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The Ear Region in Xenarthrans (= Edentata: Mammalia) Part I. Cingulates

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Walter Segall

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Murra, J. 1946. The historic tribes of Ecuador, pp. 785–821. *In* Steward, J. H., ed., Handbook of South American Indians. Vol. 2, The Andean Civilizations. Bulletin 143, Bureau of American Ethnology, Smithsonian Institution, Washington, D.C.

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Preface

When Bryan Patterson left Field Museum in 1955 to take up the Agassiz Professorship at Harvard, he took with him the only copy of this study, which had resulted from a decade of Wednesday afternoon collaborations.* This he subsequently revised, and in part revised again, but for unknown reasons it somehow never was completed and made ready for publication. I believe Patterson simply never refined it to his complete satisfaction. Aware of the scope of this ambitious project, following the deaths of Patterson in 1979 and Segall in 1981, I have attempted to pull together those parts of the scattered manuscript that could be found, and to salvage the 100+ pen-and-ink illustrations that had been rendered expressly for it, mostly by John Conrad Hanson and R. Norris. Hanson was the staff artist for the Department of Geology during most of the decade of the original collaboration, and Norris served briefly as the Zoology staff artist between 1949 and 1950. These descriptions constitute the first attempt to provide a comprehensive coverage since the work of van der Klaauw (1931), adding much that was new at the time the work was done. The study by Guth (1961) in many respects parallels this work but is difficult to obtain, and in any case covers somewhat different ground and works from a different set of specimens. It is an essential companion to this study. Subsequently, still more fossil materials have become available, notably pampatheres under study by Edmund, and the *Glyptotherium* specimens described by Gillette and Ray (1981). Except for the Field Museum specimen *Vassallia* (= *Plaina*), no attempt to incorporate new pampathere data has been made. *Glyptotherium,* to judge by the Gillette and Ray report (their figs. 7–8, 10c, 12a), fit the more or less stereotypic pattern of all glyptodontoids, and their illustrations correspond closely to those offered here (figs. 15–16).

Patterson had used the illustrations for lectures and student projects over the years, with inevitable wear and other damage resulting. In order to save those most deteriorated, Ron Testa, Field Museum photographer, photographed each on high contrast negatives to eliminate the stains and smudges and to emphasize the original pen-and-ink work. Finally, to keep the results as uniform as possible, we treated all the drawings in this manner. I then montaged them into the figures and decided on the features to be labeled. Credit for the labeling is due Marlene Werner, currently of the Museum's Scientific Services staff. In a few instances Patterson had penciled notations directly on the drawings. In those cases, I could be certain of what was intended. But for the vast majority, I have labeled them according to my interpretation of what the text called for and what I think had been intended, or according to need so as to make each illustration immediately comprehensible. For this the responsibility is entirely mine. In some cases I have modified the text either to expand upon it, or to provide greater consistency, or to conform to present terminology, eliminate repetition, or correct an occasional lapsus. Wherever this has been done in the text, I have employed the device of setting off the changes in square brackets [ ] so that the reader could distinguish between the original and my tampering.

There can be little doubt that Patterson was the senior and pivotal author of the pair, for he clearly had the broader phylogenetic and taxonomic understanding. Segall's contributions provided functional and comparative anatomic understanding, based upon his training in that subject, upon his long experience with human ear study, and upon his inquiring mind.

It is a difficult matter for a third party to join an effort of this sort, for one does not know for sure why the initial study was never finished. Were the authors unhappy with the result? Or did they just run out of time? Or would they wish to have another meddle with their effort? Would the third party be doing them an injustice?

I have carefully weighed the pros and cons. I believe that both Patterson and Segall would want the work finished. My decision to do so rests heavily on the realization that if I did not complete the work, far too great an investment in their time and effort, insight, and knowledge would be lost. By pulling together the parts of this work that could be found and by my filling the gaps, I hope I do not do the others a disservice. At least the reader should be able to be clear about separating my part of the final work from theirs, and by so doing at least the descriptive aspects and illustrations would survive and be made available to all in a useful form.

W.D.T.

* Segall, a practicing physician at the time, specializing in eye, ear, nose, and throat, had been trained in the famed Vienna Clinics. He brought to the collaboration anatomical and medical insights not usually available to the paleontologist and comparative anatomist. Wednesday afternoon was the physician's half-day off, and in this case was regularly devoted to this study by the two senior authors.

The Ear Region in Xenarthrans (= Edentata: Mammalia) Part I. Cingulates

Abstract

This report is the first of two planned works detailing the descriptive and comparative anatomy of the xenarthran ear region (basicranium and its immediate surrounds, including middle ear, but not the inner ear). The study was begun by Patterson and Segall in 1945 and continued actively well into 1955, and only fitfully by Patterson thereafter. This part, "Cingulates," covers a representation of the Cingulata (= Loricata), including dasypodoids (*Utaetus* group, *Priodontes* group, *Dasypus* group, *Euphractus* group, *Peltephilus* group, and *Chlamytherium* group) and glyptodontoids. In all, details are given for 10 living and 15 extinct species. The anatomical details largely support most accepted views of cingulate systematic relationships; there are few surprises. It is confirmed that the pampatheres have a decidedly glyptodont-like basicranium, and it is noted that Bordas had stressed this same point in a 1939b paper.

Introduction

This work ("Cingulates") constitutes Part I (the first two-fifths) of the original Patterson-Segall manuscript on the ear region of the Xenarthra. The remainder (Pilosa: Anteaters and Sloths) is now planned for publication at a later date as Part II of the whole. The original outline called for an Introduction with a general discussion of the auditory region, the main Systematics Section (descriptions with discussions), and a Conclusion. No text of any sort has been found for the first and last of these sections, which I know existed at times past. I have tried to fill these gaps as directly and briefly as possible. My introduction attempts to take cognizance of the probable thinking of the two original authors as well as to provide a framework for the study. It is cast in as nearly modern systematic terms as is compatible with their text. The main body of their text is but little changed. It includes entirely new descriptions of both fossil and Recent forms (25 taxa). The Conclusions section, which I have tried to present in the light of our current understanding of cingulate interrelationships, is entirely mine, but in it I have attempted to stress their implied or stated conclusions.

Three major goals were certainly in their minds when they began the work: (1) to increase the level of knowledge beyond that of their predecessors, especially van der Klaauw (1931) and before him van Kampen (1905); (2) to treat fossil and modern materials together; and (3) to integrate the new knowledge with the old so as to reinterpret xenarthran relationships. That this was so is evident from the detailed descriptions and discussions they wrote, from the illustrations they had made, and from Patterson's several revision attempts. The approach of both men to systematics was conservative, so it is extremely unlikely that they would overemphasize evidence drawn from a single character complex. They did of course consider the petrosal to be a generally conservative structure, and the mastoid to be far more variable, and thus the whole to be a most reliable and informative guide to understanding phylogeny, a concept dating back at least to Flower (1870).

With xenarthran systematics as uncertain as it was during the decade of this work (and in some ways as it remains today; see below), it is easily understood that Patterson and Segall would try to

bring forward new evidence from this relatively neglected source. I am convinced that Patterson's attempts to sort this out and to fathom the implications account in part for the long delays necessitated by his revision attempts. At least one insight (and probably many others) gained from this early collaboration with Segall spilled over into the Patterson and Pascual works (1968, 1972) in the form of their suggestions about xenarthran relationships, especially that of pampatheres and glyptodonts. Since Segall did not have as extensive an insight into systematics and evolution as Patterson did, he was content to have Patterson make whatever changes he thought appropriate. Hence to sort out the thinking in this area, we need only search for the clues that Patterson may have left us. One of these, and I believe this is the key one, comes from the mentioned works of Patterson and Pascual (1968, 1972) wherein the Xenarthra are subdivided in the modern way, into the Cingulata, Vermilingua, and Pilosa.[1] They included three families within the cingulates, subdivided as follows:

[1] Modern usage usually divides Xenarthra into these three subordinal groups based upon the distinctiveness of each in terms of overall morphology (Engelmann, 1985) and supported by evidence from serum protein (Sarich, 1985) and eye lens proteins (de Jong et al., 1985). As Engelmann points out, however, the older notion of there being a dichotomy rather than a trichotomy may yet prove to be correct, for the many morphologic features unite the Pilosa (sensu lato), and the modern protein evidence merely indicates remoteness.

†Palaeopeltidae:			†*Palaeopeltis* (= †*Pseudorophodon*)
Dasypodidae:	†Utaetinae:		†*Utaetus*
	Priodontinae:	Priodontini:	*Priodontes*
			Cabassous
		Tolypeutini:	*Tolypeutes*
	Dasypodinae:		*Dasypus*
	†Stegotheriinae:		†*Astegotherium*
			†*Pseudostegotherium*
			†*Stegotheriopsis*
			†*Stegotherium*
	Euphractinae:	Euphractini:	*Euphractus*
			Zaedius
			Chaetophractus
			†*Paleuphractus*
			†*Macroeuphractus*
			†*Proeuphractus*
			†*Stenotatus*[2]
			†*Prozaedius*
		Chlamyphorini:	*Chlamyphorus*
			Burmeisteria
	†Eutatinae:		†*Eutatus*
			†*Doellotatus*
			†*Proeutatus*
			†*Meteutatus*
	†Peltephilinae:		†*Peltephilus*
			†*Parapeltocoelus*
			†*Peltocoelus*
			†*Anantiosodon*
			†*Epipeltephilus*
	†Pampatheriinae (= †Chlamytherinae and = †Chlamydotheridae):		†*Chlamytherium*
			†*Holmesina*
			†*Plaina*
			†*Kraglievichia*

[2] At the time of the study, this was considered to be a stegotheriine.

			†*Vassallia*
			†*Machlydotherium*
†Glyptodontidae:	†Propalaeohoplophorinae:		†*Glyptatelus*
			†*Propalaeohoplophorus*
			†*Cochlops*
			†*Eucinepeltus*
			†*Asterostemma*
			†*Metopotoxus*
	†Sclerocalyptinae (= †Hoplophorinae):		†*Palaehoplophorus*
			†*Protoglyptodon*
			†*Eosclerophorus*
			†*Trachycalyptus*
			†*Plohophorus* (= †*Hoplophractus* and †*Hoplophorus*, in part)
			†*Parahoplophorus*
			†*Lomaphorops*
			†*Stromaphorus*
			†*Stromaphoropsis*
			†*Eosclerocalyptus*
			†*Plohophoroides*
			†*Lomaphorus*
			†*Hoplophorus*
			†*Brachyostracon* = †*Glyptotherium* [a glyptodont]
			†*Pseudoeuryurus*
			†*Urotherium*
			†*Neuryurus* (= †*Euryurus*)
	†Doedicurinae:	†Panochthini:	†*Nopachtus*
			†*Propanochthus*
			†*Panochthus*
		†Doedicurini:	†*Comaphorus*
			†*Eleutherocercus*
			†*Prodoedicurus*
			†*Xiphuroides*
			†*Plaxhaplous*
			†*Doedicurus*
	†Glyptodontinae:		
			†*Paraglyptodon*
			†*Glyptotherium*
			†*Neothoracophorus*
			†*Glyptodon*
			†*Boreostracon* = †*Glyptotherium*

The present work covers only the Cingulata. The Pilosa, the Vermilingua, and possible ancestral stock(s) will be treated in a subsequent report.

I had hoped that the long-awaited monographic study of the evolution of the Xenarthra, edited by G. G. Montgomery (1985), would shed much light upon the origin and evolution of the order. However, although many details of interrelationships are presented in it, especially those among the armadillos, the phylogenetic systematics of the order remains unclear in several respects: (1) the group's origin is still uncertain, but now it is at least demonstrably remote; (2) its closest relatives within the Mammalia remain a mystery; (3) its major

subdivisions are thus far distinct, without troublesome (or enlightening) intergradations, and these subdivisions also appear to represent early events; (4) within the cingulates, the exact relationship of armadillos and glyptodonts remains a debatable topic.

For this work the most directly useful chapters in the Montgomery volume (1985) are the first seven. That by Glass reviews the history of edentate classification and concludes with a formal proposal for use of the ordinal name Xenarthra to replace Edentata. (Bordas, 1939a,b, had done this, but except for some paleontologists [Hoffstetter, 1958, 1969], it was not widely accepted and used.) Wetzel in two other useful introductory chapters deals with identification, distribution, and taxonomy of living taxa exclusively. Sarich's (1985) report on albumin immunological evidence and de Jong's on eye lens protein structures are necessarily based upon modern materials. They add significant new dimensions to our understanding of relationships within the order by bringing to bear on the subject such different kinds of evidence from the usual classical morphological kinds. Only two of the seven works deal directly with fossil cingulates, that of Edmund (1985) on the fascinating North American pampatheres (giant armadillos); and an entirely theoretical one by Engelmann (1985), which is a thoughtful and far-reaching cladistic analysis that seeks to examine the phylogeny of the entire order.

Abbreviations used are for the most part standard; the Appendix provides a detailed listing. The systematic section of the original manuscript is written in a style that combines description with discussion and sometimes conclusions. The overall conclusions will await the final section, but matters dealing with just the cingulates are discussed and conclusions drawn by Turnbull in a Conclusions section of this work.

Dasypodoids

The *Utaetus* Group

†**Utaetus** Ameghino, 1902. Figure 1A.

A cranial fragment of *Utaetus buccatus* Ameghino, AMNH 28668, from the early Eocene Casamayor, provides the only evidence of skull structure in the Xenarthra prior to the Oligocene Deseadan and in the Dasypoda prior to the Miocene Santa Cruz. The specimen has been well described by Simpson (1948, pp. 82–83), but further study of it in light of the extended comparisons made during the preparation of this paper has revealed a little information additional to that already published.

The squamosal is the only part contributing to the auditory region that is present in the specimen. The glenoid surface is low on the skull, a point emphasized by Simpson, lower than in *Dasypus,* a form outstanding in this respect among living armadillos, but not as low as in *Peltephilus.* The articular area is almost flat, not quite transverse but extending a little anterolaterally. Behind the glenoid surface is a rather small process, compressed anteroposteriorly and terminating ventrally in a fairly sharp point, that sends a spur of bone medially in the direction of a posterolaterally extending ridge formed by the alisphenoid and the medial part of the squamosal. Simpson referred to this process when he described the glenoid fossae as being ". . . underhung by the external auditory meati posteriorly . . . ," a statement which we are inclined to question (see below). Posterior to this process there is a rectangular area gently convex transversely and decidedly concave anteroposteriorly; a large foramen is situated near the center. The rectangular area narrows ventromedially and is followed posteriorly by a second, somewhat smaller process. From the gap between the spur on the anterior process and the ridge formed by the squamosal and alisphenoid, a groove runs posteriorly in the endocranial surface of the squamosal. In the matrix that covered this area, small fragments of bone were present between spur and ridge. There can be no doubt that these were remnants of a bridge that connected spur and ridge and formed the ventral rim of a foramen leading to the groove just described.

This description has been taken from the left side of the specimen. The right side is less complete, but the foramen in the rectangular area and part of the groove medial to it in the endocranial surface of the squamosal can be seen.

These two foramina are the clues to the interpretation of the structure preserved. The medial one is posterolateral to the foramen ovale and posteromedial to the glenoid cavity, occupying essentially the same position as a similar opening described here in *Tolypeutes* (p. 12). From it, a groove in the endocranial surface of the squamosal, covered and converted into a canal by the periotic, leads posteriorly and hence in the direction of the mastoid foramen, with which the corresponding foramen in *Tolypeutes* is in communication. The

identity of the openings in the two forms would seem to be virtually certain. The foramen in the rectangular area leads to a short canal, lateral to the groove just described, that passes directly upward through the squamosal to open internally low in the cranial cavity. From this internal opening, a groove, also no doubt covered by the periotic in life, extends upward and backward to cross the low, inconspicuous tentorium. Canal and groove obviously transmitted a vein tributary to the lateral sinus system, and it is, we think, evident that this second foramen is the postglenoid. It therefore follows that the process anterior to it is a true postglenoid and that the posterior process is the posttympanic. This is a most important point; *Utaetus* is the only armadillo, and in fact the only xenarthran, thus far known in which such a process occurs. Its presence adds another significant item to the list of resemblances between *Utaetus* and the Palaeanodonta[3] drawn up by Simpson (1948, p. 88). Postglenoid and posttympanic processes are closer together than in palaeanodonts. The latter process appears to have been somewhat more independent of the mastoid than in other xenarthrans. Due to the presence of the postglenoid, it is probable that there was no open space above the porus (see below).

There is no indication whatever of an epitympanic sinus in the squamosal and indeed no certain evidence of any appreciable epitympanic recess.

It is most unfortunate that no portion of the tympanic is preserved, since the evidence of the squamosal upon the size of this element is somewhat equivocal. The size and shape of the area posterior to the postglenoid process are such as almost to suggest the existence of a well-developed bony meatus of palaeanodont or *Euphractus* type that would have underhung the glenoid to some extent; yet if such had been the case, it is wholly unlikely that the large postglenoid foramen would have occupied the position it does, where it would have been at or very near the porus. We are strongly inclined to suspect that the tympanic was simple, little or not at all advanced beyond the ring form, hence of the type that was certainly primitive for the Xenarthra and that persisted with little change to Pleistocene and Recent time in many sloths and armadillos, and, apparently, in all glyptodonts.

[3] *Epoicotherium* among palaeanodonts appears to lack this process (Simpson, 1927), and in the related *Xenocranium* it is feebly developed (Colbert, 1942).

The *Priodontes* Group

The Priodontines

Priodontes F. Cuvier, 1825. Figure 1B–C.

One young adult skull of *Priodontes gigas* E. Geoffroy, FMNH 25271, has been available to us. The tympanic is horseshoe-shaped with an irregular, slightly expanded medial border. At the junction of the rather slender anterior crus with the medial border, there is a thin, rather blunt and short styliform process that imparts a right-angled appearance to this portion of the bone. A similar but less prominent process is figured by van Kampen (1905, p. 491, fig. 43).

The bone is small in comparison with the size of the skull, being actually somewhat smaller than that of the closely related and much smaller *Cabassous*. The crista tympanica and, correspondingly, the sulcus tympanicus are well developed. A recessus meatus is present, but there is no indication of a cylindrical part. A chordafortsatz (the term applied by Bondy, 1907, to a process originating from the inside of the dorsal part of the posterior crus that runs parallel to and provides a bony support for that part of the n. chorda tympani posterior to the malleus) is present. The anterior crus approaches but is not in contact with the squamosal at the posterior extremity of the medial border of the glenoid cavity and also may contact a part of the peculiar, characteristically xenarthran process from the crista facialis of the periotic. As in most xenarthrans, the sulcus malleolaris is very well developed, and the bony anterior end of the malleus is plainly visible externally when in position. The posterior crus rests on the tympanohyal laterally and on the medial extension from this element medially. (The probability that this medial extension is the caudal entotympanic is discussed below.) It closely approaches but does not unite with the squamosal. The porus opens anteroventrolaterally and is notably deeper than wide. The squamosal does not approach the wide incisura tympanica in this and most other armadillos (in later members of the *Euphractus* group the crura meet and the superficies meatus grows down toward them), but arches high above it, leaving a conspicuous open space above the porus, in which the ossicles, when in place, may be seen in a lateral view of the skull. This is characteristic of cingulates, although conditions in *Utaetus* would suggest that it may have been primitive for the Xenarthra as a whole.

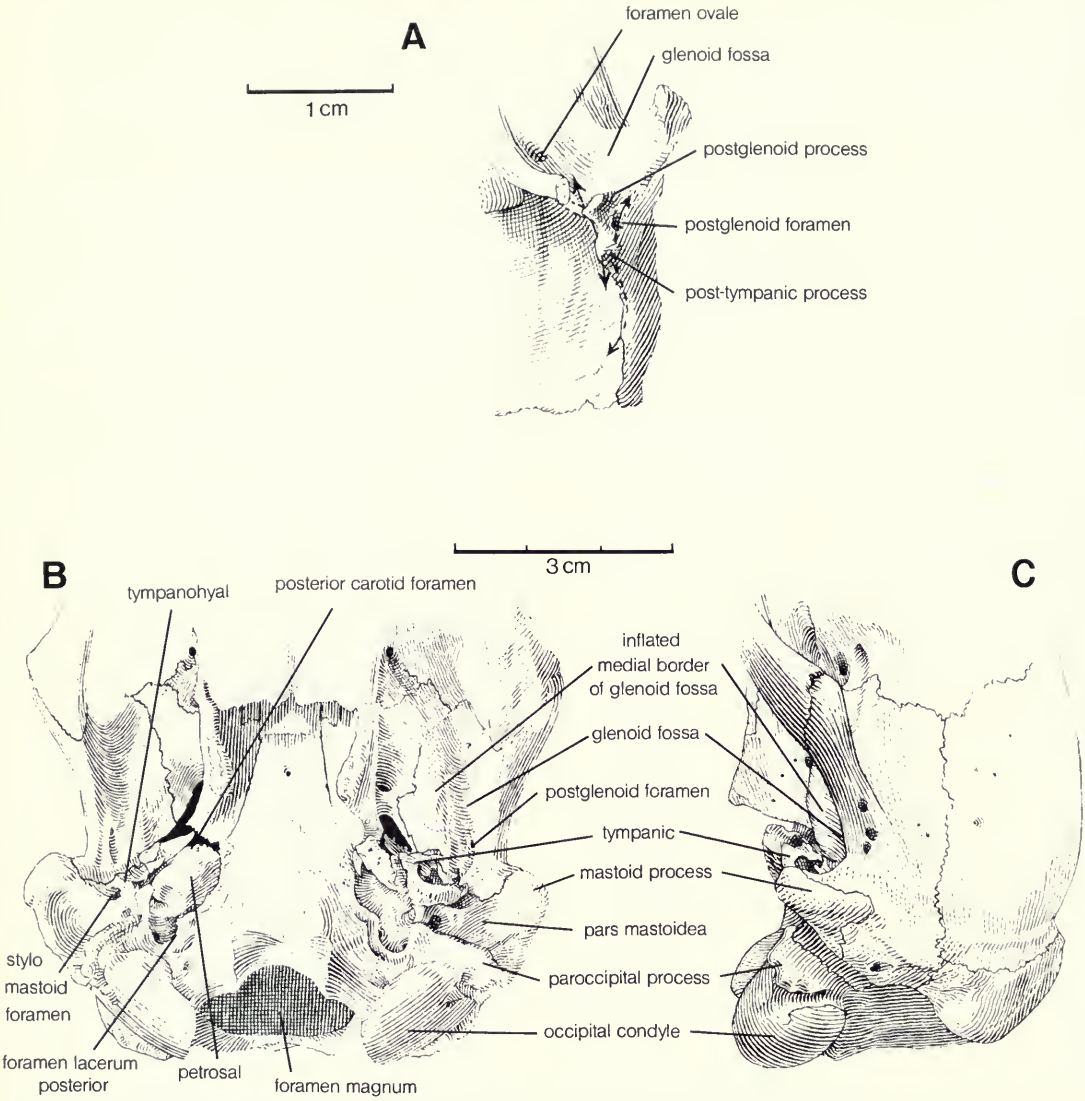

FIG. 1. *Eutatus buccatus,* AMNH 28668: **A,** cranial fragment shown in ventral view. *Priodontes gigas,* FMNH 25271: **B–C,** posterior part of skull shown in ventral and left lateral views.

The glenoid fossa is elongate anteroposteriorly and deeply concave transversely; it does not overhang the tympanic. The medial border is formed by the squamosal, which is here considerably inflated, the inflation involving part of the alisphenoid as well. [There is no developed postglenoid process.]

Van der Klaauw (1924, 1931, p. 267) has shown that two different elements (or at least centers of ossification) may enter into the composition of the entotympanic, a rostral part that is connected during early ontogeny with the cartilage of the Eustachian tube, and a caudal part that is connected with the tympanohyal. These two parts may, and very often do, grow toward each other and fuse. As a result, in most adult edentates no trace of a former separation remains. Very young specimens occasionally reveal indications of a division, and some of these are described in this paper. In some armadillos the entotympanic does not become ossified and in others ossification is not extensive. These last, exemplified by *Priodontes* and to a lesser extent by its relatives, retain traces or at least suggestions of the division into the adult stage.

Priodontes possesses what is clearly a rostral entotympanic. This is a small, irregularly shaped

bone, loosely connected to the anterointernal edge of the tympanic and thus usually lost during maceration. Van Kampen (1905, pp. 491–492) commented that he had encountered no description of it previous to his own, but stated that it had been figured by G. Cuvier (1825 [1834–1836 edition originally cited, but not seen by W.D.T.]) in the Ossemens Fossiles. The figure in question, however, is so poor as regards the auditory region that we are quite unable to determine what is or is not represented in it. Our example of this element does not appear to be as well ossified as the one figured by van Kampen; it is not as broad transversely and, as it does not extend as far posteriorly, there is a pronounced gap between it and the medial extension from the tympanohyal. The surface of the bone is pierced by numerous minute vascular foramina, by a deep, irregular groove for the carotid present in the medial face. There is a semicircular excavation on the lateral for the Eustachian tube which is not completely surrounded by bone. Anteromedially, the rostral entotympanic sends up a spur that comes in close contact with the basisphenoid. The bone does not extend forward to enclose a foramen lacerum medium.

The question of whether or not a caudal entotympanic is present in *Priodontes* is of some interest. Van Kampen (1905, p. 495) and van der Klaauw (1931, pp. 108, 243) describe tympanohyal in this form, and in *Cabassous* and *Tolypeutes* to a lesser degree, as broadening to a leaflike expansion at the tip. The expansion is anteroexternal, anteromedial and posteromedial in direction, extending posteriorly to a sutural connection with a ridge running anterointernally from the tip of the paroccipital process and anteromedially toward the rostral entotympanic. Anterolaterally the expansion extends beneath the main portion of the tympanohyal, with which its lateral extremity is fused. It is on this expansion, and not primarily upon the tympanohyal proper, that the posterior crus of the tympanic rests. It is possible that this apparent expansion of the tympanohyal is actually the caudal entotympanic. Position relation to the exoccipital and anteromedial expansion toward rostral entotympanic are all features of the caudal entotympanic rather than of the tympanohyal. No suture between tympanohyal and expansion is visible, to be sure, but if present this would have closed during intrauterine life. In the related *Tolypeutes,* Bondy (1907, pp. 349–350) regarded a comparable structure as a process from the periotic, a determination with which we are not in agreement (see below).

The tympanohyal proper is inclined posteromedially and is fused with the periotic, continuing without interruption into the crista facialis in this form, and, apparently, in all Xenarthra. It is also fused with the pars mastoidea posterior to the stylomastoid foramen. This is an age character in certain other armadillos, and possibly here also. Posterointernal to this foramen, as noted by van Kampen, the tympanohyal, together with the mastoid, exoccipital, and supposed posterior entotympanic, enclose a second opening comparable in size to the stylomastoid [foramen]. The articular surface for the stylohyal is depressed relative to the surrounding structure.

The ventral surface of the periotic [petrosal] is unusually irregular. The promontorium is elongate, oval in outline and slopes laterally more gradually than in other armadillos; it is surrounded anteriorly and medially by a flat, horizontal shelf of bone, which is not in contact with either the basioccipital or basisphenoid. A periotic [petrosal] shelf in this position is unique among Xenarthra. Posteromedial to the fenestra rotunda there is a low blunt ridge that forms the anterior border of the foramen lacerum posterior. This ridge approaches a bluntly angular process from the basioccipital, which underhangs the medial shelf of the periotic [petrosal]. The recessus epitympanicus is shallow and separated only by a slightly raised border from the glenoid cavity. There is no epitympanic sinus in the *Priodontes* group. The crista facialis is deep [i.e., is more dorsally positioned than the rest of the ventral surface of the petrosal] and has a slight inward curvature. Anterior to the apertura tympanica canalis facialis, the crista gives origin to an anteromedioventrally-directed process of irregular, although essentially tripartite, shape and delicate structure. The anterior portion of this crest is lanceolate, acutely pointed and slightly concave ventrally; posterior to this are two smaller, more ventrally directed projections with slightly expanded extremities.

This process, which reaches its greatest known development in *Priodontes,* is characteristic of the Xenarthra as a whole. Its significance as a morphological character of the group does not seem to have been fully realized heretofore, and its nature has been misinterpreted. A structure of such delicacy is particularly liable to damage during maceration of the skulls of Recent forms and to loss prior to burial or during preparation of the skulls of extinct ones. In forms with well-developed bullae, it may be reduced in complexity and is not visible externally. These reasons no doubt

account for the failure to appreciate the significance of the structure. Van Kampen (1905, pp. 476, 484; figs. 39–40, O) observed this process in sloths and described its position as medial to the processus anterior to the malleus, but failed to note its connection with the crista facialis, even describing it as loose in *Choloepeus*. He regarded it as probably homologous with the ossiculum accessorium malleoli. Van der Klaauw (1924, p. 118; 1931, p. 236) believed the process to be a part of the periotic, calling it a processus perioticus superior, although he used the abbreviation "oss. acc. mi." in several of his figures of ground sloths (1931, figs. 1, 4, 6). Curiously enough, neither of these authors refers to conditions in the armadillos, in several of which the process is well developed and its relation clear.

As will be evident from the description given above, we agree with van der Klaauw that the process is not an ossiculum accessorium malleoli. We have examined large series of xenarthrans, including many young specimens, and in none have we found any indication that it is a separate element; all the evidence—position, union with the crista facialis, and relation to other elements of the auditory region—overwhelmingly indicates that the process is a part of the periotic. Van der Klaauw's term processus perioticus superior is not strictly accurate topographically; the process is actually lateral rather than superior as regards its point of origin. We suggest the name *processus cristae facialis* in allusion to the demonstrated connection between process and crista.

The pars mastoidea of the periotic is widely exposed on the surface of the skull. It forms the posterior and inferior portions of the massive and very prominent mastoid process, and participates to a slight extent in the root of the paroccipital process. The latter is better developed than in any other living armadillo. A deep, broad excavation runs anteromedially between the two processes. The basicranial portion of the exoccipital is more extensive in priodontines than in other armadillos. In *Priodontes* a prominent ridge runs anteromedially from the tip of the paroccipital process to the supposed caudal part of the entotympanic; between this ridge and the condyle there is a triangular, concave area.

The internal carotid artery runs in the groove on the medial face of the entotympanic described above, and enters the cranial cavity through the anterior part of the wide gap between periotic [petrosal] and basisphenoid. A poorly defined groove in the medial part of the basioccipital indicates the presence of a second artery entering the skull at the same point as the internal carotid, as in other armadillos. The postglenoid foramen is situated in a slitlike recess at the posterior extremity of the glenoid cavity. The fairly large subsquamosal openings are variable in number and situated in the posterior root of the zygoma. Posterior to the foramen ovale is a wide gap between squamosal, tympanic, and periotic [petrosal] that probably gives passage to a vein (see below, *Tolypeutes*). The mastoid foramen is large and opens posteriorly on the occiput. There is no closed channel in the mastoid ventral to it. The foramen lacerum [posterior] is bordered by the exoccipital, in which it forms a deep, semilunar notch posteriorly, and by the periotic [petrosal] anteriorly. The foramen stylomastoideum primitivum is large and bordered by the tympanohyal medially; a slight groove in the mastoid process, bordered posteriorly by a sharp ridge, runs ventrally from it.

Cabassous McMurtrie, 1831. Figure 2A–C.

One skull of *Cabassous lugubris*, FMNH 22437 (fig. 2B–C), and three of *Cabassous loricatus* have been examined, including FMNH 26471 (fig. 2A), 47959, and 47960.

The tympanic is horseshoe-shaped and is slightly larger and considerably better developed than in *Priodontes*, being notably expanded in the medial direction, displaying approximately the same width throughout and forming a very slight rudiment of a cylindrical meatus laterally. In *C. loricatus*, a medially projecting styliform process is present, which borders the Eustachian tube anteriorly; in *C. lugubris* this is barely indicated. The crista tympanica, the sulcus, and the chordafortsatz do not differ from those of *Priodontes*. The spina tympanica posterior is very well defined, and the posterior crus is somewhat thickened and has an extensive attachment surface for cartilaginous or fibrous connection with the tympanohyal, the spina extending up to contact the squamosal. Anteriorly, the tympanic, as in *Priodontes*, has only a loose connection of this sort with a ridge on the squamosal, and the crus is free dorsally on the bony skull. In contrast to *Priodontes* and *Tolypeutes*, the crus does not closely approach the processus cristae facialis of the periotic. Medially, and postero- and anteromedially, the tympanic and entotympanic are in close contact in fully adult skulls. The porus, incisura tympanica, and the space above it are essentially as in *Priodontes*; the same is also true of the glenoid fossa in *C. lugubris*, but

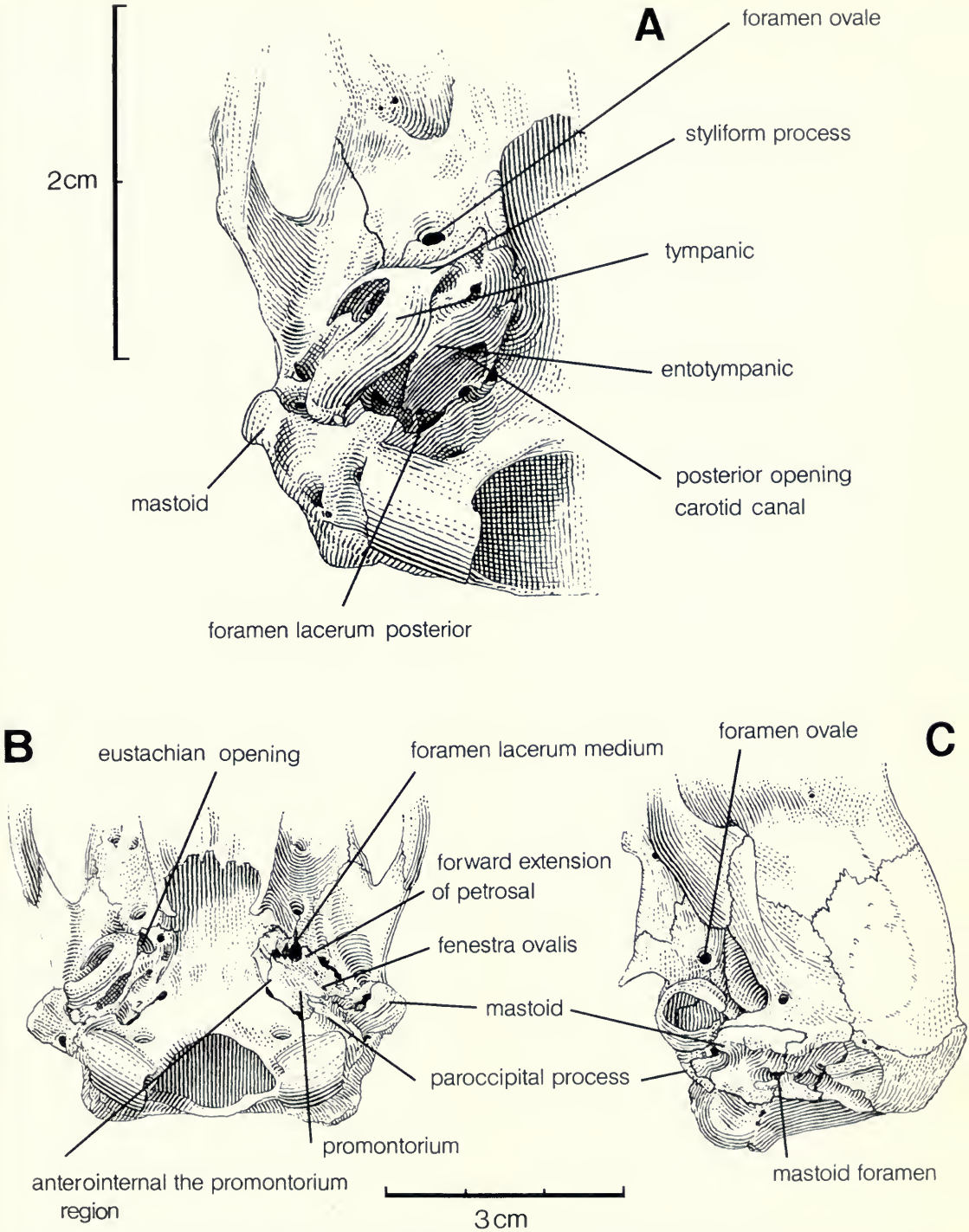

FIG. 2. *Cabassous loricatus*, FMNH 26471: **A**, right side of basicranium of skull shown in ventral view. *Cabassous lugubris*, FMNH 22436: **B–C**, posterior part of skull shown in ventral and left lateral views.

in *C. loricatus* this area is somewhat wider and flatter.

The entotympanic is much better developed than in *Priodontes* and forms, together with the tympanic, a well-developed bulla. In adult skulls, it is an irregularly shaped but essentially curved bone, pierced by several minute vascular foramina in addition to the large carotid foramen. It is united with the tympanohyal posteroexternally and has sutural connections, which may fuse in old age, with the paroccipital [paroccipital process of exoccipital], basioccipital, and basisphenoid, pterygoid, and alisphenoid. The anterior extremity curves dorsolaterally to the squamosal. The large Eustachian opening is surrounded by the entotympanic, except laterally where it is bordered by the tympanic.

The specimens at our disposal throw some light on the ossification of the entotympanic and on the relations between its rostral and caudal portions. The rostral portion, which forms rather more than half of the bone, completes its ossification first. In *C. loricatus,* ossification is completed with the growth of a spur or plate of bone that extends back to the exoccipital and thus forms the lateral border of the foramen lacerum posterior. A conspicuous gap is left between this spur and the tympanic. Concurrently with the growth of the spur, the caudal entotympanic ossifies medially from the tympanohyal, passes between the tympanic and pars mastoidea, and finally grows anteriorly to fill the gap between the tympanic and the spur or plate from the rostral portion. In one skull of *C. loricatus* (FMNH 47958) spicules and thin sheets of bone can be seen in place in the dried cartilage occupying this gap. There can, we think, be little doubt that we are dealing here with a caudal entotympanic; these conditions increase the probability that a comparable, although much less completely ossified, element is also present in *Priodontes.* In the only specimen of *C. lugubris* at our disposal, a young adult, the rostral entotympanic does not send a spur to the exoccipital.

The tympanohyal is less complex than that of *Priodontes*; in *C. loricatus* a rudiment of a vagina processus hyoidei is developed.

The ventral surface of the periotic [petrosal] is less complex than in *Priodontes.* The sulcus and crista facialis and the process from the latter are, in comparison, only moderately developed. A small, irregularly shaped, flat plate of bone, varying in degree of development, extends forward from the promontorium to partially enclose the foramen lacerum medium laterally. Anterointernal to the promontorium, the periotic [petrosal] is rounded ventrally and passes over the lateral edges of the basioccipital and basisphenoid, to which it is closely appressed. The recessus epitympanicus in *C. lugubris* is more sharply defined than in *C. loricatus* and *Priodontes.* It is not deeper than in these forms but is excavated posteriorly in such a way as to appear as a small fossa, in which the crus breve of the incus lies. The mastoid process is relatively smaller in *Cabassous* than in *Priodontes*—and much smaller in *C. loricatus* than in the larger *C. lugubris*—and the surface exposure of the pars mastoidea is in consequence less extensive. The space between mastoid and paroccipital process, the latter very small in *C. lugubris* and almost nonexistent in *C. loricatus,* is very shallow in comparison with the deep cleft present in *Priodontes.* The basicranial portion of the exoccipital is not as large, relatively, as in *Priodontes.* There is, however, a concave area immediately in advance of the condyle, and beyond this the anterior extremity of the bone curves down to meet the caudal portion of the entotympanic.

The posterior opening of the carotid canal is situated at the center of the entotympanic. The foramen lacerum medium is situated between the basisphenoid, pterygoid, and periotic [petrosal], and is completely concealed by the entotympanic. [I find this fits the condition in *C. loricatus*: f.l.m. is less concealed in *C. lugubris.*] Other minor openings, presumably vascular, lead to this foramen; in both *C. lugubris* and *C. loricatus* there is a small opening situated between basisphenoid and entotympanic near the anterior extremity of the latter, and in *C. lugubris* there is another in the ventral surface of the entotympanic anterointernal to the Eustachian tube.

Between entotympanic and basioccipital, anterointernal to the foramen lacerum posterior, there is a foramen, again presumably vascular, that is sometimes double and leads to a short canal between basioccipital and periotic [petrosal]; this opens into the cranial cavity posterointernal to the foramen lacerum medium. There is no postglenoid foramen. Possibly in correlation with this loss the subsquamosal foramina are large, as indeed they are in *Priodontes,* in which the postglenoid foramen is much reduced. Posteroexternal to the foramen ovale is a groove in the squamosal leading to a gap between the squamosal and periotic that probably transmits a vein. The mastoid foramen is in the usual position; the vein runs ventrally in a groove in the occipital surface that is partially covered by a bridge of bone supplied by the squa-

mosal and pars mastoidea of the periotic. The foramen lacerum posterior is large. The foramen stylomastoideum primitivum resembles that of *Priodontes*.

The Tolypeutines

Tolypeutes Illiger, 1811

Seven skulls of *Tolypeutes tricinctus* have been available to us. [Presumably these were FMNH 21407, 28339–28342, 28345, and 54353. Apparently Patterson and Segall thought that they resembled the priodontines closely enough that it was not necessary to have drawings made.]

The tympanic is similar to those of *Priodontes* and *Cabassous*, but shows a surprising amount of variation in medial expansion. In degree this varies from slight (no greater than in *Priodontes*) to considerable (very nearly as in *Cabassous loricatus*); in one specimen the anterior portion is much more expanded than the posterior. The skulls at hand are all adult, which suggests that the observed variability is not dependent upon age. The styliform process varies from practically absent to well developed, and is variable as to form. Crista tympanica, sulcus, spina posterior, and caudal chordafortsatz[4] are as in the preceding forms. The posterior crus rests mainly on the tympanohyal, not on the periotic as maintained by Bondy, but also extends dorsally to form a sutural union with the squamosal. The same author stated that the anterior crus is widely separated from the skull. This is only partly true. The large sulcus malleolaris together with the very well-developed anterior process of the malleus divides the anterior face of the dorsal portion of the crus into two parts. The lateral portion is freely projecting and well separated from adjoining portions of the skull, but the medial is in close contact with the ridge formed by the squamosal and the underlying processus cristae facialis, to which it is bound by fibrous tissue.

The glenoid area is similar to that of *Cabassous*, but is less concave medially and the ridge on the squamosal that forms the medial border of the area is much less pronounced.

The rostral entotympanic is similar in all respects to that of *C. loricatus*, including the development, in some specimens, of a spur of bone extending back to the rudimentary paroccipital process. Due to the variability in the degree of medial expansion shown by the tympanic, the degree of union between the two bones and the definition of the bony Eustachian tube varies. The caudal entotympanic is very poorly ossified; only a rudimentary projection from the tympanohyal is present in some of the specimens. *Tolypeutes* is thus to a considerable degree intermediate between *Cabassous* and *Priodontes* in the degree of ossification of the entotympanic as a whole.

The tympanohyal exhibits no differences from that of *Cabassous lugubris*.

The ventral surface of the periotic [petrosal] is structurally very similar to that of *Cabassous* but exhibits certain differences in its relations to surrounding elements. Anterointernally it abuts against and does not overlie the basisphenoid. The processus cristae facialis is extraordinary in that it underlies and is closely connected to the ridge on the squamosal that forms the medial boundary of the glenoid area, and thus forms a large part of the attachment surface for the anterior crus of the tympanic. The epitympanic recess is precisely as in *Cabassous loricatus*. Bondy (1907) stated that the recess was bounded laterally by the periotic. This is not entirely correct; the squamosal forms the greater part of the lateral wall, the pars mastoidea contributing posteriorly to a small degree. [Here Patterson and Segall were probably thinking "petrosal" and Bondy really meant "periotic," i.e., including petrosal and mastoid.]

The pars mastoidea of the periotic is similar to that of *Cabassous*; due to the narrow occiput the squamosal is excluded from the occipital surface. For the greatest part of its length the mastoid process is in contact with the posterior crus of the tympanic, a point of resemblance to the euphractines. The basicranial portion of the exoccipital is less extensive than in priodontines, but nevertheless a rudiment is present of the crest that in *Priodontes* runs from the paroccipital process to the presumed caudal entotympanic.

The foramina present few differences from those of *Cabassous*. The canal for the internal carotid is

[4] Bondy (1907, pp. 349–350) stated that the posterior crus of the tympanic in *Tolypeutes* rests on a process from the periotic (this is actually the tympanohyal), to which he applied the name "chordafortsatz." In the introductory part of his paper, however, he defined this term as applying to a process originating from the inside of the dorsal part of the posterior crus of the tympanum and running parallel to and providing a bony support for that part of the n. chorda tympani posterior to the malleus. His use of this term later in the same paper for a process supposedly from the periotic is difficult to understand, particularly since a caudal chordafortsatz as defined by him is present.

better developed, due to the greater degree of ossification of the rostral entotympanic, and the groove in the basisphenoid for the second artery is converted into a canal as a result of the contact of this bone and the periotic [petrosal]. A small foramen pierces the entotympanic in a dorsoventral direction, opening into the cranial cavity behind the common opening for the two arteries. A postglenoid foramen is invariably present anteroexternal to the recessus epitympanicus. Posteroexternal to the foramen ovale and immediately anterior to the tympanic there is a groove in the squamosal, as in *Cabassous*; in *Tolypeutes* this is converted into a canal by the presence of the underlying processus cristae facialis. The canal leads to the venous system of this region of the skull. The identity of this canal with the comparable one in the Casamayoran *Utaetus* is virtually certain. *Priodontes, Cabassous,* and *Tolypeutes* exhibit an interesting structural transition from the open gap seen in the first to the closed canal present in the last. Due to the close connection between mastoid process and tympanic, the stylomastoid foramen opens ventrally on the anterior side of the process, anteroexternal to the posterior crus, a point of interest in view of the conditions obtaining in the euphractines.

The *Dasypus* Group

The Dasypodines

Dasypus Linnaeus, 1758

Sixty-eight skulls of *Dasypus novemcinctus,* including FMNH 14008 (fig. 3A–B), nine of *Dasypus septemcinctus,* and two of *Dasypus kappleri* have been examined.[5] As noted in the [missing original] introduction, in much of the literature this genus is referred to as *Tatu* or *Tatusia* and the name *Dasypus* is applied to *Euphractus* and *Zaedius.*

The tympanic is of primitive ring type, the medial side enlarging to some extent toward the Eustachian tube. The styliform process is either not developed or is very poorly defined. There is some variation in the degree of expansion, but this is by no means so extreme as in *Tolypeutes.* The medial border is irregular in the majority of specimens, the indentations and projections being very marked in some. The posterior crus is attached along much of the length of the tympanohyal and also has a slight sutural connection with the squamosal, but does not come into contact with the mastoid process. As in *Tolypeutes,* the anterior crus is in contact with both the squamosal and the processus cristae facialis. Other details of structure are similar to those observed in the forms described above.

The glenoid region differs from that of all other armadillos. The articular surface is flat and relatively low on the side of the skull, being situated on a level below that of the dorsal extremity of the anterior crus of the tympanic. It is thus farther below the incisura tympanica than in other living forms (only *Utaetus* and the peltephilids among the extinct exceed it in this respect), and the postglenoid surface slopes abruptly upward to form a rather acute angle with the base of the mastoid process. The [dorsal crest of the] zygomatic process of the squamosal is more prominent than in other living forms; it sweeps upward and backward almost to the squamoso-parieto-supraoccipital junction.

The entotympanic is very poorly ossified in *Dasypus,* and in the great majority of specimens there is no trace of it whatever in the dried skull. Three specimens of *D. novemcinctus* at our disposal show conclusively, however, that ossification may take place. In one of these (14008) there are traces of a rostral element attached to the tympanic by dried cartilage posterior to the vicinity of the Eustachian tube. In another (18761) there is a suggestion of a caudal ossification near the tympanohyal. The third (43286) has a comparatively well developed rostral entotympanic that forms a posterior border for the Eustachian tube, and gradually tapers in a posterior direction; between the posterior portion and the tympanic there is a gap, precisely as in *Cabassous* and *Tolypeutes.* The bone has only a cartilaginous connection with the tympanic and does not extend very far medially; thus only a small portion of the floor of the hypotympanic sinus is formed by bone.

The tympanohyal is fused proximally with the periotic and is in close contact with the pars mastoidea distal to the foramen stylomastoideum primitivum; fusion may take place here with advancing age. The articular surface for the stylohyal projects ventrally to varying degrees and is medial

[5] The suite of materials available to Patterson and Segall during the years that this section was under study includes the following FMNH specimens:

D. novemcinctus—8858, 11089, 14008, 15857, 15967–69, 18748–61, 20537, 21131, 21405–6, 28347–49, 30476–87, 30885, 34191, 34351–53, 39304–7, 41585, 41890, 43285–87, 45354–55, 48357, 51392, 51801–2, 51962–64, 52246, 54204, 54245, 55664, 63920.

D. septemcinctus—29331–38, 52354.

D. kappleri—30348, 30350.

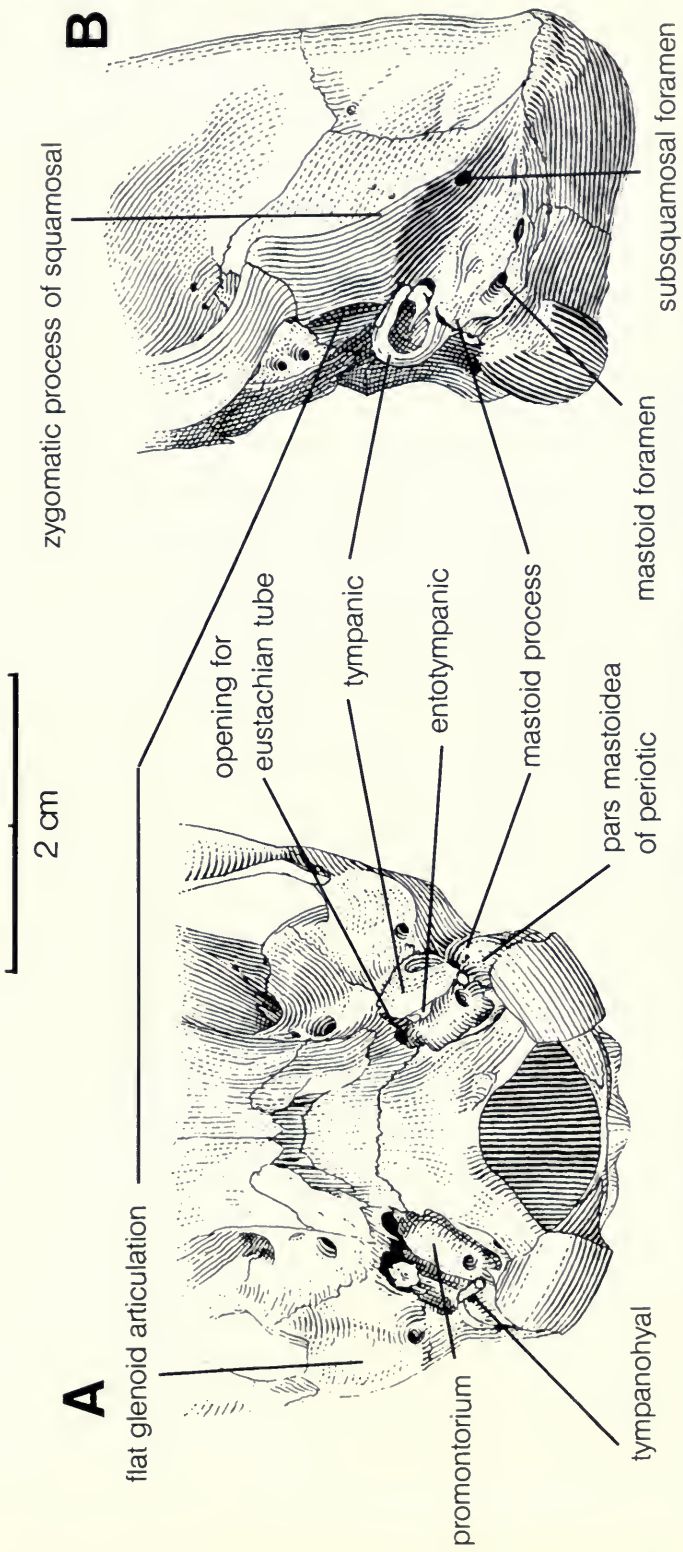

FIG. 3. *Dasypus novemcinctus*, FMNH 14008: **A–B**, posterior portion of skull shown in basicranial and left lateral views.

to the ascending portion of the posterior crus of the tympanic.

The promontorium of the periotic [petrosal] is globular in form, very much more rounded than in any of the forms described above. Medial to it there is a moderate shelf. The processus cristae facialis is well developed, decidedly expanded distally, where it is concave and in some specimens actually cup-shaped. The epitympanic recess is small and variable in depth and extends posteriorly, although not to so marked a degree as in *Cabassous* and *Tolypeutes.* There is no epitympanic sinus.

The surface exposure of the pars mastoidea is small in comparison with those of the forms hitherto described, widening only slightly as it passes to the ventral surface of the skull. It contributes equally with the squamosal to the formation of the short, blunt mastoid process. The basicranial region is narrow in comparison with those of other armadillos and the mastoid processes extend but little laterally beyond the level of the condyles. There is no trace of a paroccipital process. The condyles reach well below the level of the tympanic, a condition not shown by any other living armadillo except *Priodontes.*

The course of the internal carotid cannot be determined in the dried skull; no trace of a groove for its reception is present in the most complete rostral entotympanic preserved. There is, however, no reason to doubt that it lay medial to this element and entered the cranial cavity through the gap anteromedial to the periotic [petrosal]. The groove for the second artery may be seen in the basisphenoid. The postglenoid foramen is immediately behind the glenoid surface and at nearly the same level. Two subsquamosal foramina may be present, one in the zygomatic root above and lateral to the postglenoid, the other caudocranial from it and near the point of origin of the upswept ridge of the zygomatic portion of the squamosal. The former is frequently absent, the latter more constant. The mastoid foramen, or foramina, and enclosed groove ventral to it are in the usual position. The foramen stylomastoideum primitivum is anteromedial to the mastoid process.

The Stegotheriines

†Stegotherium Ameghino, 1887

Two skulls of *Stegotherium tesselatum* Ameghino, PU 15565 (fig. 4A–B) and 15566, both studied previously by Scott (1903, p. 16) and by van der Klaauw (1931, pp. 312–313), have been examined. Scott called attention to the many features in which *Stegotherium* resembled *Dasypus* and expressed the opinion that the two were closely related. Detailed study of the auditory region thoroughly supports this view.

The tympanic, present on the right side [of the illustration, the left side of the specimen] of 15566, is similar to that of *Dasypus* in structure, degree of expansion, and points of attachment of the crura. The incisura tympanica is likewise steeply arched. As van der Klaauw (1931) has pointed out, the malleus is in position, a feature not clearly shown in Scott's figure (1903, pl. 3, fig. 6), which is inaccurate in certain other respects as well.

The glenoid cavity agrees with that of *Dasypus* in being equally low on the skull—an important point, but here the resemblance ends. The articular surface is long and semicylindrical, much as in *Priodontes.* Scott (1903–1904) has given a detailed description of the very peculiar jugal; the descending process of this bone projects straight ventrally well beyond the lateral surface of the glenoid articulation. Some specimens of *D. novemcinctus* show a slight reduction of the ventral surface of the zygomatic process of the maxillary and thus exhibit an approach to the extreme degree of reduction that has occurred in this region in *Stegotherium. Dasypus kappleri* has a much larger jugal than either *D. novemcinctus* or *D. s. septemcinctus,* and the upper border of the zygoma is straighter than in these species; in both characters this large species resembles *Stegotherium* to a greater extent than do the smaller ones.

There is no trace of an entotympanic in either specimen despite the fact that a tympanic is present in one of them. This is an important resemblance to conditions in the dried skull of *Dasypus* and strongly suggests that the entotympanic was largely cartilaginous here also. Van der Klaauw (1931, p. 275) stated that Scott's (1903–1904) account of a part of the petrosal might have referred to an entotympanic. From the specimens and Scott's account itself, however, it seems clear that the part under description was the promontorium.

The tympanohyal, pars petrosa, and pars mastoidea of the periotic, recessus epitympanicus, and mastoid process are all essentially as in *Dasypus*; only the promontorium differs, being less globular. A paroccipital process is equally lacking. The processus cristae facialis is broken away in the specimens.

The very close similarity with *Dasypus* is also

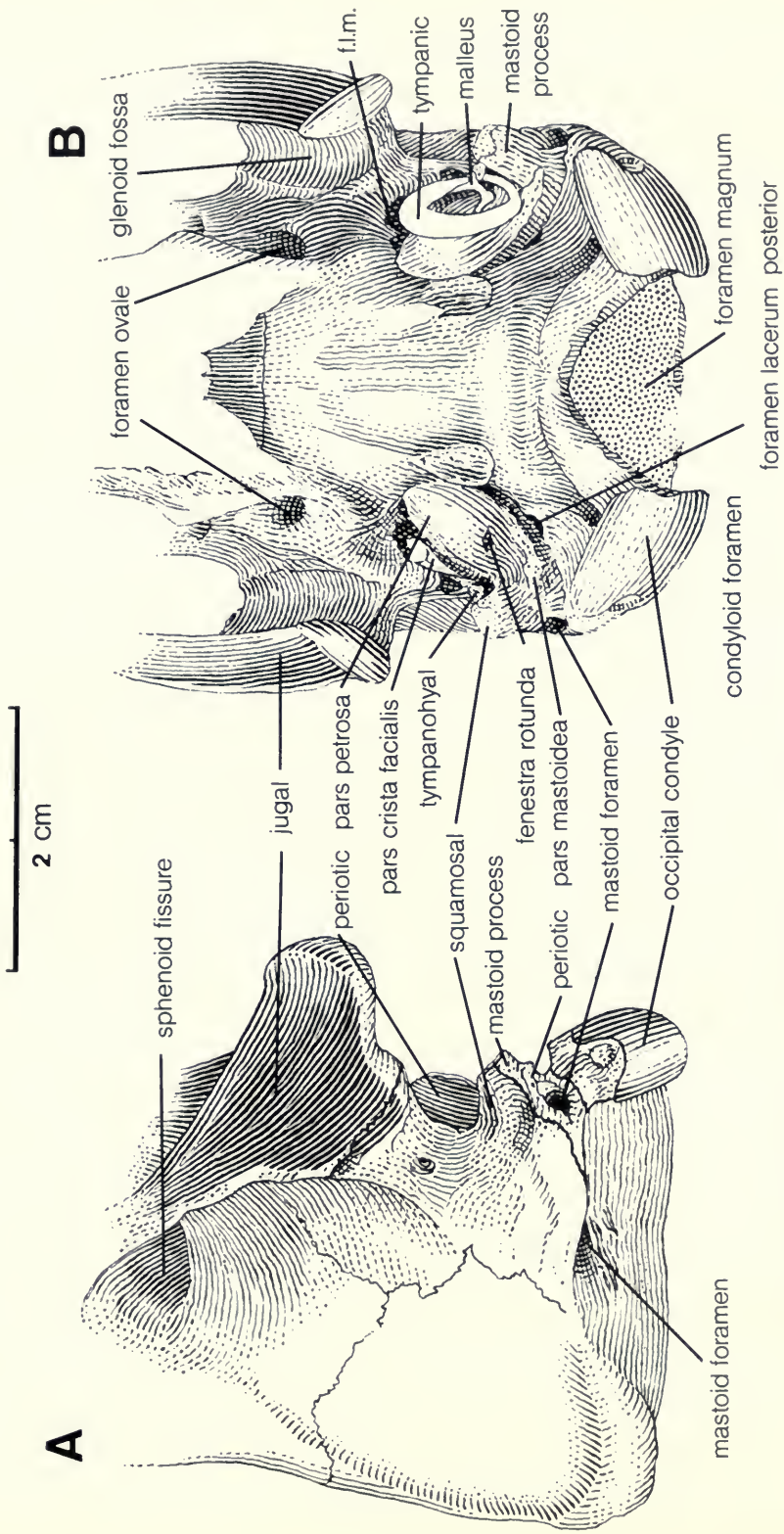

FIG. 4. *Stegotherium tesselatum*, PU 15565: **A–B**, posterior portion of skull shown in right lateral and ventral views.

apparent in the foramina, with the exception of the venous system which, save for the mastoid foramen, is reduced in comparison with that of other armadillos.

The *Euphractus* Group

The Euphractines

Euphractus Wagler, 1830, and **Zaedius** Ameghino, 1889

Thirteen skulls of *Euphractus sexcinctus* Linnaeus, seven of *Euphractus villosus* Desmarest [now usually placed in *Chaetophractus*], and ten of *Zaedius pichiy* Desmarest have been available for study.[6] [Two of *E. sexcinctus,* FMNH 28350 (fig. 5A–C) and 34348 (fig. 6A–B), one of *Chaetophractus* (*Euphractus*) *villosus,* FMNH 63865 (fig. 7A–C), and one of *Z. pichiy,* FMNH 23809 (fig. 8A–B) are illustrated.] *Euphractus, Chaetophractus,* and *Zaedius* are so similar in all characters of the auditory region that they may most conveniently be described together. As already noted, the name *Dasypus* is applied to these genera in much of the literature. Some authors place *E. villosus* in a distinct genus, *Chaetophractus* Fitzinger (1871).

Members of the *Euphractus* group, and particularly the euphractines, possess well-developed, inflated bullae, better developed than in any other armadillos with the exception of members of the *Peltephilus* group. In these (q.v.) the bulla is equally as complete but the structural details are quite different.

Van Kampen (1905, p. 492) suspected but was unable to prove that the bulla was compound in the euphractines. Van der Klaauw (1924) found a cartilaginous entotympanic in an embryo of *E. sexcinctus* and accordingly believed that two elements were involved. This is completely confirmed by a very young individual of *C.* (*E.*) *villosus* (FMNH 63865, fig. 7A) in which ossification of the entotympanic is well advanced but fusion with the tympanic has not yet taken place. Slightly more than half of the bulla is formed by the tympanic, whose medial border extends in a rather irregular line from the opening for the Eustachian tube to a point just lateral to the external margin of the condyle. Tympanic and entotympanic fuse early in life, leaving no or at most very little indication of a previous separation.

Externally, the inflated portion of the tympanic is on the whole smoothly convex, the smoothness being interrupted by a wide, shallow groove running anterointernally from the vicinity of the mastoid process and by a prominence anterior to it that extends medially from the ventral border of the meatus. Both groove and prominence are much more pronounced in *Euphractus* [and *Chaetophractus*] than in *Zaedius.* Internally, crista tympanica and sulcus tympanicus are well developed, the abrupt medial border of the crista forming a sharply defined boundary to the sinus hypotympanicus. The tympanic extends but little beyond the crista in its posterior and central portions, but, anterointernally [where it may in part be rostral entotympanic], the space between the crista and the opening for the Eustachian tube is extensive, more so in *Zaedius* than in *Euphractus* [and *Chaetophractus*]. The bone forms a complete ring below and medial to the inwardly sloping superficies meatus. This is obscured in adult specimens, but is particularly well shown in the young *C.* (*E.*) *villosus* mentioned above. Here the two crura may be seen to meet [and fuse] beneath the superficies meatus, forming a rather deep, very thin plate of bone, which continues anteriorly and posteriorly into the crista tympanica. An oblique suture is still present between the crura. This reveals that the anterior crus runs for the entire length of the superficies of the squamosal, thus forming the greater part of the bony plate, while the posterior crus does not extend anteriorly beyond the pars mastoidea of the periotic. A clearly defined recessus meatus is present.

The attachments of the crura in euphractines are quite different from those in the forms hitherto described. The anterior crus is not loosely attached by soft parts but on the contrary has a complete and extensive sutural connection to the adjacent part of the squamosal. The posterior crus retains the usual relationship with the tympanohyal, but this is here unimportant in comparison with the much more extensive sutural connections with the mastoid portion of the mastoid process laterally and with the squamosal medially, which go far beyond anything seen in the *Priodontes* or *Dasypus* groups. The proximal portions of both crura have enlarged to meet each other in the manner just

[6] The suite of materials available to Patterson and Segall during the time that this section was under study includes the following FMNH specimens:

E. sexcinctus—21403–4, 26427, 28350–54, 34346–49, 54325.

C. (*E.*) *villosus*—24331–35, 54352, 63865.

Z. pichiy—1 uncat., 21711, 23809–11, 25617, 28505–7, 49942.

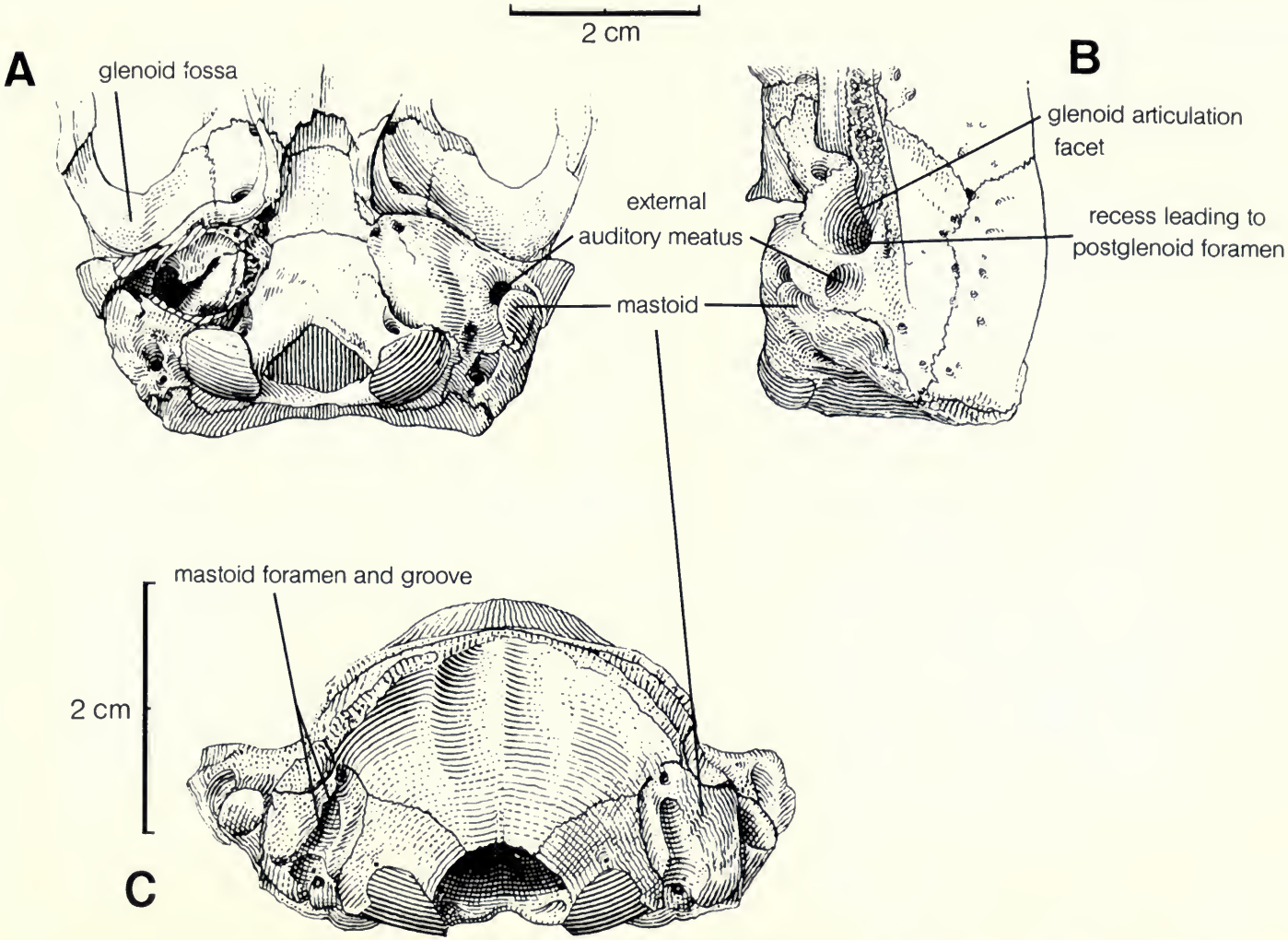

FIG. 5. *Euphractus sexcinctus*, FMNH 28350: **A–C**, posterior portion of skull shown in ventral, left lateral, and posterior views.

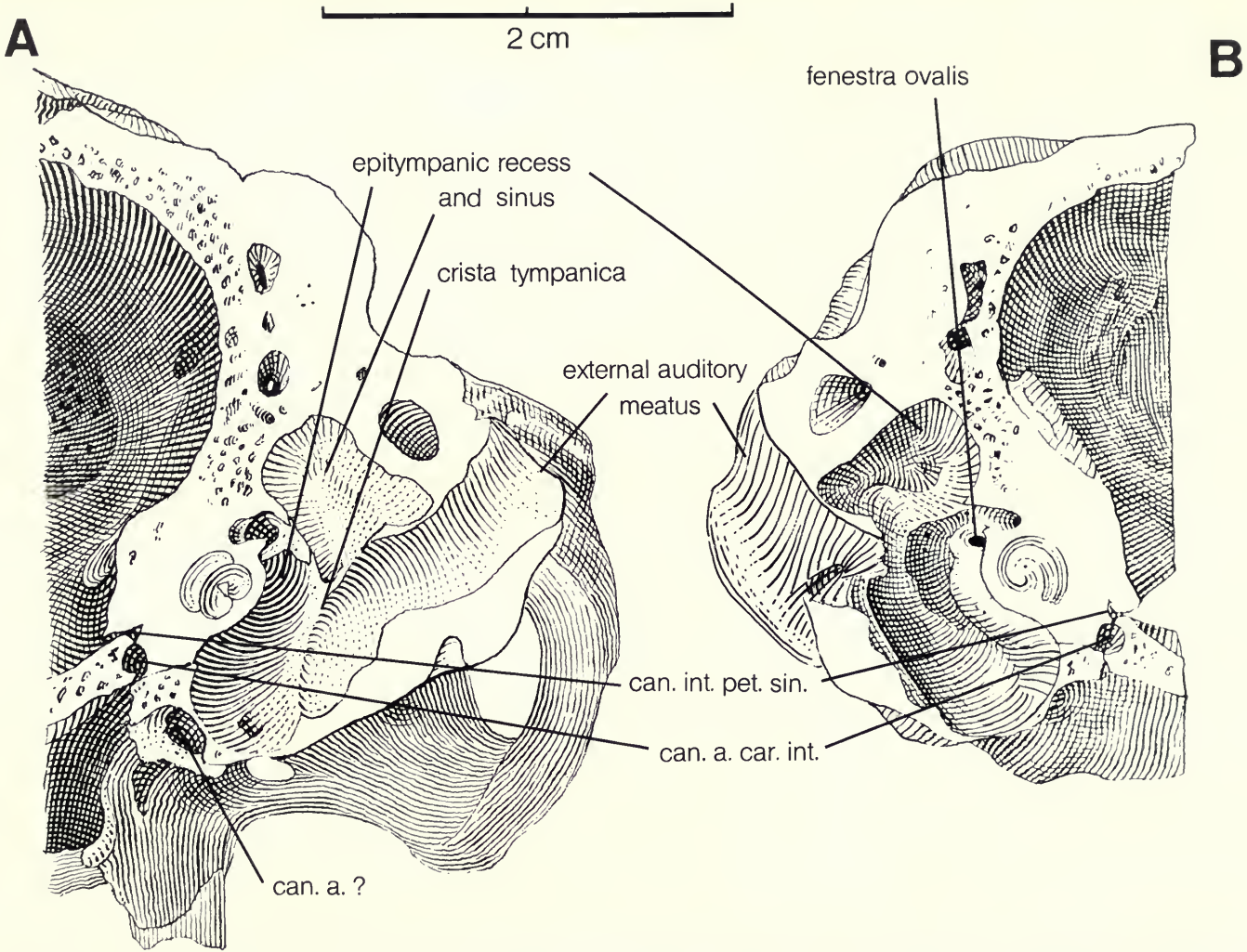

FIG. 6. *Euphractus sexcinctus*, FMNH 34348: **A–B,** sectioned skull, with cut running through meatus, bulla, petrosal, and braincase, shown in views toward anterior and posterior sides of cut.

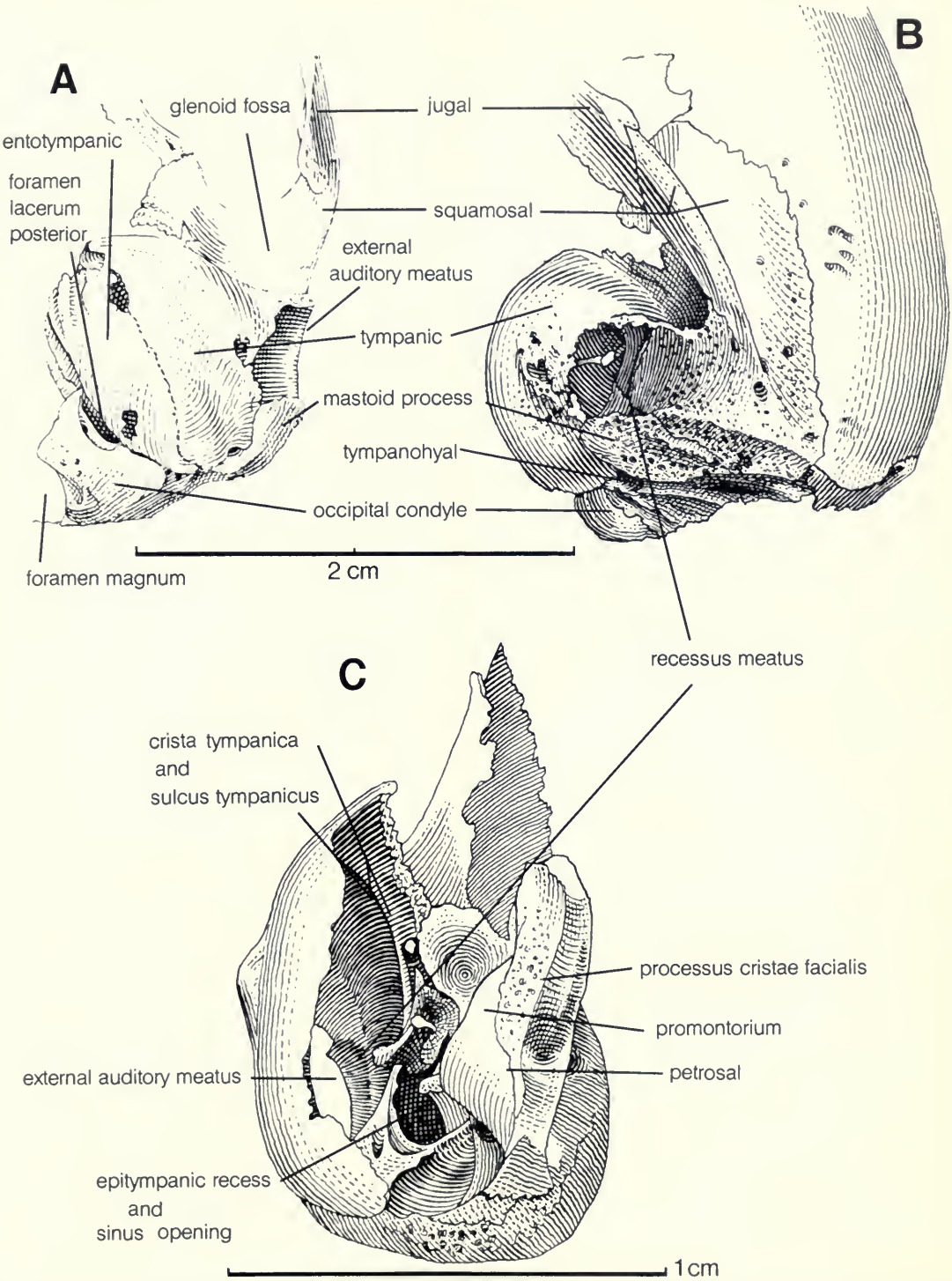

FIG. 7. *Chaetophractus* (= *Euphractus*) *villosus*, FMNH 63865: **A–B,** left bulla and part of cranium shown in ventral and lateral views; **C,** broken right bulla (shown at larger scale), looking anterodorsolaterally into the bulla through the gap afforded by the missing entotympanic and basicranial elements.

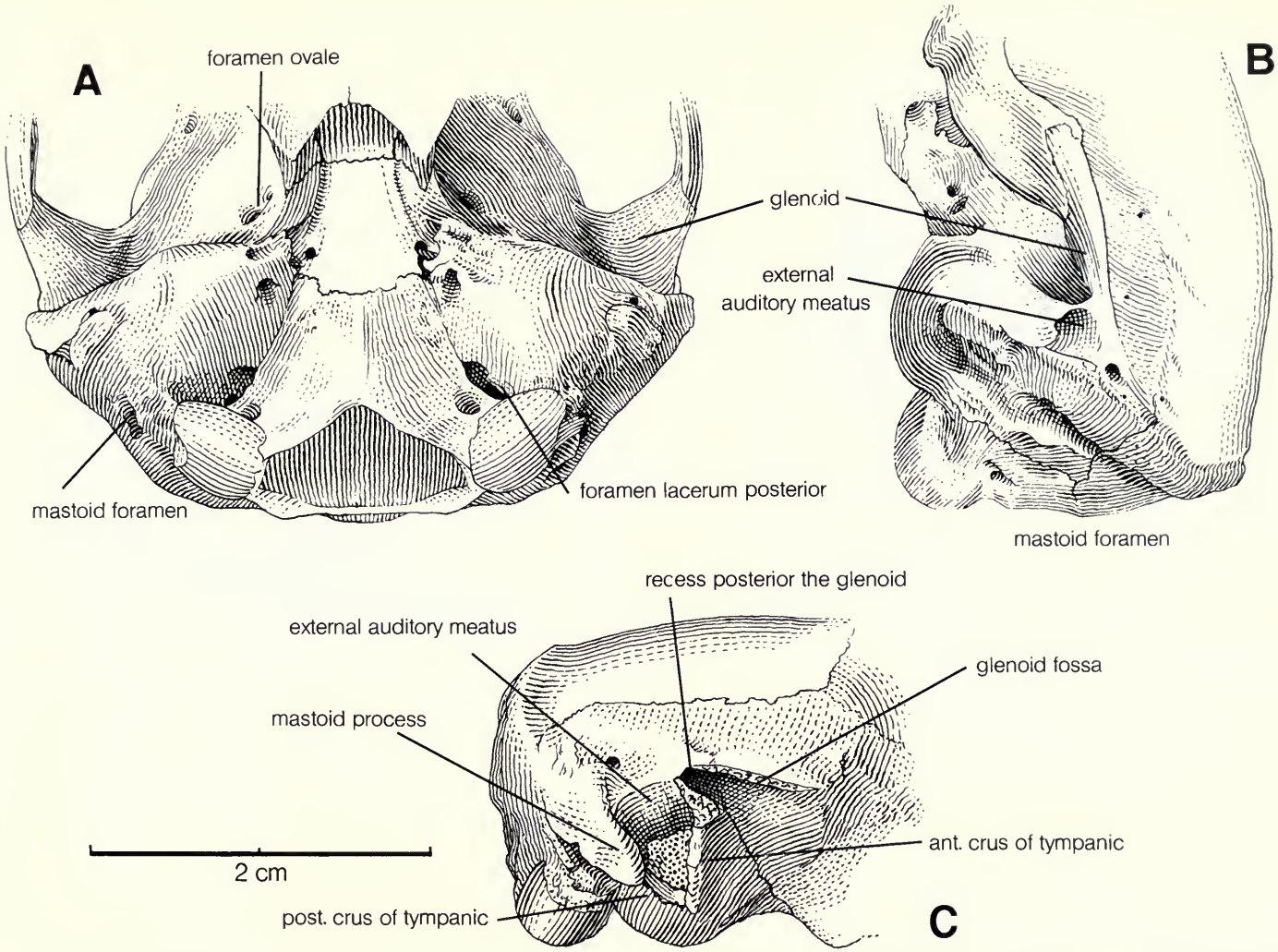

FIG. 8. *Zaedius pichiy,* FMNH 23809: **A–B,** posterior part of skull shown in ventral and left lateral views. *Paleuphractus argentinus,* FMNH P14412: **C,** cranium shown in right lateral view.

described. Due to the extensive union between tympanic and squamosal, the sulcus malleolaris becomes obscured early. It is plainly visible in the young *Chaetophractus,* and the tip of the processus malleolaris may be seen forming part of the bulla wall in some adults. In the interior of the bulla the tympanic fuses with the adjacent portion of the processus cristae facialis of the periotic [petrosal].

A very well developed external auditory meatus, which ossifies early in postnatal ontogeny, is present. It is inclined dorsolaterally and the porus presents upward and outward, the inclination being more pronounced in the smaller *Zaedius.* The ventral and anterior surfaces of the meatus ossify from the anterior crus of the tympanic, which in these forms is very much more extensive than the posterior, and come into sutural contact with the mastoid process, which forms the greater part of the posterior wall. In old individuals the suture becomes obliterated. Lateral to the stylomastoid foramen, the meatus sends down a short, blunt process in some individuals. The posterior crus, which is small in comparison with the anterior although equal in relative size to the posterior crura in the *Priodontes* and *Dasypus* groups, is largely concealed by the mastoid process in lateral view and contributes very little to the posterior wall. The dorsal wall, lateral to the tympanic ring, is formed largely by the squamosal, the anterior crus contributing at the margin. In the very young specimen of *Chaetophractus,* the meatus has barely begun to ossify and there are traces of a cleft extending medially between the crura. This is an interesting point of resemblance to the eutatines and to the Tertiary euphractines described below.

The glenoid surface is high on the skull and slightly convex. Posterior to it is a large, deep recess in the squamosal that extends back above and internal to the auditory meatus; the large postglenoid foramen opens in the caudal extremity of the recess. The structure of this area is a characteristic feature of the entire *Euphractus* group.

The entotympanic has sutural contacts with the exoccipital posteriorly—the contact here extending ventrally almost to the level of the condyle, the basioccipital, and to a slight extent the basisphenoid medially. It reaches the pterygoid anteriorly, the two bones forming a short crest above the level of the Eustachian opening. Laterally, it extends above the anterior margin of the tympanic, between this element and the alisphenoid, to the squamosoalisphenoid junction, as in *Cabassous* and *Tolypeutes.* Internally, the entotympanic is smooth, and its posterior extremity forms a sharp, prominent transverse ridge that continues upward into the crista facialis. There is no trace, in this or any other xenarthran, of a septum bullae, a structure that frequently occurs in other mammals with a compound bulla. Anteroexternally it fuses extensively in adult specimens with the processus cristae facialis. The medial wall of the bone is thickened and cancellous. The aperture for the Eustachian tube is completely surrounded by this element and by the tympanic. The entotympanic may be a compound bone, formed from rostral and caudal elements in these genera, but the material at hand, even the young individual of *Chaetophractus,* throws no light on the matter. The paleontological evidence suggests, however, that the part, if any, played by the caudal portion was minor.

The tympanohyal is in the usual position. It is clearly visible in very young specimens, in which it may be seen as a thin strip of bone lying medial to the united crura of the tympanic, but later becomes fused with the surrounding elements. A slight depression for the reception of the stylohyal sometimes remains to mark its position in *Euphractus,* into which, as noted by van Kampen (1905), the tip of the otherwise fused tympanohyal occasionally protrudes.

The ventral surface of the pars petrosa of the periotic shows no outstanding peculiarities. The promontorium is prominent but not as globular as in *Dasypus,* being quite similar to that of *Tolypeutes.* The processus cristae facialis is a very well developed, gently concave bony plate that is rounded anteriorly and sharply triangular posteriorly. As noted above, it fuses during postnatal ontogeny with the tympanic and entotympanic. The recessus epitympanicus passes directly into a large epitympanic sinus, which extends anteriorly beneath the posterior part of the recess behind the glenoid articulation and posteriorly into the pars mastoidea. In the young specimen of *Chaetophractus* already referred to, it is partially divided by a horizontal septum into two portions, of which the lower, and smaller, appears to correspond in part to the posterior evagination of the recessus epitympanicus seen in *Cabassous* and *Tolypeutes.* Van Kampen noted the presence of an epitympanic sinus in *Euphractus* and *Zaedius* but was uncertain as to whether it lay wholly in the squamosal. Our material shows that it is bounded medially by the periotic.

In correlation with the width of the cranium, the pars mastoidea is widely exposed on the occipital surface. It forms the whole of the mastoid

process, which is wide transversely, compressed anteroposteriorly, and inclined anteroventrally. The relations between this process and the tympanic have been described above. The process is in contact laterally for most of its length with the outgrowth from the anterior crus of the tympanic; the rounded tip may project for a very short distance in some specimens. The posterior face bears a small protuberance near the center. Between the process and the exoccipital there is a wide, shallow groove [leading from the mastoid foramen]. No trace of a paroccipital process is present.

The internal carotid enters a canal in the anterior part of the entotympanic, and passes to the cranial cavity via the concealed foramen lacerum medium in all specimens but one of *Zaedius,* all of *C.* (*E.*) *villosus,* and slightly under half of *E. sexcinctus.* In the single *Zaedius* and the remaining *E. sexcinctus,* there is a groove in the entotympanic, and the foramen lacerum medium is visible in the dried skull. The artery enters the cranial cavity by a small opening situated directly dorsal to the foramen lacerum medium and posterolateral to the sella turcica. A second artery enters the skull immediately anterointernal to the foramen lacerum posterior and runs anteriorly in a canal, formed by the entotympanic below, periotic laterally and basioccipital medially, that opens in the cranial cavity at the posterolateral extremity of the sella. Several small squamosal foramina, rarely a single large one, occur above the porus in *Euphractus.* In *Zaedius* there is usually a single foramen above and behind the porus, and occasionally one or two smaller ones as well. The mastoid foramen is in the usual position with a channel running ventrally from it, which is only exceptionally bridged over in part by bone. Above it is a second, smaller venous opening. Both foramina lead into canals that pass anteriorly above the auditory region, through the diploe in this very thick part of the cranial wall, to open in the posterolateral part of the cerebral cavity. Here the dorsal of the two canals (which becomes ventral in position posteriorly) receives a sinus that enters the cerebral cavity through a venous opening in the posterior part of the orbit. Both canals are in communication with each other posteriorly and also with the transverse sinus, the canal from the postglenoid foramen, the subsquamosal foramina, and the numerous small venous openings in the vicinity of the squamosoparietal suture. The foramen lacerum posterior, as usual, is oval and situated between exoccipital and entotympanic.

The course of the facial nerve in armadillos of the *Euphractus* group is rather unusual. The nerve follows the usual course within the tympanic cavity and then turns laterally to pass through a canal formed by the pars mastoidea posteriorly and the tympanohyal and posterior crus of the tympanic posteriorly. On emerging from this canal at the foramen stylomastoideum definitivum, it runs anteroventrolaterally along the sulcus in the anterior face of the mastoid process—and hence lies within the external auditory meatus—and finally leaves the skull at a point near the tip of the mastoid process, between this element and the outgrowth of the anterior crus of the tympanic. In young animals, this is in a slit between the two, but as ossification of the crus progresses the point of exit is converted into a foramen, a "foramen stylomastoideum tertium," so to speak.

†Paleuphractus Kraglievich, 1934

Two skulls of *Paleuphractus argentinus* Moreno and Mercerat, FMNH P14412 (fig. 8C) and P14442, from the Andalgalense of Catamarca, have been available for study. Both have suffered to some extent from distortion and breakage.

The tympanic, as far as revealed, is very similar to those of *Zaedius* and *Euphratus,* differing only in the structure of the anterior crus. In degree of enlargement and lateral projection, this portion of the bone is comparable to that of *Zaedius* but it is not reflected posteriorly to floor the meatus. The well-defined ventral slit, here V-shaped, between anterior crus and mastoid process is therefore present, as in all extinct euphractine genera now known. The relation of the anterior wall of the tympanic to the deep recess, posterior to the glenoid surface, is precisely as in the living forms.

The boundary between tympanic and entotympanic is visible in the posterior half of the bulla. It corresponds closely with conditions seen in the young specimen of *Euphractus* [*Chaetophractus*] described above, except that here again, as in *Proeuphractus,* there is a gap posteriorly between the two elements and no contact between exoccipital and entotympanic at the level of the condyle. The gap is smaller than in that form and is confined entirely to the posterior face of the bulla. This lack of ossification in the immediate vicinity of the tympanohyal, coupled with the absence of any indication of a division in the entotympanic of the young *Euphractus* [*Chaetophractus*], strongly suggests that the caudal portion of the entotym-

panic played a very minor role, if indeed it participated at all, in the formation of the bone.

The ventral surface of the pars petrosa of the periotic is comparable in all respects with that of *Euphractus*. The same is true of the pars mastoidea, save that the mastoid process projects freely in the cranioventral direction, due to the lack of reflection of the anterior crus of the tympanic.

All foramina that can be seen in the auditory region differ in no respect from those of the living forms, except that due to the lesser degree of ossification of the anterior crus, there is no "foramen stylomastoideum tertium" between crus and mastoid process.

†**Proeuphractus** Ameghino, 1886

Two specimens of *Proeuphractus scalabrinii* Moreno and Mercerat, FMNH P14360 (fig. 9A–B) and P15435, from the Andalgalense of Catamarca, have been available; both are unfortunately incomplete, but nevertheless most of the structure can be determined. *Proeuphractus* and its close relative *Macroeuphractus* are similar in general to *Euphractus* and *Zaedius* and it will suffice here to discuss those points in which they differ.

The bulla is less inflated than in the living forms and its anterior border shows an uninterrupted, gently concave sweep when seen in ventral aspect, a feature that is even more pronounced in the giant *Macroeuphractus* (Lydekker, 1894, pl. 35). The external meatus is as long as in *Euphractus* and *Zaedius* but is not closed ventrally by bone. The bony extension of the anterior crus, as in *Macroeuphractus,* did not turn posteriorly to meet the mastoid process, thus leaving an open V-shaped cleft between the two elements. The bony extension continues ventrally below the porus, forming a groove between the crura. Tympanic and mastoid are united medially to the point of exit of the facial nerve. The mastoid process is broken in our material; in *Macroeuphractus* it is very massive. In only one other character is there a major difference between *Proeuphractus* and the living euphractines. As in the Santacruzian *Prozaedius* (see below), a cleft, reaching almost to the middle of the bulla, separates the entotympanic and tympanic posteriorly. The position of the cleft is the same as that occupied by the caudal portion of the entotympanic in *Cabassous,* etc., a fact which suggests that this portion of the bone remained unossified in *Proeuphractus*. There is thus no connection between entotympanic and exoccipital at the level of the condyle. It is rather remarkable to find these primitive characters persisting in so large and specialized a form. Both available specimens appear to be fully grown, so that the lack of ossification can hardly be regarded as due to immaturity. The later, *Macroeuphractus retusus* Ameghino, has a fully ossified bulla, to judge from Lydekker's figure.

It is probable that an epitympanic sinus is present in this and other Tertiary euphractines, but sections would be necessary to conclusively demonstrate its presence.

†**Prozaedius** Ameghino, 1891

An excellent skull of *Prozaedius exilis* Ameghino, PU 15579 (fig. 10A–B), from the Santa Cruz Formation of Patagonia, permits the following rather full account of this earliest euphractine. Scott's description of the skull (1903, pp. 70–72), which includes a brief summary of the auditory region, was largely based on this specimen, and van der Klaauw (1931, pp. 312–313) has published a brief note upon it.

The bulla of this form is, as would be expected, more primitive than in any later euphractine, and resembles the bulla of the Pliocene eutatine *Doellotatus* (see below) in several respects.

The tympanic retains some trace of the primitive ring form,[7] being only moderately expanded medially in the posterior portion. It is considerably prolonged anteromedially, however, in the vicinity of the Eustachian tube. The external auditory meatus is barely developed, and above it there is a parallel-sided cleft between the mastoid process and anterior crus, which is U-shaped at the base. The shorter, V-shaped cleft of the Pliocene *Paleuphractus* indicates that formation of the tubular meatus in euphractines involved bone growth at the base of the cleft as well as extension of the anterior crus posteriorly. The anterior crus forms a straight, nearly vertical ridge sharply edged laterally; there is a steplike indentation at the upper extremity, as in *Doellotatus*. In contrast to the living forms, there is no posterior continuation from the anterior portion of the crista tympanica, and

[7] It should be noted that what appears at first glance to be a tympanic in Scott's figure (1903, pl. 6, fig. 20) of the closely related but longer skulled *Stenotatus patagonicus* Ameghino is actually the occipital condyle, which, as he states (p. 81), is deeply incised laterally.

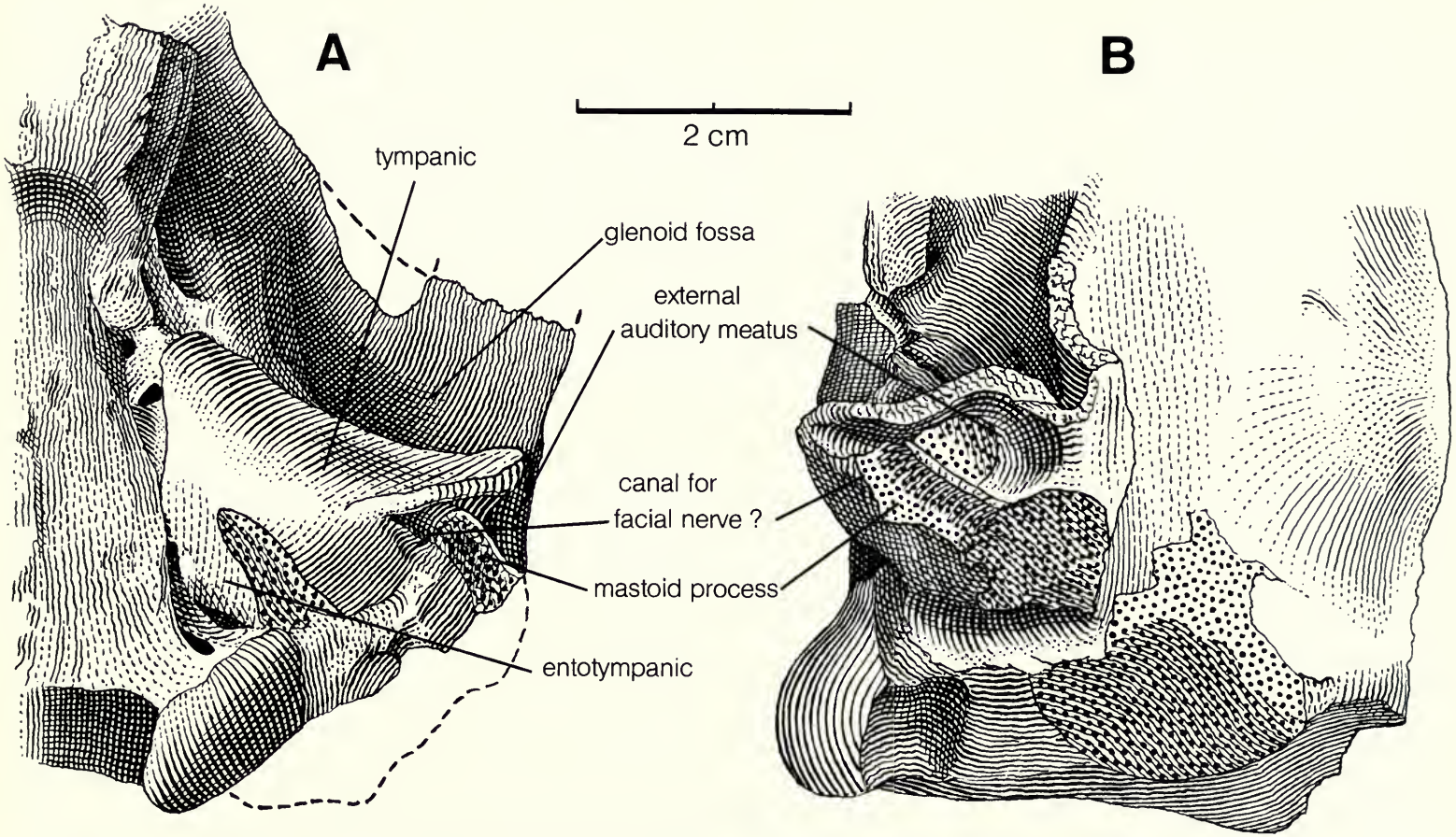

FIG. 9. *Proeuphractus scalabrinii*, FMNH P14360: **A–B,** posterior portion of skull shown in ventral and left lateral views.

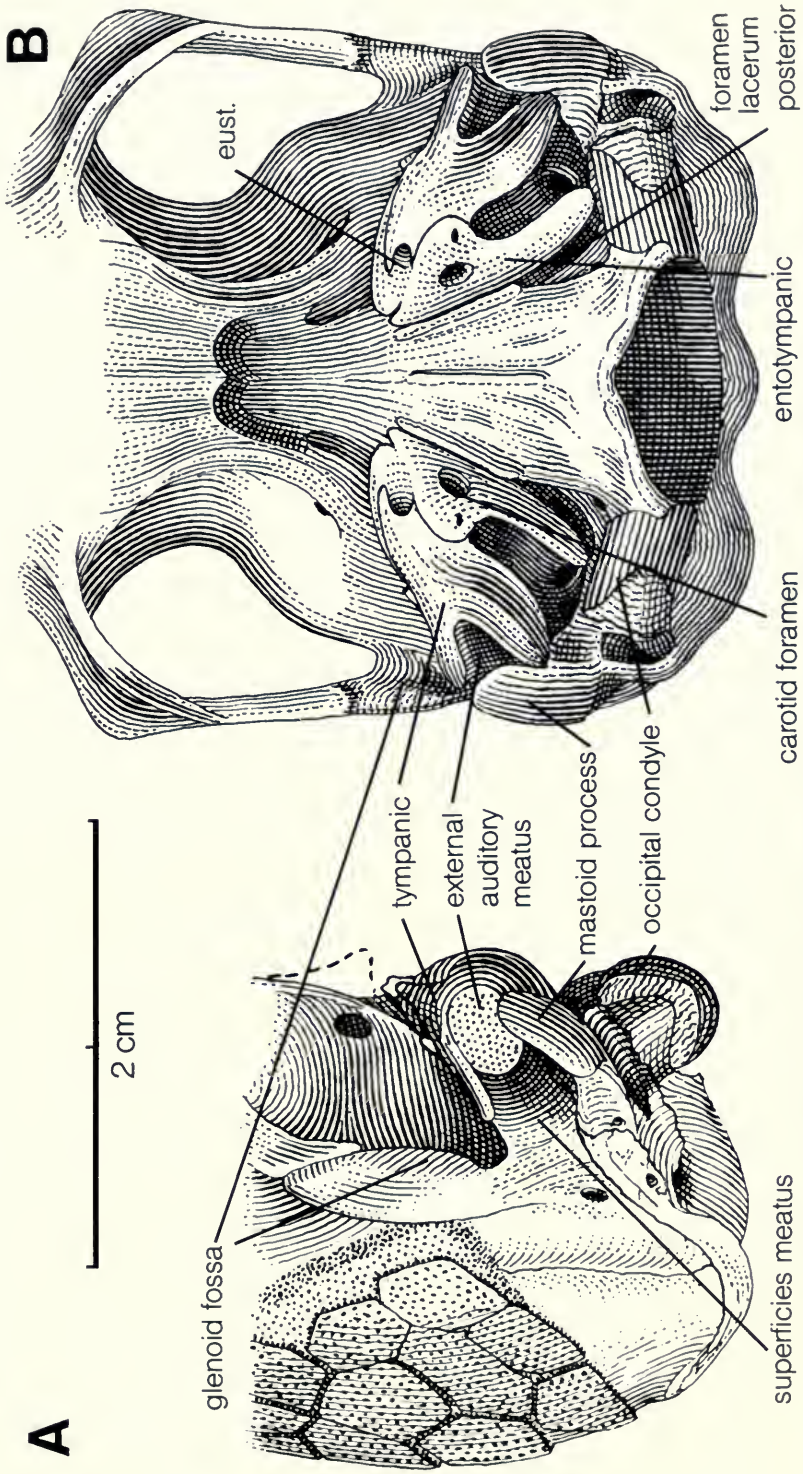

FIG. 10. *Prozaedius exilis*, PU 15579: **A–B**, posterior portion of skull shown in right lateral and ventral views.

the tympanic consequently does not form a complete ring. The posterior crus is, as usual in this group, short in comparison with the anterior and curves upward medial to the mastoid process, which conceals its upper portion when the skull is viewed from the lateral side. As far as its attachment is concerned, it is nearly identical with *Euphractus,* the only difference being that the sutural connection to the mastoid process is less extensive.

Prozaedius thus shows conclusively that, of the two crura, it is the posterior that earlier attains the definitive form and relationships encountered in the later members of the *Euphractus* group. This is not surprising since the structure here is merely an exaggeration of that seen in incipient form in the *Priodontes* and *Dasypus* groups, whereas the modification of the anterior crus has been much more extensive. The superficies meatus is nearly vertical, as in *Doellotatus* and juvenile Recent euphractines. In contrast to these later forms and due to the fact that the tympanic ring is not complete, there is a gap between the arched ventral border of the superficies and the incisura tympanica, in which the malleus and incus are visible [but not shown in fig. 10, however]. This is a primitive character and an interesting point of resemblance to armadillos of the *Priodontes* and *Dasypus* groups. The projecting tip of the anterior process of the malleus may be seen on both sides of the specimen.

The fossa in front of the anterior wall of the meatus and behind the glenoid surface which is so characteristic of the entire *Euphractus* group is less extensive in *Prozaedius* than in later euphractines, being narrower transversely, due to the less expanded zygoma and anterior crus, and not extending so far posterodorsally.

The relations between tympanic and entotympanic are very clear, the bulla not being "broken up into pieces" as van der Klaauw supposed. The rostral portion of the entotympanic, the only part ossified, is less developed than in later forms. Anteriorly, it completely fills the space between the tympanic and neighboring elements, extending laterally on the anterior face of the bulla to the projecting tip of the processus anterior of the malleus, as in *Cabassous* and *Tolypeutes,* and forming a curved suture posterior to the Eustachian tube with the anterior half of the medial border of the tympanic. Due to a fracture, it is impossible to be certain whether or not a pterygoid-entotympanic crest was present. This anterior portion of the bone is cancellous. Posteriorly, the entotympanic diverges from the tympanic, forming a fairly wide medial strip that extends back to the exoccipital. A wide gap is thus formed between the two bones (not within the tympanic, as van der Klaauw thought might be the case), in which no trace of a caudal entotympanic is to be seen. In later forms this gap is closed by progressive ossification of the rostral portion. As already stated, there is no clear evidence that a caudal portion participated at all in the formation of the bulla. The form and position of the opening for the Eustachian tube are as in the living forms.

In degree of prominence, the promontorium resembles those of *Euphractus* and *Zaedius.* The recessus epitympanicus is well developed; the presence of the ossicles makes it impossible to determine whether or not a sinus was present. The pars mastoidea is comparable to that of these Recent forms in its degree of exposure, but, due to the much less expanded posterior root of the zygoma, the anterior half faces laterally rather than posterolaterally. The mastoid process projects more freely than in later forms, and bears a conspicuous buttress on the lateral edge a short distance below the junction with the occipital crest. Its squamosal component extends far ventrally, reaching to the posterior crus of the tympanic.

Prozaedius resembles *Paleuphractus* in the absence of a "foramen stylomastoideum tertium." The other foramina in the vicinity of the auditory region are precisely as in the living forms. Van der Klaauw's (1931, p. 313) "opening in the rostromedial part of the bulla" is the usual carotid foramen in the entotympanic.

The Chlamyphorines

Chlamyphorus Harlan, 1825

Specimens of this and of the related, somewhat larger *Burmeisteria* are rare in collections, and we are fortunate to have been able to examine a skull of *Chlamyphorus truncatus* Harlan, PU 538 (fig. 11A–B), an adult individual. The extraordinary little animals, so distinctive in external characters and in the relations of the pelvis and tail to the posterior portion of the carapace, are dwarfed relatives of the euphractines, from which group they almost certainly arose. We thus agree with Simpson's remark (1927, p. 292) that *Chlamyphorus* is ". . . a peculiar and highly aberrant derivative of an essentially *Dasypus* [i.e., *Euphractus*]-like form." So far as the auditory region is concerned, this is not open to question, and evidence from other parts of the body would appear to be in accord.

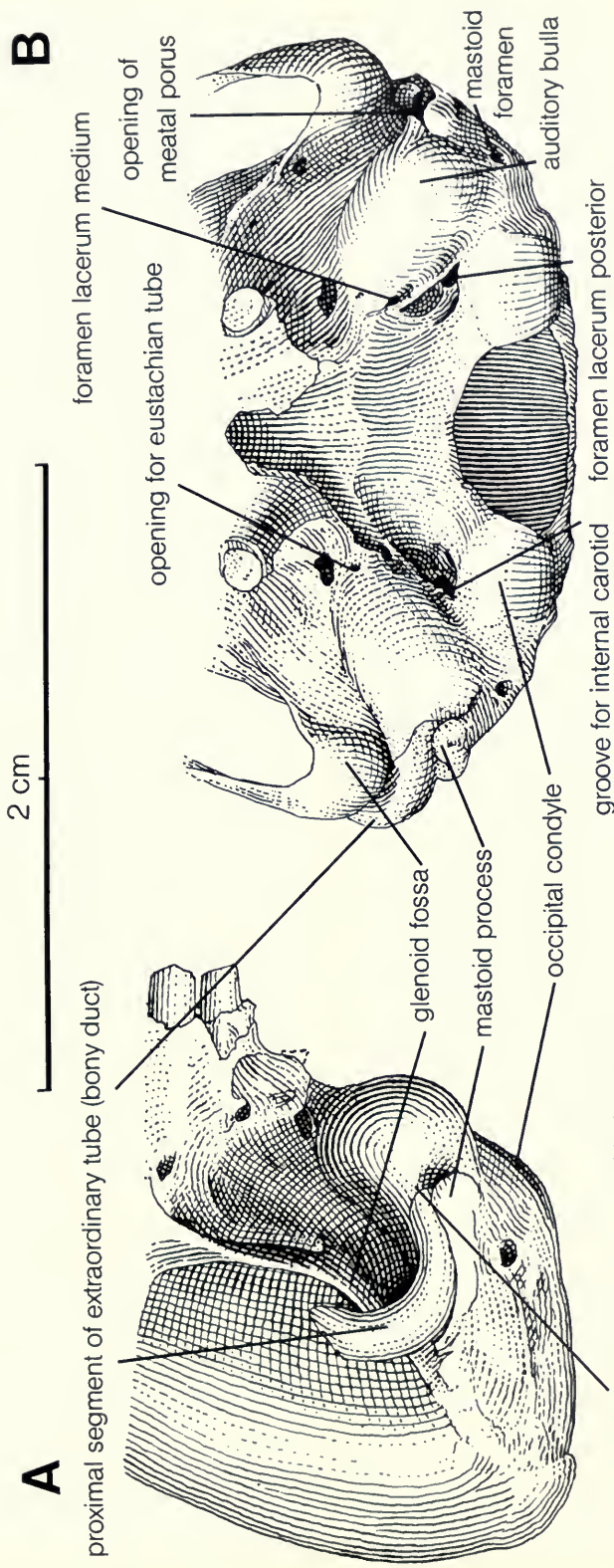

FIG. 11. *Chlamyphorus truncatus*, PU 538: **A–B**, posterior portion of skull shown in right lateral and ventral views

The striking features of the skull of *Chlamyphorus,* those immediately noticed on comparison with skulls of euphractines—triangular appearance, wide, deep, and short cranium, zygomata narrowing anteriorly, frontal protuberances, reduced orbits, relatively enormous foramen magnum, and so on—are all consequent upon the size reduction undergone by the chlamyphorines. They are the results of adjustments that have taken place in the head. Compromises have ensued beween overall size reduction and disproportionate reduction of various parts, some of which (e.g., brain, depth of teeth, sinuses) have undergone relatively less reduction, while others (e.g., eyes) have undergone more. In the auditory region and vicinity, adjustment to the relatively large size of the brain has resulted in certain differences from the euphractines in general appearance. For example, the recess posterior to the glenoid cavity, so conspicuous in euphractines, is here reduced. The well-inflated bullae are aligned more obliquely, and, as van Kampen has noted, lie in a more ventral plane relative to the basicranium. Posteromedially the bullae have rather extensive contacts with the occipital condyles, which are situated farther forward than in euphractines and greatly expanded in the anteroposterior direction. These distinctions are relatively minor, however, and in no way disguise the fundamental similarity between chlamyphorines and euphractines in this area.

The bulla closely resembles that of *Zaedius* in shape, but is smoother and more convex. There is no trace of the prominence extending medially from the meatus, and the groove running anterointernally from the vicinity of the mastoid process is barely discernible; both these features, it will be recalled, were less prominent in the smaller *Zaedius* than in the larger *Euphractus.* [It should be noted that Segall has subsequently studied *C. truncatus* (1976) and in that work this feature does not appear on the specimen illustrated (Segall, 1976, fig. 1, p. 433; MCZ 3209).] That portion of the tympanic anterointernal to the crista tympanica, between this crest and the opening for the Eustachian tube, is relatively more extensive than in *Zaedius,* in which, in turn, this part is relatively larger than in *Euphractus.* The attachments of the crura are as in the euphractines, the posterior being partially concealed by the mastoid process and the anterior united suturally with the squamosal.

In the structure of the auditory meatus, however, *Chlamyphorus* is sharply distinct from the Pliocene and later euphractines. The external canal is short, the anterior crus not extending laterally and posteriorly to form a long bony meatus. The porus is consequently low on the side of the skull, at a level only slightly above that of the tip of the mastoid process. It is nearly circular in outline, presents upward and outward, and has a prominent lip. From it a groove, situated mainly in the squamosal, curves upward and forward, terminating immediately lateral to the occipital crest. In this groove, and fitting over the lip of the porus, lies the extraordinary tube (van Kampen, 1905, p. 493), ossified from the cartilaginous meatus,[8] which has attracted the attention of all who have studied the chlamyphorine auditory region, from Harlan (1825) and Hyrtl (1854) on [and including Segall (1976, p. 431)]. The tube extends beyond the groove, curves forward over the root of the zygoma, and ends above the glenoid articulation. [Segall's 1976 dissection (pp. 433, 437) shows this to be a two-part tube, the proximal part occupying the groove, the articulating distal part extending more freely forward nearly to the frontal protuberance and the eye.] The structure of this area is, of course, decidedly different from that of the Recent and Pliocene euphractines, but is derivable from that of the earlier forms. Acquisition of an ossified tube by forms comparable in meatal structure to the Santacruzean *Prozaedius* would lead to the conditions seen in the chlamyphorines.

The position of the glenoid articulation is exactly as in the euphractines, but the articular surface is rather more convex transversely. As a result of the dwarfing of the animal and the disproportionate [lesser] reduction in brain size, the posterior root of the zygoma stands out from the side of the cranium to a greater extent than in euphractines, and, as already noted, the recess behind the articular surface is reduced, although still fully recognizable.

No trace of a suture between tympanic and entotympanic remains, but there can be no doubt that the bulla is compound. The crest formed by the entotympanic and pterygoid is prominent, but, as in *Euphractus* and *Zaedius,* it is above the level of the opening for the Eustachian tube, which is here very small.

The tympanohyal is completely fused with the surrounding elements and no details of its structure can be seen. A small pit on the occipital surface immediately above the bulla and medial to the mastoid process marks the position of the attachment of the stylohyal.

[8] Van der Klaauw (1931, p. 257) implies that the meatus in *Euphractus* and *Zaedius* is formed in the same way. We do not believe this to be the case.

External examination and X-ray photography fail to reveal any trace of an epitympanic sinus. If present in the ancestry of *Chlamyphorus,* as may have been the case, elimination of this cavity is to be attributed to dwarfing.

The pars petrosa of the periotic is not visible in the specimen at our disposal. The sutures between the pars mastoidea and the squamosal and occipital elements cannot be seen, but, from the position of the mastoid foramen, it is evident that the pars mastoidea forms the ventrolateral corner of the occipital surface. In comparison with the euphractines, the mastoid process is small and extends laterally to a lesser degree. It conceals the posterior crus of the tympanic in side view and may contribute in a minor way to the formation of the groove in which the meatal tube lies.

The medial face of the entotympanic is grooved for the reception of the internal carotid but no canal is formed, the artery passing anteriorly to the foramen lacerum medium, which opens at the anterior extremity of the groove. The second artery passes forward in a second, more dorsally situated groove between entotympanic and basioccipital, runs beneath a bar formed by the entotympanic and pterygoid, and also enters the cranial cavity via the foramen lacerum medium. The postglenoid foramen, as in euphractines, is situated at the posterior extremity of the recess behind the glenoid surface; it is relatively enormous in comparison with the size of the skull. There are no subsquamosal foramina. The mastoid foramen occupies the same position as in euphractines, but there is no groove running ventrally from it. The foramen lacerum posterior resembles those of *Euphractus* and *Zaedius.* The stylomastoid foramen, again as in these forms, leaves the skull between tympanic and mastoid process.

The Eutatines

†Doellotatus Bordas, 1932

Three specimens that are apparently referable to *Doellotatus prominens* (Moreno & Mercerat),[9] FMNH P14351 (fig. 12D) and P14358 (fig. 12C) from the Araucanense and P14526 (fig. 12A–B) from the Corral Quemado, Catamarca, Argentina, have been examined. None of the three is complete and all are either broken or somewhat crushed, but between them most of the structural details can be determined.

The tympanic in the later eutatines is an extraordinary bone, thick and so dense that it resembles the pars petrosa of the periotic in texture. The porus, due to the prominence of the crura, is deep set in the bulla, and has a rather irregular border. The anterior crus is high, reaching to the root of the zygoma, and very robust, expanded in the transverse plane, and with a sharp lateral margin. The upper extremity is indented in steplike fashion. There is no indication of a posterior reflection, such as occurs in Recent euphractines, but its posterior wall is concave, forming a recess above and slightly anterior to the porus. The posterior crus, as in euphractines, is short and largely covered laterally by the mastoid process, but it also has a prominent lateral margin; the attachments are also almost precisely similar. The margins of both crura continue ventrally beyond the porus, with the result that a conspicuous groove is formed in the lateral face of the bulla, as in *Proeuphractus.* The crura meet above the porus, as in *Euphractus,* excluding the narrow superficies meatus of the squamosal from its border. The sutures in this region can be seen clearly in FMNH P14526 (fig. 12A–B).

As already mentioned above (p. 28), the glenoid area, and in particular the fossa posterior to it, agrees in all essentials of structure with that of the euphractines.

The entotympanic, nearly complete on the left side of FMNH P14351 (fig. 12D) and on the right of P14526, resembles that of Recent euphractines. It is cancellous in its anterior half, extends laterally above the medial half of the anterior face of the tympanic, where it is concealed externally by the enlargement of the squamosal in this area, and posteriorly to the foramen lacerum posterior. The bulla is thus completely enclosed by bone, in sharp contrast to the Miocene and Pliocene euphractines in which the entotympanic is not completely ossified posteriorly. The Eustachian tube and styliform process are comparable to those of *Euphractus.*

[9] Described as *Eutatus prominens.* Bordas (1933, p. 584) makes only passing mention of this species in his discussion of the eutatines and leaves the reader in doubt as to the generic assignment. Associated carapacial material permits at least tentative specific identification of our specimens, and the skulls are very similar to that of *Doellotatus inornatus* Rovereto, the type species, leaving no doubt as to the generic determination. [Earlier, Ameghino (1891) had equated *E. prominens* of Moreno and Mercerat with his species *Eutatus distans.*]

The ventrolateral face of the pars petrosa of the periotic is rather flat, and has a rounded anterior extremity. [Here I suspect that Patterson has seen some other specimen(s), for only the anterior tip and ventromedial edge are exposed on the petrosals of the specimens listed here. The best exposure is seen in FMNH P14351.] The promontorium is low and inconspicuous in comparison with that of the euphractines. The ventral portion of the medial face is deeply grooved, and lower border of the groove forming a sharp edge. [The cranial side of FMNH P14526 possibly may have been further prepared subsequent to the Patterson-Segall study of it. That surface is irregular, and the meatus internus acusticus is prominent and deep.] Unfortunately, nothing can be seen of the crista facialis or recessus epitympanicus in any of the specimens. Whether or not an epitympanic sinus was present is uncertain.

Doellotatus resembles *Prozaedius* in the degree of expansion of the posterior root of the zygoma, and the surface exposure of the pars mastoidea is consequently as much lateral as posterior in position, as in that form. The freely projecting mastoid process is stouter and less flattened anteroposteriorly than in *Prozaedius*; its base is closer to the condyle than in any euphractine. It bears a buttress on the lateral edge, exactly as in *Prozaedius,* and a second eminence, dorsal to this and above and behind the meatus, to which the squamosal contributes.

There is no groove or opening in the entotympanic for the carotid, and there would appear to have been a visible foramen lacerum medium anterointernal to the bulla, as in certain living euphractines. The arterial canal between entotympanic, periotic and basioccipital was present, occupying the groove in the medial face of the pars petrosa. The postglenoid foramen, as in euphractines, opens at the posterior extremity of the deep fossa posterior to the glenoid surface. The subsquamosal foramina vary in number and size and are situated above the meatus. The mastoid foramen is ventral in position, opening between the base of the mastoid process and the vestigial paroccipital process. In euphractines, the vein runs down the occiput in a groove, which is here completely bridged over by bone. The narrow foramen lacerum posterior resembles that of the euphractines very closely. As in the Tertiary members of this group, the stylomastoid foramen opens laterally between the posterior crus of the tympanic and the mastoid process.

†Eutatus Gervais, 1867

Examination of a specimen of *Eutatus seguini* Gervais in the American Museum of Natural History (AM 11231, type of *Eutatus brevis* Ameghino) permits the statement that this latest and largest eutatine is in nearly every respect comparable to the earlier and much smaller *Doellotatus.* [This also appears reasonable, to judge by the figure given by Ameghino (1906, p. 380, fig. 236).]

†Proeutatus Ameghino, 1891

Three skulls of *Proeutatus oenophorus* Ameghino, FMNH P13197 (fig. 13A–B), P13199 (fig. 13C–D), and P13203, from the Santa Cruz Formation of Patagonia, have been examined.

Scott (1903, p. 44) has stated that "the tympanic, which was loosely attached, is a small, incomplete ring of bone, with large, irregular external meatus." It was not attached in any of the skulls that he figured. An incomplete tympanic is fortunately preserved in FMNH P13199, permitting us to confirm and to some extent amplify the brief account just quoted. [Unfortunately, it is now lost, or at least is no longer with the specimen. It is good that Patterson and Segall discussed and illustrated it, for that is now all we have to go on.] The specimen is incomplete anteriorly, the proximal end of the anterior crus being broken off. In contrast to *Doellotatus,* the tympanic is of primitive type, comparable in general to those of *Dasypus* and of the *Priodontes* group. The posterior portion is more expanded than the anterior, and the two parts meet in a very sharp angle, almost precisely as in *Priodontes.* Again as in this form, there is no groove in the region of the Eustachian tube. No trace is apparent of the thickening that is so striking a feature of *Doellotatus.* The porus, as Scott states, is irregular; the outline corresponds closely to that of *Priodontes.* The spina tympanica posterior is conspicuous, the bony meatus short, and the crista, sulcus, and recessus well developed. The posterior crus is attached mainly to the tympanohyal, with only the spina extending up to the squamosal as in the *Priodontes* and *Dasypus* groups; more of it is visible in lateral view than in later eutatines, due to the relatively smaller and shorter mastoid process. The anterior crus is evidently broken off immediately distal to the sulcus malleolaris. The small part of the ascending portion that is preserved is very slender, and it would seem

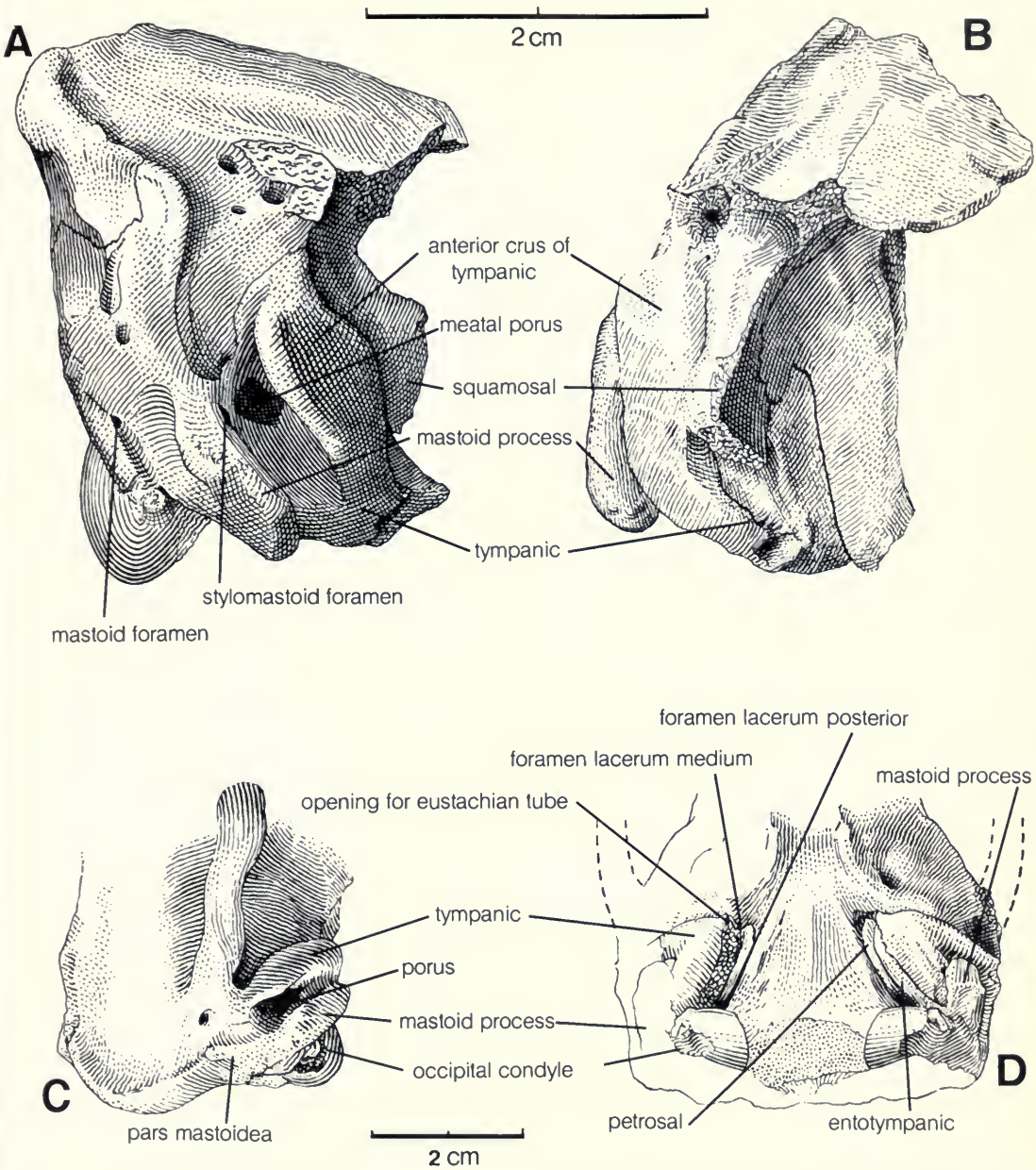

FIG. 12. *Doellotatus prominens*: **A–D,** three partial skulls shown in right lateral and anterior views (FMNH P14526), right lateral view (FMNH P14358), and ventral view (FMNH P14351).

likely that the missing portion was similarly constructed. In all probability the whole resembled the anterior crus in the *Priodontes* and *Dasypus* groups, was bound to the squamosal by soft parts only, and did not extend dorsally much above the level of the posterior crus. The structure of the malleus confirms this inference. The adjacent surface of the squamosal, anterointernal to the superficies meatus, forms a conspicuous, thick ridge, second in prominence only to *Priodontes* among the forms studied.

The recess in the squamosal posterior to the glenoid area, characteristic of all members of the *Euphractus* group, is present in *Proeutatus* also.

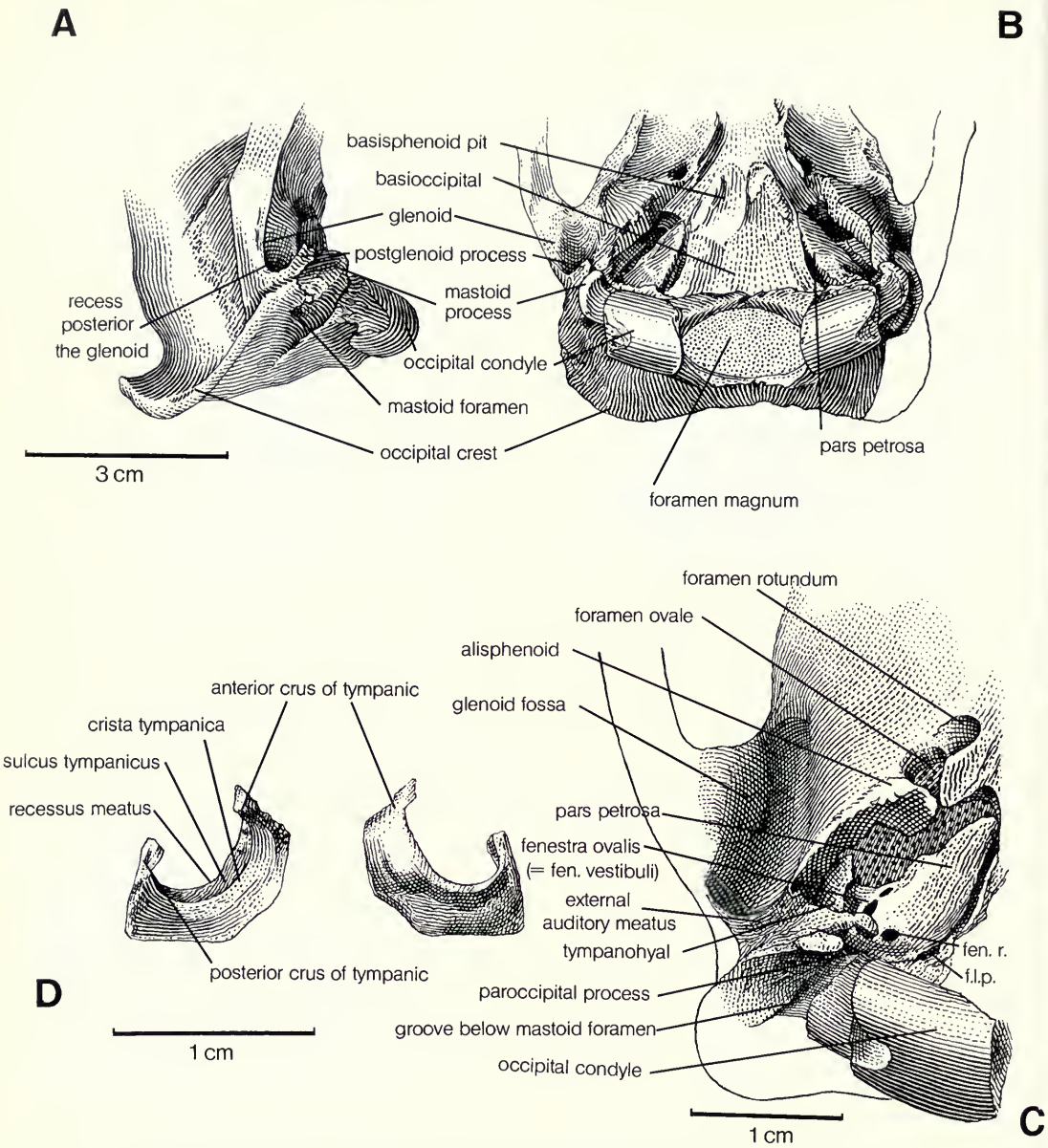

FIG. 13. *Proeutatus*: **A–C,** two partial crania shown in right lateral and ventral views (*P.* cf. *oenophorus,* FMNH P13197) and ventral view (*P. oenophorus,* FMNH P13199); **D,** right tympanum shown in internal (left) and external views (FMNH P13199).

In this form, however, the distance between the base of the mastoid process and the rim of the recess is much less than in other members of the group, the arched superficies meatus actually being anterior to the rim rather than posterior to it as in *Prozaedius. Proeutatus* thus indicates that acquisition of the postglenoid recess preceded, and may have been the structural prerequisite for, enlargement of the anterior crus in members of the *Euphractus* group, but at the same time shows that enlargement of the crus was accompanied by further enlargement of that portion of the squamosal forming the rim of the process.

No trace of an entotympanic is present in our material nor in that figured by Scott.

The tympanohyal is very well preserved in FMNH P13199. At the base it is indistinguishably fused with the crista facialis and curves laterally,

providing a base of attachment for the posterior crus of the tympanic. The posterior surface is grooved for the passage of the facial nerve.

The pars petrosa of the periotic runs to a blunt point anterointernally, and has a sharp ventromedial border that is only slightly above the level of the basicranium. Above this border, as in *Doellotatus,* there is a groove in the medial face of the bone. The promontorium agrees with that of *Doellotatus* in being notably less prominent than in euphractines. The crista facialis is very sharply defined and bears the usual xenarthran process, which is unfortunately broken away anteriorly in the available specimens. The recessus epitympanicus is rather shallow toward the lateral side but is sharply bounded medially due to the prominence of the crista facialis. There is no epitympanic sinus. The pars mastoidea is less extensive than in *Doellotatus,* and is more widely exposed on the occipital than on the lateral surface of the skull. The mastoid process is very notably smaller and shorter than in any other member of the *Euphractus* group, and is further distinguished by being widened in the anteroposterior rather than in the transverse direction.

Due to the absence (or lack of ossification of the entotympanic) nothing can be said concerning the carotid foramen. To judge from the space between the anterior extremity of the pars petrosa and the alisphenoid, a foramen lacerum medium was present. The groove in the medial surface of the pars petrosa, which is converted into a canal by the basioccipital, extends toward a foramen that pierces the alisphenoid anterior to the tip of the petrosal. This in turn leads to a canal that opens in the posterior part of the sella. The postglenoid foramen, as in other members of the *Euphractus* group, is situated in the posterior portion of the postglenoid recess. There are several small venous foramina above the recess. The mastoid foramen is in the usual position; the groove running ventrally from it does not appear to have been roofed over by bone. The foramen lacerum posterius has the usual slitlike form. The stylomastoid foramen is situated between the tympanic and mastoid process, and is lower in position than in other members of the group.

It will be evident from the figure that the foramen ovale and the opening of the transverse canal are more lateral in position than is usual in edentates, the transverse canal opening occupying the usual position of the foramen ovale. Although outside of the auditory region, a note on the transverse canal may be interpolated here; among armadillos, the canal is present in the *Dasypus* and *Euphractus* groups and absent in the others. Glyptodonts, anteaters, and sloths do not have it, and there has been no record of its occurrence in palaeanodonts.

The *Peltephilus* Group

†Peltephilus Ameghino, 1887

Two skulls of *Peltephilus pumilus* (= *Peltephilus ferox*) Ameghino (PU 15391, fig. 14A–B; AM 9524) from the Santa Cruz Formation of Patagonia have been examined. The peculiarities of structure exhibited by these remarkable armadillos extend also to the auditory region, the group being highly distinctive in the structure of this area.

The bulla is complete and well inflated. The tympanic forms a long tubular meatus as in Recent euphractines, but the resemblance between the two ends here. In *Peltephilus* the meatus extends not only dorsally but anteroexternally to a marked degree as well, a unique feature. Both crura, and not the anterior alone, contribute to the formation of the ventral half of the tube. How much of the dorsal half may be supplied by them and how much by the superficies meatus of the squamosal cannot be determined. Scott (1903, p. 90) states that the dorsal surface is formed by the zygomatic process of the squamosal and the anterior by the postglenoid process. This is quite uncertain and at least partly erroneous. There is no postglenoid process, and it is virtually certain that a strip from the anterior crus of the tympanic lines the anterior part of the meatus, and [it is] possible that it may extend to the dorsal surface as well. Whatever its composition, the dorsal half is less arched than in other armidillos. In consequence, the porus is oval with the long axis in the anteroposterior direction. The anteroexternal inclination of the meatus is so pronounced that its anterior portion actually lies above the external portion of the wide glenoid cavity; the tympanic and squamosal are indistinguishably fused in this area. Again as a result of the direction of the meatus, the posterior crus is well separated from the mastoid process. The ventral surface of the meatus bears a rounded, irregular ridge that curves posteriorly to the vicinity of the tympanohyal, and joins the bulla proper in an irregular manner. Anteriorly, the bulla extends almost to the glenoid cavity, the two being separated only by a rather shallow but well defined fissura Glaseri. The posterior end of the bulla is in very close contact with and in places fused with the

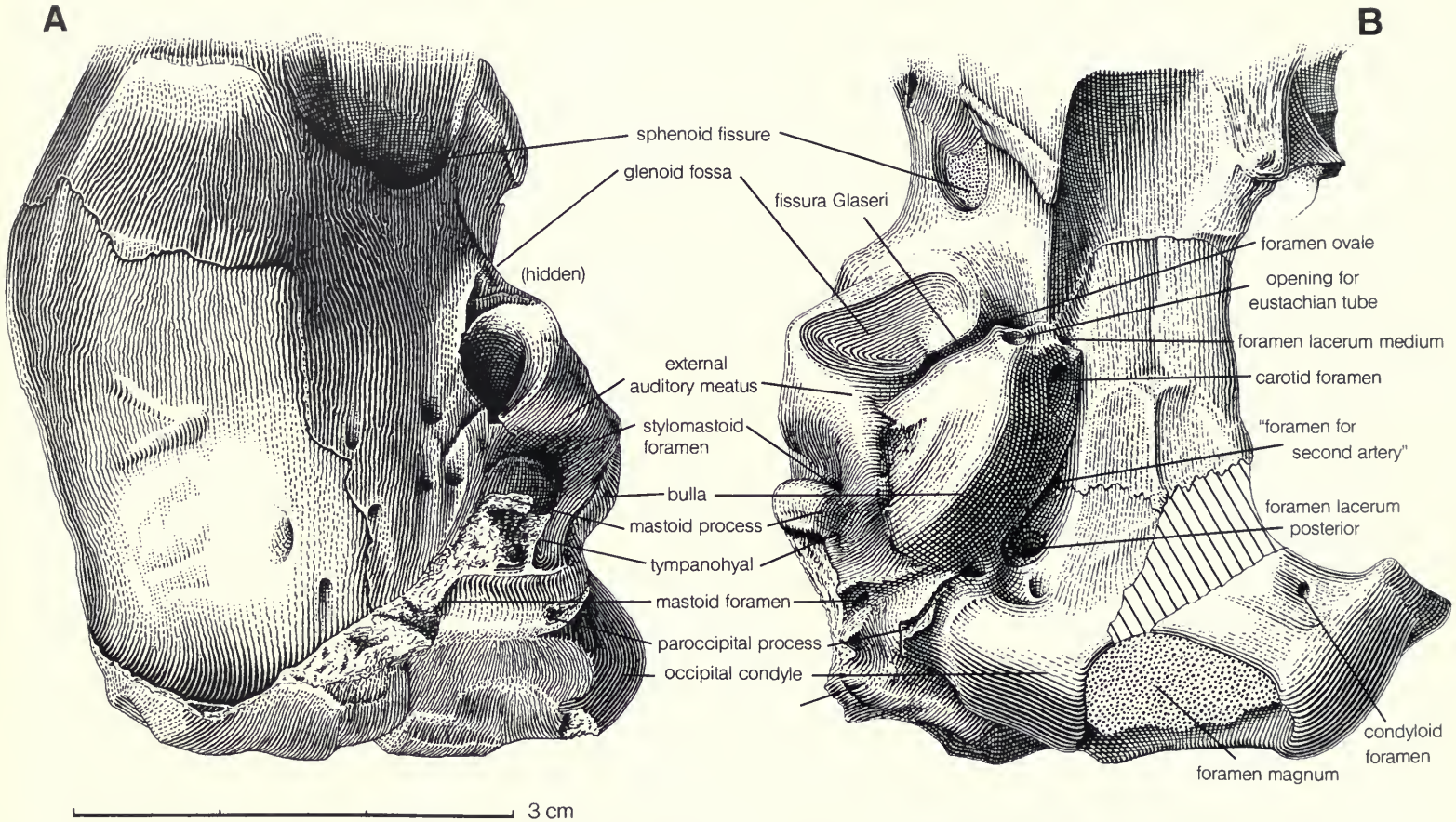

FIG. 14. *Peltephilus ferox*, PU 15391: **A–B,** posterior part of skull shown in right lateral and ventral views.

adjoining portion of the pars mastoidea of the periotic. The glenoid cavity, it should be noted, is lower on the skull than in any other armadillo.

The boundary between entotympanic and tympanic cannot be determined. There is no reason to doubt, however, that the relations of the two bones were essentially as in *Euphractus* and allies. The opening for the Eustachian tube is in the same position as in these forms, but is larger.

As Scott has noted, *Peltephilus* is the only Santa Cruz armadillo that has a completely ossified bulla. Members of this group are in fact the first xenarthrans known to have acquired this condition. The Myrmecophagidae are a close second, but there is some doubt (see below) as to whether the tympanic is completely fused with the surrounding elements in the Santa Cruz *Promyrmephagus*.

The tympanohyal cannot be distinguished; it is, however, almost surely fused with surrounding elements in the shallow depression medial to the mastoid process.

Nothing can be seen of the pars petrosa in our material, except for a narrow strip anterior to the foramen lacerum posterius that is not covered by the bulla. The pars mastoidea is very well developed, and is broadly exposed both on the occiput and on the lateral side of the skull. The mastoid process is massive and rather short, situated laterally on the skull and sharply set off from the posterior crus of the tympanic by a wide and deep groove. The extent to which the squamosal participates in the process cannot be seen in the specimens. The lateral extension of the exoccipital beyond the condyle is well separated from the mastoid process.

The carotid foramen and canal occupy the same position as in the *Euphractus* group. The presence of the second arterial canal is uncertain; if present it was small and ran forward between the dorsal surface of the entotympanic and the ventral surface of the periotic. There is a small foramen lacerum medium at the anterointernal corner of the bulla. In other edentates the foramen ovale is situated well in advance of the bulla, and is hence outside the region under consideration. In *Peltephilus,* however, as Scott noted, it adjoins the bulla, being above and slightly in front of the opening for the Eustachian tube. There is no postglenoid foramen, but a number of vascular foramina occur in the dorsal surface of the squamosal. The mastoid foramen is in the usual position, and a very well defined groove runs ventrally from it. Some minor foramina, presumably vascular, are present around the posterior margin of the bulla. The foramen lacerum posterior is larger than in members of the *Euphractus* group. The stylomastoid foramen is slitlike and opens externally at the ventromedial extremity of the cleft between the meatus and the mastoid process.

The *Chlamytherium* Group

†Plaina Castellanos, 1937[10]

A magnificent skull of this form, referred tentatively to *Plaina subintermedia* Rovereto, has been available and is currently under study by A. G. Edmund. The specimen, FMNH P14424 (fig. 15A–B), comes from the Corral Quemado horizon, Catamarca, Argentina.

The tympanic and entotympanic (if this element was ossified) are missing in this specimen and in other skulls of chlamytheres thus far described (Castellanos, 1937; Bordas, 1939b; the bulla indicated in fig. 1 of this paper is the ventral surface of the periotic[11]). There can be no doubt that the tympanic was of the primitive, horseshoe-shaped type seen in such forms as *Priodontes* and *Dasypus,* and was, likewise, loosely attached by soft parts to the squamosal anteriorly and resting almost entirely on the tympanohyal posteriorly. The meatus faced laterally and was farther posterior to the glenoid cavity than in other armadillos, a point of resemblance to the glyptodonts.

The glenoid surface differs from that of other armadillos and strongly resembles that of the glyptodonts. The articular surface is at right angles to the long axis of the skull, narrow anteroposteriorly, wide transversely and gently convex in both these directions. A very large, U-shaped notch separates the glenoid articulation from the mastoid process; this is labeled as the glenoid cavity in Bordas's Figure 1. Between the glenoid surface and the auditory region proper there is a conspicuous, ventrally facing fossa within which the postglenoid foramen is situated. The fossa is separated from the auditory region by the thick ridge formed by

[10] [A. G. Edmund, who is reviewing the Pampatheres, tells me that *Plaina* will have to be abandoned, since its genus type is a synonym. *Vassallia* is the appropriate replacement generic name, the species being *V. maxima* Castellanos, 1946.]

[11] Bordas appears to have been influenced in his account of the auditory region of *Chlamytherium* by the works of Huxley (1865) and Burmeister (1870–1874) on glyptodonts. Van Kampen's correction of the errors made by these authors was apparently not available to him.

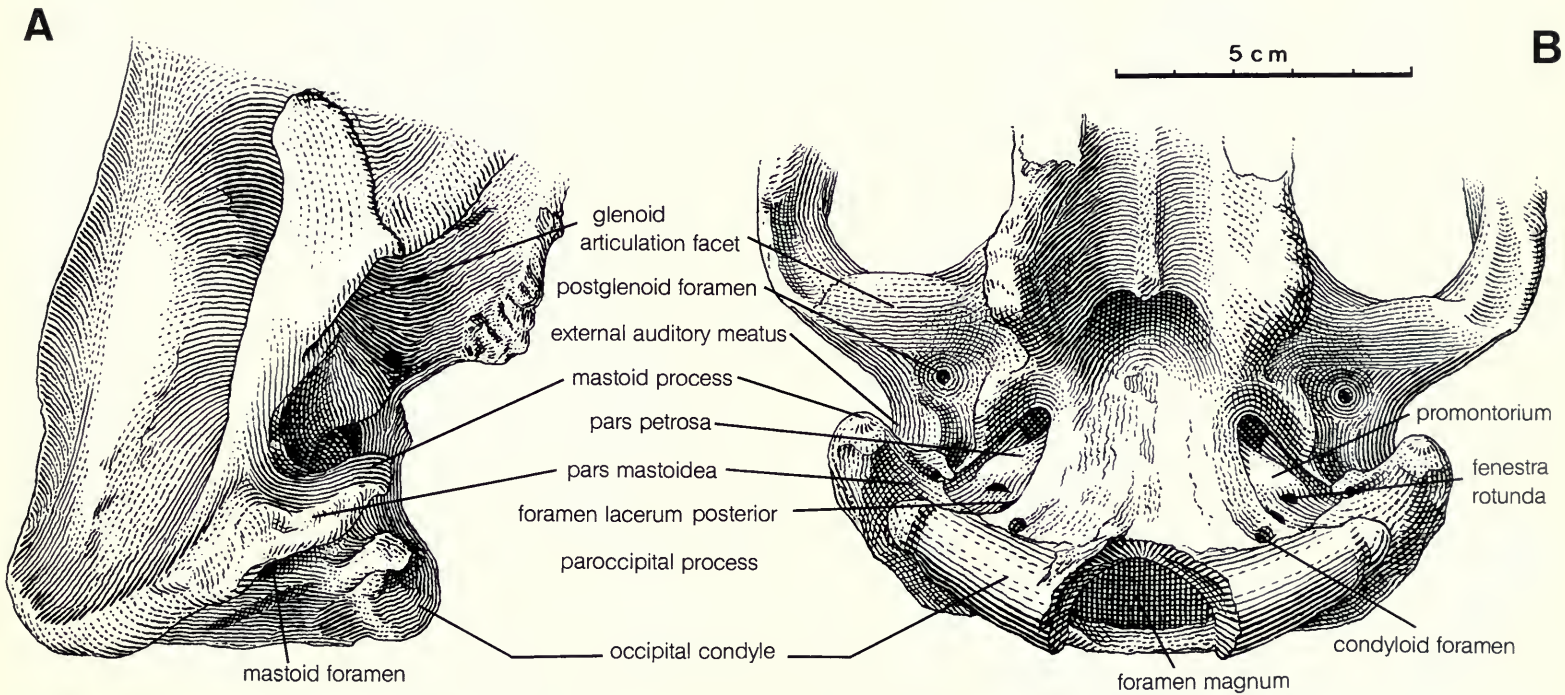

FIG. 15. *Plaina* cf. *subintermedia*, FMNH P14424: **A–B,** cranium shown in right lateral and ventral views.

the squamosal, which is so characteristic a feature of the Xenarthra. In the somewhat earlier, late Miocene *Kraglievichia,* this ridge would appear to have been more prominent than in *Plaina,* to judge from Castellanos's figure (1937, fig. 2).

The tympanohyal is present, although incomplete ventrally, on the right side of the skull. Here it projects medially, as a continuation of the crista facialis, as in other armadillos.

The promontorium is well rounded, and slopes evenly upward and forward to the rather sharp anterointernal tip [of the petrosal], which is, however, less pointed than in glyptodonts. There is a wide gap anteriorly between periotic [petrosal] and neighboring elements. Behind this promontorium and set off from it by a groove, the ventral surface of the pars petrosa forms a rather flat shelf. The fenestra rotundum ("fosa para el atrohial" in Bordas's figure) is situated in the posterior part of the promontorium just beneath the junction of promontorium and shelf. The recessus epitympanicus is comparable in degree of definition to those of other armadillos. There is no indication of an epitympanic sinus. The crista facialis has evidently been damaged somewhat, especially in its posterior portion, during the preparation of the skull from the very hard matrix that enveloped it. On the left side, part at least of the processus cristae facialis remains; the extremity is thick and blunt, much as in the glyptodonts. The pars mastoidea has a large occipital exposure and forms the ventrolateral corner of the occiput. The mastoid process (referred to as the postglenoid process by Bordas), nearly all of which is formed by the pars mastoidea, is a massive structure directed anteroventrally and terminating in a blunt tip. On the lateral side, near the junction of process and occipital crest, there is a prominent protuberance. As in *Priodontes,* and [as in that form] presumably correlated with large size, the paroccipital process is well developed—for an armadillo.[12] Situated immediately lateral to the condyle, it consists of a ventrally projecting knob of bone, which, again as in *Priodontes,* descends slightly lower on the side of the skull than the mastoid process. The two processes are separated by a deep and rather narrow cleft, considerably narrower than the corresponding one in Priodontes.

The internal carotid evidently entered the cranial cavity via the gap anterior to the periotic. Bordas identifies the lateral portion of this gap as the foramen ovale, but this is not the case; the foramen ovale opens farther forward, well within the alisphenoid, as in all edentates. The second arterial canal appears to have run forward, as usual, between the periotic and the basicranial elements. The postglenoid foramen is small and is situated within the fossa posterior to the glenoid articulation, as noted above; in glyptodonts the same foramen is similarly situated. The small subsquamosal foramen opens in a groove between the root of the mastoid process and the ridge that forms the upper border of the zygomatic process of the squamosal, a position precisely similar to that occupied by this foramen in glyptodonts. In *Chlamytherium* the subsquamosal is evidently larger than in *Plaina.* Bordas identified this as the porus, which is certainly not correct (the parts labeled as external auditory meatus and crista meati in his fig. 1 are evidently portions of the mastoid process). The mastoid foramen is in the usual position. The foramen lacerum posterior, as noted by Bordas, is relatively small. The facial nerve, after leaving the foramen stylomastoideum primitivum, ran ventrally in a groove in the medial surface of the mastoid process.

The general appearance of the auditory region and of the surrounding parts of the chlamythere skull, taken as a whole, is highly distinctive. The very broad, ventrally convex, tuberculate basis cranii with the periotics set well above it; the bluntly terminating processus cristae facialis; the close approximation of the mastoid process and exoccipital; the wide, transversely aligned glenoid surface and the zygomata that are so notably wider than the cranium; the fossa posterior to the glenoid surface, into which the postglenoid foramen opens; the relatively short basicranial region; the stout pterygoid processes—all these combine, as observed by Bordas, to form a whole that is decidedly glyptodont-like.

Glyptodontoids

Glyptodontidae

Available material of this group is limited in extent.[13] Fortunately, this lack is not particularly

[12] Large euphractines show no such development, but in these forms formation of a paroccipital process would appear to have been prevented by union of bulla and pars mastoidea immediately lateral to the occipital condyle.

[13] This was true when Patterson and Segall did the study; while still somewhat limited today, such materials are more abundant now than when that statement was

serious, since the glyptodont auditory region is stereotyped in comparison with the diversity encountered among armadillos and sloths. In this section, therefore, individual descriptions are not given and a general account only is presented, based on the following skulls (those in Field Museum's collections bear "P" prefix): *Propalaeohoplophorus australis* Ameghino, P13205, from the early Miocene Santa Cruz Formation of Patagonia; *Stromaphorus compressideus*[14] Castellanos (fide Hoffstetter, 1958) from the Andalgala Formation, Catamarca, Argentina; *Hoplophractus proximus* Moreno and Mercerat, P14501 (fig. 16A–B); and *Eleutherocercus solidus*[14] Rovereto, P14475 (fig. 17), both from the Corral Quemado formation, Catamarca, Argentina. [These last two skulls are nearly complete, and are deserving of additional study. For example, that of *Hoplophractus* preserves the right premaxillary, which is small and endentulous but has a pair of anteriorly directed pits, one dorsal to its tip, the other ventral and adjacent the midline. To me these suggest attachment surfaces for tendons of a proboscis. Gillette and Ray (1981) did not find a preserved premaxillary in any of their *Glyptotherium* material, but they conclusively inferred its presence on the basis of thickness and form of the adjacent bones.]

No trace of a tympanic or an entotympanic has yet been found in any glyptodont. Description of parts of the tympanic by earlier authors, Huxley (1865) and Burmeister (1870–1874), are now known to be erroneous and to have been based on misidentifications of other parts of the auditory region (see below). The tympanic very evidently was of the primitive horseshoe-shaped type, loosely attached to the tympanohyal posteriorly and to the squamosal ridge anteriorly; this ridge is more rounded and much more massive than in armadillos. Ridge and tympanohyal are well separated, and the incisura tympanica must therefore have been relatively wide. It is clear that the meatus was situated far behind the glenoid articulation, notably farther posteriorly than in all armadillos except the chlamytheres.

The glenoid articulation is highly characteristic of the group. It is very wide transversely and narrow anteroposteriorly, and stands out at a right angle to the skull. Posterior to and above the medial portion there is a large fossa [mandibular fossa] in which the postglenoid foramen (or foramina) is situated.[15] [Gillette & Ray (1981) show the mandibular fossa in their illustrations of *Glyptotherium taxonicum* and *Glyptotherium arizonae* (their figs. 7–8, 10b–c), but they make no mention of a postglenoid foramen. In both Field Museum specimens here described, that foramen opens into the fossa.] Glyptodonts differ from all armadillos, again with the exception of the chlamytheres, in the structure of this area.

The tympanohyal is best shown in our material on the left side of the skull of *H. proximus,* and even in this specimen the bone may not be complete ventrally. [Since this was written there has been further damage, so it is fortunate that the illustration, fig. 16B, was made at an earlier date.] As preserved, it is a relatively stout bar extending posterointernally from the crista facialis and pars mastoidea to the posterior portion of the ventral surface of the pars petrosa, where it comes in contact with a small spur from this surface.

The ventral surface of the periotic [petrosal] is extensive. The promontorium is not at all sharply defined, no more so than in the eutatines, which are outstanding among armadillos in this respect. Anterior to it is a laterally compressed anteroventromedially extending portion that terminates more sharply than in any armadillo. Medial and dorsal to this compressed portion is a shelf, varying in width in the different forms, that slopes down to a large quadrangular, somewhat irregularly surfaced area behind the promontorium. This area, which is much larger than in any armadillo, continues posterolaterally into the pars mastoidea. On the left side of *H. proximus,* above the medial extremity of the tympanohyal, the quadrangular area sends down a small, posteriorly curving process, with which the tip of the tympanohyal comes into contact. [This can now only be seen on the right side due to subsequent damage.] No such process is to be seen on any of the other specimens available to us, but a small structure of this sort

written. There is as yet undescribed new material from South America, and two significant published works considerably improve the situation for glyptodont cranial study: that of Vinacci Thul (1945) [which Patterson and Segall were unaware of], whose description of the skull appears to be the first serious attempt in that direction since Burmeister (1870–1874) and Owen (1845), and the more recent thorough and detailed monograph of the North American glyptodonts by Gillette and Ray (1981).

[14] [The species *compressideus* is a Moreno and Mercerat species that Ameghino (1891) denied belonged to the genus *Neuryurus,* where M. & M. had placed it. The species *solidas* was named by Ameghino (1891) and questionably assigned to the genus *Protoglyptodon.*]

[15] Several of Lydekker's plates (1894, pls. 8, 16, 22, 31–32) show the condyle of the jaw resting in this fossa and not in articulation with the glenoid surface.

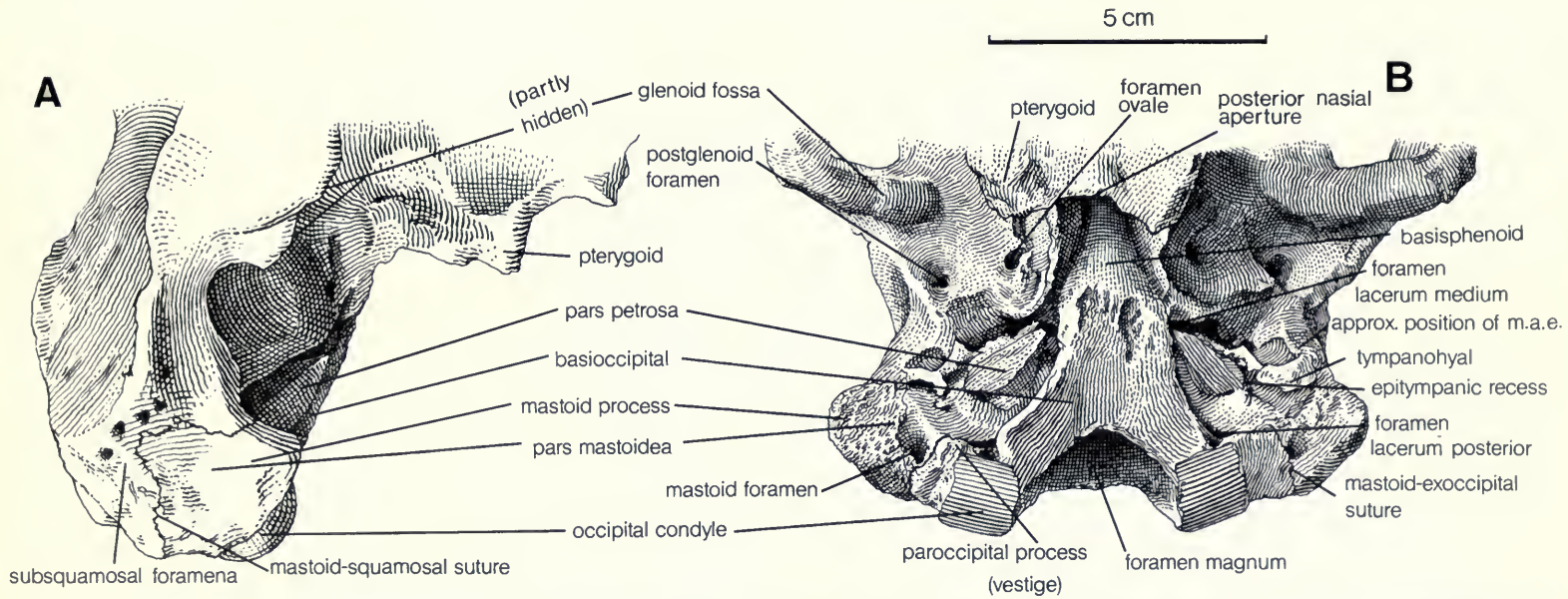

FIG. 16. *Hoplophractus proximus*, FMNH P14501: **A–B**, cranium shown in right lateral and ventral views. [The drawings are identified as glyptodont (lateral view) and *Plohophorus cuneiform*.]

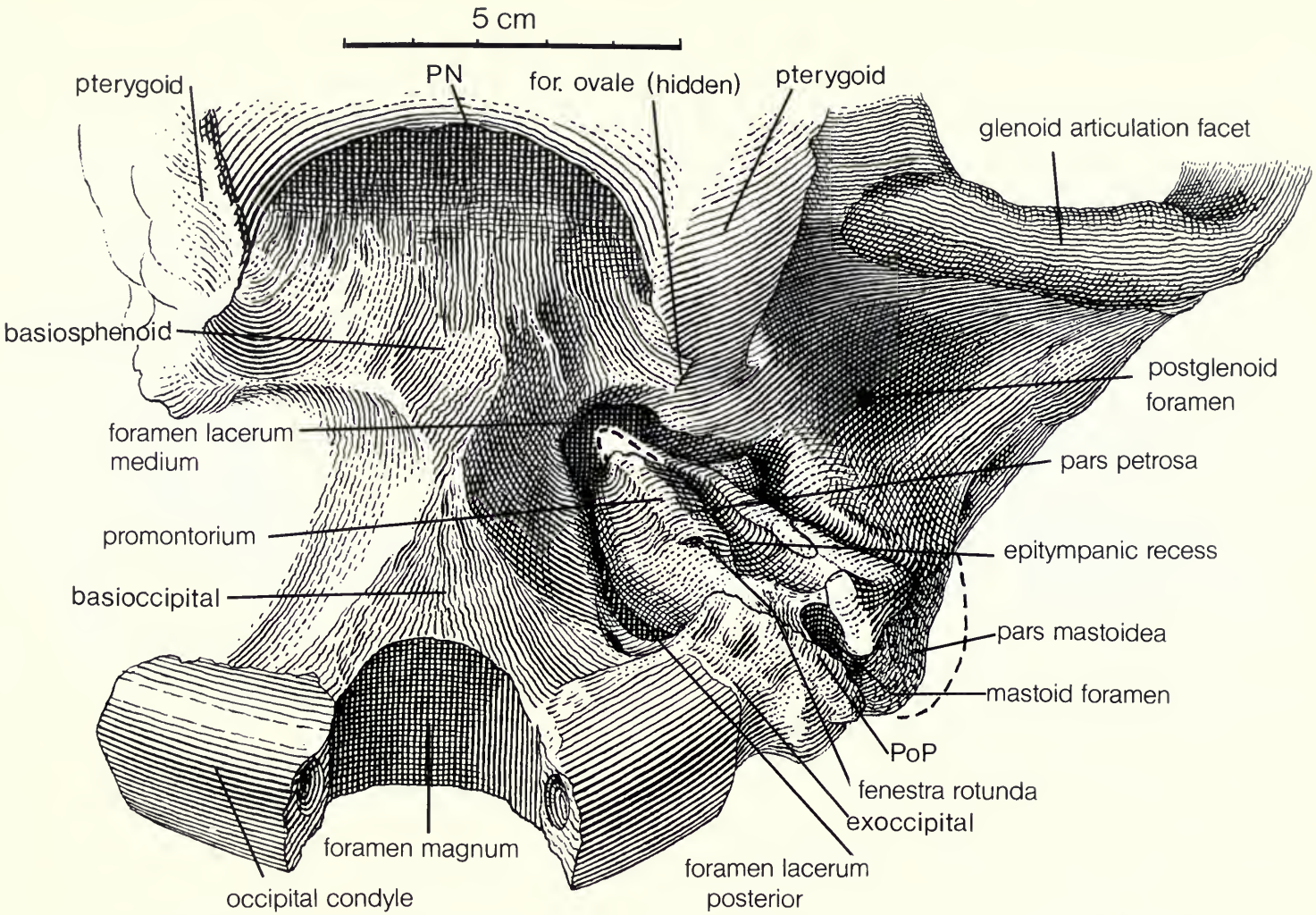

FIG. 17. *Eleutherocercus solidus* Rovereto, FMNH P14475: basicranium and left otic region of skull shown in ventral view. [The drawing was labeled *E. tucumanus*.]

would be very liable to damage during preparation. That it was characteristic of at least some of the later glyptodonts would appear to be demonstrated by Burmeister's figure of *Glyptodon* (1870–1874, pl. 23, fig. 5), in which the tympanohyal (p.t.) is shown fused to a small process from the periotic. Development of the epitympanic recess varies considerably within the family. In *Eleutherocercus* it is very small, no larger relatively than in *Plaina,* whereas in *Hoplophractus,* P14501, it is considerably larger, pear-shaped in outline, and very sharply defined. In accordance with van Kampen's (1905) findings, there is no indication of an epitympanic sinus.[16] The crista facialis has a more robust ventral margin than in armadillos. The processus cristae facialis is poorly preserved in our material; an anterior projection, representing part of it, at least, may be seen on the left side of *H. proximus,* and all specimens show a decided thickening of the crista lateral to and above the apertura tympanici canalis facialis. The pars mastoidea, although large, plays a relatively small part in the formation of the occipital surface, the greater part of its exposure being lateral where it forms the major portion of the mastoid process. The process is massive, comparatively long anteroposteriorly, directed laterally as well as anteroventrally, and short, not extending below the level of the condyle. That portion of the exoccipital lateral to the condyle is more extensive and rugose in most glyptodonts (but not in all; *Stromaphorus,* for example, has only a very slight lateral portion) than it is in most armadillos, although no paroccipital process in the strict sense is developed.

No details can be given concerning the courses of the arteries going to the circle of Willis. The postglenoid foramen (or foramina) is invariably present and opens at or near the base of the fossa posterior to the medial portion of the glenoid articulation. The subsquamosal foramen (or foramina), as in chlamytheres, is situated in the groove between the root of the mastoid process and the overhanging dorsal rim of the zygomatic process of the squamosal. The mastoid foramen usually opens ventrally near the mastoid-exoccipital suture. In some specimens, e.g., *E. solidus,* it is more dorsal in position, and a short, deep, narrow groove is present in the posterior portion of the pars mastoidea. The foramen lacerum posterior is relatively small and slitlike. After leaving the foramen stylomastoideum primitivum, the facial nerve ran ventrolaterally in a groove in the anteromedial surface of the mastoid process.

The earlier writers on glyptodonts, Owen (1845), Huxley (1865, pp. 55–56), and Burmeister (1870–1874), were all to varying degrees mistaken in their descriptions of the auditory region. Most of their errors have been pointed out and corrected by van Kampen, with whose interpretations we are in hearty agreement, but for the sake of completeness a brief report of them may be included here. Owen's account (1845, pp. 384–385) is a straightforward description of the structure seen in *Glyptodon,* which goes astray only in the identification of certain of the foramina. Thus, he mistook the mastoid foramen for a perforated depression for the digastric muscle, believed that the jugular vein went through the foramen lacerum medium (his foramen lacerum), and stated that the "wide apertures" (postglenoid foramina) in the "deep excavation behind the glenoid articulation . . . seem to comunicate with the tympanic cavity." Huxley (1865, pp. 55–56), who studied the same specimen described by Owen, correctly recognized that the jugular left the skull by the foramen lacerum posterius and that the postglenoid foramina did not, as Owen had supposed, communicate with the tympanic cavity but with the cranial cavity. Unfortunately, however, he conceived the idea that *Glyptodon* had a tympanic of *Euphractus* type and this led him into one error after another. He believed the mastoid process (Owen's "petromastoid below the digastric depression") to be a part of the tympanic, and this in turn led him to suppose that the paroccipital portion of the exoccipital included the pars mastoidea. He mistook the mastoid foramen (Owen's "perforated depression for the digastric") for the external auditory meatus, commenting, in some surprise, on so small a passage in so large an animal. The characteristic rugosities for muscle attachment on the ventral surface of the basicranium were stated to "mark the place where the thick inner walls of the bullae impinge upon the basioccipital." The basis for this last statement is hard to imagine, since in no armadillo, not even in the dwarfed *Chlamyphorus,* do the bullae encroach medially upon the basicranium. All these errors might have been avoided had Huxley selected an armadillo with an unspecialized auditory region, such as *Dasypus* or *Priodontes,* as his standard of comparison. Burmeis-

[16] The cavity in the squamosal described by Burmeister (1870–1874, pp. 15, 248, 253–254, 267, pl. 28, fig. 2r) is, we suspect, an excavation for the reception of a venous sinus. His passing mention of a connection between this cavity and the cavum tympani is, as van Kampen suspected, certainly erroneous.

ter (1870–1874, pp. 12–13, 255) correctly recognized that the tympanic was missing in the specimens studied by him. He supposed the tympanic to have been large, reaching to the exoccipital posteriorly (p. 255), whereas the position of the tympanohyal clearly shows that a gap existed between the two bones, as in *Priodontes* and *Dasypus*. As a result, he mistook the posterior portion of the sulcus facialis for the auditory meatus (pp. 18, 255; pls. 12, fig. 28, figs. 5–6i). Like Huxley, Burmeister was misled by comparing the glyptodonts with *Euphractus*. [Had Patterson and Segall been able to have the Gillette & Ray (1981) monograph before them, doubtless they would have commented on the basic similarities of the basicranium in South and North American forms. The few differences I see are minor: the presence of a postglenoid foramen in the South American forms, its apparent absence in the North American ones, and the degree of development of the paroccipital process (PoP). Gillette & Ray label one, while in this paper we comment that none is developed *in the strict sense* in *Hoplophractus*. This is really a difference in emphasis, for the details of the region as shown in their fig. 8 and in our fig. 16 are quite alike. In the FMNH specimen of *Eleutherocercus*, however, the paroccipital process is definitely a well-formed feature, being low, massive, and with a rugose surface.]

Summary and Conclusions

When Patterson left Chicago for Harvard, there was a Conclusions section to the original work, but it has not survived among any of the drafts or revisions that he had made. It is clear to me that he wanted to revise it further, but I do not know either the original content or anything about plans for its revision. I shall therefore here try briefly to set forth the points that seem to be most important as regards this portion of the whole study. Quoted material is taken directly from original text (descriptive sections).

1. For *Eutatus*, the postglenoid foramen is identified from its position and from its connection into the cranial cavity. Building upon this evidence, the posttympanic process is identified and the concluding point is made that "its presence adds another significant item to the list of resemblances between *Eutatus* and the Palaeanodonta drawn up by Simpson (1948, p. 88)." It is speculated, based upon location of a number of structures, that the tympanic was a simple [type?], "little or not at all advanced beyond the ring form, hence of the type that was certainly primitive for the Xenarthra and that persisted with little change to Pleistocene and Recent time in many sloths and armadillos, and, apparently in all glyptodonts."

2. For *Priodontes* it is expressly noted that the crista facialis gives origin to a delicate tripartite process that is characteristic of the Xenarthra as a whole, a feature not fully realized heretofore (p. 8) and for which the name *processus cristae facialis* is suggested.

3. For *Cabassous* new information on ossification of the entotympanic is presented in which rostral and caudal portions are described.

4. For *Tolypeutes* the degree of ossification of the entotympanic is intermediate between those of *Cabassous* and *Priodontes*. In most other respects *Tolypeutes* was found to be similar to *Cabassous*. As regards the degree of enclosure of the venous canal between squamosal and processus cristae facialis, *Priodontes, Cabassous,* and *Tolypeutes* "exhibit an interesting structural transition from open gap seen in the first to closed canal in the last."

5. For *Dasypus* the unique condition of the glenoid region among all other armadillos is stressed, and variation in degree of ossification of the entotympanic is described.

6. For *Stegotherium* the many features in which *Stegotherium* resembles *Dasypus* as noted by Scott (1903–1904) had suggested to him that the two were closely related. This work reinforces that conclusion.

7. For the *Euphractus* group, six genera are illustrated showing the basically similar morphologies for all. For the modern genera the suites of specimens included young and adults which enabled developmental data to be presented.

8. For the eutatines the description of the extraordinarily thick and dense tympanic of the later forms (*Doellotatus*) is a contribution significant in its contrast with the primitive condition seen in *Proeutatus*.

9. For the *Peltephilus* group, in Patterson and Segall's words, "the peculiarities of structure exhibited by these remarkable armadillos extend to the auditory region, the group being highly distinctive in the structure of this area." The bulla is complete, well inflated, with the tympanic forming a long tubular meatus as in Recent euphractines. The glenoid cavity is lower on the skull than in any other armadillo.

10. For the *Chlamytherium* group the glyptodont-like form of the auditory region and its immediate surrounding cranial area is stressed.

11. For the glyptodonts it is concluded that "the tympanic very evidently was of the primitive horseshoe-shaped type, loosely attached to the tympanohyal posteriorly and to the squamosal ridge anteriorly. . . ." Further, the glenoid articulation is characteristic for the group, being very wide transversely and narrow anteroposteriorly.

This section, comprising about half of the original, is the first and most straightforward of the two currently planned publications. It makes but a few suggestions for changes in the systematics of the cingulates (cf. Hoffstetter, 1958; Engelmann, 1985), and is notable for its depiction of the extent of diversity of morphology of the otic regions among the armadillos. In contrast, and equally striking, is the uniformity of that area in glyptodonts, a point stressed in the text. The few systematic changes that had been suggested by earlier workers, usually upon other grounds, are confirmed by the ear region structures. For the sloths (to be reported in the subsequent companion volume) there is far more uncertainty in this regard, and so the ear region study offers more and greater insights. However, discussions of those considerations, as well as any broad conclusions relating to the entire study, will await the publication of that second section of the work.

It is unfortunate that the extensive data set represented by this effort by Patterson and Segall was not published 25 to 30 years ago, for it would have provided a far broader base for others—such as Guth (1961), whose important study most closely parallels this one, MacIntyre (1972), Szalay (1972), Hunt (1974), Novacek (1977), Archibald (1977), Hunt and Korth (1980), Wible (1980, 1983), Gillette and Ray (1981), Engelmann (1985), and Wyss et al. (1987)—to have worked from. All of them worked with a broad comparative perspective as regards their several concerns with therian otic region development and evolution. Equally, it is a pity that Patterson and Segall were not aware of the Guth study, which probably was being prepared at about the same time as their early draft, or the Vinacci Thul study of *Glyptodon* (1945), which appeared about the time that they began this work, for both are directly pertinent. At this point, we can only move on, for the past is past. If the xenarthran stock is truly one of the basic early adaptive lines of the eutherians, as it appears now to be (McKenna, 1975; Hoffstetter, 1958; Wyss et al., 1987), then the better based our understanding of that group is, the more meaningful should be all broad extrapolations from it to the metatheria and to the various other stem eutherians. At least now, at this late date, this documentation for cingulate ear region morphology is finally available.

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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.

FMNH = Field Museum of Natural History, Chicago (prefix P indicates a paleontological specimen; numbers lacking a prefix indicate specimens in the Recent mammal collections).

MCZ = Museum of Comparative Zoology, Harvard University, Cambridge, Mass.

PU = Princeton University, Princeton, N.J.

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

ant. crus of tympanic = anterior crus of tympanic

can. a. car. int. = canal for internal carotid artery

can. a. ? = arterial canal ?

can. int. pet. sin. = canal internal the petrosal sinus

eust. = opening for Eustachian tube

fen. r. or fen. rotunda = fenestra rotunda (= fen. cochleae)

f.l.m. = foramen lacerum medium (= entocarotid foramen)

f.l.p. = foramen lacerum posterior

m.a.e. = meatus auditorius externus

PoP = paroccipital process

post. crus of tympanic = posterior crus of tympanic

PN = posterior nasal aperture

p.t. = processus tympanohyal.

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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