedially.

The tympanohyal is clearly visible in transverse section; it is a stout, ventrally directed pillar situated between the periotic and tympanic and fused dorsally with the ventrally directed portion of the crista facialis. It continues ventrally to form the anteroexternal portion of the large, circular fossa for the reception of the stylohyal. The mastoid appears to form the posteroexternal and posterior portions of this fossa, and the entotympanic the medial.

The tympanic cavity is slightly deeper than wide and quite short anteroposteriorly. Its floor is formed, for the most part, by the entotympanic; the tympanic participates laterally to a much smaller extent. A narrow cleft separates the two bones. The most anterior of the foramina seen externally in the deep, sinuous groove between the tympanic laterally and the entotympanic and stylohyal process medially (van der Klaauw, 1930a, p. 135) leads into a canal that opens internally into the tympanic cavity within this narrow cleft. That portion of the floor supplied by the entotympanic slopes gently upward into a wedge-shaped process between periotic and tympanohyal. The lateral border of this wedge and the adjacent portion of the tympanic form a semilunar notch beyond which the tympanohyal leaves the cavity. Between these three elements is a large foramen leading to two canals, a larger lateral and a smaller medial, that open ventrally anterior and medial to the foramen stylostastoideum definitivum in the posterior part of the sinuous groove referred to above. Dorsal to the apex or the wedge formed by the entotympanic is another large foramen leading to a canal that opens externally in the posterior portion of the deep groove for the carotid artery. Judging from its position, this canal could have transmitted the stapedia artery. In the medial wall there is a nar-

row fissure between the entotympanic and the laterally projecting periotic. A small canal between these two bones leads from the fissure to the carotid groove where it opens anterior to the canal just described. In the anterior portion of the cavity the medial border of the tympanic forms a sharp ridge that constitutes the lateral boundary of the large opening for the Eustachian tube. Ventrally, this opening is bounded by the entotympanic and, to a lesser extent, tympanic, medially by the entotympanic. The anterior wall of the opening is formed, to a large extent, by the pterygoid.

The walls of the tympanic cavity converge dorsally to a slight extent to form the large foramen pneumaticum leading to the recessus epitympanicus [lapsus: epitympanic sinus]. [Note that van der Klaauw (1930a, p. 131) claims that the epitympanic recess lacked any "entrance to accessory cavities".] The recess [sinus] is larger than the tympanic cavity but is much less extensive than in either *Bradypus* or *Choloepus*, projecting to only a moderate degree anteriorly, and not at all posteriorly, beyond the level of the tympanic cavity. Laterally it extends slightly beyond the level of the sulcus tympanicus and medially it overlies the periotic for about half of its width. Several ridges radiate from the margins of the pneumatic foramen and a number of small bony projections are present. This is a point of resemblance to *Bradypus* and of contrast to *Choloepus*. The periotic is more posteriorly situated, relative to the tympanic cavity, than in either *Bradypus* or *Choloepus*, and does not extend anteriorly beyond the level of the anterior margin of the external auditory meatus. The fenestrae accordingly occupy a posterior position within the tympanic cavity, the fenestrae cochleae being barely visible in the section. The internal auditory meatus is oval, bony, and directed posteromedially. The division for the facial and acoustic nerves cannot be seen from the orifice. The hiatus subarcuatus [i.e., subarcuate fossa] occupies the same position as in the tree sloths. The cranial surface of the periotic is overlapped dorsally by a downgrowth of the squamosal. The limits of the mastoid portion of the periotic cannot be seen. This element probably formed most of the irregularly triangular, depressed area between the occiput and the root of the zygoma.

The groove between the basis cranii and the entotympanic for the internal carotid artery has been described above. At the anterior end of this groove, opposite the external auditory meatus, the artery entered a short canal that runs dorsal to the periotic and then turns sharply medially to open

into the braincase. After leaving this canal, the artery ran medially in a well-drained [lapsus?: well-defined] channel in the dorsal surface of the basisphenoid. The canals connecting the carotid groove and the tympanic cavity have been described above.

The main drainage of the transverse sinus system is through the large foramen lacerum posterium. [Traces of the transverse sinus system are visible as a series of grooves on the internal surface of the braincase. The superior petrosal sinus is marked by a deep groove running posteriorly along a lappet of the squamosal bone that covers the dorsal portions of the petrosal. This groove empties into a wider but somewhat shallower groove in the presumed vicinity of the squamosal-supraoccipital junction. The wide groove is clearly a remnant of the sigmoid sinus, and it runs in a gentle S-shaped curve ventrally and slightly anteriorly to empty into the foramen lacerum posterium. The groove for the sigmoid sinus is also joined by a deep groove apparently representing the transverse sinus. This groove curves medially in a U-shaped arc, first dorsally, then ventrally, and then splits near the midline into a vessel that opens out onto the external surface of the occiput, and one that travels dorsally to connect with the midline groove for the superior sagittal sinus.] Several minute venous openings in the squamoso-tympanic junction behind the glenoid cavity and a series of larger openings along the squamosoparietal suture are tributaries to this system [as are the postglenoid foramina]. The mastoid foramen occupies the usual position. The inferior petrosal sinus ran back in a small groove beneath the medial edge of the periotic, between this element and the basisphenoid. Near the anterior end of the periotic this groove bends sharply laterally and then ventrally, where it is only incompletely separated from the carotid canal. After a short distance it turns posteriorly to continue as a canal that runs back to the foramen lacerum posterium above the carotid groove.

The course of the facial nerve is well shown. The exposed part of the canalis facialis within the tympanic cavity is short. The crista facialis is well developed and deep; it continues anteriorly into a rather structureless mass of bone that is wedged between the anterior end of the pars petrosa and the ventral wall of the epitympanic sinus. This bony mass is clearly the homologue of the rather elaborately developed anterior processes of the crista facialis seen in other edentates, particularly the armadillos. Posteriorly the crista unites with

the tympanohyal. The facial canal runs between the periotic and the tympanohyal, this part of its course being, by definition, the foramen stylo-mastoideum primitivum, and then continues posteriorly to open, between tympanic and periotic, in the foramen stylo-mastoideum definitivum situated at the posterior end of the sinuous groove on the base of the skull described above. Lateral and slightly dorsal to the upper end of the tympanohyal is the opening for the entrance of the middle ear to the tympanic cavity. [It is unclear which opening Patterson and Segall are referring to in this sentence. The opening for the Eustachian tube is located *medial* and dorsal to the upper end of the tympanohyal, whereas the foramen pneumaticum (i.e., the opening into the epitympanic sinus) is lateral and dorsal to the upper end of the tympanohyal. It is possible also that they are referring to the stylomastoid foramen, which is anterior, lateral, and dorsal to the *lower* end of the tympanohyal.] The canal of Huguier [a.k.a. fissura Glaseri] for the exit of the chorda [tympani] is in the usual position medial to the spina tympanica anterior. The canal opens externally lateral and slightly dorsal to the orificium tubae. A small groove in the posterior part of the glenoid fossa leads to the opening for [this canal].

Megatherium (Pseudomegatherium) lundii

A fairly well-preserved although somewhat distorted specimen from the Pleistocene of Tarija, Bolivia, FMNH P14216, is available for study.

The auditory region is very similar to that of [*Eremotherium*] (*Megatherium*), the difference being of rather a superficial kind. Both tympanic and entotympanic are less prominent, particularly in their ventral portions, which are much less extended and less rugose. The external extension of the tympanic forming the ventral wall of the external auditory meatus is much smaller and the porus consequently faces more ventrally. The meatus is relatively shorter and smaller and diminishes in size medially until the internal diameters are only half those at the porus. The sinuous groove between the tympanic and the process for the stylohyal is, for the most part, lacking. The process for the stylohyal reaches farther ventrally, due largely to the lesser development of the tympanic and entotympanic, and anteriorly, where it extends forward beneath the posterior portion of the external auditory meatus. There is a large opening anterior to and continuous with the orifice of the

foramen lacerum posterium in which the periotic is widely exposed. This opening was filled in part by the internal carotid, which here did not run in so well-defined a groove as in [*Eremotherium*] (*Megatherium*). The opening of the condylar foramen is farther forward, directly behind the foramen lacerum posterium. A distinct postglenoid foramen is present. The stylomastoid foramen is directed more laterally and is more readily visible, due to the lesser development of the tympanic. Again due to this last factor, the foramen appears to be a foramen primitivum rather than a definitivum.

The majority of the differences are clearly to be correlated with the lesser degree of development of the tympanic in *M. (Pseudomegatherium)*. In the absence of a series of specimens they cannot properly be evaluated. We have observed that in *Bradypus* this element may show considerable variability in individuals of apparently similar ages.

[As with their descriptions of the mylodont ear region, Patterson and Segall included with their description of *Megatherium* a critique of a paper by van der Klaauw (1930a) on the tympanic region of megatheres. In many cases, as with the mylodonts, they agreed with the descriptions of van der Klaauw, and many of the points of disagreement have been discussed already in the descriptions above. Still, there are certain points of contention with the earlier work that are not discussed above, and yet were obviously considered significant by Patterson and Segall. These criticisms have been edited and presented in the following few paragraphs.]

[In contrast to the description given by van der Klaauw (1930a, p. 130),] the posterior horn [of the tympanic] does not appear to be fused with the "processus pro stylohyale." [Van der Klaauw (1930a, p. 131) describes the bulla itself as being oriented rostromedial to caudolateral.] We suspect that [he] has mistaken the anterior portion of the bulla for a postglenoid process. We believe the long axis of the bulla to run caudoventrally to rostrolaterally. [In describing the external surface of the bulla, van der Klaauw (1930a, p. 134) mentions an] infundibulum posteromedial to the styloform process. [We find this] difficult to understand; we suspect he is dealing with a broken remnant of the pterygoid sinus.

[We] question the presence of a fissure between the promontorium and dorsal margin of the entotympanic [as was claimed by van der Klaauw

(1930a, p. 130).¹⁷ Van der Klaauw (1930a, p. 131) states that the entotympanic formed not only the anterior wall, but also a small portion of the lateral wall of the posterior lacerate foramen, the remainder of the wall being formed by the exoccipital. We feel that the] entotympanic probably forms only the anterior [wall and that the] basioccipital forms the medial and the exoccipital the posterior and lateral walls.

[Van der Klaauw (1930a, pp. 132–134) describes a groove between the tympanic and pterygoid that terminates caudally in at least one, and possibly two (depending on the specimen) openings. The larger and more posterior of the openings he calls the ostium tympanicum tubae. The smaller, more anterolateral opening he suggests might be a foramen for the tensor tympani muscle.] Insofar as we can follow the involved description, we agree, but the possible opening for the m. tensor tympani is anterior to, much smaller than, and not separated from the ostium tympanicum tubae. Van der Klaauw may have been confusing the foramen for the chorda tympani in his account.

The *Schismotherium* Group

Schismotherium fractum based on FMNH P13137, Miocene Santa Cruz Formation, Argentina. Figure 12.

The tympanic is as small as but slightly more expanded than in *Pelecycodon* and diverges posteriorly from the entotympanic to a greater degree (agreeing in this with *Choloepus* to some extent) but is not otherwise different. The ridge formed by the squamosal that runs posterointernal to the glenoid fossa is much less pronounced than in *Pelecycodon*, exposing much more of the anterior portion of the tympanic. Anteriorly there is a rather large gap between the tympanic and the squamosal. The squamosal is somewhat grooved in this region, which contributes to the size of the gap. This groove is variably developed in *Hapalops*, and its function is not clear.

The entotympanic is a relatively small, straight bony plate; its ventral margin is narrowed posteriorly and slightly wider anteriorly than in *Pelecycodon*. It is directed a little less medially than in that

¹⁷ [W T. and T.G. note the presence of van der Klaauw's fissure laterally, although it does not appear to be present on the medial side of the entotympanic.]

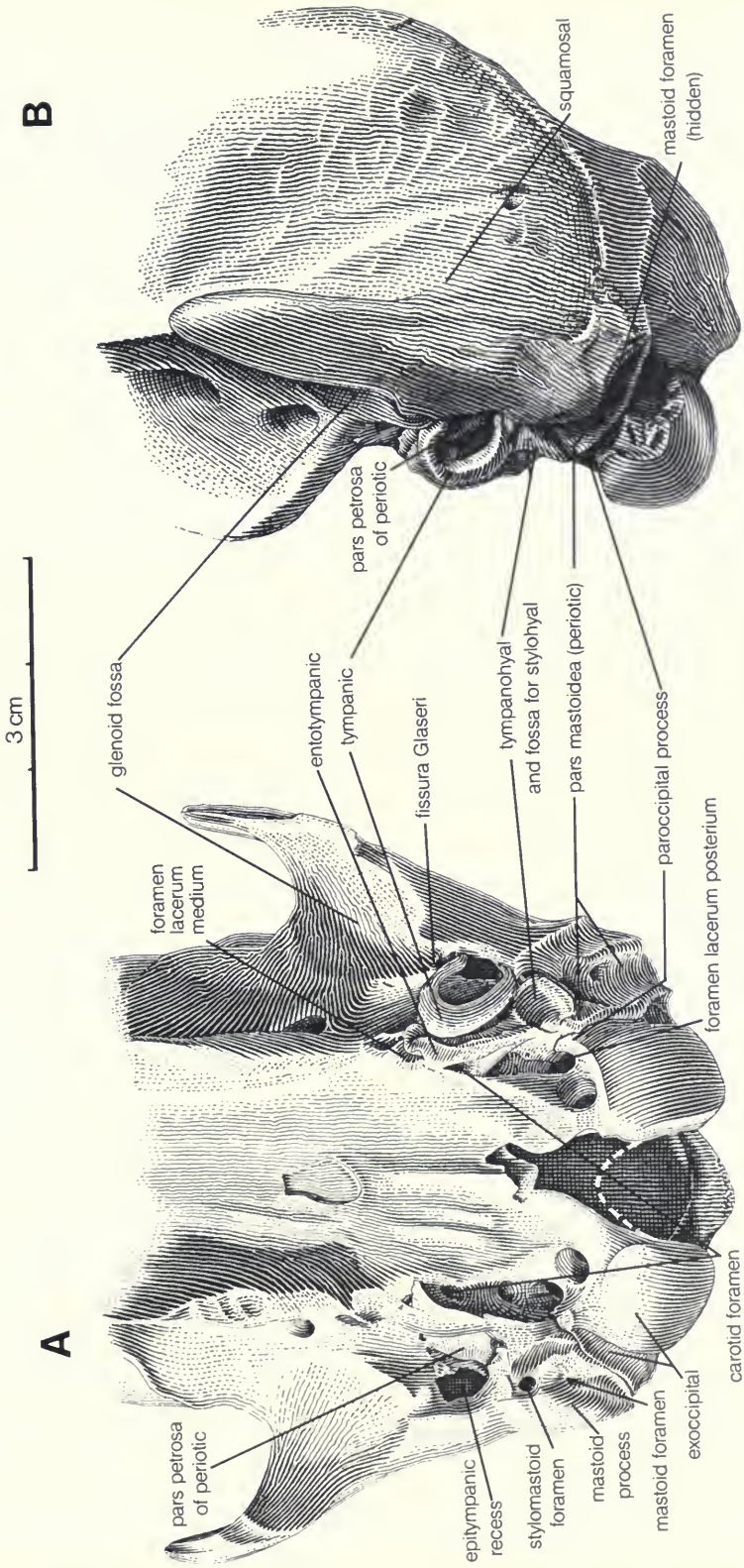


FIG. 12. *Schismotherium fractum*, FMNH P13137: A-B, posterior portion of skull shown in ventral and left lateral views.

genus and is not in contact with the tympanic except at a point immediately posterior to the [opening for the] Eustachian tube. Posteriorly it is continuous with the insignificant paroccipital process. Ventrally, it descends below the level of the basicranium, the basicranial protuberance that is present in *Peleciodon* being absent in *Schismothe-rium*. The medial process is less expanded posteriorly and the carotid groove consequently shorter. Due to the slight contact of tympanic and entotympanic, the [opening for the] Eustachian tube is poorly defined. Its position is indicated by a very small rudiment of styloform process on the tympanic.

The tympanohyal is considerably larger than in *Peleciodon*, and is, indeed, relatively larger than in any sloth. It forms the whole of the fossa for the stylohyal, neither the entotympanic nor the mastoid participating at all. Only in *Choloepus* is a situation at all comparable to be encountered. The fossa faces ventrally and is situated directly behind the cleft between the tympanic and the entotympanic. It is flatter and less excavated than in *Peleciodon*.

The pars petrosa of the periotic presents no difficulties [i.e., it bears a morphology typical of at least some sloths, and in fact is much like the petrosal of *Hapalops*]. The epitympanic recess leads directly into the very large epitympanic recess [lapsus: sinus]. The mastoid portion is not clearly determinable, but presumably ran as usual in the wide groove between exoccipital and mastoid process. The latter is prominent, sharp-edged ventrally and caudally, and is formed by the squamosal.

The carotid foramen has the usual position and relations to surrounding bony elements. There is no postglenoid or subsquamosal foramen. The mastoid foramen is relatively large and opens posteriorly in the groove between exoccipital and stylo-mastoid process. The foramen lacerum medium is small. The foramen lacerum posterium is egg-shaped, continuing anteriorly in a progressively shallowing groove that is longer than in *Peleciodon* or *Hapalops*. The stylo-mastoid foramen is definitely a foramen primitivum, and differs in no essential feature from that of other related forms. The course of the chorda tympani can clearly be seen. It entered the tympanic cavity through a rather large opening between the posterior portion of the tympanic and the tympanohyal. It left by a smaller opening between tympanic and squamosal near the lateral end of the fissura Glaseri.

Peleciodon sp., based on FMNH P13126, Miocene Santa Cruz Formation, Argentina. Figure 13A–B.

The tympanic is small, ringlike and only very slightly expanded medially in that part where the horizontal portion continues upward into the anterior crus. It is inclined somewhat more than 45 degrees to the horizontal. The anterior crus is concealed anteriorly by a broad ridge, formed by the squamosal, that bounds the glenoid fossa postero-internally. Medially the tympanic is in close contact with the entotympanic, the two bones diverging to form the bony opening for the Eustachian tube, posteriorly with the tympanohyal. The longest diameter of the oval porus is inclined posterodorsally-anteroventrally. The posterior crus turns forward to run for a short distance along the ventral side of the superficies meatus.

The entotympanic is in contact laterally with the tympanic; it extends rather more ventrally than the tympanic in the region of contact and a shallow groove runs between the two. As is usual, the entotympanic is a rather simple, straight bone, varying but little in width throughout its course. On the medial surface it is grooved posteriorly and pierced anteriorly for the passage of the carotid. At its anterior extremity it sends down a triangular projection that lies against an elongate protuberance on the lateral side of the basis cranii. This protuberance is more anterior in position and more prominent than that of *Hapalops*, and appears to involve the posterior extremity of the basicranial portion of the pterygoid as well as the anterolateral portion of the basisphenoid. The pterygoid wings diverge posteromedially [lapsus: posterolaterally] as they approach the base and sides of the cranium and continue dorsolaterally into the ridge, formed by the squamosal, that borders the tympanic anteriorly (see above). The opening for the Eustachian tube is situated behind and slightly medial to the root of the pterygoid wing. The posterior end of the entotympanic forms a part, although not a large one, of the fossa for the stylohyal, which it [borders] anteromedially and medially. Posteriorly, the entotympanic continues without interruption into the low paroccipital process.

The tympanohyal is relatively large, and faces ventrally and a little posteriorly. It forms approximately half of the fossa for the stylohyal, which has a rather high and sharply defined border. The fossa is slightly posteromedial to the line of the tympanic-entotympanic junction.

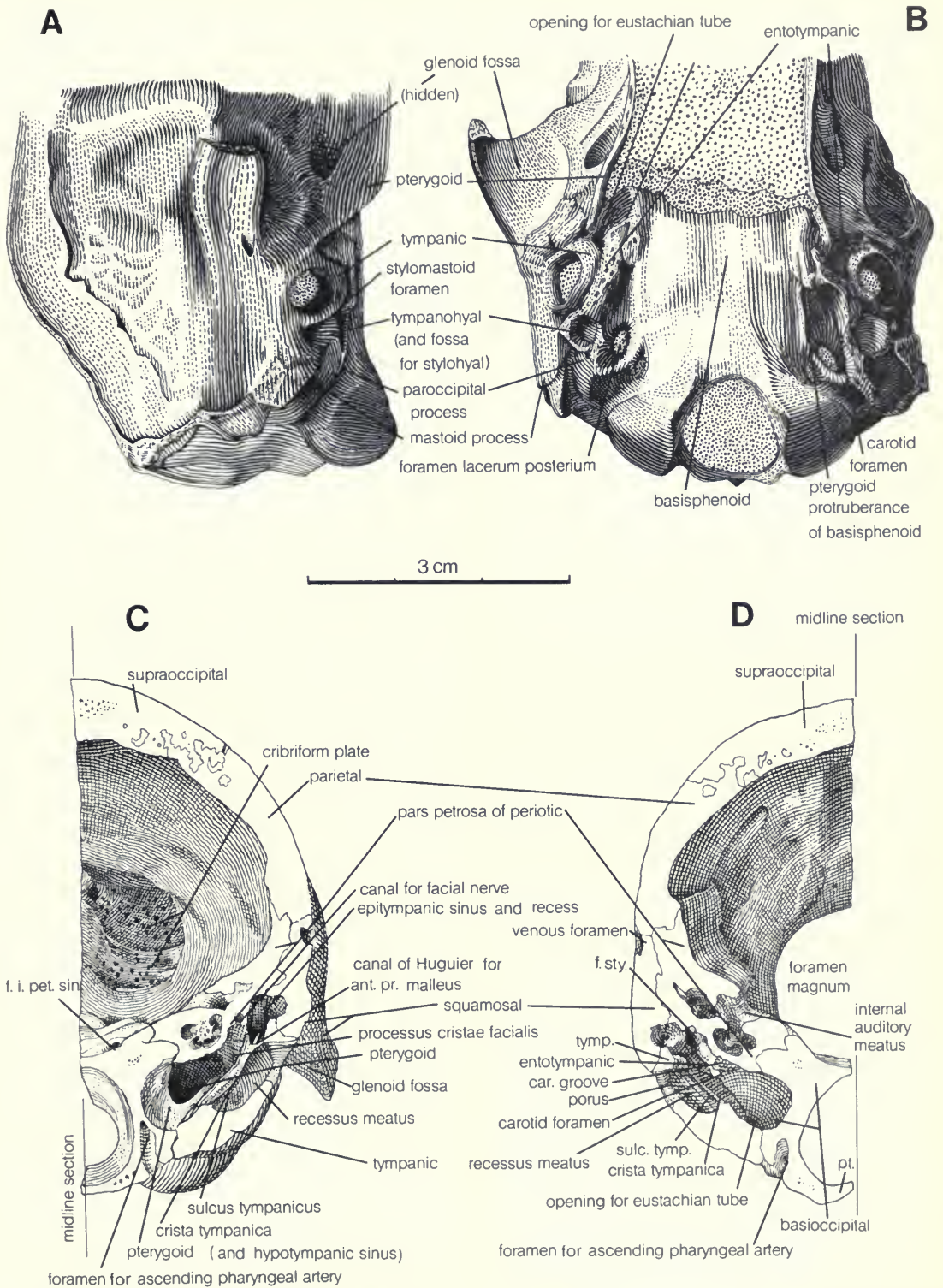


FIG. 13. *Pelecycodon* sp., FMNH P13126: A-B, posterior portion of skull shown in right lateral and ventral views. *Myrmecophaga tridactyla*, FMNH 49342: C-D, sectioned skull, with cut running through bulla, petrosal, and braincase, shown in views toward anterior and posterior sides of cut.

The pars petrosa of the periotic and the recessus epitympanicus are concealed by matrix. The pars mastoidea is prominent, concave posteriorly, and forms a rather sharp crest laterally that continues down from the occipital crest to end ventrally in the blunt mastoid process.

The carotid ran in the usual groove formed by the entotympanic and the basisphenoid, and entered the entotympanic through the carotid foramen, which is situated in the usual position. There is no definitive postglenoid foramen, but several venous openings are present above or on the side of the root or the zygoma; there are, in addition, several small openings in the lateral surface of the squamosal. Similarly there appears to be no well-defined mastoid foramen but in its place some irregularly placed minor perforations at the base of the mastoid process. The foramen lacerum medium is a very small opening at the anterior extremity of the bulla. The foramen lacerum posterium is large and oval in outline with the long diameter directed anteroposteriorly. The stylo-mastoid foramen, which in this form is a foramen primitivum, opens at the bottom of a pit on the side of the skull immediately posterior to the tympanic and above the fossa for the stylohyal.

Anteaters

Myrmecophaga Linnaeus and *Tamandua* Frisch;

M. tridactyla, *T. mexicana*, *T. tetradactyla*.¹⁸

Figures 13C–D, 14A–B.

Sixteen skulls of *M. tridactyla* Linnaeus and 36 of *T. tetradactyla* Linnaeus have been examined.

¹⁸ [The following specimens of *Myrmecophaga* and *Tamandua* were examined:

M. tridactyla—B.P. & W.S.: FMNH 15966, 20014, 26561–62, 28309, 28309 (these latter two specimens were given the same catalog number), 28310, 44081–86, 49338, 49342 (illus. in fig. 13). W.T. & T.G.: FMNH 60688, 87898–901, 88490, 88890–91, 92078, 95014, 98159, 104936.

T. mexicana—B.P. & W.S.: FMNH 13169–70, 14210, 14476, 15163, 15965, 18764–65, 22397, 30740 (illus. in fig. 14), 44070, 49846, 58545, 63918–19, 74915. W.T. & T.G.: FMNH 68922–27, 69596–98, 80972, 89238, 90062–64, 93095, 121192, 123994.

T. tetradactyla—B.P. & W.S.: FMNH 37, 20973, 21338, 24218–19, 25261, 26470, 26862, 34325, 34333–35,

[Note: Wetzel (1985) has recently provided an update on the species-level taxonomy of anteaters. He divides the genus *Tamandua* into two species, *T. tetradactyla* and *T. mexicana*. We examined 88 *Tamandua* skulls (see footnote 18 for specimen numbers) and identified them to species using the characters given by Wetzel. Wetzel's cranial characters were somewhat variable within each species, so when necessary the skin accompanying a given skull was examined for aid in specific identification. Out of Patterson and Segall's 36 original specimens, 16 could be placed in *T. mexicana*, the remaining 20 belonging to *T. tetradactyla*. From the 52 additional specimens available to us, 17 were identified as *T. mexicana*, and the other 35 as *T. tetradactyla*. It should be noted here as well that in addition to the 16 skulls of *Myrmecophaga* examined by Patterson and Segall, we had available another 12 skulls. Any significant differences in ear region morphology noted between the three taxa are discussed in the text.] The differences in auditory region structure between these two forms are minor and they will accordingly be described together. We have also had before us a good skull of "*Neotamandua*" *conspicua* Rovereto, FMNH P14419, from the Pliocene of Catamarca, Argentina. This species is close to *Myrmecophaga tridactyla* in all characters, and does not appear to be generically distinct.

Acquisition of termite-eating habits and the structural changes attendant thereupon have led to rather profound modification of the myrmecophagid auditory region, with the result that the group is the most distinctive among the Edentata in this as well as in numerous other anatomical features.

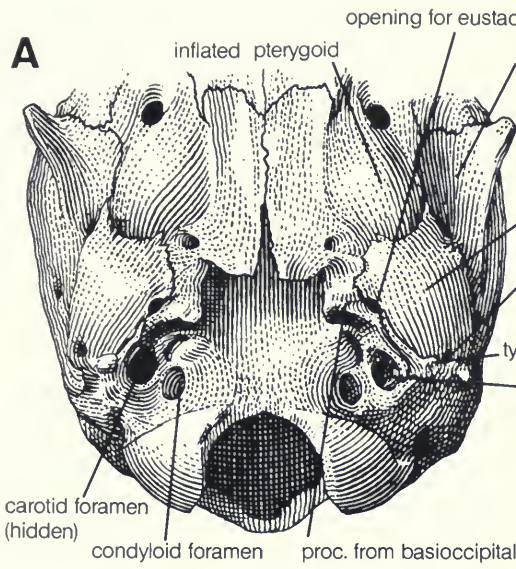
The tympanic in very young specimens is horse-shoe-shaped and in contact with the skull only by the crura, a narrow gap being present between its medial margin and the basioccipital and pterygoid. The porus at this stage is circular. The crura are expanded anteroposteriorly at their dorsal extremities and approach each other closely. A short descending wedge of the squamosal partially covers the approaching extremities of the crura on the

34671, 46202, 50886, 54290, 61852, 64289, 70815, 75124, 105841. W.T. & T.G.: FMNH 60093, 60547, 60640, 84242–43, 86889–92, 87902–04, 89853, 92074–77, 92359, 92965, 93176, 93514, 93537, 95439–42, 96001, 96202, 98917, 119370, 123020, 127284–85, 137419.]

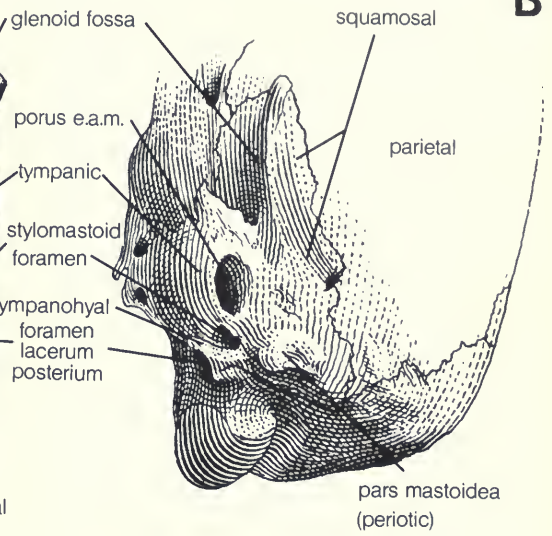
FIG. 14. *Tamandua mexicana*, FMNH 30740: A–B, posterior portion of skull shown in ventral and left lateral views. *Cyclopes didactylus*, FMNH 30741: C–D, posterior portion of skull shown in right lateral and ventral views.

2 cm

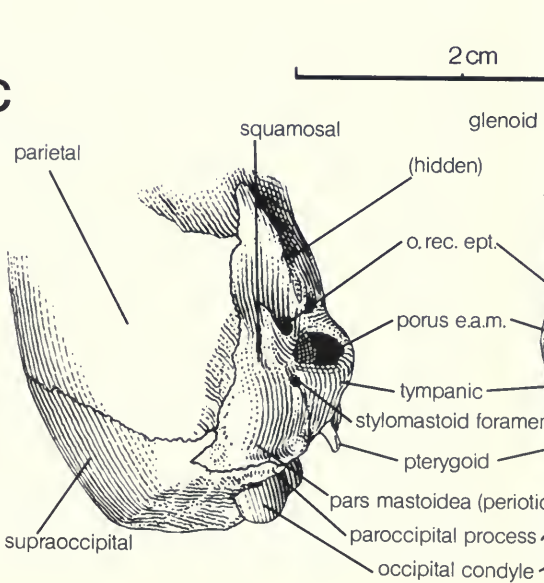
A



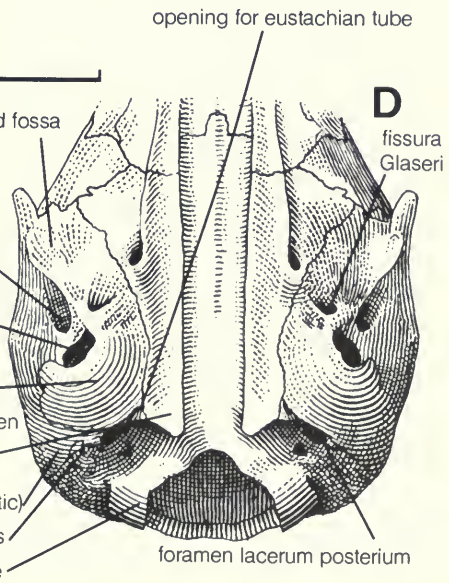
B



C



D



2 cm

lateral side. With advancing age, the gap between tympanic and pterygoid and basioccipital closes, the crura meet to form a complete ring, the anterior sending back a spur to the posterior,¹⁹ and the descending wedge of the squamosal loses its identity.

Enlargement of the tympanic on the medial side of the crista is limited, save for a triangular extension posterior to the pterygoid sinus, but on the lateral side it grows laterodorsally, forming a recessus meatus and changing the outline of the porus from circular to oval. A tubular meatus is never formed, there being no dorsal wall. In *Myrmecophaga*, but not in *Tamandua*, the bone thickens greatly with advancing age. Sulcus tympanicus and crista tympanica are prominent. The sulcus malleolaris is visible in specimens of all ages. In the vicinity of the sulcus there is frequently a conspicuous process, sometimes triangular, sometimes pointed, projecting anteroventrally from the adjacent surface of the tympanic. This process, which may range from practically absent to very large, appears to have no function, at least dissection failed to reveal any to us.

A conspicuous difference distinguishing the Myrmecophagidae from all other edentates is the major part played by the basioccipital and especially by the pterygoid in the formation of the bulla. The basioccipital sends down a ventrally directed process ("processus basiptyergoideus" of Parker, 1886, p. 71) that forms the posterointernal portion [see *Cyclopes* below, however], and the pterygoid contributes the anterointernal portion. The suture between these two bones is obliterated in adults, but in very young specimens its lateral course may be seen running obliquely upward and forward from the anterior margin of the ventral extremity of the basioccipital process. A section through the bulla reveals a large hypotympanic sinus that is formed mainly by these two bones, the tympanic contributing to a small extent on the lateral side of the floor, and the entotympanic participating posteriorly. Anteriorly, as has long been known, the bulla is in wide communication with the extensive, inflated sinus in the pterygoid. The two cavities are only partially separated by a low, nearly transverse septum formed by the pterygoid. The pterygoid sinus forms a conspicuous prominence on the ventral surface of the skull, larger in

Myrmecophaga than in *Tamandua*,²⁰ that extends ventrally to a lower level than the bulla. The tympanic overlaps the pterygoid sinus to a slight extent externally, but the two bones remain separate and a conspicuous fissura Glaseri is present.

The opening for the Eustachian tube, as shown independently in 1904 by Zuckerkandl, Denker,²¹ and Boenninghaus, is in an extraordinary position. Pari passu with the elongation of the hard palate and the posterior shifting of the internal narial opening, the Eustachian tube was displaced from its well-nigh universal anterointernal position to the posteromedial portion of the bulla. As shown by Zuckerkandl (1904) and by Denker (1904), it is not cartilaginous but fibrous in structure. The bony opening varies from round to oval and presents posteroventrally. [In *T. mexicana* this opening is always oval in shape, although in *Myrmecophaga* and *T. tetradactyla* its shape is indeed variable.] It is bounded mainly by the tympanic on the lateral side and by the basioccipital process on the medial, both bones being notched in adult but not in very young specimens. [In all the specimens that we examined, the basioccipital was notched by the opening for the Eustachian tube. Some of the younger specimens lacked a corresponding notch, however, in the tympanic bone.] Participation of the pterygoid in the anterior extremity of the opening is variable. Among specimens young enough to show the sutures in this area we found that in *Tamandua* the pterygoid participates in about 50 percent of the cases and in *Myrmecophaga* in no case. The probability that the entotympanic takes part to a slight extent posteriorly is discussed below.

The glenoid cavity is immediately anterior to the tympanic and on a level with the upper margin of the porus, is gently concave transversely, and enlarges from behind forward. In structure, it most closely resembles that of the mylodont sloths among the other Edentata.

The existence of an entotympanic is difficult to detect. In those xenarthrans with well-developed tympanic and entotympanic, the entotympanic runs from the sulcus malleolaris, anteriorly, to the

²⁰ In *Tamandua* there is a large sinus in the palatine and alisphenoid that extends posteriorly above the pterygoid sinus. There is no communication between the two, the palatine-alisphenoid sinus opening to the narial passage (Paulli, 1900, p. 564, pl. 28, fig. A).

²¹ A correction of an earlier study (1899), in which this author, in agreement with Hyrtl (1845), had concluded that the tube was absent. More than half a century earlier, however, von Rapp (1852) had demonstrated the true position (van Kampen, 1905, p. 488).

¹⁹ This is quite apparent in adults. Van Kampen (1905, p. 487) stated that a complete ring was present in a young *Myrmecophaga* examined by him. Presumably his specimen was somewhat older than the very young *Tamandua* available to us.

typanohyal, posteriorly. There is no certain trace of an entotympanic anterior to the Eustachian opening in anteaters. Some young individuals of *Myrmecophaga* show a thin strip of bone extending from the sulcus malleolaris to the vicinity of the Eustachian opening that appears to be only partially fused with the medial margin of the tympanic. A faint groove, which may be a remnant of a former division, is present between the two. In other specimens, however, the groove is wholly lateral to the Eustachian opening, and in no xenarthran is this opening surrounded by the entotympanic. This suggests that the medial portion demarcated by the groove is actually an increment of the tympanic, which at birth is but little expanded. The presence of the entotympanic in this portion of the bulla is therefore very doubtful—the pterygoid having replaced it functionally—although the possibility of the existence as a vestige, perhaps varying in individuals, cannot perhaps be ruled out entirely. Posteriorly, the picture is clearer. Van Kampen (1905, pp. 487–488) mentioned a bony lamella in *Myrmecophaga* between periotic, basioccipital, exoccipital, and tympanic. He noted the resemblance in position to the posterior portion of the entotympanic in *Choloepus*, and accordingly suspected that this lamella might be the entotympanic, although he was unable to detect sutures separating it either from the tympanic or the pars mastoidea. Among our material, both of *Myrmecophaga* and *Tamandua*, there are specimens that clearly show this element to be distinct, some of them showing that it extends to the vicinity of the typanohyal and others indicating that it may extend to the posterior margin of the Eustachian opening. [A contact between the entotympanic and typanohyal was much more common in these genera than an entotympanic participation in the rim of the opening for the Eustachian tube.] It would appear that there is considerable individual variation in the degree of ossification attained. This small bone fulfills all the requirements of an entotympanic and we accordingly have no hesitation in so identifying it. It is not yet ossified in the very young *Tamandua* shown in the figure, the future position there being marked by a gap between the neighboring elements. [The figured specimen has a small but clearly ossified entotympanic. It is possible that Patterson and Segall had intended to include a figure of a somewhat younger specimen, and that it is this younger specimen that they are referring to, but we have found no such figure in the material left to us.]

In only one skull of *Myrmecophaga* have we seen the surface exposure of the typanohyal distinctly delineated from the surrounding elements; here it is situated midway between the orifices of the stylomastoid and posterior lacerate foramina. In all other specimens of this genus, and in all of *Tamandua*, it is fused with one or more of the surrounding elements; even in the very young *Tamandua* figured, in which ossification of the typanohyal is apparently not complete, the extremity is united with the pars mastoidea.

The pars petrosa in young specimens is globular in ventral view, slightly pointed anterointernally and hardly at all expanded medially beyond the promontorium. With advancing age a heavy shelf expands on the medial side to form an extensive suture with the basioccipital. The lateral side of the promontorium bears a groove for the internal carotid artery. The crista and sulcus facialis are prominent. The processus cristae facialis is large and bluntly triangular in outline; it has a long sutural connection with the squamosal in the recessus epitympanicus. Its tip is concave and is perforated by a small evidently vascular foramen, which leads, via a groove in the lateral face of the process in very young specimens, to the cranial wall. In adults the groove is covered by bone. In young specimens the tympanic is not in contact with the process. [The contact between the tympanic and the processus appears to be somewhat variable. The youngest specimen available to us (*T. mexicana*, FMNH 15163) lacks such a contact, but a slight contact is visible in several slightly older specimens (*Myrmecophaga*, FMNH 87899 and 88490), and one juvenile specimen (*T. mexicana*, FMNH 58545) showed a clear extensive contact between the two elements.] In adults the relations in this area are obscure, but the contact, if any, between the two is slight. The recessus epitympanicus is large in juvenile specimens and in adults enlarges still further to form a sinus epitympanicus. The pars mastoidea is lateral in position and roughly quadrangular in outline on the surface of the skull, except at the anterointernal corner where a thin strip runs forward above the posterior crus of the tympanic. [Our youngest specimen would seem to indicate that this thin strip of mastoid is a surface exposure of the typanohyal that later on fuses to the mastoid.] There is no mastoid process. The exoccipital projects ventrally, but there is no freely projecting paroccipital process, the tip being joined to the mastoid, typanohyal, tympanic and entotympanic. On the cerebellar surface of the periotic, a conspicuous but presumably un-

important difference between the two forms may be observed. In *Tamandua* a very large and deep subarcuate fossa is present. *Myrmecophaga* exhibits only a shallow depression in this area.

The internal carotid artery enters the bulla by a foramen opening in the anterior part of the foramen lacerum posterium, crosses the [petrosal] in the groove described above, and leaves by a foramen between petiotic and pterygoid at the dorsal extremity of the partial septum formed by the latter bone. From this point the artery runs anterointernally to the circle of Willis in a canal that opens beside the posterior extremity of the sella turcica. The ascending pharyngeal artery runs forward under the basioccipital process to a foramen in the pterygoid posterointernal to the sinus. [Patterson and Segall do not indicate the basis for the claim that this vascular channel is for the ascending pharyngeal artery. Guth (1961) claims that this foramen is for a vein connecting the transverse sinus and the external jugular vein.] The artery then turns upward and forward within a canal that joins the carotid canal near the opening at the sella turcica. The size of the foramen and canal for the ascending pharyngeal artery is variable; frequently, although not invariably, the canal sends a branch anterointernally to transmit an arterial twig to the narial passage. There are no postglenoid or squamosal foramina. Venous foramina on or near the squamoso-parietal suture vary greatly in number and size. In *Tamandua* the inferior petrosal sinus runs within the basioccipital, in *Myrmecophaga* over the inner surface of this bone for a part of its course. There is no large and constant mastoid foramen, such as occurs in armadillos, the main venous drainage in this area leaving the skull by the posterolateral portion of the foramen lacerum posterium. [Patterson and Seagll's comments on the venous drainage of the posterior portion of the cranial cavity are probably based on the presence of large but rather faintly marked grooves for the transverse and sigmoid sinuses on the internal surface of the cranial cavity. However, their interpretation is also in accordance with the observations of Guth (1961) on the venous drainage of the head in anteaters.] This foramen, or rather the fossa into which it opens, is of great size due to the fact that it serves not only for the exit of [cranial nerves] IX, X, and XI, which leave the cranial cavity through its anterointernal portion, but also as a vestibule into which are gathered the internal carotid, the main venous drainage of the posterior part of the skull, and various other, and minor, vascular channels. The stylomastoid foramen, a

foramen definitivum, opens between tympanic and mastoid a short distance behind the porus. The chorda tympani emerges near the dorsal extremity of the fissura Glaseri.

Cyclopes Gray; *C. didactylus*.²² Figures 14C–D, 15.

With regard to the systematic position of *Cyclopes*, although thoroughly agreeing with Reeve (1940) that the characters sometimes employed to place *Cyclopes* in a subfamily (Winge, 1941) or even a family (Pocock, 1924) of its own are without value in this connection, we nevertheless believe on other grounds that this little anteater has had an evolutionary history of its own, distinct from that of *Myrmecophagus* and *Tamandua*. With so little known of the early history of the group, however, it would be altogether premature to attempt now to express this in any formal way.

Fourteen skulls of *C. didactylus* Linnaeus have been available. [We examined an additional 11 specimens (see footnote 22 for specimen numbers).] While agreeing in the main with *Myrmecophaga* and *Tamandua*, the auditory region of *Cyclopes* is distinctive in several characters, some of which, at least, would seem to be attributable to the small size of the animal.

The tympanic differs from that of other myrmecophagids in several respects. The anterior crus is more internal in position than in these forms. In consequence, the areas of attachment for the crura are aligned on an anterointernal-posteroexternal line rather than on an anteroposterior one, the axis of the external meatus is directed anterolaterally rather than transversely, and the anterior portion of the bone is reduced relative to the posterior. The posterior crus is vertical [within 10 degrees or so of vertical], and abuts against the descending wedge of the squamosal. In young specimens of *Cyclopes* this wedge is relatively larger than it is in the young *Tamandua* described above, and the posterior crus has a more extensive sutural connection with it. This is due to the absence of the thin strip of the pars mastoidea that in the young *Tamandua* runs forward above the

²² [The following specimens of *Cyclopes* were examined:

B.P. & W.S.: FMNH 19500–01, 20033, 21719, 24796, 30741 (illus. in fig. 31C–D), 34247, 44055–56, 50907, 51890, 51931 (illus. in fig. 32A–C), 64187, 64188 (illus. in fig. 32D). W.T. & T.G.: FMNH 51899, 58802, 61853–54, 69969–71, 71002, 93175, 121653, 122699.]

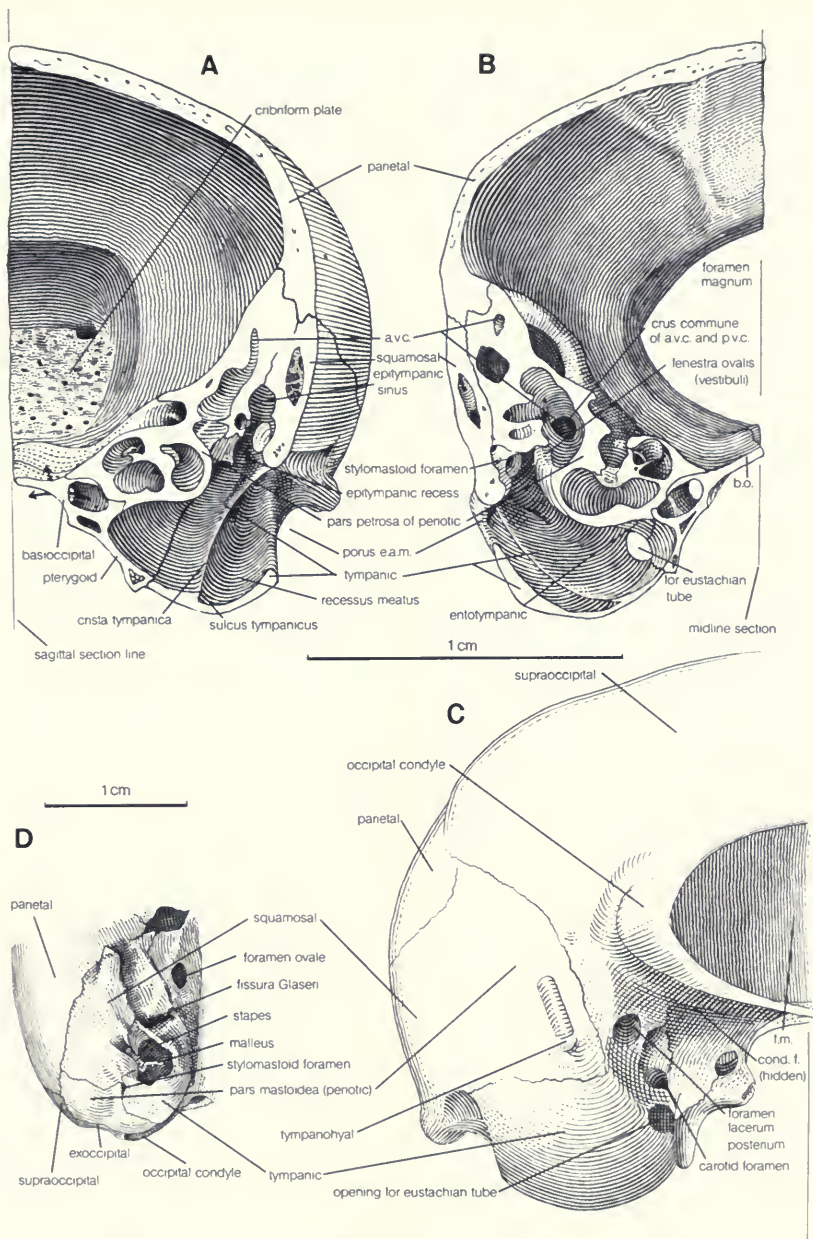


FIG. 15. *Cyclopes didactylus*, FMNH 51931: A-B, sectioned skull, with cut running through bulla, petrosal, and braincase, shown in views toward anterior and posterior sides of cut; C, left side of skull shown in posterior view. *Cyclopes didactylus*, FMNH 64188: D, posterior portion of juvenile skull shown in ventral view.

posterior crus. The anterior crus is not vertical, as it is in other anteaters, but is inclined anteriorly. Its area of attachment is thus farther forward, in addition to being more internal in position. [The forward inclination of the anterior crus makes it appear to attach more anteriorly. However, the anterior limit of the tympanic lies well behind the glenoid, in contrast to the situation found in the

other anteaters, where the tympanic lies just behind the glenoid. The attachment of the anterior crus in *Cyclopes* is closer to the foramen ovale than in the other forms, but this seems to be due to a posterior shift of the foramen. In *Cyclopes*, the foramen ovale lies at or posterior to the level of the glenoid. In the other anteaters it is anterior to the level of the glenoid.] A wide gap between

the two crura is thus left, which is only partially filled in, in young specimens, by the descending wedge of the squamosal. The result is a cleft in the lateral surface of the squamosal between the wedge and the area of attachment for the anterior crus. The epitympanic recess is thus in wide communication with the exterior, and the ossicles may be seen in place in anterior view. A spur of bone from the anterior crus extends back beneath the cleft. With advancing age, this spur grows backward to the squamosal wedge and to the posterior crus and fuses with them. It thus obliterates the identity of the wedge and converts the cleft into an opening of varying size. Presumably this was filled by connective tissue during life, but we have no embalmed or alcoholic material with which to test the supposition. Nothing resembling this peculiar arrangement is to be seen elsewhere in the Edentata.

The bulla is inflated and much wider posteriorly than anteriorly. As a result of the internal position of the anterior crus of the tympanic, the fissura Glaseri is limited in extent, being confined to a small area bounded laterally by the anterior crus and medially by a highly variable antero-internal extension of the tympanic. [Although this antero-internal process of the tympanic is not discernible externally in most specimens, the position and size of the fissura Glaseri are highly variable.] The pterygoid runs posteriorly along the medial length of the bulla to cap, and in some cases extend beyond, the descending process of the basioccipital. Regarding a pterygoid sinus there is some difference of opinion, Denker (1904) denying and van Kampen (1905) affirming its presence. We believe that both are in a measure correct. There is no conspicuous sinus, only partially connected with the bulla, as in *Myrmecophaga* and *Tamandua*, but the pterygoid is hollowed out to form the antero-internal portion and the medial wall of the bulla. As is well known, the pterygoids and the posterior portions of the palatines do not unite in the midline to form a bony tube for the narial passage.

In the youngest specimen of the series at our disposal [fig. 15D, FMNH 64188], the medial portion of the tympanic is fully developed, but the meatus has not yet attained the adult form. The ventral wall is not yet ossified, and a conspicuous notch is therefore present between the anterior and posterior walls. In adults this notch becomes closed and a recessus meatus similar to those of *Myrmecophaga* and *Tamandua* is formed. As in these forms, there is no cylindrical auditory meatus. The

porus is round to rounded-triangular in outline. The glenoid articulation is similar in structure to that of the other forms.

The opening for the Eustachian tube occupies the same remarkable position as that seen in *Tamandua* and *Myrmecophaga*. As in these forms, there is no certain indication of an entotympanic anterior to the opening. In one specimen there is a small, distinct lamina of bone lying between tympanic and pterygoid anteriorly. No other indication of a separate ossification here is to be seen, not even in the youngest specimens of our series. Van Kampen (1905, p. 488) stated that the posterior part of the entotympanic is better developed than in other myrmecophagids, excluding the descending process of the basioccipital from participation in the internal wall of the bulla. Our material is on the whole confirmatory. Sutures may be seen in adult, but not aged, individuals between basioccipital, pterygoid, and tympanic plus entotympanic, and these show that the basioccipital apparently does not form part of the internal wall. In our youngest specimen, the tympanic, as noted above, is almost fully [developed], but the entotympanic, which forms the posterointernal portion of the bulla and extends back to the paroccipital process, is still cartilaginous. Evidently, entotympanic and tympanic fuse shortly after ossification of the former is complete. Later on, both become fused with the squamosal and pars mastoidea. [The size and position of the entotympanic are very difficult to determine from the specimens at hand. The above description seems somewhat at odds with itself, at one point stating that there is no sign of an entotympanic anterior to the opening for the Eustachian tube, and yet referring to a juvenile specimen (FMNH 64188) with a cartilaginous entotympanic that clearly lies anterior to the location of the adult Eustachian tube. Unfortunately, it is difficult to say how informative such juvenile specimens are for determining the positions of bones in the adult—obviously there are major rearrangements going on over the course of development. The juvenile specimen in question does not yet show the growth of the tympanic under the tympanic bulla so characteristic of adult specimens. Our interpretation of the adult entotympanic largely follows that of Guth (1961), who stated that the entotympanic has a short anterior lamina in the posterointernal portion of the bulla which is fused dorsally to the petrosal and forms the medial wall to the canal for the internal carotid artery (see fig. 15B–C). Thus, we feel that there are

indications of an entotympanic anterior to the Eustachian tube,²³ as shown in juveniles with unossified entotympanics, and have labeled the figures accordingly. This interpretation is in contrast to the above statement given by Patterson and Segall.]

The tympanohyal is completely fused with the mastoid in all specimens of our series, and there is no indication at the surface to mark its position. In two specimens, however, parts of the hyoid arch are still attached, and these reveal that the extremity of the tympanohyal lies immediately lateral to the paroccipital process [and protrudes from the posteroventral corner of the mastoid]. This agrees very well with conditions shown in Parker's figure of a late embryo (1886, pl. 10, fig. 1).

The ventral surface of the pars petrosa bears a relatively larger promontorium than in other anteaters, and this is not grooved for the internal carotid, that artery not passing through the bulla in *Cyclopes*. The processus cristae facialis is large but simple in structure, consisting so far as can be seen in our material of a thin plate of bone, that is in contact with the anterior crus of the tympanic. The recessus epitympanicus is large, and a small epitympanic sinus is present; the extraordinary anterior opening in the recessus has been described above. The pars mastoidea is much as in *Myrmecophaga* and *Tamandua* but lacking, as already stated, the small strip that runs forward above the posterior crus in these forms. Again as in these forms, there is no mastoid process and the paroccipital process is united at the extremity with the neighboring elements. *Cyclopes* has a fossa subarcuata that is even larger, relatively, than in *Tamandua*. Unlike conditions in that form, there is a large gap in the posteroventral part of the wall of the fossa, between the anterior-vertical, semi-circular canal and the pars mastoidea.

The internal carotid did not pass through the bulla, a contrast to the other living anteaters. Instead, as Denker (1904) showed, it enters a foramen situated above the Eustachian opening and in the presumed entotympanic. Anteriorly, the artery runs in a canal between basioccipital and peri-

otic, which opens at the Circle of Willis. A small foramen in the posterior wall of the bulla is presumably for the entrance of the stapedia artery. A second foramen, medial to the internal carotid, is situated either within the descending process of the basioccipital or between this and the pterygoid. The foramen leads to a short canal that enters the internal carotid canal. Shortly before emerging at the circle of Willis, the carotid canal gives off a small branch canal that passes anteriorly and ventrally through basioccipital and pterygoid to open in the side wall of the narial passage. We believe that the second foramen and the canal leading from it is the homologue of that situated in the posterior part of the pterygoid, behind the pterygoid sinus, in *Myrmecophaga* and *Tamandua*. This foramen, it will be recalled, also leads to a canal that runs into the carotid canal and, in some specimens, gives off a small canal leading to the narial passage. We suspect that foramen and canal transmit the ascending pharyngeal artery, and that a twig from this vessel passes to the narial passage. Conditions in other xenarthrans tend to bear this out. Denker (1904), however, thought that the artery concerned was the internal maxillary. This we doubt, but the absence of material for dissection prevents us from coming to a positive conclusion. The remaining cranial foramina present no striking differences from those of other anteaters.

Protamandua Ameghino; P. rothi

Two partial skulls, referred to *Protamandua rothi* Ameghino, from the Early Miocene Santa Cruz Formation of Patagonia, PU 15267 and FMNH P13134, have been available for study [figs. 16 and 17, respectively]. These are the earliest known examples of the myrmecophagid skull. The presence of anteaters in the Santa Cruz was announced nearly 50 [90] years ago by Ameghino, who described this species on a calcaneum and two others, *Promyrmecophagus euryarthrus* and *Promyrmecophagus dolichoarthrus*, on the basis of isolated astragali (1904, pp. 277–278). FMNH P13134 includes some postcranial elements, among them by great good fortune the calcaneum and astragalus. The authorities of the Museo Argentino de Ciencias Naturales very kindly sent excellent casts of Ameghino's types, thus enabling us to make direct comparisons. Ameghino's descriptions are, as usual, accurate, and the distinctive features pointed out by him are real. Examination of a series of

²³ [This entotympanic would presumably be homologous to the rostral portion of the entotympanic in other xenarthrans. Note that the entotympanic in *Myrmecophaga* and *Tamandua* is located posterior to the Eustachian tube, and seems more likely to be derived from the caudal portion of the entotympanic of other xenarthrans, suggesting that the two anteater lineages may have reduced the entotympanic in a very different manner.]

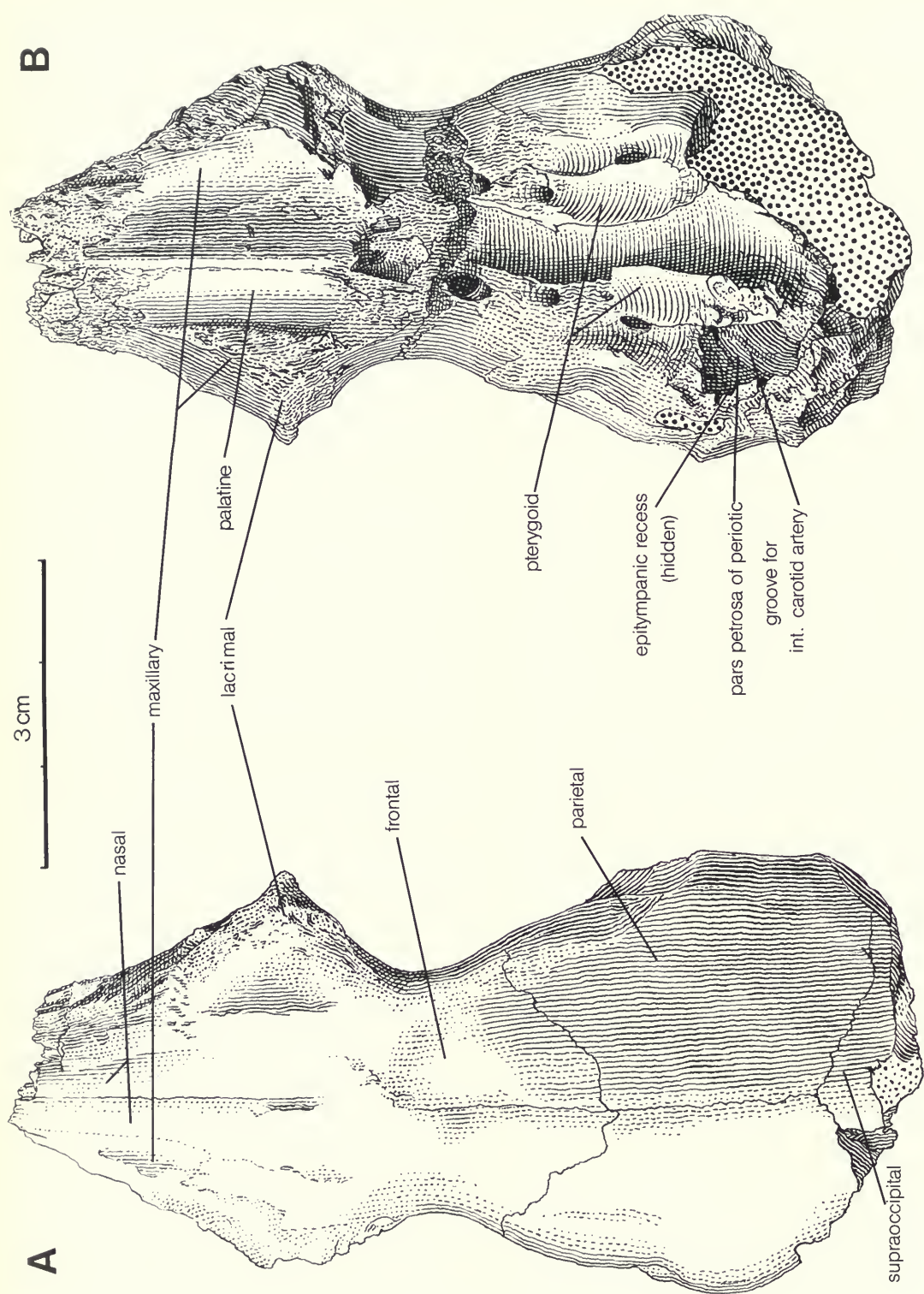


FIG. 16. *Protamandua rothi*, FMNH P13134: A-B, skull shown in dorsal and ventral views.

Recent myrmecophagids reveals considerable variation in the foot bones, however, suggesting these three named species may actually be one and the same. This is not the place for a taxonomic discussion, and we accordingly limit ourselves to stating that the calcaneum of *P. rothi* (the species enjoying page priority) and the calcaneum of FMNH P13134 are sufficiently similar to permit specific identification of our material. It is an ironic footnote to the history of paleontology that Scott, who scouted Ameghino's identification, doubted to the end of his life that there were anteaters in the Santa Cruz, and should have lived for over 50 years in close but unconscious proximity to such positive proof of their existence as is provided by the skull described and figured below. The specimen was labeled "*Hapalops*, juv." Thus disguised, the likelihood is that Scott never even saw it, or, if he did, gave no more than a passing glance to it as it lay, dorsal side up, in its cotton-filled box. The Field Museum of Natural History specimen was likewise labeled in the field as a poorly preserved "*Hapalops*" and in consequence went unprepared for many years. The moral would appear to be that all specimens of "*Hapalops*," whether in the field or in the laboratory, deserve more than casual inspection.

The tympanic is as massive as in *Myrmecophaga*. Medial to the crista tympanica, it is moderately expanded, about equally so along the entire periphery. On the lateral side of the crista, the ventral wall of the auditory meatus is expanded to almost the same extent as in *Myrmecophaga* and *Tamandua*, forming a fairly large recessus meatus. The porus is rounder than in adults of these forms, although not as deep dorsoventrally as in *Cyclopes*. The crura lie in an anteroposterior line and meet above the porus. The pterygoids are unfortunately not complete in either skull, but it is nevertheless clear that they are fully comparable to those of later forms in the degree of their participation in the bulla. It is evident also that a pterygoid sinus is present and in broad communication with the interior of the bulla. Although the details are not very clear, the specimens suggest that, both in degree of prominence and in relations with the hypotympanic sinus, the pterygoid sinus is intermediate between the vestigial condition in *Cyclopes* on the one hand and the very large, well demarcated sinuses of *Myrmecophaga* and *Tamandua* on the other. As in *Cyclopes*, the pterygoids and posterior portions of the palatines do not meet in the midline to floor of the nasal passage. The descending processes of the basioccipital are fully

comparable to those of the living forms, and, as in *Myrmecophaga* and *Tamandua*, form the posteroventral portion of the bulla. The glenoid surfaces, so far as preserved, are of the usual myrmecophagid type.

The specimens reveal nothing of the entotympanic, but there is no reason to suspect that it was appreciably different from that of *Myrmecophaga*. The position of the opening for the Eustachian tube is indicated by slight notches in the tympanic and in the basioccipital process of PU 15267. It was therefore in the same remarkable position as in the later forms.

Nothing can be seen of the tympanohyal.

The ventral surface of the pars petrosa closely resembles those of *Myrmecophaga* and *Tamandua*; it is similarly grooved for the passage of the entocarotid [i.e., internal carotid] artery. The processus cristae facialis, so far as preserved, is thin and platelike. Very little can be seen of the recessus epitympanicus, although it is certain that no anterior opening, such as occurs in *Cyclopes*, is present, and we are unable to say whether or not there is a sinus epitympanicus. The limits of the pars mastoidea cannot be seen. As in other anteaters there is no mastoid process. The paroccipital process appears to have had the same relations to the surrounding elements as in the living forms.²⁴

What can be seen of the cranial foramina accords completely with conditions in *Myrmecophaga* and *Tamandua*.

Protamandua clearly shows that by Early Miocene time every one of the several characters that so sharply distinguish the auditory region as the Myrmecophagidae had been acquired. The glimpses of the rest of the anatomy afforded by FMNH P13134 reveal a similar situation. The maxilla is edentulous, for example, and the forefoot already shows the characteristic enlargement of metacarpal III.

Palaeonodonta

Metacheiromyidae

The two known genera of the family, *Palaeonodon* and *Metacheiromys*, have been so thoroughly described and illustrated by Matthew (1918) and by Simpson (1931a) that detailed descriptions

²⁴ The degree of prominence and the apparent independence of this process in PU 15267 are due to crushing.

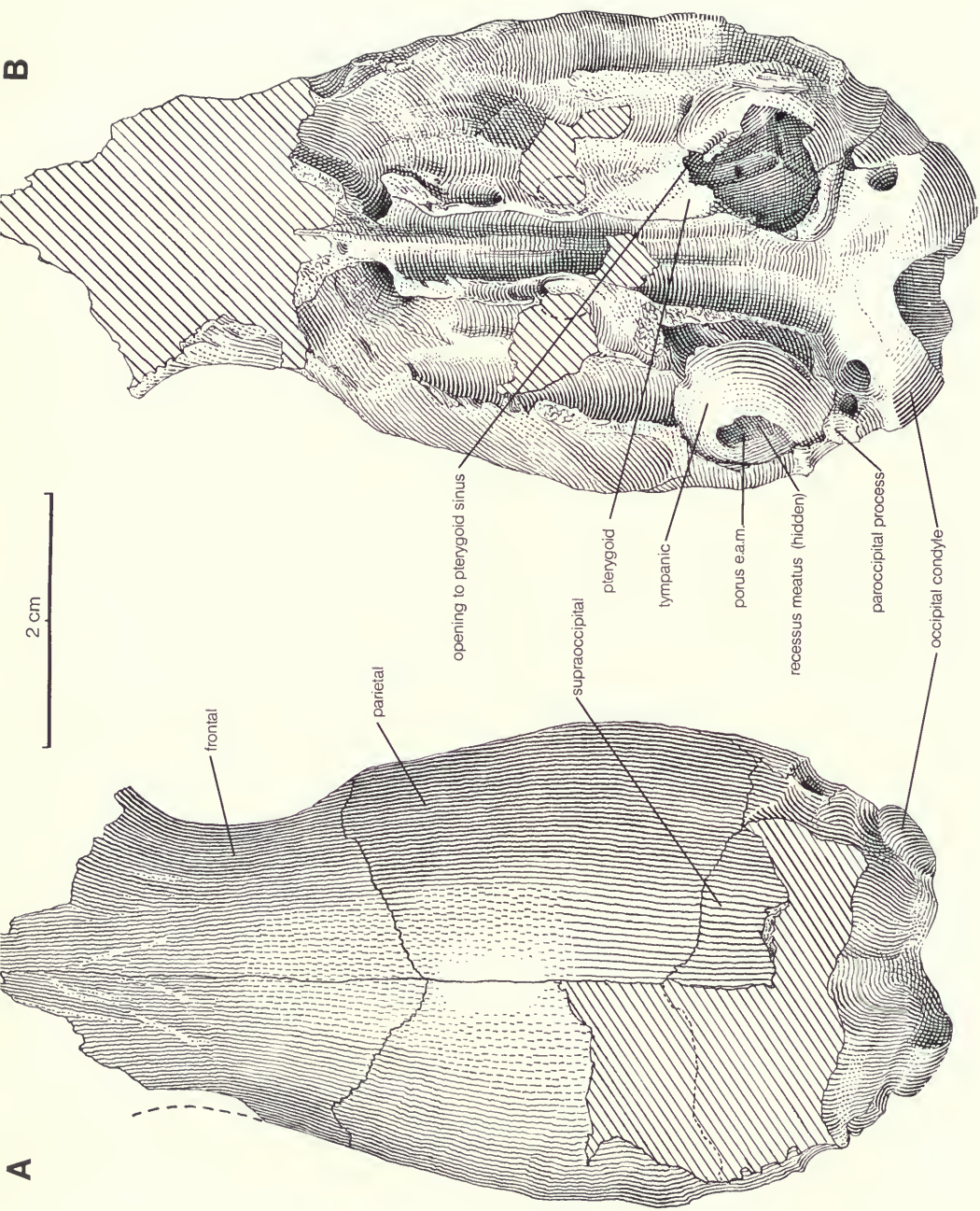


FIG. 17. *Protamandua rothi*, PU 15267: A-B, skull shown in dorsal and ventral views.

would be superfluous. Examination of these Late Paleocene and Eocene edentates [from North America] in the light of this study has suggested certain reinterpretation of Matthew's work on *Palaeonodon*, raised one or two minor points in regard to Simpson's work on *Metacheiromys*, and permitted a few additions. The following notes are therefore strictly supplementary to the studies of these authors, which should be consulted in this connection.

Palaeonodon Matthew

Palaeonodon ignavus, AMNH 15086

Simpson's figure [of the cast of the cranial and nasal cavities] is very accurate; the surface of the cerebrum is badly weathered, thus the fissuration is perhaps better developed than the cast would suggest.

There is no indication of the transverse cerebral fissure in *Palaeonodon* that is so well developed in *Epoicotherium* (fig. 19A–D) and *Chlamytherium*. The cerebellum is much lower in relation to the dorsal surface of the cerebrum in *Epoicotherium* than in *Palaeonodon*.

The tentorium is median, anterior to the median lobe of cerebellum in both palaeonodonts, a contrast to *Chlamytherium*. The olfactory bulbs and indeed the brain as a whole, is very much shorter in *Epoicotherium* than in *Palaeonodon*.

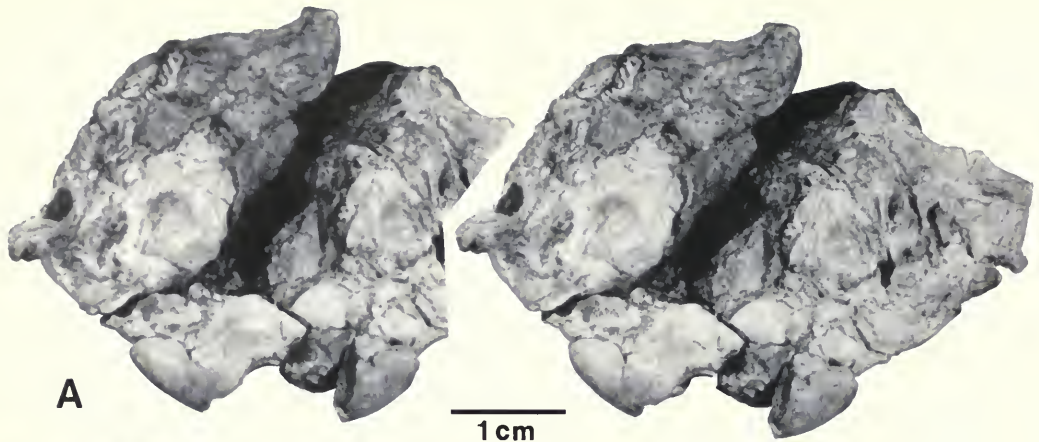
There are five prominent ridges in the posterior part of the nasal chamber of *Palaeonodon* with four grooves separating them, a sharp contrast to *Epoicotherium* in which there are only two grooves, one very lateral. This region is weathered in *Palaeonodon*, but the median area may correspond to the nasal cast in *Epoicotherium*.

The right tympanic in the type of *P. ignavus* Matthew (AMNH 15086 from the Wasatchian of Wyoming) has been displaced medially and somewhat dorsally. [The bone also seems to have shifted slightly posteriorly and to have been rotated counterclockwise in ventral view.] The crura have then been removed from their points of attachment, which appear to have been the same as in the specialized armadillos and sloths, and the entotympanic has been crushed and broken (see below). Matthew stated that the tympanic did not possess a tubular auditory meatus. This may well have been the case but it cannot be proved from the specimen. [The left side of the specimen has

been subsequently prepared, and clearly demonstrates the presence of an undisturbed tympanic extended laterally to form a tubular auditory meatus.] The meatal rim is incomplete anteriorly and centrally, and it is therefore possible that a bony external meatus may have been partially formed from the anterior crus, somewhat in the manner of the euphractine armadillos.

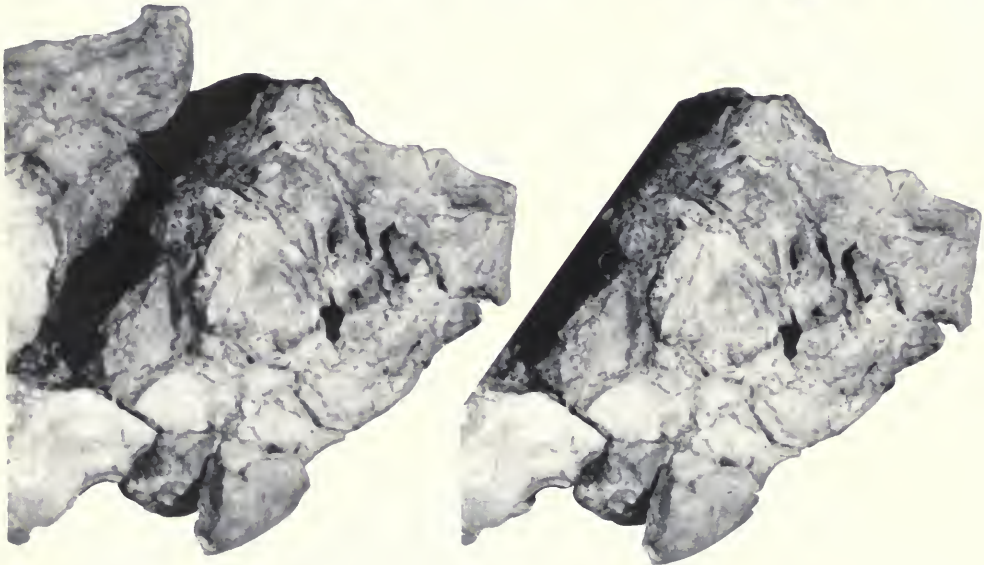
Matthew made no mention of an entotympanic. We agree with van der Klaauw (1931b, pp. 275–288) that this element was present. The evidence consists of three fragments disposed around the rim of the tympanic, only one of which is clearly figured by Matthew (1918, fig. 39, *pet.*; p. 623). The first of these is a rather thin strip of crushed cancellous bone lying between the tympanic and basisphenoid and retaining a very slender connection with the second. This, [which is] smooth and gently concave on its lateral side, has been displaced medially almost to the midline of the basioccipital. An attempt was made in Matthew's figure to restore this fragment to its supposed original position. The result, however, gives the impression of a ventrally directed process from the basioccipital, similar to that of the Myrmecophagidae, which was certainly not the case. The third, and largest, fragment lies posterior to the tympanic, with which it is in contact. Its relations with the basioccipital and pars mastoidea are by no means as clear as Matthew's figure would suggest, conditions here actually being obscure in the specimen. [On the left side of the specimen, further preparation has exposed a clear suture between the entotympanic and basioccipital.] The structure, position, and relations of these three fragments are precisely what would obtain if they were remnants of a well-developed entotympanic that was broken and partially displaced at the same time that the tympanic was displaced medially. No other interpretation of them is possible; this is true whether the comparison be made with xenarthrans or with *Metacheiromys*. The apparently cancellous nature of the anterior fragment agrees with xenarthran entotympanic structure; the smooth concave lateral side of the central one can only be part of the inner wall of the bulla, whereas the posterior fragment (Matthew's "petrosal crest"), as van der Klaauw has pointed out, is fully comparable to the caudal part of the xenarthran entotympanic. There can be little doubt that the entotympanic was almost if not quite as well developed as in *Metacheiromys*.

The two small bones in the tympanic cavity



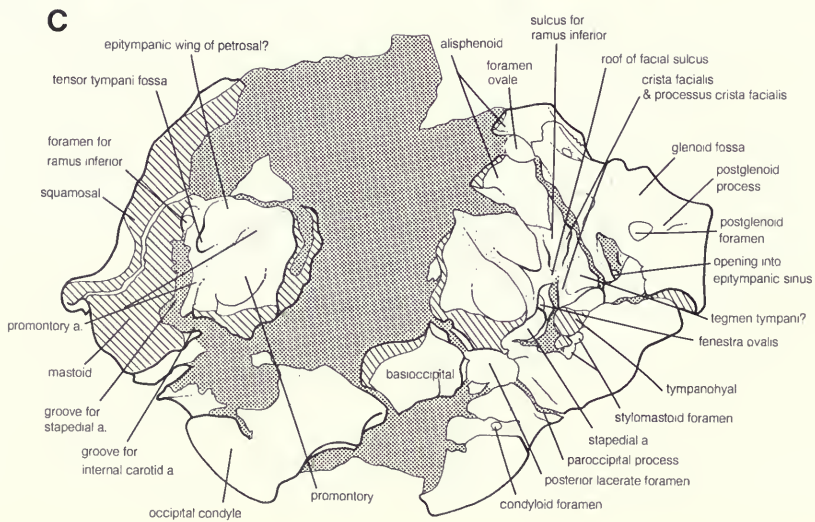
A

1 cm



B

1 cm



("frg., fragments possibly of tympanic ring" in Matthew's figure caption, fig. 39) cannot be interpreted with any certainty. Conceivably they are auditory ossicles, perhaps malleus and incus, but the preparation necessary to confirm or disprove this would be dangerous to the specimen; they do not appear to be processes from the periotic and are too robust to be regarded as broken parts of the tympanic.

[The preparation on the left side of the type specimen has exposed the internal surface of the tympanic cavity. Moreover, Dr. Ken Rose has kindly loaned to us a new specimen of *Palaeonodon* (USGS 21876, fig. 18). This specimen consists of an uncrushed braincase in which the petrosals on either side were exposed due to the absence of the tympanics and entotympanics. We have subsequently prepared the entire middle ear cavity on the left side of the skull, which was largely undamaged in burial, and the medial portion of the right side, which was damaged laterally. The following then is a brief description of the heretofore undescribed middle ear cavity of *Palaeonodon*, based on the type and the new specimen.

The promontorium of the petrosal is small, ovoid, and only slightly inflated. It is separated from the basioccipital by a broad medial shelf that is continuous anteriorly with what appears to be a large epitympanic wing of the petrosal (terminology of MacPhee, 1981). These shelves give the ventral surface of the petrosal a broad, flat appearance that stands in sharp contrast to the large, globose petrosal characteristic of *Metacheiromys* and most xenarthrans (see, however, *Priodontes*, Patterson et al., 1989). The epitympanic wing continues anterolaterally and dorsally to the promontorium to form a large, deep fossa for the origin of the tensor tympani muscle.

The stapedial arterial system of *Palaeonodon* appears to have been quite well developed, in contrast to the xenarthrans, which have lost the stapedial artery (Bugge, 1979; Wible, 1984, 1987). The posterior process of the right petrosal in USGS 21876, a process which marks the beginning of a groove for the promontory artery, forms the ventralmost point on the petrosal. It would seem to indicate from its position that the internal carotid

artery entered the tympanic cavity from a ventral position in the posterior wall. In the type, this area is occupied by the entotympanic, and this bone presumably had a posteroventral carotid foramen. In *Metacheiromys* and the xenarthrans, this carotid foramen is situated much farther anteriorly, along the medial wall of the tympanic cavity. The internal carotid appears to have traveled a short distance anterolaterally from the carotid foramen and then split into two large branches that traversed grooves on the lateral surface of the petrosal—a dorsal stapedial artery and a ventral promontory artery. The latter artery continued on in a groove that ran anteriorly for a short distance before curving over the ventral surface of the promontorium in an anteromedial arc to reach the very anterointernal corner of the petrosal. No such groove is present in *Metacheiromys*, and among xenarthrans it is only found in the anteaters. The former artery flowed anterodorsally and laterally, its groove ending at the posteroventral rim of the fenestra ovalis. The artery must have then passed through the stapes (see the description of *Metacheiromys* stapes below) and continued on to form a large ramus inferior and possibly a smaller ramus superior, although there is no evidence for the latter. The ramus inferior passed under the roof of the facial sulcus and from there ran anteriorly and ventrally in a very large groove located lateral to the tensor tympani fossa. The lateral wall of this groove is formed by a ridge of the petrosal bone. This ridge is continuous posteriorly with the crista facialis and bears a broken surface laterally, which appears to match a similar broken surface on the squamosal, separated from the ridge by a narrow groove. At its ventral extremity, the ridge is sutured to the alisphenoid. The positional relationships of this ridge—medial to the squamosal and the presumed tegmen tympani (the structure so labeled in the figure is similar in position to the tegmen of xenarthrans), lateral to the petrosal proper, and posterior to the alisphenoid—and the fact that it forms a direct continuation of the crista, suggest to us that this ridge, and the floor of the ramus inferior groove along with it, may be homologous with the processus cristae facialis of xenarthrans. If we are correct in homologizing the

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FIG. 18. *Palaeonodon* sp., USGS 21876: **A**, stereophotographs of braincase in ventral view; **B**, stereophotographs showing enlarged view of left auditory region in ventral view; **C**, line drawing of braincase in ventral view, with structures labeled. Hatched lines indicate a broken surface, stippling indicates the presence of matrix.

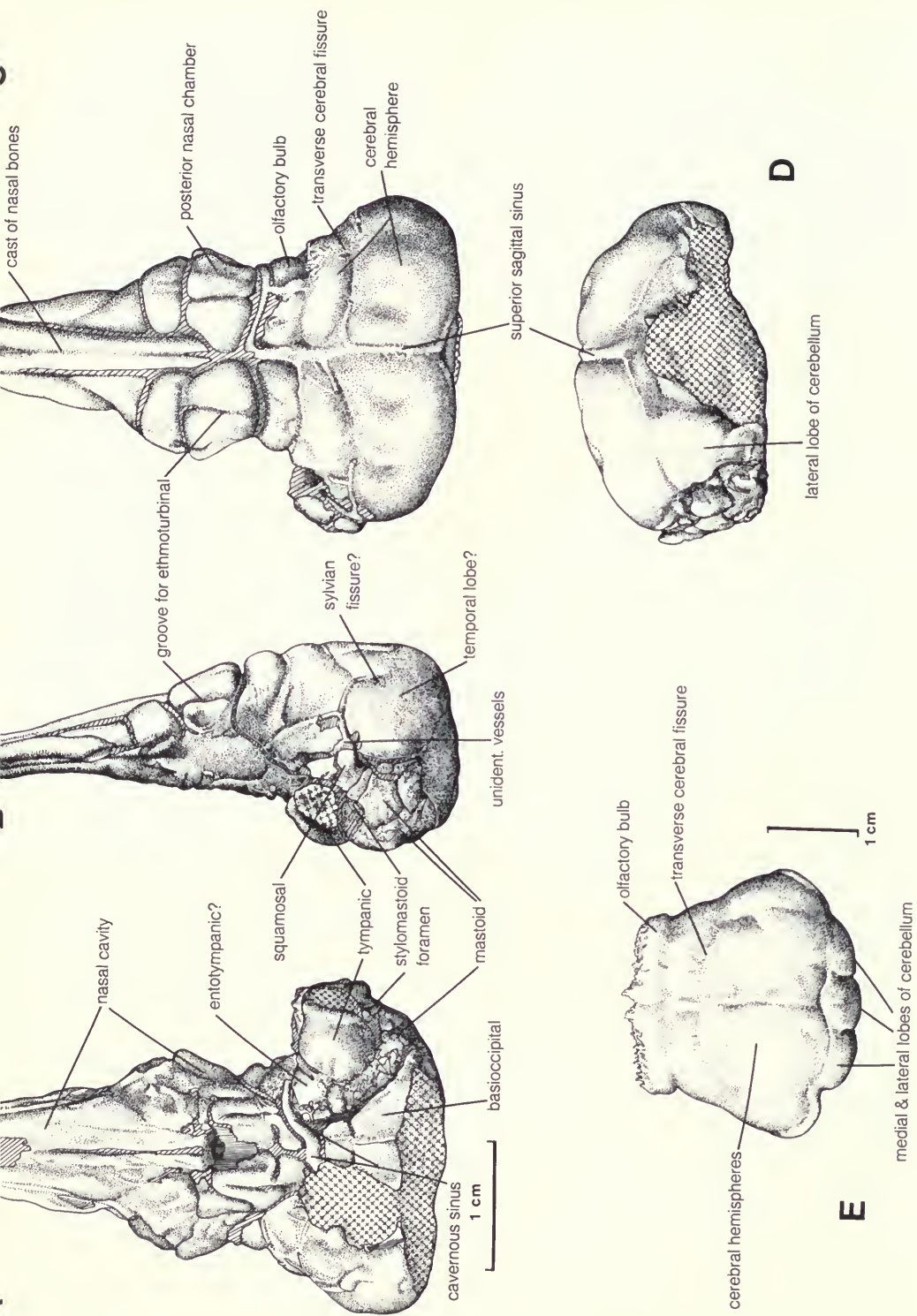


FIG. 19. *Epicotherium* sp., FMNH UM483: A-D, skull and endocranium shown in ventral, lateral, dorsal and posterior views. *Epicotherium* sp., AMNH 9245: E, endocranium shown in dorsal view.

two processes, it would constitute very strong evidence of a palaeodont/xenarthran relationship, as noted by Patterson and Segall below.

USGS 21876 has one more large vascular groove traveling through the auditory region. This groove crosses the medial surface of the petrosal, ventral to the position of the entotympanic in the type, and ends posteriorly in the large, deeply recessed posterior lacerate foramen. Almost certainly this groove served to carry the inferior petrosal sinus (Wible, 1986.)

Matthew very tentatively determined as the hyoid articulation a depression in the ventral surface of the pars mastoidea (?hy in his fig. 39). This pit narrows to a foramen, however, and there is another, smaller foramen posterior to it. These two openings correspond well in position to foramina regarded as vascular by Simpson in *Metacheiromys* and we so regard them in *Palaeanodon*. [Similar vascular foramina occur in the entotympanic of *Metacheiromys* (Simpson, 1931a, fig. 7v), in accordance with the condition in some sloths and armadillos.] The tympanohyal and the stylomastoid foramen were almost surely situated in the now open and matrix-filled space that has been left medial to the pars mastoidea by the displacement of the tympanic and entotympanic. [The subsequent preparation of the type on the left side has exposed the tympanohyal and stylomastoid foramen. The tympanohyal, which faces laterally, is situated posterior to the medial portion of the meatal tube of the tympanic. The stylomastoid foramen lies just anterolateral to the tympanohyal, and hence also behind the meatal tube. It is thus a foramen definitivum. Note that in the figure of USGS 21876, the tympanohyal faces posteriorly and lies anteromedial to the hourglass-shaped stylomastoid foramen. It would seem that the tympanohyal, which is broken off in this specimen, must have been enlarged posteriorly and ventrally as in xenarthrans (see footnote 7), contacting the mastoid and thus completely enclosing the "foramen primitivum" (*sensu* Patterson and Segall). From this "foramen primitivum," the facial nerve apparently curved around the lateral surface of the tympanohyal so that the stylomastoid foramen ("foramen definitivum," *sensu* Patterson and Segall) came to lie anterolateral to the tympanohyal at the surface of the skull. As to the hourglass shape of the foramen, it is possible that there was an arterial twig accompanying the facial nerve into the tympanic cavity, much as Guth (1961) describes in *Bradypus* and *Choloepus*.] Matthew has described and figured the very large pars mastoi-

dea of the periotic. We may add that the ventral position is slightly inflated, foreshadowing conditions in the later *Metacheiromys*.

The foramen lacerum posterum is unusually large and round, as noted by Matthew. It notes the basioccipital (and mastoid?)²⁵ to a degree equaled by few xenarthra. Matthew's figure shows it as sharply set off from the groove between the bulla and basioccipital by a sutural connection between the caudal part of the entotympanic ("petrosal crest") and the basioccipital. The supposed suture is, however, an artifact brought about by the medial displacement of tympanic and entotympanic. [As mentioned above, in this specimen Matthew would seem to have been correct. Subsequent preparation has revealed a basioccipital-entotympanic suture.] Relations between foramen and groove were no doubt as in *Metacheiromys* and the Xenarthra.

Matthew stated that, on the basis of the skull, "... one might hesitate to say whether the genus stood nearer fundamentally to the armadillo or to the pangolins." Incomplete as the only known skull is, it permits a more positive conclusion than this. *Palaeanodon* possesses a well-developed entotympanic, a very large pars mastoidea, and occipital crest—all characters present, in varying degree, among the Xenarthra. In the Pholidota (see further below) the entotympanic is represented only by a small nodule of bone between the tympanohyal and the anterior part of the basioccipital (if indeed this is an entotympanic at all), which is not present

²⁵ In the Xenarthra, the suture between exoccipital and pars mastoidea runs lateral to the foramen. In Matthew's figure of *P. ignavus* and in one, but not both, of Simpson's basicranial figures of *Metacheiromys dasypus*, the suture is shown as running to the foramen. Examination of the materials permits some doubt as to whether the suture actually followed that course in palaeodonts. [Matthew's figure of *Metacheiromys* (PU 18107) shows a clear contact between the entotympanic and the reduced paroccipital process, which itself lies medial to the mastoid. This contact excludes the mastoid from participation in the rim of the posterior lacerate foramen. The entotympanic continues on laterally to this contact to form a lateral connection with the tympanohyal and a posterior connection with the mastoid. The situation is less clear in *Palaeanodon*. The area is covered with matrix in this area, making sutures difficult to distinguish. Certainly the entotympanic approaches the paroccipital process. USGS 21876, however, has relatively small exoccipitals, and the mastoid appears to form part of the paroccipital process. Given the size of the mastoid participation in the rim of the posterior lacerate foramen in this specimen, it seems likely that the entotympanic (which is missing in this specimen) would exclude mastoid exposure in the rim of the foramen.]

in all species, the surface exposure of the pars mastoidea is minute and there is no occipital crest. Of such pangolin characters as the lateral wings of the basioccipital and the smaller lateral surface of the squamosal there is no trace in *Palaeanodon*. For us, then, there can be no hesitation: the skull is fundamentally edentate and shows no significant resemblance to the pangolins.

Metacheiromys Wortman²⁶

The auditory region has been well described and figured by Simpson. The metacheiromyids are extremely precocious in the degree of evolution shown by the auditory region. Nothing comparable was achieved by the *Xenarthra* until post-Santacruzian time. The structure is not exactly like anything later achieved by the xenarthrans, the euphractines coming the closest in tympanic structure. The most aberrant feature, from a xenarthran standpoint, is the greatly inflated mastoid, as Simpson identifies the inflated element behind the tympanic. There is a decided possibility, however, that much of this inflated area may be entotympanic, in which case the difference would not be great since the entotympanic extends laterally behind the tympanic to participate in the fossa for the stylohyal in many xenarthrans, e.g., ground sloths.

Simpson's figures of *M. dasypus* (AMNH 11718, type, from the Bridgerian of Wyoming) show what appears to be a suture between entotympanic and mastoid that runs anteriorly and ventrally from the foramen lacerum posterium to the tympanic. This is not mentioned in his text. [To us] it does not appear to be a suture but a combination of a crack and a small groove running from a vascular foramen to the foramen lacerum posterium. [Patterson and Segall's observations are completely corroborated by PU 18107.] We believed that the entotympanic, rather than ending at this point, continued laterally to the tympanohyal, as in *Xenarthrans* and *Palaeanodon*. [Again, the new specimen confirms this unequivocally.] Vague indications of a division between entotympanic and mastoid in this area can be seen both in *M. dasypus* and in the type of *M. tatusia* (AMNH 11549), but it is not certain that these are really sutural. The

²⁶ [In addition to the type, the description below was compared to PU 18107, a beautifully preserved and wholly uncrushed skull which is approximately one-third smaller than the type specimen. The information on the stapes was derived from USNM 452349, which Robert Emry kindly allowed us to examine.]

fact remains that what must be mastoid is notably more inflated than in xenarthrans, but this difference does not by any means offset the very positive resemblance between the two groups in the auditory region as a whole. In *Palaeanodon ignavus* (type) there is no such great inflation posterior to the bulla and there is no clear separation between the two tympanics, possibly due to the greater age of specimen.

A conspicuous difference from the *Xenarthra* that has not hitherto been described is that there is no groove or canal in the entotympanic for the internal carotid. [In this matter, Patterson and Segall are incorrect. PU 18107 shows a clear groove on the external surface of the left entotympanic that runs anteromedially from the posterior lacerate foramen to a carotid foramen located just posterior to the midpoint of the entotympanic.] The second artery [see footnote 12] may have passed forward to the cranial cavity from the groove described by Simpson between basioccipital and entotympanic. There is no postglenoid foramen in metacheiromyids, nor is there any venous opening posterior to the foramen ovale, but a mastoid foramen of xenarthran type may be seen in *M. tatusia*. [*Palaeanodon* does not have a mastoid foramen per se, but USGS 21876 does possess a clear groove traveling dorsally and slightly anterolaterally across the front of the mastoid. This groove presumably served the same purpose as the mastoid foramen and canal of xenarthrans—to carry the occipital artery (Tandler, 1899). We have not examined *M. tatusia* personally, and hence we do not know whether its “mastoid foramen” is a ventral opening for the occipital artery or a more dorsal opening for the arteria diploetica magna. The USGS specimen also clearly possesses a postglenoid foramen, which as Patterson and Segall note, is absent in *Metacheiromys*.] A postglenoid process is present in both *Palaeanodon* and *Metacheiromys*, but is situated farther anterior to the mastoid process than in *Utaetus*, the only xenarthran to possess a postglenoid process.

The ventral surface of the pars petrosa of the periotic is exposed on the left side of *M. tatusia*. It is rounded, only slightly longer than wide, and decidedly convex transversely, resembling that of *Dasypus* among living armadillos. There is no indication of shelving around the promontorium, such as occurs in armadillos. The fenestrae are relatively large, especially the f. vestibuli, which is larger than in *Dasypus* and *Euphractus*. The apertura tympanica canalis facialis is visible but the crista facialis is broken. This is most unfor-

fortunate, because it would be of great interest to learn if the Palaeonodonta possessed the process from the anterior part of the crest that is so characteristic a feature of the Xenarthra. The great size and marked degree of inflation of the pars mastoidea has been commented on by Simpson. The relation of this inflation to the bulla is unknown. If the inflation is not cancellous but consists of a single large cavity, this may well be epi- rather than hypotympanic in nature. [Although the nature of this mastoid inflation is unknown in *Metacheiromys*, preparation of the USGS specimen of *Palaeonodon* has demonstrated that its mastoid inflation is not connected to the middle ear cavity. The middle ear cavity does, however, possess a large epitympanic sinus that opens ventrally through a foramen pneumaticum situated lateral to the presumed tegmen tympani. This sinus has a small anterior extension into the squamosal over the glenoid fossa.]

[Lastly, we have been permitted to examine a specimen of *Metacheiromys* (USNM 452349) in which the ear ossicles are preserved. The stapes of this animal is a typical, therian bicurrate stapes. It is short and wide, so that the width of the footplate appears to exceed the height of the bone. There is a small head situated on top of the confluence of the two crura, and the crura themselves, both of which are somewhat damaged, appear to be either hollow or deeply grooved, much as in the anteaters *Myrmecophaga* and *Tamandua*. The footplate itself forms an elongate oval transversely and is surrounded by a high rim. The incus is incompletely exposed and the malleus damaged; thus, descriptions of these bones will not be included here.]

Epoicotheriidae

As in the case of the *Metacheiromyidae*, the available materials, consisting of one skull each of the remarkable little *Epoicotherium* Douglas from the Chadronian of Montana and of the even more extraordinary *Xenocranium* Colbert from the Orellan of Wyoming, have been so well described (Simpson, 1927; Colbert, 1942) that the discussion will be limited to a few supplementary remarks. [We have no copy of these remarks, only the figure of one poorly preserved skull and endocast of an epoicotheriid of indeterminate affinities from the Early Oligocene of South Dakota and one endocast of another epoicotheriid specimen from the American Museum (fig. 18A–D, FMNH UM 483; 18E, AMNH 9245). The poor state of preservation of this

specimen prevents any attempt at a description of the ear region beyond what is noted on the figure. For a discussion of the bony anatomy of the auditory region in this family, the reader is referred to the aforementioned works, as well as to the work of Rose and Emry (1983).]

The Auditory Ossicles

William D. Turnbull and Timothy Gaudin

Patterson and Segall had illustrations prepared of the auditory ossicles of fossil and extant xenarthrans from all three infraorders. Unfortunately, we have found no descriptive text to go with these figures. There are no such descriptions appended to the accounts of individual genera in the systematics section of either Part I or Part II. We have assumed that these descriptions were to be grouped together in a separate section to be placed somewhere within the manuscript as a whole, but we have no clear evidence that this is so, or where such a segment was to be placed. It is clear that these ossicle illustrations were prepared either before or after the figures accompanying the main systematic sections, as they are drawn in a very different style. It may very well be that the reason we have no manuscript for this section is that Patterson had decided not to include this section in the final published version. We will assume, however, that since he and Segall had the illustrations made, they intended them to be included in the study. We have montaged these illustrations into two figures (figs. 20–21) and written a descriptive text to accompany them.

The auditory ossicles of most of the living genera of xenarthrans have been carefully described by Doran (1878) and later by Fleischer (1973). The morphology of both the xenarthran stapes (Novacek & Wyss, 1986a) and malleus (Segall, 1976) has been addressed by subsequent workers. Notes on the ossicles of fossil xenarthrans are more difficult to come by, but descriptions are available in the works of Woodward (1900), Stock (1925), Lull (1929), and Guth (1956b, 1957, 1961). Because there is already a substantial body of literature describing these bones, we have treated this portion of the text as supplementary to the earlier works, and have not prepared an exhaustive description of the ossicles of all genera for which they are available. Rather, we have concentrated on describing the ossicles for the genera for which we have figures, or for which we were able to ob-

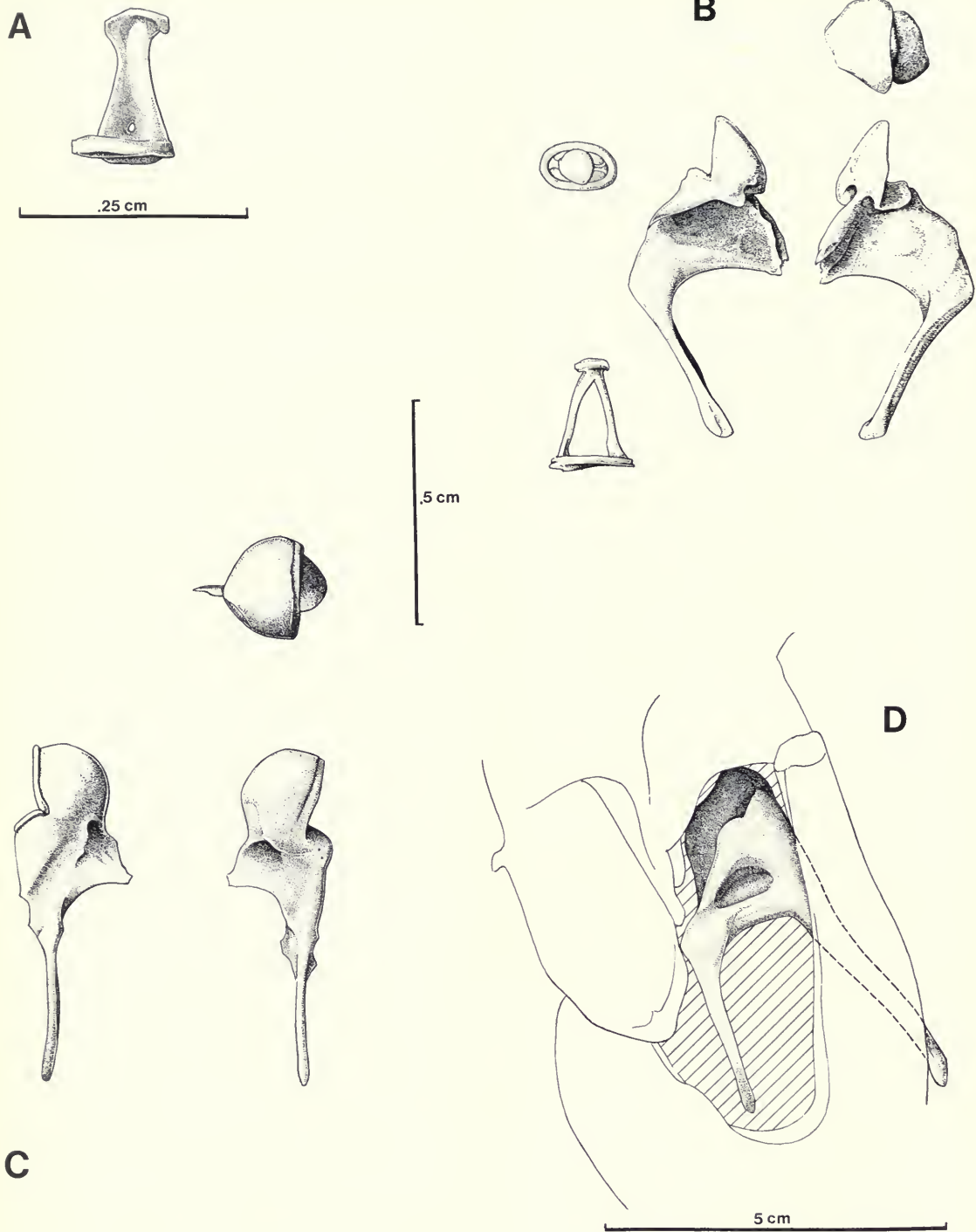


FIG. 20. *Tolypeutes t. matacus*, FMNH 28340: A, stapes shown in ventral view. *Dasypus novemcinctus mexicana*, FMNH 63921: B, malleus shown in dorsal (above), lateral (left), and medial views, stapes shown in lateral (above) and ventral views. *Chaetophractus (= Euphractus) villosus*, FMNH 63865: C, malleus shown in dorsal, lateral (left), and medial views. *Prozaedius exilis*, PU 15579: D, right malleus and portion of tympanic ring shown in lateral view.

tain specimens not available to the original authors. For other xenarthran taxa, we provide no more than an overview, and the reader is referred to the aforementioned studies for the details.

Armadillos

Figure 20 illustrates the morphology of the malleus and stapes in several genera of living and extant armadillos. One can divide the armadillos into two groups based on the morphology of the malleus. This first group, typified by the malleus of *Dasypus* in Figure 20B, corresponds roughly with Engelmann's group Dasypodidae (Engelmann, 1978, 1985, although it includes the extinct form *Prozaedius*, which Engelmann considers to be an early euphractine). The second group, represented by the malleus of *Chaetophractus* in Figure 20C, corresponds with a clade to which Engelmann gives the name Euphracta.

The malleus of *Dasypus* is characterized by a dorsoventrally elongate head that is somewhat triangular in lateral view, with the apex of the head pointed straight dorsally. The articular surface is divided by a deep groove into two facets which lie at an acute angle to one another in lateral view. The upper facet is much larger than the lower. It is flat, vertically oriented, and faces posteriorly and slightly medially. The lower facet, which is also turned slightly medially, is convex upward. The malleus has a large anterior process (terminology of Segall, 1976, equivalent to the processus gracilis of Doran, 1878), which is connected by a broad lamina to the head. The lamina has a medially thickened anterodorsal border, and bears on its lateral surface a deep fossa which receives the tip of the anterior crus of the tympanic. The neck of the malleus is short and mediolaterally compressed. The lateral process (processus brevis of Doran, 1878) is not distinct. The manubrium is sabre-shaped in anterior view, with a broad base that narrows distally to a laterally recurved tip. It is quite thin in lateral view, with a spatulate distal expansion. The manubrium is set off from the neck of the malleus by a 60–70-degree angle in dorsal view, whereas in lateral view, the angle between the two is about 110 degrees.

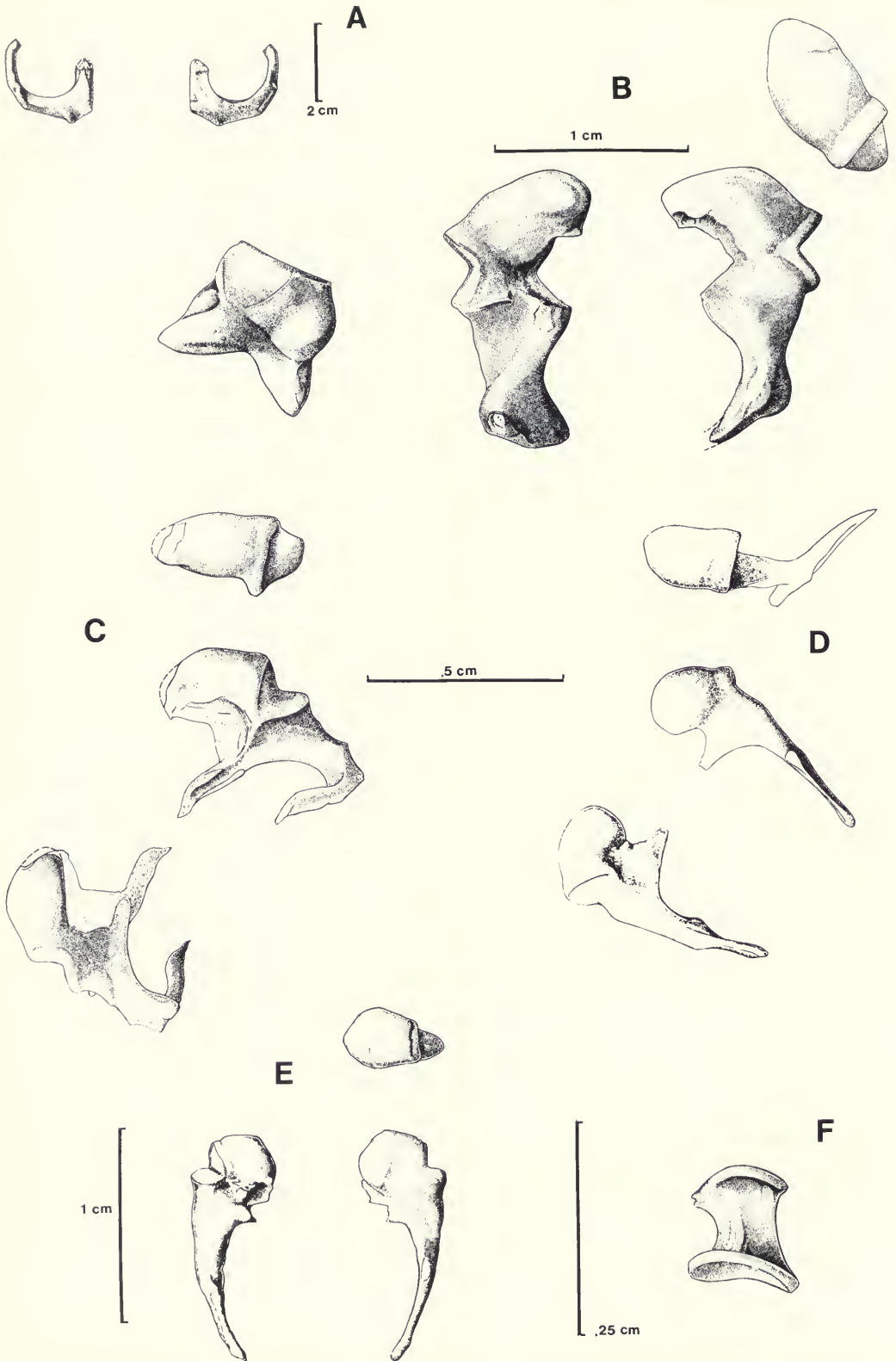
The mallei of *Priodontes* (FMNH 25271), *Cabassous* (FMNH 47960), and *Tolypeutes* (FMNH 28341 and 21407) were examined and found to be very similar to that of *Dasypus*. In *Priodontes* the head is more compressed anteroposteriorly, whereas in *Cabassous* the head is more globose, the anterior process is noticeably thickened, and the articular

facets face more dorsally and medially. *Tolypeutes*, as in *Priodontes*, has a more compressed head than *Dasypus*; but, more strikingly, it bears an enormously elongate anterior process that runs along the full length of the sulcus malleoli of the tympanic. Such an elongate process was found in a *Dasypus* juvenile by Doran (1878), and in a *Dasypus* adult by Guth (1961). It is also present in the fossil form *Prozaedius*, which we have not been able to examine personally, but which is illustrated in Figure 20D. The malleus of this genus appears to be quite similar to that of the other dasypodids. Given its position as an early and rather primitive euphractine, it seems reasonable to suggest that this "dasypodid-type" malleus, with or without the greatly elongate anterior process, may be primitive for armadillos as a whole.

The malleus of euphractine armadillos shows substantial differences from that of the dasypodids, contra the descriptions of Doran (1878). As illustrated in Figure 20C by the malleus of a juvenile specimen of *Chaetophractus* (FMNH 63865), the head of these forms is much larger relative to the size of the whole bone itself, and much more globose. The articular facets for the incus are set at an obtuse angle to one another; otherwise they are similar to those of *Dasypus*. The anterior process of the malleus is quite small, with a corresponding reduction in the size of the lamina. The lateral process of the malleus is much more distinct than that of *Dasypus*, though the shape of the manubrium is much the same as in the latter genus. In strong contrast, however, to the malleus of *Dasypus*, the manubrium is in line with the neck in lateral view, and forms an obtuse angle of about 100 degrees with the neck in dorsal view.

The mallei of *Zaedius* (FMNH 25617) and *Chlamyphorus*, the latter as described in Guth (1961) and Segall (1976), are broadly similar to that of *Chaetophractus*. The anterior process and lamina are further reduced in *Zaedius*, and even further reduced in *Chlamyphorus* (contra Fleischer, 1973, who illustrates a large anterior process for *Chlamyphorus*). *Chlamyphorus* exhibits several other small differences from the mallei of *Zaedius* and *Chaetophractus*, including differences in the shape of the articular facets, lateral process, and manubrium, all attributable, according to Segall (1976), to adaptation to the animal's fossorial way of life.

The stapes of armadillos, as exemplified by that of *Dasypus* (fig. 20B), is of a fairly standard eutherian bicurrate type, albeit with somewhat dorsoventrally compressed crura. Such a widely perforate stapes is unquestionably primitive for cingulates as a whole (Novacek & Wyss, 1986a),



and is present in living and in some extinct forms, e.g., *Eutatus* and *Glyptodon* (Guth, 1957, 1961). However, there is variation in stapedia morphology within the group. The stapes of *Tolypeutes* (fig. 20A) has only a very small, distally located stapedia foramen. The crura are confluent proximally, forming an elongate neck below the head. A neck is variably present in the genus *Cabassous* (Guth, 1961, pers. obs.). A neck is also found in the stapes of *Glyptodon* (Guth, 1957, 1961) and *Chlamyphorus* (Guth, 1961; Segall, 1976, but cf. Fleischer, 1973), although in these forms the stapedia foramen is a good deal larger than in *Tolypeutes*. The three other glyptodont genera in which Guth (1957, 1961) figures the stapes show a completely imperforate morphology. However, in two of these forms Guth describes the bone as having two thickened crura that have fused medially. Given this fact, and the condition in *Glyptodon* and other cingulates, it is most parsimonious to conclude that a perforate stapes (i.e., one with unfused crura, and perhaps with an elongate neck) is primitive for glyptodonts.

Sloths

Much as with the armadillos, extinct and extant sloths can be divided into two groups on the basis of malleus morphology. The first group, typified by the malleus of *Bradypus* (FMNH 16557, fig. 21D), corresponds to the *Bradypus/Megatherium* division of the main systematics section of this study. The second group, as exemplified by the malleus of *Choloepus* (FMNH 30731, fig. 21C), corresponds to the *Choloepus/Megalonyx* and *Myodont* divisions of this work.

The malleus of *Bradypus* is similar in many respects to that of the euphractine armadillos. Like the latter group, the head of the malleus is large and bulbous. However, it is directed slightly anteroventrally and is much more elongate antero-posteriorly than in euphractines, so that in dorsal view the sides of the head run parallel to one another (fig. 21D). As Segall (1976) has noted, such a dorsal contour is common to all living sloths and anteaters except *Cyclopes*, and stands in contrast

to the more semioval or semicircular head characteristic of *Cyclopes* and extant cingulates. The articular facets of the malleus in *Bradypus* are similar in morphology to those of *Chaetophractus*, except that the groove dividing the facets is shallower, the two facets are approximately subequal, and the upper facet is directed posteroventromedially (not simply posteromedially). The neck is slender and of similar relative length as that of *Chaetophractus*. As in the latter form, the anterior process is small. The lamina is somewhat larger than in euphractines, due to the lengthening of the head, but as in these forms it lacks a distinct lateral facet for articulation with the tympanic bone. The lateral process of the malleus is enlarged over the condition seen in euphractines, so that it actually forms a free-standing projection dorsally. The manubrium is reduced in length relative to the cingulate condition, but is otherwise similar in shape. In lateral view, as in euphractines the manubrium is in line with the neck. In dorsal view, it sits at a more obtuse angle than is seen in *Chaetophractus*, forming about a 130-degree angle with the neck.

Although we have not been able to examine the specimen personally, the malleus of *Nothrotheriops* as illustrated in Figure 21E closely approximates the morphology described above in *Bradypus*, with some slight differences. The groove dividing upper and lower incudal facets is deeper. The head is slightly less elongate. The most noteworthy difference between the malleus of *Nothrotheriops* and that of *Bradypus*, indeed between *Nothrotheriops* and all other sloths and anteaters save *Cyclopes*, is that the dorsal contour of the head is ovoid, with the sides not subparallel but bowing out from one another. This condition is very reminiscent of the morphology seen in cingulates (Segall, 1976).

We have only a sketchy diagram provided by Guth (1961) of the malleus of *Megatherium*, but it would seem to conform as well to the general shape of the bone in *Bradypus*. It is likely that such a malleus is characteristic of the whole *Bradypus/Megatherium* division.

As Doran (1878) noted, the malleus of *Choloepus* shows clear differences from that of *Bradypus*. It also demonstrates some interesting similarities

FIG. 21. *Paramylodon*, AMNH 22609: A, isolated left tympanic ring shown in medial and lateral views. *Lestodon myloides*, AMNH 11270: B, right malleus shown in dorsal, medial (left), and lateral views, incus shown in dorsomedial view. *Choloepus hoffmani*, FMNH 30739: C, left malleus shown in dorsal (above), medial (middle), and lateral views. *Bradypus tridactylus*, FMNH 16657: D, right malleus shown in dorsal (above), lateral (middle), and medial views. *Nothrotheriops shastense*, YPM 13198: E, right malleus shown in dorsal, medial (left), and lateral views. *Cyclopes didactylus*, FMNH 51931: F, stapes shown in ventral view.

to the dasypodid malleus. More so than in any other xenarthran, the head of the malleus is tremendously elongated anteroposteriorly. Like *Bradypus*, this head is directed somewhat anteroventrally. The anterior process, like that of the dasypodids and unlike that of *Bradypus*, is quite long, and the lamina correspondingly large. The articular facets for the incus are like those of *Bradypus*, except that the groove separating upper and lower facets is deeper. The lateral process is about the size of that present in *Chaetophractus*—larger than that of the dasypodids, smaller than the lateral process of *Bradypus*. The manubrium is similar in shape and in length to that of *Bradypus*, but is oriented at a much different angle relative to the rest of the bone. In lateral view, the manubrium forms an angle of approximately 110 degrees to the neck, much as in the Dasypodidae. In dorsal view, the manubrium forms a more acute angle with the neck than is the case in *Dasybus*, being offset about 45 degrees laterally from the neck.

The only megalonychid specimen in which auditory ossicles were available to us for examination was AMNH 17722, the *Acratocnus* specimen described in the main systematic section and illustrated in Figure 5. The malleus of this form, which can be seen in the figure, is not isolated, but from the portion that is exposed it appears to show a *Choloepus*-like morphology, with a long anterior process and a manubrium that sits at a 100–110-degree angle to the neck in lateral view.

The mylodont sloths also conform closely to the malleolar morphology of *Choloepus*. Figure 21B shows the malleus of *Lestodon* in medial, lateral, and dorsal view. The head and incudal facets are very *Choloepus*-like. The lamina and anterior process are broken, but what remains of the lamina would seem to indicate a structure of similar size to that found in *Choloepus*. The manubrium is also missing from the specimen, but the proximal remnants of this structure show that it formed a large angle with the neck of the malleus when viewed laterally.

Figure 22 illustrates ossicles of the genus *Glossotherium*, including those of a juvenile specimen lent to us by the Page Museum (LACMHC 12230), and two adults sent to us by the Idaho Museum of Natural History (IMNH 35015/15141, 55005/16072). The mallei in both cases are badly damaged, with only the head and articular facets preserved. Stock (1925, pl. 23), however, provides a figure of a malleus from the same genus, shown in posterior view. The bone in Stock's figure preserves all but the distal portion of the manubrium.

The bone in this genus is unusual in several respects. The lower articular facet is inflated more than is typical for xenarthrans, and the bone has a curious sigmoid curvature in dorsal view. Both the anterior extremity of the head and the incudal facets are deflected somewhat medially, while the neck turns back laterally. The anterior process in Stock's specimen appears to be broken, so that its size cannot be determined. As in *Choloepus*, however, the malleus has an elongate head that seems to have borne a large lamina on its ventral surface, and the manubrium sits at an obtuse angle to the neck.

Guth (1956b, 1961) illustrates the mallei of a number of other mylodont genera, including *Myloodon*, *Glossotherium*, *Scelidotherium*, *Analcitherium*, and *Nematherium*. These are also, for the most part, like the malleus of *Choloepus*, although some show interesting resemblances to the malleus of *Bradypus*. The malleus of *Scelidotherium* appears to lack the long anterior process of *Choloepus*; however, this may be attributable to post-mortem breakage. *Analcitherium* does not appear to have the greatly elongate head characteristic of *Choloepus*, though it is otherwise quite similar. In *Myloodon* and *Glossotherium*, the manubrium is in line with the neck of the malleus in lateral view, as in forms from the *Bradypus*/*Megatherium* division. The elongate malleolar head, and, in the case of *Myloodon*, elongate anterior process are, however, much more reminiscent of the morphology in *Choloepus*.

Figures 21B and 22C–E illustrate the morphology of the incus in *Lestodon* and *Glossotherium*, respectively. Because Patterson and Segall included such a drawing in their auditory ossicle figures, we will briefly mention that the morphology of these bones is typical for sloths as a whole (Doran, 1878; Woodward, 1900; Guth, 1961; Fleischer, 1973). The body is short and squat, and the long and short processes are approximately equal in length. This is in contrast to the incudi of cingulates and of *Tamandua* and *Cyclopes*, in which the short process is much reduced relative to the long process (Doran, 1878).²⁷

Patterson and Segall included no figures of the stapes of any sloth. However, given the recent attention focused on the primitive morphology of

²⁷ There is some disagreement as to the relative size of these processes in *Myrmecophaga*—Doran (1878) and Fleischer (1973) describe the short process as being reduced, but Field Museum specimens and those of Guth (1961) bear processes that are much closer to one another in length.

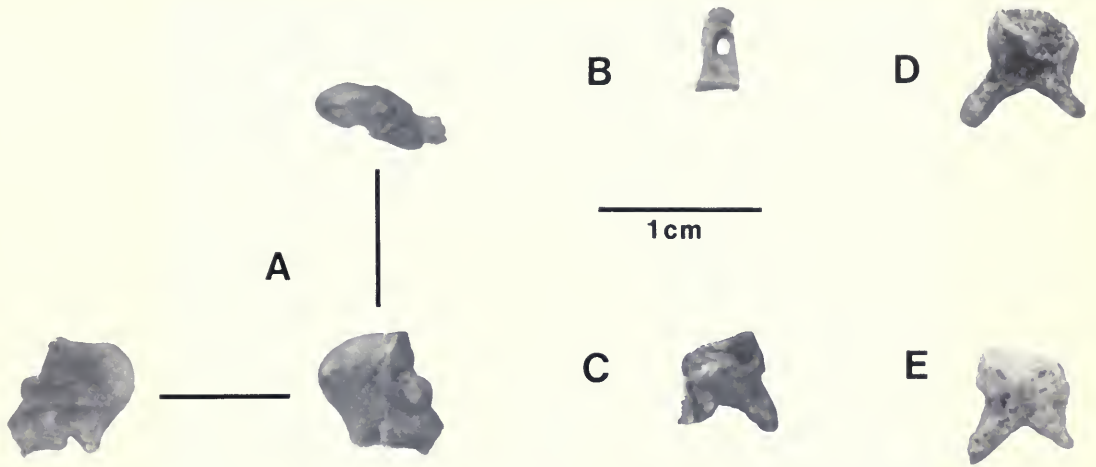


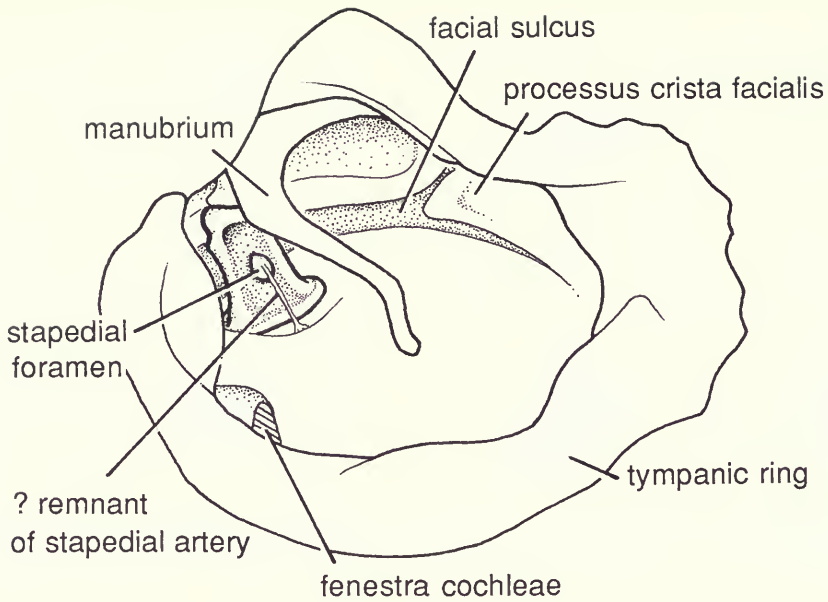
FIG. 22. *Glossotherium harlani*, LACMHC 12230: A, partial right malleus shown in dorsal, lateral (left), and medial views; B, right stapes shown in ventral view; C, right incus shown in medial view. *Glossotherium harlani*, IMNH 35015/15141: D, incus shown in lateral view. *Glossotherium harlani*, IMNH 55005/16072: E, incus shown in lateral view.

the stapes for Eutheria as a whole and edentates in particular (Segall, 1970; Fleischer, 1978; Novacek & Wyss, 1986a), as well as the importance of the stapes as a character useful in sorting out eutherian relationships (Novacek, 1982, 1986; Novacek & Wyss, 1986b; Shoshani, 1986; Novacek et al., 1988), we felt a few paragraphs on the stapedia morphology of both fossil and extant sloths might prove enlightening. Novacek and Wyss (1986a) have suggested that an imperforate stapes, much like that figured for the pygmy anteater *Cyclopes* (fig. 21F), is primitive for sloths as well. Certainly an imperforate stapes is quite common in the two extant sloth genera. However, as Doran (1878) has pointed out, both genera at times possess a small, slitlike aperture between two thickened columnar crura. This stapedia morphology is variably present among individuals, and even between left and right sides of the same skull.

The ontogeny of the stapes in both genera demonstrates that this slit results from an incomplete closure of a much larger foramen present in immature individuals. We have observed a large, circular stapedia foramen in our youngest juvenile specimens of *Choloepus* (FMNH 44053 (illus. in fig. 23A–B), 60586). This large foramen is retained on at least one side of the skull in some older juveniles (FMNH 84522, 127421) and even some skulls in which the cranial sutures are beginning to close (FMNH 1206 and 127422). In one early juvenile specimen (FMNH 128409), as well as in a few older juveniles (FMNH 14183, 14185, 14186, and 60585), the foramen is narrowed and may be represented

by nothing but a small slit, but all *Choloepus* juveniles in the Field Museum collections possess a perforated stapes. Specimen FMNH 44053, an early juvenile, appears to retain a vestige of the stapedia artery passing through the stapedia foramen. This vestigial artery, as illustrated in Figure 23A, is embedded in a ligament that arises from the external surface of the promontorium ventral to the fenestra ovalis and passes through the stapedia foramen into dried connective tissue filling the facial sulcus. The stapedia foramen is absent in all juvenile specimens of *Bradypus* contained in the Field Museum collections. However, Schneider (1955) has described the stapedia foramen in fetal *Bradypus*, indicating that a rudiment of the stapedia artery passes through this opening. According to Schneider, both the artery and the stapedia opening degenerate fairly early in ontogeny.

A secondary loss of the stapedia foramen in *Choloepus* and *Bradypus* is proposed not only on the basis of the ontogeny of the stapes in these extant forms, but also on phylogenetic information. The morphology of the stapes is well known among extinct ground sloths of the family Mylodontidae, the purported sister group to the megalonychoid clade that contains the living tree sloths. This stapedia morphology is well illustrated by a juvenile *Glossotherium* specimen from the Page Museum (fig. 22B). The stapes possesses a large proximally situated stapedia foramen. The crura run essentially parallel to one another, in contrast to the distally diverging crura of cingulates (fig. 20B), and are connected to one another by a thin



A

FIG. 23. *Choloepus hoffmani*, FMNH 44053: A, line drawing of the right ear region based on photograph in B, showing a close-up of the tympanic ring, auditory ossicles, and middle ear. (Continued on p. 67.)

lamina situated beneath the stapedial foramen. The posterior crus, again unlike that of cingulates, is thickened dorsoventrally and bears a strong muscular process. The stapes of the genus *Myiodon*, described and figured almost 100 years ago by Woodward (1900), is essentially identical to that described above for *Glossotherium*. Guth (1956a, 1961) also illustrates the stapes of several mylodont genera, including the Pleistocene forms *Myiodon*, *Glossotherium*, and *Scelidotherium*, and the Miocene genus *Analcitherium*. All these forms bear large stapedial perforations. *Myiodon* and *Glossotherium*, according to Guth, lack any sort of plate connecting the crura, so that the stapes closely resemble those typically found in the anteaters *Myrmecophaga* and *Tamandua*.

In addition to the information on the mylodont stapes, we have recently uncovered a stapes from a fossil megalonychoid, the Santacrucian genus *Eucholoeps*. The left stapes of FMNH P13139 was found in place, sitting within the vestibule with its head poking out of the fenestra ovalis. Its morphology (fig. 23B) is reminiscent of that found in our juvenile *Choloepus* specimens. It is short and triangular in dorsoventral view, with two thick

crura that diverge slightly from head to footplate. The posterior crus is not noticeably thickened as it is in *Glossotherium* (see fig. 23B, posterior view), though it bears a blunt process for the stapedius muscle posteriorly and lacks a neck separating the head from the crura, as in the latter genus. Like *Glossotherium*, the stapes of *Eucholoeps* has a small dorsal lamina that connects the two crura beneath the stapedial foramen. The foramen, though partially obscured by matrix, is clearly circular and quite large.

In all fossil and extant sloths for which the stapes is known, the bone exhibits a well-defined stapedial foramen at some point during ontogeny. Although more data on the morphology of the stapes in extinct sloths, particularly among the megalonychids²⁸ and megatheriids, could provide important corroborating evidence, we feel that all

²⁸ We have recently discovered a stapes preserved on the right side of a skull of *Megalonyx* from AMNH (F:AM 99194). The stapes was damaged during preparation (it was broken through the middle of both crura) but clearly bore a large stapedial foramen.



B

1cm



1mm

C

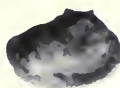


FIG. 23. Continued. **B**, photograph of posterior portion of skull (FMNH 44053), ventrolateral view. *Eucholoeps ingens*, FMNH P13139; **C**, left stapes shown in (clockwise from upper left) dorsal, ventral, lateral, and posterior view.

current ontogenetic and phylogenetic information supports the claim that the stapes in primitive sloths was of a typical eutherian bicurate form. This bicurate form was subsequently lost in adult

Bradypus and *Choloepus*. A bicurate stapes is present in two of three genera of vermilinguas and is almost certainly present primitively in cingulates, as discussed above. It thus seems highly

probable that a widely perforate stapes is primitive for the whole order. Given this fact, and the aforementioned presence of a bicurrate stapes in palaeonodons, the absence of a stapedia foramen is unlikely to serve as a valid character separating edentates from the rest of Eutheria (*contra* Novacek, 1982, 1986; Novacek & Wyss, 1986b; Shoshani, 1986; Novacek et al., 1988).

Anteaters

Apart from the stapes of *Cyclopes*, no figures of anteater ear ossicles were prepared by Patterson and Segall, and little mention has been made of these bones so far in this text. As these bones have been described elsewhere (Doran, 1878; Guth, 1961; Fleischer, 1973), we will not describe them in detail, except for the following brief discussion of mallear morphology. The mallei of the three genera of extant vermilinguas are similar in most respects to that of *Bradypus*. The head is antero-posteriorly elongate (although directed straight anteriorly, not anteroventrally as in the latter form), and the anterior process and lamina are small (*contra* Guth, 1961, and Fleischer, 1973, who depict the anterior process and lamina in these forms as being considerably larger). In *Cyclopes*, the manubrium forms a 180-degree angle to the neck in lateral view, just as in *Bradypus*, whereas in the other two genera the angle is only slightly lower, closer to 150 degrees. Similarly, in dorsal view the manubrium forms an obtuse angle with the neck as in *Bradypus*. From the point of view of Patterson and Segall's implied phylogenetic relationships, the similarities of the malleus in the anteaters, the *Bradypus/Megatherium* sloth division, and the euphractine armadillos would almost have to be considered convergent. Interestingly, these three groups of xenarthrans are the three major subgroups that are characterized by animals that possess completely ossified auditory bullae. The dasypodid armadillos, as well as *Choloepus* and the megalonychid and mylodont sloths, which share a common mallear morphology, are for the most part lacking a completely ossified auditory bulla. This would seem to imply that the morphological differences between the two malleus types, including differences in length of the anterior process and orientation of the manubrium, may have important functional differences—differences correlated with the differing resonant properties of fully ossified versus partly membranous middle ear cavity walls.

Conclusions

William D. Turnbull and Timothy Gaudin

It has already been pointed out, both in the Conclusions to Part I and in the Introduction to this paper, that we have not been able to find any formal written conclusions in association with the manuscripts of either Part I or Part II. This is despite the fact that we know such a Conclusions section, summarizing the systematic implications of this work, existed at some time. It seems likely that Patterson never finished the manuscripts to his complete satisfaction, in large measure owing to the difficulty he had in drawing systematic conclusions from the work. Although we have no written version of Patterson's final thoughts on this matter, we do have clues as to what Patterson and Segall thought this study might imply in terms of xenarthran phylogeny. The organization of the Descriptive Anatomy section of this paper into divisions, groups, and subfamilies serves as the main source of insight into the thinking of the two original authors. The xenarthran phylogeny of Patterson and Pascual (1968, 1972) was based largely on Patterson's earlier work on the anatomy of the auditory region, and although it is only a very general phylogeny of the order, it provides additional insights. Last, the Descriptive Anatomy section of this paper has conclusions embedded within the descriptions themselves. The descriptions are the only source of character data to support the relationships deduced from the above sources, but their support of these groupings is very uneven, with some such groupings (perhaps those Patterson was less comfortable with?) receiving little or no attention. In writing this Conclusions section, we have tried not only to piece together the systematic conclusions of Patterson and Segall, but to provide the evidence for these conclusions as well, emphasizing those relationships that are the best supported. Figure 24 and Table 1 are provided as a summary of these phylogenetic relationships and the supporting evidence. One of us has performed a cladistic analysis of pilosan phylogeny based upon characters of the ear region drawn from these descriptions (Gaudin, 1990). Although this is not the place to discuss those results in detail, they will be mentioned in cases where they provide additional support for Patterson and Segall's conclusions, or where they may serve to clear up ambiguities in the relationships the original authors attempted to draw.

In the last paragraph of their description of *Palaeanodon*, Patterson and Segall state, "For us then there can be no hesitation: the skull [of *Palaeanodon*] is fundamentally edentate and shows no significant resemblances to pangolins." This sentence is a strong endorsement of the earlier work of Simpson (1931a, 1945), who placed palaeanodonts in the suborder Palaeanodonta within the order Edentata (= Xenarthra). However, as discussed in the introduction, the work of Emry (1970) criticizing Simpson's allocation of the palaeanodonts to the Xenarthra, and suggesting instead pholidotan affinities, seems to have raised serious doubts in Patterson's mind as to the correctness of his earlier views on palaeanodonts. In Patterson and Pascual (1972), the systematic relationships of palaeanodonts are mentioned briefly, and although these authors do not endorse Emry's views, neither do they come out in favor of a palaeanodont/xenarthran linkage. It would seem that Patterson, as in most of the recent literature on the group (Rose, 1979; Rose & Emry, 1983; Rose et al., 1991), chose to consider the group as a suborder *incertae sedis*. The characters used by Patterson and Segall to support the common ancestry of palaeanodonts and xenarthrans are not as strong as their above statement would seem to indicate. Two of their three characters, the strong occipital crest and large mastoid exposure, are most likely primitive eutherian features (Kielan-Jaworowska, 1981, 1984; Novacek, 1986; Novacek & Wyss, 1986b; Novacek et al., 1988). The third character, a large entotympanic, although clearly not a primitive eutherian feature (Novacek, 1977), is also problematic. Novacek lists 13 higher categories of mammals that have a large entotympanic contribution to the auditory bulla, raising the strong possibility that this resemblance between xenarthrans and palaeanodonts is merely convergent.

Our examination of new specimens of *Palaeanodon* and *Metacheiromys* has shed new light on this problem of palaeanodont affinities. Like Patterson and Segall, we find little reason, based on auditory region anatomy, to consider palaeanodonts and pangolins to be closely related. Emry (1970) briefly discusses the auditory region of the two groups, and suggests that the inflated mastoid of palaeanodonts is actually an epitympanic inflation of the squamosal, which would cover the mastoid posteriorly—a feature characteristic of the Pholidota. However, both *Palaeanodon* (USGS 21876) and *Metacheiromys* (PU 18107) have a clear suture between mastoid and squamosal showing that, unlike pangolins, the squamosal does not have

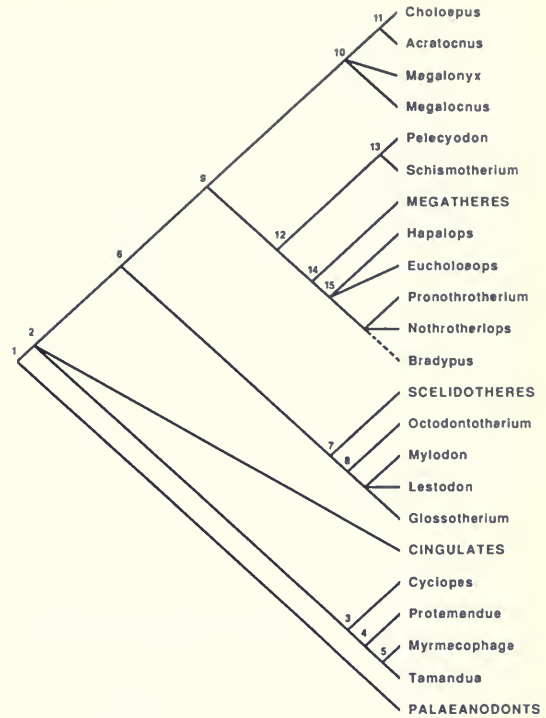


FIG. 24. Inferred phylogeny, based on Parts I and II of this work and the work of Patterson and Pascual (1968, 1972). Characters supporting the numbered nodes are given in the Conclusions and in Table 1.

an occipital exposure. In addition, a break in the squamosal of USGS 21876 has permitted preparation of the epitympanic sinus, showing that it is clearly separate from the air spaces filling the mastoid, and that the sinus not only extends posterior to the auditory meatus, as in pangolins but not xenarthrans, but also anterior to the meatus, coming to lie above the glenoid, as in xenarthrans but not pangolins. The only real resemblances between the ear regions of palaeanodonts and pangolins are characters, like the large epitympanic recess and large posterior lacerate foramen, that are shared by xenarthrans as well and, if anything, indicate the possible monophyly of the cohort Edentata (*sensu* Novacek, 1986).

Unlike the situation with palaeanodonts and pholidotans, there are several characteristics of the auditory region that would seem to indicate a close common ancestry of palaeanodonts and xenarthrans. Two such features were discussed above in the descriptions of *Palaeanodon* and *Metacheiromys*: the groove or canal in the mastoid for the occipital artery, and the processus cristae facialis. In addition, the anterolateral position of the stylo-mastoid foramen relative to the tympanohyal is

TABLE 1. Characters supporting the Patterson and Segall phylogeny. Those characters in bold type are strong characters (i.e., their distributions among relevant taxa are essentially the same as described by Patterson and Segall), those in normal type are questionable in some way or another.

-
- Node 1: Palaeanodonts + Xenarthra: **Large entotympanic**; large mastoid exposure on occiput; well-developed occipital crest.
- Node 2: Xenarthra: **Enlarged entoglenoid process**; squamosal arches high above incisura tympanica, exposing the auditory ossicles in lateral view; processus crista facialis present; tympanohyal continuous with crista facialis; foramen ovale located within the alisphenoid.
- Node 3: Vermilingua: **Pterygoids extended posteriorly to participate in the wall of the tympanic cavity; opening for Eustachian tube located at posteromedial corner of tympanic cavity; descending wedge of squamosal separates tympanic crura in juvenile skull; mastoid process absent; recessus meatus well developed; glenoid gently concave transversely and enlarges from behind forwards.**
- Node 4: *Protamandua* + *Tamandua* + *Myrmecophaga*: **Internal carotid artery crosses surface of promontorium within groove; basioccipital process participates in wall of tympanic cavity; tympanic cavity communicates anteriorly with pterygoid sinus.**
- Node 5: *Tamandua* + *Myrmecophaga*: **Pterygoids meet in midline.**
- Node 6: Sloths: **Large rounded stylohyal fossa made up of contributions from mastoid, tympanohyal, and entotympanic; anterior crus of tympanic larger than posterior.**
- Node 7: Mylodontidae: **Epitympanic sinus absent**; root of zygoma directed anterolaterally; glenoid situated well anterior and dorsal to porus acousticus; glenoid shallow, concave, extending well onto the zygoma, with internal descending portion slight; entotympanic firmly attached to the petrosal; entotympanic contacts exoccipital and tympanohyal; entotympanic with saddle-shaped sulcus for the internal carotid artery lying between medial and lateral plates.
- Node 8: Mylodontinae: **Pterygoid inflated; tympanohyal directed ventrally and posterolaterally.**
 Scelidotheriinae: **Paroccipital process enlarged; stylohyal fossa reduced in size; groove in which mastoid lies somewhat narrowed; tympanohyal directed ventrally.**
- Node 9: Megalonychoidea: Tympanic expanded medially.
- Node 10: Megalonychidae: **Large, circular posterior lacerate foramen; lateral plate of entotympanic thin with a medial expansion; glenoid transversely expanded; dorsal contour of skull evenly convex in lateral view; root of zygoma directed laterally; processus crista facialis large, flat, and concave; stylomastoid foramen a foramen primitivum.**
- Node 11: *Acratocnus* + *Choloepus*: **Paroccipital process enlarged; *Acratocnus* intermediate between large megalonychids and *Choloepus* in the following characters—ventral position of stylohyal fossa in lateral view, position of glenoid relative to porus acousticus (both dorsoventrally and anteroposteriorly), length and width of mastoid groove and size of mastoid process, rugosity and medial expansion of tympanic.**
Megalocnus + *Choloepus*: **Extensive area of attachment between anterior crus of tympanic and squamosal; skull heavily pneumatized.**
- Node 12: Megatheriidae: **Tympanic large relative to size of skull; posterior lacerate foramen elongate anteroposteriorly; epitympanic sinus rough-walled; Eustachian tube oriented vertically.**
- Node 13: *Schismotherium* Group: **Basioccipital tubera present.**
- Node 14: Megatheriinae + Nothrotheriinae: **Stylomastoid foramen directed ventrally; anterior crus of tympanic does not diverge laterally; tympanic unattached to the pterygoid or squamosal ventrally; anterior portion of tympanic expanded ventrally and medially; tympanic laterally expanded; auditory bulla fully ossified.**
- Node 15: *Pronothrotherium* + *Nothrotheriops*: **Vomer with elongate ridge bearing a sigmoid curvature; glenoid similar in shape.**
Pronothrotherium + *Bradypus*: **Mastoid process enlarged; relationship of tympanic crura to squamosal similar.**
Nothrotheriops + *Bradypus*: **Anterior portion of entotympanic extends laterally beneath tympanic.**
Megatherium/*Eremotherium* + *Pronothrotherium*: **Postglenoid foramina present; entotympanic with large anteroventral process.**
-

a shared feature of xenarthrans and palaeanodonts. This latter feature is not unique to these two groups of eutherians, as discussed above, but it is relatively uncommon and is almost certainly not a primitive feature of eutherian auditory regions. The possession of a large entotympanic does not itself constitute strong evidence for a clade containing both xenarthrans and palaeanodonts, but the morphological details of the entotympanics in these two groups do support their monophyly. In both groups, the entotympanic is a plate-like bone forming the entire medial wall to the

auditory bulla, as well as a portion of the posterior wall and a small portion of the ventral wall. The entotympanic participates in the wall of the posterior lacerate foramen and bears a foramen for the internal carotid artery. In addition, both forms possess an ostium tympanicum tubae that emerges between the entotympanic, tympanic, and basiocranium. Of the 11 other higher categories of mammals listed by Novacek (1977) as having a well-developed entotympanic, only the Carnivora possess all the details listed above that characterize the palaeanodont and xenarthran entotympanic

(van der Klaauw, 1930b, 1931b; Simpson, 1931b; McKenna, 1963; Hunt, 1974; Hunt & Korth, 1980; MacPhee, 1981; Novacek, 1986; Wible & Novacek, 1988; MacPhee et al., 1989). As discussed by Wible and Novacek (1988), the absence of any trace of an entotympanic in the earliest true carnivorans, the miacids, suggests that the entotympanic was independently derived within the Carnivora; thus, any similarity in the carnivoran and palaeonodont/xenarthran entotympanic must also be independently acquired.

We are not aware of any modern systematic treatment of the Xenarthra that considers them as anything other than a "natural group" or monophyletic clade, with the possible exception of Engelmann's Ph.D. thesis (1978), in which he suggests pangolins were derived from within anteaters. Certainly Patterson and Segall accepted the monophyly of the order, and although there is little discussion of ordinal level features in this paper, Part I mentions several auditory characters that typify the order as a whole. Only one of these characters seems to provide strong support for xenarthran monophyly. Patterson and Segall describe a large ridge of the squamosal bone posterointernal to the glenoid that forms the anterior border of the tympanic cavity in all xenarthrans. This ridge appears to be homologous to the entoglenoid process of McDowell (1958), and an enlarged entoglenoid process such as the one present in xenarthrans is, according to MacPhee (1981), a derived feature within Eutheria. The high squamosal arch over the incisura tympanica as described in *Prionodontes* (Patterson et al., 1989, p. 5) is also indicated as a primitive feature of all xenarthrans. This conclusion is seemingly contradicted in the description of *Utaetus* on the same page, where Patterson and Segall state that "due to the presence of the postglenoid [process], it is probable that there was no open space above the porus." The other characters given by Patterson and Segall as characteristic of the order appear to be primitive at some other level. The processus crista facialis has already been discussed as a character shared with palaeonodonts. The connection of the tympanohyal to the crista facialis is common to all mammals (Goodrich, 1930; Wible, 1990). The position of the foramen ovale within the alisphenoid appears to be primitive for eutherians. This character is notable in that Novacek (1986), Novacek and Wyss (1986b), and Novacek et al. (1988) have claimed that the foramen ovale in xenarthrans only notches the back of the alisphenoid in xenarthrans and pholidotans, and have used this character, as well

as the supposed imperforate nature of the stapes in these two orders, to set them as the sister-group to all other eutherians. In the section on auditory ossicles, we show that an imperforate stapes is unlikely to be primitive for xenarthra as a whole. This, coupled with Patterson and Segall's observations on the position of the foramen ovale, would seem to suggest that the hypothesis of a monophyletic Epitheria, including all eutherian orders except the Pholidota and Xenarthra, warrants serious reconsideration.

We note here briefly that the analysis of Gaudin (1990) has provided some auditory characters that are synapomorphous for xenarthrans, including: pterygoid participation in the wall of the tympanic cavity, the presence of an entotympanic/pterygoid connection, and a reduction in relative length of the postglenoid region of the skull.

Patterson and Pascual (1968, 1972) depict the relationship between the three xenarthran infraorders as an unresolved trichotomy. Patterson and Segall treat these infraorders in a like manner, considering each independently without discussing the possibility of a close relationship between any two. Segall, in a later work on the auditory anatomy of *Chlamyphorus*, supports a monophyletic Pilosa, linking sloths and anteaters on the basis of a shared feature of the mallei of the two groups, wherein the head of the malleus is elongate in dorsal view, with parallel sides and without an anterior spine. As stated in the introduction, the work of Gaudin (1990) has uncovered a number of auditory characters that would support a monophyletic Pilosa, including: large posterior lacerate foramen, posterior lacerate foramen below and behind the petrosal (see Engelmann, 1978, 1985), presence of an entotympanic/paroccipital process contact, and stylomastoid foramen located directly lateral to the surface exposure of the tympanohyal.

Of the three xenarthran suborders, the Vermilingua is perhaps the most distinctive. Patterson and Segall discuss a number of characteristics that unite these taxa, including the unusual posterior extension of the pterygoids and the posterior location of the opening for the Eustachian tube. These authors state that the form of the glenoid is a distinctive character of the infraorder, yet earlier in this paper they note the similarity of the anteater glenoid to the glenoid of mylodonts. This would seem to indicate that this type of glenoid may be primitive for all pilosans.

Within the Vermilingua, Patterson and Segall place *Cyclopes* as the sister-group to the other three described genera—*Protamandua*, *Tamandua*, and

Myrmecophaga. This arrangement, which coincides with that of Engelmann (1985), is supported by the fact that *Cyclopes* lacks a basioccipital participation in the tympanic cavity and a connection between the pterygoid sinus and tympanic cavity. *Cyclopes* also has an internal carotid artery that courses medial to the tympanic cavity, and does not cross the promontorium as in other anteaters. *Cyclopes* does possess a large subarcuate fossa like that found in *Tamandua*. However, this characteristic is absent in *Myrmecophaga* and other xenarthrans, and considering the overwhelming similarity between *Tamandua* and *Myrmecophaga*, is probably convergent. Patterson and Segall place *Protamandua* as the sister-group to *Tamandua* and *Myrmecophaga*, an arrangement that is again in agreement with the phylogeny of Engelmann (1985). *Protamandua* does not have pterygoids that meet in the midline as in *Tamandua* and *Myrmecophaga*, but its porus and tympanics are intermediate in shape between that of *Cyclopes* and those of *Tamandua* and *Myrmecophaga*, and it possesses a promontory artery and a basioccipital and pterygoid sinus participation in the tympanic cavity. We would like to note here that Engelmann (1985) united *Cyclopes* and the Pliocene genus *Palaeomyrmidon* into a clade he termed the Cyclopinini, partly on the basis of the lack of midline pterygoid fusion in these two forms. The lack of fusion in *Protamandua* as well would suggest that this is a primitive feature for the Vermilingua as a whole.

Patterson and Segall consider the sloths to be a monophyletic group made up of three families: the Mylodontidae, Megatheriidae, and Megalonychidae. However, apart from the presence of a large, round stylohyal fossa formed by contributions from the mastoid, tympanohyal, and entotympanic, and perhaps the anterior crus of the tympanic being larger than the posterior (though the latter feature is also present in some anteaters and armadillos and hence may be primitive), they provide little support from the ear region for the monophyly of sloths. The two original authors depart from the usual trichotomous arrangement of the three sloth families (Hoffstetter, 1958; Engelmann, 1985), placing the Megatheriidae and Megalonychidae into a monophyletic group Megalonychoidea. They then split the remaining sloth family of traditional classifications, the two extant genera of tree sloths in the family Bradypodidae (Simpson, 1945), by placing *Choloepus* in the Megalonychidae and *Bradypus* in the Megatheriidae. These conclusions are perhaps the most unusual

and interesting results of this entire paper. The latter conclusion, that of bradypodid diphyly, is well supported and will be discussed below when relationships within the megatheriids and megalonychids are considered. The former conclusion, that of a monophyletic Megalonychoidea, is very poorly supported. We can find only a single character, the possession of a medially expanded tympanic ring, that Patterson and Segall would use to support this grouping. Even this character is absent in the Santacrucian megatheriid genera *Schismotherium* and *Pelecycodon* and in the extant form *Choloepus* (although in the case of *Choloepus*, Patterson and Segall imply that this is a secondary reduction, contra Guth, 1961, who uses an unexpanded tympanic as a character linking *Choloepus* and mylodontids). Certainly the mylodontids are more divergent morphologically (especially dentally) from the other two families than those families are from each other (Webb, 1985), but it is unclear if the similarities, dental and otherwise, between the megatheriids and megalonychids are derived or simply primitive. This is a hypothesis in need of much more supporting evidence; unfortunately, the work of Gaudin (1990) does not provide such evidence, nor does it support a monophyletic Megalonychoidea.

Of the three sloth families, it is perhaps surprising that the Mylodontidae, which as noted above is in many features the most distinctive family, is the least well-supported by characters of the ear region in Patterson and Segall's work. Many of the features described by these authors as characteristic of the mylodontid auditory region are primitive at another level, e.g., the anterolaterally directed zygomatic root and glenoid well separated from the porus acusticus are primitive for all xenarthrans, the glenoid shape characters and the position of the glenoid dorsal to the porus are primitive for pilosans, and the contact between entotympanic and tympanohyal and entotympanic and exoccipital are primitive for all sloths. The shape of the internal carotid sulcus is not unique, but its ventral location at the level of the basicranium does appear to characterize mylodontid sloths. The lack of an epitympanic sinus is also a solid character. The analysis of Gaudin (1990) would support this clade with additional characters, including the flat lateral profile of the ventral edge of the entotympanic, the enlarged lateral exposure of the mastoid, and the uniform size of the tympanohyal along its entire length.

Within the Mylodontidae, the subfamily Scelidotheriinae is clearly defined by a number of fea-

tures, among them the large paroccipital process and reduced stylohyal fossa. The genus *Octodontotherium* was figured by Patterson and Segall, but the description was written by Turnbull and Gaudin. It is placed in the subfamily Mylodontinae on the basis of Patterson and Pascual's phylogeny (1968, 1972). This placement of *Octodontotherium* conflicts with the phylogeny of Engelmann (1985), in which this taxon is placed outside both the subfamilies Mylodontinae and Scelidotheriinae, but our placement is corroborated by a couple of characters from the ear region, including the presence of an inflated pterygoid and a ventrally and posterolaterally directed tympanohyal. The remaining mylodontine genera, *Myiodon*, *Lestodon*, and *Glossotherium/Paramyiodon*, are shown as forming an unresolved trichotomy in Figure 24. Patterson and Segall do not discuss any features that are unique to the three forms, but they undoubtedly recognized their close relationship exclusive of *Octodontotherium* and the scelidotherines, as have other recent workers (Hoffstetter, 1958; de Paula Couto, 1979; Engelmann, 1985; Webb, 1989). Gaudin (1990) provides several characters linking these three mylodontine taxa, including a circular stylohyal fossa and a laterally directed stylomastoid foramen.

The relationships within the Megalonychidae, and indeed its identity as a monophyletic group, are perhaps the best supported and most clearly worked out of all the systematic conclusions of this paper. Patterson and Segall give at least six features that support the monophyly of this group: circular posterior lacerate foramen, entotympanic lateral plate thin, glenoid transversely expanded, zygomatic root directed laterally, dorsal contour of skull evenly convex (though not in *Megalonyx*), and stylomastoid foramen a foramen primitivum (though not in *Megalocnus*). Of these, all but the last (which, as the name implies, is probably primitive) appear to be relatively robust supportive arguments.

The taxa *Megalonyx* and *Megalocnus* form an unresolved trichotomy with the other megalonychid genera in Figure 24. Patterson and Segall are unclear in their discussions as to which taxon is the closest to *Acratocnus* and *Choloepus*, with each showing resemblances the other lacked. This uncertainty is exacerbated by the incompleteness of our specimen of *Megalocnus*. No such uncertainty is evident, however, in the placement of *Acratocnus* as the sister-group to the extant genus *Choloepus*. Patterson and Segall note that *Acratocnus* is intermediate in morphology between *Megalonyx*/

Megalocnus and *Choloepus* in a host of features, including the ventral position of the stylohyal fossa, the expansion and rugosity of the tympanic ring, the position of the glenoid relative to the porus, and the development of the mastoid region. In addition, it shares with *Choloepus* an enlargement of the paroccipital process. This analysis thus provides additional evidence for Webb's (1985) placement of *Choloepus* within the Megalonychidae, which in his analysis was supported by only a single character. It conflicts, however, with the megalonychid phylogeny of Webb and Perrigo (1985) in deriving *Choloepus* from within the antilean ground sloth radiation, rather than setting it as the sister-group to all Plio-Pleistocene megalonychids.

Patterson and Segall provide a number of characters that support the monophyly of their megatheriid clade, the *Bradypus/Megatherium* division. Unfortunately, relationships within the group are in many cases rather poorly resolved and somewhat confusing. The characteristics used by the original authors to support the megatheriid division are as follows: tympanic large relative to the size of the skull, posterior lacerate foramen elongate anteroposteriorly, Eustachian tube directed ventrally (a feature that is not well developed in the Santacrucian taxa), and epitympanic sinus rough-walled, the latter feature observable only in *Bradypus* and *Eremotherium*. We might also add to this list features of the mallear morphology discussed in the auditory ossicle descriptions, namely that the manubrium forms an obtuse angle with the neck of the malleus in dorsal view but is in line with the malleus in lateral view.

The Santacrucian taxa *Schismotherium* and *Peleciodon* have been separated from the other megatheres into their own group in the systematics section of this work. This arrangement, coupled with the absence in these genera of many characters that were stated in the text as characterizing the entire *Bradypus/Megatherium* division, implies to us that these forms were intended to fall outside the other megatheriids, as depicted in Figure 24. There appears to be little support for joining these two taxa into a monophyletic group, the only character given being the presence of basioccipital tubera (see Descriptive Anatomy: The *Schismotherium* Group), a feature found in a number of other sloths. This is the relationship suggested by the arrangement of the systematics section, however, and may have been supported by other cranial, postcranial, or dental characteristics.

The remaining taxa in this family are split

roughly into two subfamilies, the Megatheriinae and the Nothrotheriinae. These two groups would seem to form a monophyletic group, united by the following auditory characters: stylomastoid foramen directed posteriorly, anterior crus of the tympanic not diverging laterally (as in the *Schismotherium* group), ventral portion of the tympanic unattached to pterygoid or squamosal, tympanic expanded ventrally and medially in its anterior portion, tympanic laterally expanded, and auditory bulla fully ossified. It should be noted, however, that the latter three characters are not present in the Santacrucian members of the Nothrotheriinae.

The nothrotherines are grouped together without any characters, so far as we were able to ascertain, that support their monophyly. The auditory regions of *Eucholoeps* and *Hapalops*, which are placed in this subfamily by the original authors, do not seem to us markedly different from the other Santacrucian forms, save perhaps for a somewhat more medially expanded tympanic ring in the latter genus. It may be that this is another arrangement based on the morphology of other regions of the animals in question. The monophyly of *Pronothrotherium* and *Nothrotheriops* is better established, based on the shared possession of a truly bizarre elongate and curved vomerine ridge, as well as similarities in the shape of the glenoid. The position of *Bradypus* is much more difficult to elucidate. Patterson and Pascual (1968, 1972) show *Bradypus* as having been derived from somewhere within the Nothrotheriinae, but where exactly it goes is not specified, nor is it specified anywhere in their text. Patterson and Segall list several similarities between *Bradypus* and *Pronothrotherium*, including a similar relationship between the tympanic crura and the squamosal, as well as the presence of a large mastoid process. They also note that in both *Bradypus* and *Nothrotheriops* the entotympanic extends laterally beneath the tympanic at its anterior end. Because of these similarities, we have tentatively placed *Bradypus* in a trichotomy with the other two genera. We would like to mention a third possibility, however, a sister-group relationship between *Bradypus* and the megatherines. The work of Gaudin (1990) strongly supports such an arrangement, based not only on the shared possession of a rough-walled epitympanic sinus, but also on the following characters: tympanic forms a posterior wall to the glenoid, ossified auditory meatus present, porus circular, tympanohyal directed posteromedially, and tympanic contact with the pterygoid.

Whether one chooses to place *Bradypus* in the Nothrotheriinae or the Megatheriinae, its separate derivation from the other extant sloth genus *Choloepus* is a remarkable result of this study. Moreover, this study provides the evidence on which this suggestion, put forward over 20 years ago by Patterson and Pascual (1968), was based. The evidence it provides in this regard is nicely supplementary to that compiled by Webb (1985), who also allied *Bradypus* with the megatheriids.

As mentioned in the Conclusions of Part I, it is a pity that this body of information was not published 25 to 30 years ago. With its broad coverage of auditory anatomy within the Xenarthra and Palaeanodonta, it would have served not only as an important source of information for those workers interested in the systematics of this order in particular, e.g., Guth (1961) and Engelmann (1985), but also any number of studies concerned with the development and evolution of the therian otic region, and indeed the evolution of the Theria itself. The study suggests a number of novel (at least at the time it was being prepared) changes in xenarthran systematics, including the alliance of glyptodonts and pampatheres, the diphyly of the Bradypodidae, and the monophyly of the Megalonychoidea, and, at least in the case of the first two hypotheses, provides important and heretofore unavailable supporting evidence for these relationships. The study has even broader implications, providing important information on the relationship of palaeanodonts and xenarthrans and the relationship of the Xenarthra to other eutherian orders. Therefore we feel certain that this study, even though it has waited some 30 years for publication, will still serve as an important work for students of mammalian evolution in the years to come.

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Appendix

The following abbreviations are used to designate institutions, usually in relation to specimens:

AMNH	= American Museum of Natural History, New York.
AMNH F:AM	= Frick Collection, American Museum of Natural History, New York.
FMNH	= Field Museum of Natural History, Chicago (prefix P indicates a paleontological specimen; numbers lacking a prefix indicate specimens in the Recent mammal collections).
IMNH	= Idaho Museum of Natural History, Idaho State University, Pocatello, Idaho.
LACMHC	= George C. Page Museum, Los Angeles, California.
MCZ	= Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts.
PU	= Princeton University, Princeton, New Jersey.
USGS	= United States Geological Survey, Washington, D.C.
USNM	= United States National Museum of Natural History, Smithsonian Institution, Washington, D.C.
YPM	= Peabody Museum, Yale University, New Haven, Connecticut.

The following abbreviations are used in the text, figures, or figure captions:

ant. crus tympanic	= anterior crus of the tympanic
ant. pr. malleus	= anterior process of the malleus
a.v.c.	= anterior vertical semicircular canal
b.o.	= basioccipital
car. groove	= groove for the internal carotid artery
cond. f.	= condylar or condyloid foramen
crus commune of a.v.c. and p.v.c.	= crus commune of the anterior vertical and posterior vertical semicircular canals
e.i.r.	= epitympanic recess
ext. orifice of canal of Huguier	= external orifice of the canal of Huguier (a.k.a. the fissura Glaseri)
fen. cochleae	= fenestra cochleae
f. i. pet. sin.	= foramen for the inferior petrosal sinus
f.l.p.	= foramen lacerum posterium
f.m.	= foramen magnum
fen. ovalis	= fenestra ovalis
f. sty.	= stylomastoid foramen
fen. vestibuli	= fenestra vestibuli
o. rec. ept.	= opening into the epitympanic recess
porus e.a.m.	= porus acousticus, opening of the external auditory meatus
post. crus tymp.	= posterior crus of the tympanic
proc. from basioccipital	= tympanic process of the basioccipital
pt.	= pterygoid
sulc. tymp.	= sulcus tympanicum
stmf.	= stylomastoid foramen

The dagger symbol (†) is used to indicate that the two senior authors are deceased; in systematic references, the dagger designates an extinct taxon.

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