Chapter 14

The Basicranial and Posterior Cranial Anatomy of the Families of the Toxodontia

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ABSTRACT

The basicranial and posterior cranial anatomy of the extinct suborder Toxodontia (order Notoungulata) is described using representatives from the five constituent families, Isotemnidae, Homalodotheriidae, Leontiniidae, Notohippidae, and Toxodontidae. New traits of intratympanic anatomy in toxodontians are identified. Based on observations presented here, some previous anatomical interpretations are clarified or corrected. The morphology of the bulla does not imply a compound bony origin; it is apparently comprised solely of ectotympanic bone. Additionally, previous osteological evidence offered to support the presence of an internal carotid artery could not be confirmed, leaving open the question of the source of intracranial blood supply.

INTRODUCTION

The focus of this paper will be the description of the external and internal anatomy of the ear region and posterior cranium of toxodontian notoungulates. The suborder as currently constituted was defined by Simpson (1967), who merged the former entelonychians with the toxodontans, and includes the families Isotemnidae, Homalodotheriidae, Leontiniidae, Notohippidae, and Toxdontidae (Simpson, 1967; McKenna and Bell, 1997). Simpson (1967) used Toxodonta, Scott's (1905) name for the suborder; more recently Toxodontia, Owen's (1853) name for the order, has been used at subordinal rank (McKenna, 1975; Mones, 1987; McKenna and Bell, 1997).

The scope of the paper has been arbitrarily limited to anatomical description because of length constraints. The work presented here forms the basis of a detailed character analysis that will be used to assess phylogenetic affinities of the toxodontians. Comparative assessment of other notoungulates and pertinent outgroups will be presented in the character analysis of a second manuscript in preparation.

Santiago Roth published a work in 1903 on South American ungulates in which he dealt extensively with notoungulates. Roth (1903) focused on the comparative anatomy of the temporal bone of notoungulates with respect to other ungulate orders. (Note: "temporal bone" was Roth's designation and stems from the fact that his frame of reference for the study began with human anatomy.) A large "auditory chamber" on the posterodorsal aspect of the cranium was identified and its homology to the mastoid antrum of human anatomy was specified by the name it was given, the pars mastoidea. This structure is, as Roth suspected, a unique structure in notoungulates, but it is more accurately named the squamosal epitympanic sinus (Klaauw, 1931). It is not homologous with the mastoid antrum in humans, which is formed by inflation of the pars mastoidea of the petrosal. In a survey of other South American ungulates, such as litopterns and astrapotheres, Roth did not discover any comparable feature of the posterior cranium. The "true" mastoid was designated as the protuberancia petrosa; his description of the position of the protuberancia petrosa doubtless describes an occipital exposure of the mastoid (Roth, 1903: 12). Roth argued that the pars mastoidea (epitympanic sinus) is a structure that developed independently from the rest of the cranium, although he admitted

that it had been difficult locating a suture that separated it from the squamosal and parietal in most notoungulate genera.

In 1912, Scott presented results from the Princeton-Patagonia Expeditions of 1896–99. These included monographic treatments of two suborders, the Toxodonta (Notohippidae, Leontiniidae, Toxodontidae) (Scott, 1912a) and the Entelonychia (Notostylopidae, Isotemnidae, Homalodontotheriidae) (Scott, 1912b), subsumed under the order Toxodontia (= Notoungulata Roth). Scott concurred with Roth's findings about the pars mastoidea (epitympanic sinus of the squamosal) of notoungulates and noted that its expression in toxodontans was not as impressive as that observed in hegetotherian typotheres. He commented on its condition in toxodontans (Scott, 1912a: 113) by noting that the pars mastoidea made a larger contribution to the occiput than it did in other notoungulates.

Scott's (1912a, 1912b) interpretation of the auditory region of toxodontians is complicated. Roth's protuberancia petrosa, which Roth designated on the occiput, was misconstrued as the crista tympanica of the external auditory meatus. The crista tympanica is composed of ectotympanic, not petrosal. The styloid process was also misidentified as the stylohyal. The styloid process, which is typically at the anteromedial aspect of the auditory region, serves as an attachment for muscles of the nasopharynx. The stylohyal, on the other hand, is the secondmost proximal ossification of the hyoid apparatus, which attaches to the skull posterolateral to the auditory region. Based on the anteromedial designation of the stylohyal, Scott noted the difference between its anteromedial position in toxodontans and the posterolateral position of the stylohyal in typotheres. The hyoid recess was also misidentified as the stylomastoid foramen. These two features are posterior to the auditory meatus, but the hyoid recess is medial and the stylomastoid foramen is lateral.

Without doubt, the works of Bryan Patterson during the 1930s, when he was at the Field Museum, represent the largest contribution to our knowledge of toxodontian auditory anatomy. Patterson became interested in the auditory regions of typotherian, entelonychian, and toxodontan notoungulates

while curating the collection from the First Marshall Field Paleontological Expeditions to Argentina and Bolivia. The first paper (Patterson, 1932) was a compilation of detailed anatomical descriptions of the external basicranial and occipital anatomy of eight genera. In this paper, Patterson aimed to demonstrate that these South American ungulates were similar to other ungulates (artiodactyls were most frequently cited): ''The result of the studies presented . . . shows that they present no very radical differences from other ungulates'' (Patterson, 1932: 5). Patterson's comparative work was limited and there is no sense of how anatomical traits were distributed among ungulate taxa versus notoungulate taxa only. Nevertheless, Patterson was able to generate a list of characters that were common to all the notoungulates that he studied. The list of traits included an inflated bulla, a tubular auditory meatus (presumably meaning an *ossified* tubular meatus), an epitympanic sinus, a deep hyoid recess posterolaterally placed, invariant position of the stylomastoid foramen between the tubular meatus and the posttympanic process of the squamosal, a styliform process at the anteromedial corner of the bulla, little or no occipital exposure of the mastoid, and a prominent, ventrally projecting crest on the tubular meatus.

In addition, Patterson (1932) cleared up several misinterpretations made by Roth (1903) and Scott (1912a, 1912b). He corrected Roth's identification of the epitympanic sinus as the mastoid and the mastoid as the protuberancia petrosa, but noted that Roth (1903) had accurately identified the tubal meatus as being of (ecto)tympanic origin.

Patterson clarified Scott (1912a) in which the mastoid, hyoid position, and stylomastoid egress in toxodontians were misidentified. He redesignated Scott's stylohyal as the styliform process and then designated the feature previously named the stylomastoid foramen as the hyoid recess. In addition, he pointed out that Scott's description of the mastoid was, in fact, that of the tubular auditory meatus, which is of tympanic origin.

Patterson continued to publish his research on various notoungulates. Most of this concerned cranial anatomy (Patterson, 1934a,

1934b, 1934c; Patterson, 1935; Riggs and Patterson 1935). Throughout, he maintained the list of characters that he had published in 1932 as the comparative standard. Then, in 1936, Patterson published a paper that dealt specifically with the intratympanic anatomy of some notoungulate crania in the Field Museum collection. This was the first attempt to gather phylogenetically pertinent data from the middle ear region of a notoungulate taxon.

Patterson's (1936) study included members of Typotheria, Toxodonta, and Entelonychia, although *Homalodotherium* was the only taxon representing Entelonychia. When feasible, Patterson (1936) identified a route for the internal carotid system. In all taxa except the typotherian *Hegetotherium*, he designated a posterior carotid foramen that was confluent with the posterior lacerate foramen and an anterior carotid foramen situated anteromedially within the tympanic cavity very near the opening (called a ''foramen'' by Patterson) for the auditory tube.

Another important finding reported by Patterson (1936) concerned the anatomy of bullar septa in typotherians, toxodontans, and entelonychians. He reported a vertical septum, or its putative vestiges, in the typotherian taxa. On the other hand, a horizontal septum was described for toxodontans and entelonychians (i.e., *Homalodotherium*). Patterson cited Klaauw (1931) to support his argument that the typotherian condition indicated that the bulla was compound, i.e., it was made up of ectotympanic and entotympanic elements. He went on to suggest that the septum in toxodontans and entelonychians was homologous to the one in the typotheres. ''Provided that this small ridge is not a neomorph, it is homologous with the [typotherian] septum since in that family (the typotheres) the hypotympanic sinus is lateral to the tympanic cavity and the septum consequently vertical, while those forms in which the septum is horizontal the hypotympanic sinus is below the tympanic cavity. The large size of the hypotympanic sinus in the Toxodonta and *Homalodotherium*, and its sharp demarcation from the tympanic cavity, could be regarded as evidence that it was formed by a separate element'' (Patterson, 1936: 222–223).

Patterson (1977) revised his previous list of notoungulate characters to include the presence of a hypotympanic sinus, as well as some primitive traits such as the Eustachian tube at the anterior pole of the tympanic cavity and the presence of cranial venous sinuses anterior to the squamosal. Notably, he changed his opinion concerning the occipital exposure of the mastoid, deciding instead that it was too small to contribute to the occiput. Patterson cited Simpson's (1936) study of *Oldfieldthomasia* as evidence that the element designated as the mastoid in *Rhynchippus* and *Homalodotherium* was, in fact, adventitious bone that overlay the true mastoid.

Since Patterson's studies, no additional work on the notoungulate ear region has been published. His work has remained the standard with respect to notoungulate auditory anatomy and has been incorporated wholly into subsequent systematic analyses (e.g., Cifelli, 1993). While Patterson's contribution was authoritative, advances in morphological analysis and the discovery of additional fossil specimens provide the opportunity to re-examine the auditory anatomy of toxodontians for new anatomical and systematic information.

MATERIAL AND METHODS

Currently, the suborder Toxodontia includes the families Isotemnidae, Notohippidae, Leontiniidae, Homalodotheriidae, and Toxodontidae (Simpson, 1967; McKenna and Bell, 1997). Table 14.1 lists the specimens from each family used to generate the anatomical descriptions. Juvenile or ''young'' specimens of *Toxodon* housed at the Museo de la Plata, La Plata, Argentina were also examined; however, their ear regions were unprepared, which confined observations to external features. Young adult specimens of *Nesodon* (FMNH P13105) and *Andinotherium* (FMNH P13110) at the Field Museum of Natural History, described in Patterson (1936), were included in this work. With a few exceptions, only the tympanic side of the petrosal was prepared in specimens for which permission to prepare was granted. No attempt was made to exhume wholly the petrosal from the cranium in the study specimens. Descriptions of petrosal aspects other than the tympanic side are drawn from iso-

TABLE 14.1
Toxodontian Taxa Used in this Analysis
All locations are in Argentina.

Taxon	Specimen number	Locality
Family Isotemnidae		
Pleurostylodon sp.	MLP 74-IV-27-1	Casamayoran, Colhuehuapí, Chubut
Periphragnis sp.	MLP 69-III-24-286	Mustersan, La Gran Hondonado, Chubut
Family Notohippidae		
Puelia sp.	MLP 67-II-27-27	Mustersan, La Gran Hondonado, Chubut
Rhynchippus equinus	FMNH P13420, P13410	Deseadan, Cabeza Blanca, Chubut
Family Leontiniidae		
Leontinia gaudryi	FMNH P13285	Deseadan, Cabeza Blanca, Chubut
Ancylocoelus frequens	AMNH 29595, 29614	Deseadan, Puerto Deseado, Chubut
Scarrittia canquelensis	FMNH P14715	Deseadan, Scarritt Pocket, Lopez
Family Homalodotheriidae		
Homalodotherium segoviae	FMNH P13092	Santacrucian, Santa Cruz Fm., Santa Cruz
Family Toxodontidae		
Adinotherium robustum	AMNH 9532	Santacrucian, Coy Inlet, Santa Cruz
Adinotherium ovinum	FMNH P13110, P13109	Santacrucian, Coy Inlet, Santa Cruz
Adinotherium sp.	FMNH P13231	Santacrucian, Rio Coyle, Santa Cruz
Nesodon imbricatus	AMNH 9292	Santacrucian, Halliday Estancia
	FMNH P13105	Santacrucian, Rio Coyle, Santa Cruz
	FMNH P13227	Santacrucian, Coy Inlet, Santa Cruz

lated petrosals or from crania that permitted access to the other surfaces. The description of the petrosal as a tetrahedron, comprising tympanic, cerebellar, mastoid, and squamosal aspects, follows MacIntyre (1972). Foramina are described in the context of bones with which they are associated. Names assigned to foramina are based on positional and morphological criteria derived from observation and anatomical literature. When appropriate and possible, nomenclature for the descriptions follows the Nomina Anatomica Veterinaria, 4th ed. (World Association of Veterinary Anatomists, International Committee on Veterinary Gross Anatomical Nomenclature, 1994). A short discussion about the cranial vascular anatomy of toxodontians follows the anatomical descriptions. Space limitations did not permit the illustration of all auditory traits. Illustrations were chosen to maximize the number of traits shown.

DESCRIPTION

BASICRANIAL AND OCCIPITAL ANATOMY

ECTOTYMPANIC: The ectotympanic bone forms the auditory bulla and the external au-

ditory meatus (EAM). It forms the bulla by expanding and inflating the medial edge (i.e., the edge medial to the attachment of the tympanum) toward the occipital bone; similarly, it expands, but does not inflate, the lateral edge to form the external auditory meatus. The bulla is roughly oblate and the EAM is tube-shaped (figs. 14.1, 14.2).

The balloonlike bulla covers the tympanic surface of the petrosal. The ventral and medial expansion and inflation of the ectotympanic to form the bulla is accomplished via a broad aditus ventral to the petrosal. Thus, the septum described by Patterson (1936) appears to be the medial margin of the ectotympanic, which, due to ventromedial inflation, recurves on itself laterally and dorsally (fig. 14.3). This ectotympanic septum divides the bulla into hypotympanic and tympanic cavities as observed by Patterson. The bulla does not fuse to the lateral edge of the occipital bone along the region of the basicochlear fissure; however, the ectotympanic overlaps the sphenoid rostromedially and the occipital posteromedially (fig. 14.1). The ectotympanic also touches the rostral surface of the jug-
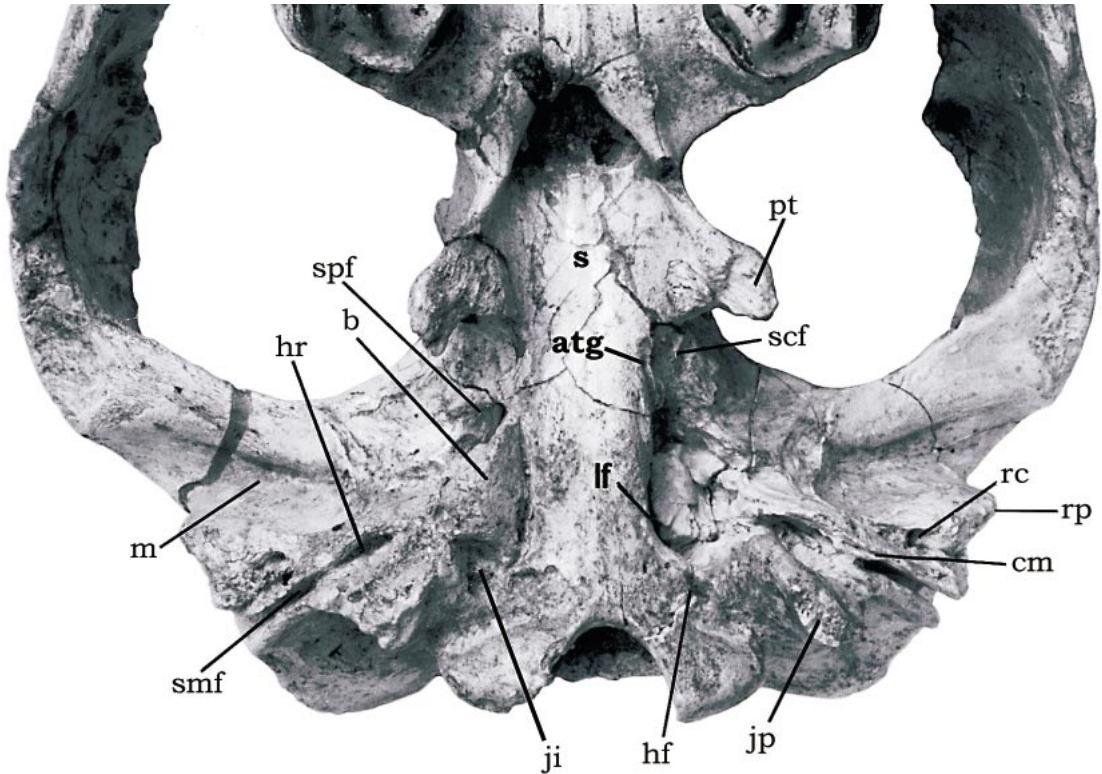
Fig. 14.1. *Periphragnis* sp. (MLP 68-III-24-286). Basicranial view. Rostral toward top of page. Abbreviations: **atg,** groove for the auditory tube; **b,** bulla; **cm,** crista meatus; **hf,** hypoglossal foramen; **hr,** hyoid recess; **ji,** jugular incisure; **jp,** jugular process; **lf,** lacerate foramen; **m,** mandibular fossa; **pt,** pterygoid hamulus; **rc,** retroarticular canal; **rp,** retroarticular process; **s,** sphenoid; **scf,** scaphoid fossa; **smf,** stylomastoid foramen; **spf,** sphenotympanic fissure.

ular process and the exoccipital component of the occipital bone, posterolateral to the jugular incisure.

There is no structural evidence in any of the taxa that permits the identification of a separate bony element contributing to the bulla in addition to the ectotympanic. Klaauw (1931) defined entotympanics as features of the ventral bulla that are ontogenetically independent of other bullar elements, though some entotympanics developed from cartilage associated with or near the Eustachian tube or the tympanohyal. Klaauw (1931: 210) described the anatomy thus, ''The septum bullae always shows a free upper margin, the rostral, under, and caudal margins being attached to the bulla.'' Though Klaauw's description implies a vertical septum, Patterson (1936) considered the presence of the horizontal septum in toxodon-

tians as support for a compound bulla made up of ento- and ectotympanic elements. Based on the cross-sectional structure of the ectotympanic bulla and the absence of anatomical features that can be associated with an entotympanic, it is tentatively proposed here that the bulla of toxodontians is composed only of ectotympanic bone. Figure 14.3 illustrates a working hypothesis that could account for the presence of a septum through the inflation of the ectotympanic alone. Ontogenetic sequences would be required to determine definitively whether an entotympanic element contributed to the bulla of toxodontians.

There are several distinct features on the ventral surface of the ectotympanic bone. One, along the anterolateral aspect of the bulla, is a linear rugosity of unknown function, if any. It is present in *Periphragnis*,
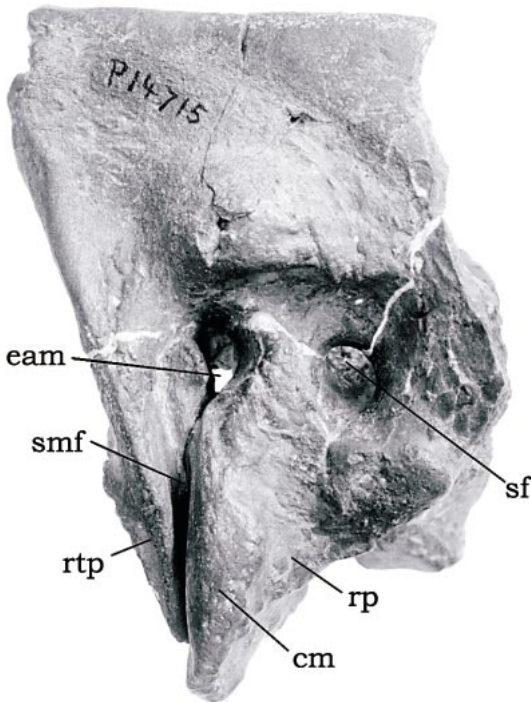
Fig. 14.2. *Ancylocoelus frequens* (FMNH P14715). Lateral view of right ectotympanic-squamosal fragment. Dorsal toward top of page; rostral to right. Abbreviations: **cm,** crista meatus; **eam,** external auditory meatus; **rp,** retroarticular process; **rtp,** retrotympanic process; **sf,** suprameatal foramen; **smf,** stylomastoid foramen.

Homalodotherium, and possibly *Rhynchippus*. In *Leontinia* and the toxodontids, this rugosity is replaced by the anterolateral ectotympanic plate. A styliform process juts anteromedially from the plate on *Homalodotherium*. On the ventral surface of the EAM is a small crest termed the meatal crest of the external auditory meatus (fig. 14.2). Immediately rostral to the jugular process (paroccipital process), the ectotympanic bone forms the rostral wall to the hyoid recess, which houses the articulation between the tympanohyal and the stylohyal. The stylomastoid foramen, which transmits the facial nerve, is wedged between the posterior face of the EAM and the retrotympanic process of the squamosal. It is posterolateral relative to the hyoid recess (figs. 14.1, 14.2). A posterior carotid foramen piercing the bulla was not found in any of the specimens studied.

The opening for the auditory (Eustachian) tube is formed ventrally by the bulla and dorsally by the sphenoid complex. As usual, it passes anteromedially in a gutter on the sphenoid bone.

Only the squamosal-ectotympanic fragment of *Scarrittia* shows the medial, or intratympanic, aspect of the ectotympanic. In this specimen the tympanic sulcus and the tympanic annulus, which suspended the tympanum, are well preserved.

SQUAMOSAL: The ventral surface of the squamosal comprises the zygomatic process, the mandibular (glenoid) fossa, the retroarticular (postglenoid) process, the retroarticular (postglenoid) foramen, and the retrotympanic (posttympanic) process (fig. 14.4). In addition, the medial edge of the squamosal, rostral to the bulla, makes a small contribution to the lateral wall of the Glaserian fissure, which gives passage to the chorda tympani nerve. The fissure is defined largely by the sphenoid, which is described below. The zygomatic process is unremarkable. It meets the jugal about midway along the length of the zygomatic arch. The mandibular fossa is wider transversely than sagittally. The retroarticular process is distinct. In toxodontians, with the exception of *Pleurostylodon*, the retroarticular process is large and becomes associated with the anterior wall of the EAM (fig. 14.2). The retroarticular foramen is in the usual place, i.e., on the posterior wall of the retroarticular process, and opens ventrally between the process and the EAM. The condition in *Puelia* is remarkable in that there is a groove in the posterior aspect of the retroarticular process that leads ventrally from the retroarticular foramen. There was no identifiable retroarticular foramen found in the squamosal-ectotympanic fragment attributed to *Ancylocoelus*. In all other toxodontians except *Pleurostylodon* and *Puelia*, the fusion between the large retroarticular process and the EAM encloses the retroarticular foramen in a canal (fig. 14.1). Based on anatomy of *Bos* and *Equus*, this canal is thought to convey the dorsal cerebral vein or its emissary (Sisson, 1975). *Leontinia* presents a problematic morphology in this regard: the retroarticular process fuses medially but not laterally with the EAM, leaving a laterally facing sulcus for the pas-
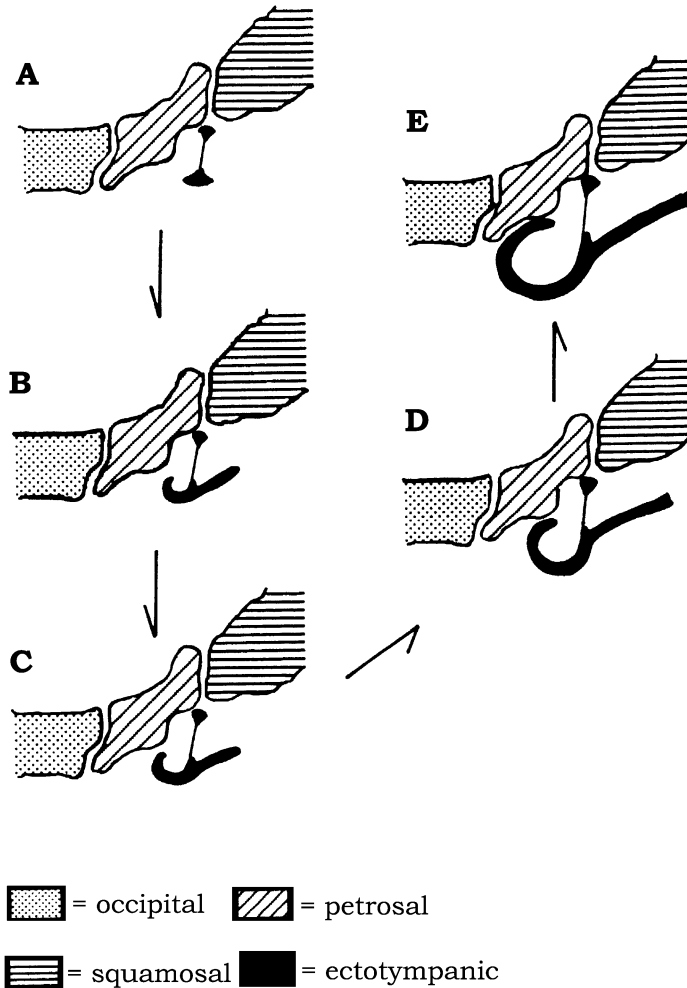
Fig. 14.3.   Schematic representation of the interpretation of ectotympanic bulla development. Cross-section through the ventral cranium, midline of the petrosal. Stippling indicates (basi)occipital; diagonal lines indicate petrosal; horizontal lines indicate squamosal; solid black indicates ectotympanic. **A,** ring-like ectotympanic supports tympanum; **B,** medial and lateral edges of ectotympanic develop; **C,** medial edge begins to inflate beneath ventral surface of petrosal and lateral moiety begins to expand, forming external auditory meatus; **D,** ventral inflation proceeds faster than medial edge development, causing appearance of medial recurving; **E,** ectotympanic bulla covers petrosal, recurved medial edge of ecto-tympanic lies ventral to, but does not fuse with, petrosal, giving appearance of septum.

sage of veins. It is possible this is an artifact of preservation. The retrotympanic process is larger than the retroarticular process. It also has greater ventral extent than the latter. Together the retroarticular and retrotympanic processes form the rostral and caudal boundaries, respectively, of a trough that cradles the EAM (fig. 14.2).

From lateral view, the mandibular fossa has a sigmoid outline. The anterior part of the fossa is convex ventrally; the posterior part is concave ventrally. The difference in size between the retroarticular and retrotympanic processes is most noticeable from this view. The EAM has variable relationships with respect to the mandibular fossa in the taxa included in this study. In *Rhynchippus*, the leontiniids, and the toxodontids, there is a suprameatal foramen dorsorostral to the EAM (fig. 14.2). The suprameatal foramen is
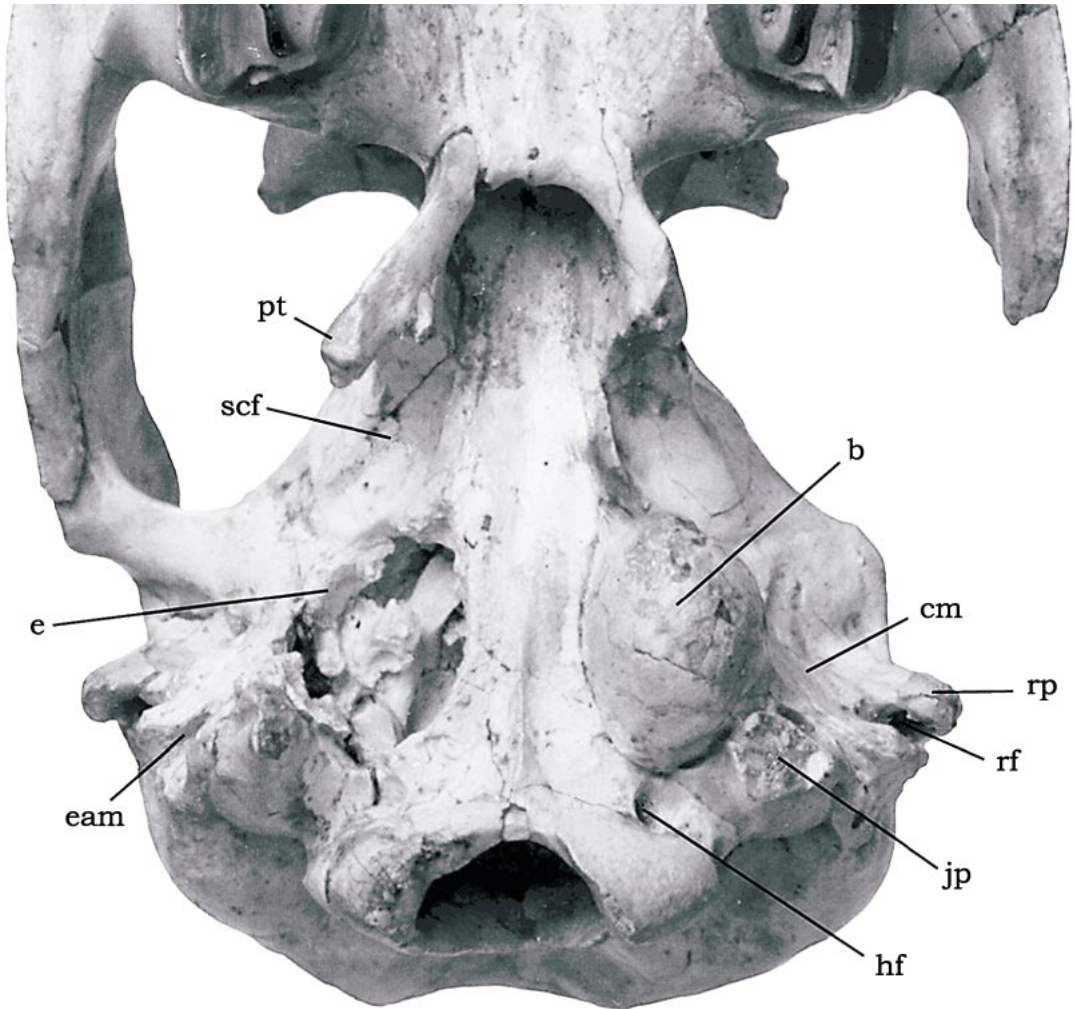
Fig. 14.4. *Puelia* sp. (MLP 67 II 27 27). Basicranial view. Rostral toward top of page. Abbreviations: **b,** bulla; **cm,** crista meatus; **e,** ectotympanic; **eam,** external auditory meatus; **hf,** hypoglossal foramen; **jp,** jugular process; **pt,** pterygoid hamulus; **rf,** retroarticular foramen; **rp,** retroarticular process; **scf,** scaphoid fossa.

continuous most likely with the temporal meatus (described below) and the retroarticular canal. Dorsally, two prominent features can be observed: a bulge in the posterior part of the squamosal that represents the epitympanic sinus (ETS) and variable numbers of fenestrations along the sutural boundary between the squamosal and parietal bones. The ETS is observed to be in communication with the tympanic cavity via a pneumatic foramen that opens into the epitympanic recess in ectotympanic-squamosal fragments assigned to *Scarrittia* and *Ancylocoelus*. The

function of the ETS is not known, though epitympanic sinuses are common in mammals (Klaauw, 1931; MacPhee, 1981). Since there is communication between the ETS, the tympanic cavity, and the hypotympanic cavity, the three spaces could play a functional role in hearing frequency range; however, this line of research is beyond the scope of this study.

The morphology of the ETS in toxodontians (in fact, in all notoungulates) is unique among mammals because it lies in the posterior and dorsal part of the squamosal. More

commonly, the ETS is located in the lateral or anterolateral part of the squamosal, as in *Orycteropus* (Klaauw, 1931). The interior of the sinus, in the specimens permitting access, is invariably hollow. Other dorsal squamosal features are the parietal-squamosal fenestrations, which convey veins from the temporal region to the cerebral veins.

Also present on the dorsal aspect of the squamosal, near the beginning of the zygomatic process, is a distinct and, in most cases, large temporal meatus. It is confluent with the retroarticular foramen and was probably involved in draining the temporal fossa along with the parietal-squamosal fenestrations mentioned above. The temporal meatus is not present in *Pleurostylodon*.

SPHENOID: The sphenoid complex has a number of features similar to those seen in other ungulates (fig. 14.1). The sphenoid in toxodontians is shortened anteroposteriorly, a condition that is commonly observed in horses, cows, pigs, fossil artiodactyls, and fossil tapirs, to name a few. This may be related to the enormous growth of the palatal region concomitant with herbivory. The pterygoid bones are present on the lateroventral aspects of the sphenoid complex. On the posterior aspect of the pterygoids, fanning out onto the sphenoid, there are distinct triangular depressions. Two low crests, one curving posterolaterally and the other posteromedially from the hamulus, demarcate each depression. These fossae are interpreted as the origins of the tensor veli palatini muscles, which raise the soft palate. There is no nomenclature for this feature in extant ungulates, which lack distinct osteological markers for this origin. The fossa will be referred to as the scaphoid fossa in reference to its shape (fig. 14.4). Its morphology is unusual, as it requires the tendon of the tensor palatini muscle to pass ventrally in a groove that splits the pterygoid hamulus instead of passing laterally to the hamulus as is the case in extant ungulates (Sisson, 1975; Nickel et al., 1983). Medial and posterior to the medial crest of the fossa is the groove for the auditory tube.

The posterior border of the sphenoid participates in the formation of the sphenotympanic fissure, as well as providing all but the lateral wall of the Glaserian fissure (fig. 14.1). (Note: the N.A.V. designates the Glas-

erian fissure as the petrotympanic fissure; unfortunately, this does not describe precisely the bony relationships in ungulates and so the eponymous name for the exit of the chorda tympani nerve is preferred here.) A comment on the morphology of the sphenotympanic fissure is required. Based on the anatomy of extant ungulates, the piriform fenestra is actually part of a single large lacerate foramen that curves around the petrosal medially and rostrally. The lacerate foramen results from loss of the two cartilaginous commissures that attach the petrosal medially to the developing basicranium (De Beer, 1937). In study specimens where the bulla is missing or has been removed, this same condition of the lacerate foramen is observed. When the bulla is present, there appears to be a distinct piriform fenestra. This large teardrop-shaped opening is actually ventral to the position of the former piriform fenestra and is a superficial feature in toxodontians, formed by bullar overlap of the sphenoid. Therefore, the term ''sphenotympanic fissure'' will be used to describe this feature. In toxodontians, the sphenotympanic fissure is thought to convey the mandibular branch of the trigeminal nerve (as there is no oval foramen), nerves of the pterygoid canal, and any derivative of the internal carotid artery, if one existed. Contrary to Patterson (1936), no anterior carotid foramen was found in any of the taxa. This is consistent with the presence of the large lacerate foramen, since the anterior carotid foramen would have been formed by chondrocranial commissures, the absence of which formed the confluent lacerate foramen.

OCCIPITAL: The occipital bone does not present any radical departures from that observed in most ungulates (figs. 14.1, 14.5). From a ventral perspective, two large tuberosities occupy either side of the midline; they serve as the insertion for the long head muscles. A single, large hypoglossal foramen is in the condylar fossa, opposite the jugular incisure (posterior lacerate foramen). The jugular incisure probably conveyed the internal jugular vein as it does in extant ungulates. Posterolateral to the hypoglossal foramen is a robust jugular process (paroccipital process). The occipital complex makes up the basal, median, and caudodorsal part of the occiput. The parietal and squamosal con-
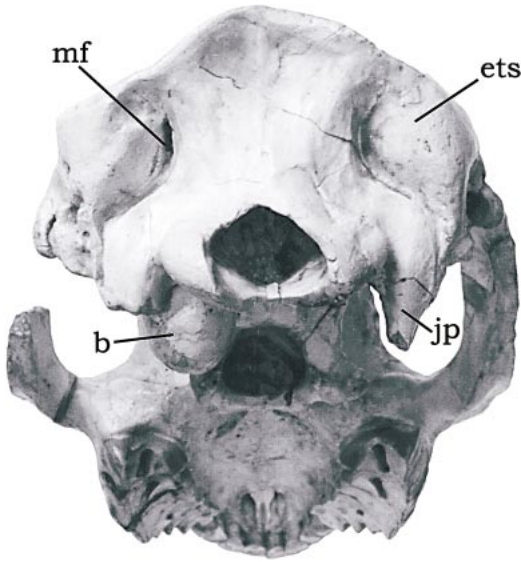
Fig. 14.5.   *Puelia* sp. (MLP 67 II 27 27). Occipital view. Abbreviations: **b,** bulla; **ets,** epitympanic sinus of the squamosal; **jp,** jugular process; **mf,** mastoid foramen.

tribute the superior and lateral portions. From caudal view, the occiput is very broad. The ETS causes the squamosal to bulge prominently on the lateral and dorsal aspects of the occiput. The lambdoid crest is large and curves laterally and rostrally, meeting the dorsocaudal border of the zygomatic process of the squamosal. Finally, there is a distinct mastoid foramen on the occiput between the squamosal and occipital bones. On the medial wall of the foramen is a small sliver of bone that originally was considered to be part of the mastoid process visible on the occiput (Roth, 1903). Examination of crania in which the squamosal and parietal had been damaged reveals that the mastoid does not contribute to the medial wall of the mastoid foramen, though the mastoid is very closely positioned to the mastoid foramen. The separate element in the medial wall is most likely adventitious growth from the (supra)occipital bone. The mastoid foramen minimally conveyed a vein (or its emissary) that drained from the transverse sinus (Nickel et al., 1983; Wible, 1984).

Prior to this study the skull of *Leontinia* was hemisected, revealing the internal surface of the cranial vault. The confluence of

the transverse and temporal sinuses can be seen at the dorsoposterolateral corner of the petrosal. The intracranial apertures of the temporal meatus and the retroarticular canal can be seen in the rostral part of the temporal sinus, which they drain. Also present ventral to the petrosal, near the aperture of the hypoglossal foramen, is the ventral opening of the condyloid canal. The dorsal aperture of the canal is not visible, but most likely it was continuous with the confluence of sinuses as is the case in extant bovids. It possibly carried a condylar vein from the confluence to join the vertebral vein, based on extant bovid anatomy (Sisson, 1975).

ORBITOTEMPORAL FOSSA: The foramina of the orbitotemporal fossa are similar to those observed in extant artiodactyls. There is a foramen orbitorotundum in the posterior half of the fossa. It probably conveyed the maxillary and ophthalmic branches of the trigeminal nerve, as well as the oculomotor, abducens, and trochlear nerves. Rostrodorsal to the foramen orbitorotundum are the optic and ethmoidal foramina. These conveyed the optic nerve and the ethmoidal nerve, and associated vessels, respectively. The optic foramen is located close to the foramen orbitorotundum (Sisson, 1975).

PETROSAL ANATOMY

TYMPANIC ASPECT: The most striking feature of the tympanic side of the petrosal in toxodontians is the medial margin. It is expanded, fanlike, toward the occipital bone and is heavily crenulated (fig. 14.6). This morphology of the medial edge encompasses the posteromedial, medial, and rostromedial margins of the petrosal. There is no fusion of the petrosal to the occipital along the area of the basicochlear fissure. Attachment of the petrosal to the cranium is accomplished by fusion to the (putative) exoccipital complement of the occipital and the squamosal only, resulting in confluency of the piriform fenestra, the basicochlear fissure, and the jugular foramen to form the lacerate foramen (fig. 14.1). Even when the ectotympanic bulla fuses with bones of the basicranium, forming pseudo-foramina such as a "jugular foramen" and a "piriform fenestra", this rela-
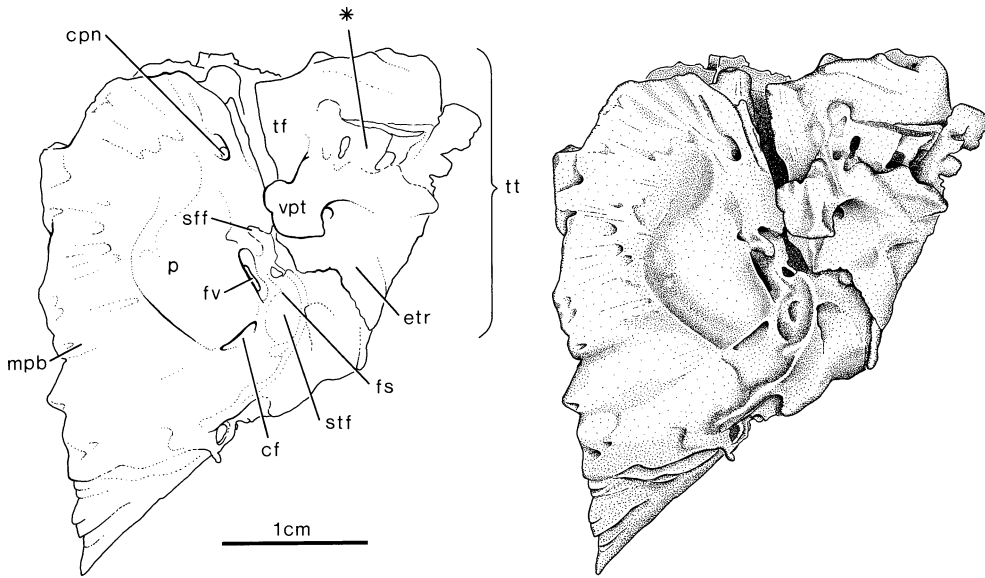
Fig. 14.6. *Scarrittia canquelensis* (AMNH 29614). Isolated left petrosal; tympanic aspect. Rostral toward top of page; medial to left. Asterisk (*) marks squamosal articular surface. Abbreviations: **cf,** cochlear fossula; **cpn,** canal for greater petrosal nerve; **etr,** epitympanic recess; **fs,** facial sulcus; **fv,** fenestra vestibuli; **mpb,** medial petrosal border; **p,** promontorium; **sff,** secondary facial foramen; **stf,** stapedius fossa; **tf,** tensor tympani fossa; **tt,** tegmen tympani; **vpt,** ventral process of the petrosal.

tionship between the petrosal and the sphenoid and occipital remains unchanged.

The promontorium of the cochlea is oriented along a subvertical axis; in other words, it sits on edge. The vestibular fenestra (the oval window) faces ventrolaterally and the cochlear fenestra (the round window) faces posteriorly (fig. 14.6). The processus recessus of the petrosal, which makes up the medial wall of the cochlear fenestra, is large and creates a deep recess. The cochlear fenestra is located inside this recess. Accordingly, this feature of the cochlear fenestra and the developed processus recessus is termed the cochlear fossula (MacPhee, 1981). The secondary facial foramen is opposite the midpoint of the promontorium. The canal for the greater petrosal nerve (hiatus fallopii) is rostral to the facial foramen, opening into the tympanic cavity. The exception to this is found in *Periphragnis*, where the canal opens into the cranial cavity. The facial foramen opens into a trough, the facial sulcus, that is directed caudally and follows the lateral curvature of the promontorium. Medial to the posterior extent of the sulcus

is a well-delineated depression for the origin of the stapedius muscle.

The tegmen tympani in toxodontians is greatly enlarged dorsolaterally (fig. 14.6). In specimens where it has been damaged, it is possible to see that it is filled with cancellous bone. The rostral half of the tegmen is for articulation with the squamosal, which forms a shelf under the tegmen. In some specimens, it is possible to see a small conical projection from the tegmen (ventral process of the tegmen). It is possibly an articular surface, either for what was the anterior crus of the ectotympanic or perhaps simply for the squamosal. A distinctive feature of the tegmen in toxodontians is the tensor tympani fossa, which is more commonly found on the lateral wall of the cochlear housing. It has the form of a large, shallow trough that begins beneath the ventral projection of the tegmen and continues rostrally. The tensor tympani fossa occurs at what would have been the distal extent of the Eustachian tube, which provides additional support for this unorthodox interpretation. (Note: the tensor tympani muscle shares a common ontogenetic origin with the
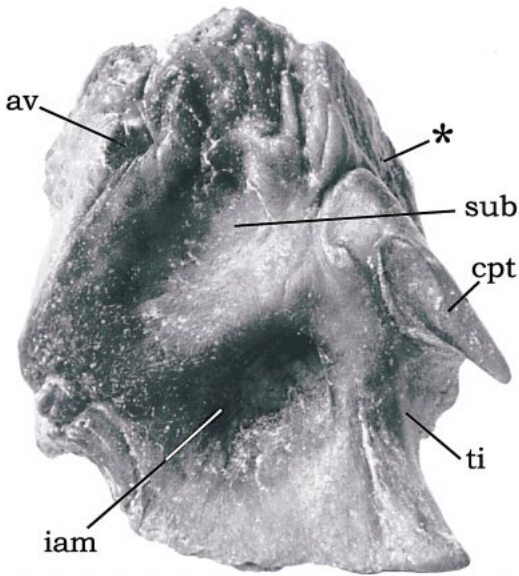
Fig. 14.7. *Adinotherium ovinum* (FMNH 13110). Isolated left petrosal; cerebellar aspect. Dorsal toward top of page; rostral to left. Asterisk (*) indicates the petrosal contribution to midcranial fossa. Abbreviations: **av,** vestibular aqueduct; **cpt,** tentorial ossification of crista petrosa; **iam,** internal auditory meatus; **sub,** subarcuate fossa; **ti,** trigeminal impression.

tensor veli palatini muscle, which develops in close approximation to the tympanic aperture of the auditory tube in mammals [De Beer, 1937].) The epitympanic recess (ETR) forms in the posterior half of the tegmen. It is ellipsoid in shape and has two small mammillate concavities at the rostral and caudal poles. The caudal concavity is the incudal fossa. The floor of the lateral semicircular canal can be seen posterior and medial to the ETR, lying laterally to the facial sulcus.

CEREBELLAR ASPECT: The two major features of this petrosal surface are the internal auditory meatus (IAM) and the subarcuate fossa (fig. 14.7). The primary facial foramen that conveys cranial nerve VII (facial nerve) is in the anterodorsal aspect; the vestibulocochlear foramen that gives passage to cranial nerve VIII (vestibulocochlear nerve) is posteroventral. The subarcuate fossa is well defined, but not particularly deep; it is immediately dorsal to the IAM. Rostral to the subarcuate fossa is a rounded linear eminence, the petrosal crest, which is the medial boundary of a fossa that contributed to the middle cranial fossa. The lateral aspect of this fossa is contributed by the enlarged tegmen tympani. There is a tentorial ossification (the tentorium cerebelli attachment to the petrosal crest) at the rostroventral extent of the crest. The ossification is a small projection directed rostroventromedially; it forms a small roof over the impression for the trigeminal nerve, which is immediately beneath it. The perilymphatic foramen opens through a slit posterodorsal to the subarcuate fossa. The cochlear aqueduct also opens through a slit; it is at the ventromedial corner, next to the mastoid process of the pars canalicularis.

MASTOID ASPECT: The mastoid part of the pars canalicularis is a long, thin, crescent-shaped wedge on the medial side of the pars canalicularis. It is aligned dorsoventrally and is convex laterally. Laterally it articulates with the squamosal and ventrally, medially, and dorsally, with the occipital. It is located near the mastoid foramen but does not contribute to it; therefore, it has no occipital exposure. There is small "mastoid eminence" posterior to the cochlear fossula.

SQUAMOSAL ASPECT: The dorsolateral margin of this face of the petrosal, which is comprised of the enlarged tegmen, contributes the medial wall of the temporal sinus. The ventrolateral aspect provides an articular surface for the squamosal. At the rosterolateral margin, a groove courses ventrolaterally. It is positioned such that it would join the retroarticular foramen; therefore, it probably conveyed an emissary vein from the dorsal cerebral vein (Sisson, 1975).

CRANIAL VASCULAR ANATOMY

Patterson (1936) proposed a distinct cranial vascular pattern for toxodontians based on his research of their auditory anatomy. He suggested that toxodontians had an intratympanic course for their internal carotid artery (ICA). As evidence, he designated a posterior carotid foramen on the posteromedial aspect of the bulla, deep within the jugular foramen and opening into the posterior lacerate foramen. Patterson also identified a foramen for the internal carotid at the anterior pole of the tympanic cavity. The analysis conducted here did not support those observations. All

toxodontian specimens cited in Patterson (1936) were examined in this study. A posterior carotid foramen piercing the posteromedial aspect of the bulla was not found. As described above, the anterior carotid foramen (median lacerate foramen) is confluent with the lacerate foramen in toxodontians; thus, there is no separate foramen for the passage of an ICA into the cranium. It is conceivable that, had there been an ICA, it entered the horizontal gap between the bulla and the petrosal caudally by way of the tympano-occipital fissure, crossed the tympanic cavity dorsal to the septum, and then entered the braincase through the rostromedial part of the lacerate foramen. This scenario is possible even in the absence of osteological markers of the ICA path. With the possible exception of one of the Scarrittia petrosals, there were also no osteological markers on the ventral surface of the petrosal supporting the ICA path proposed by Patterson. As there was no other constraining anatomy suggesting the presence and path of the ICA, none was reconstructed in this analysis. This does not deny that an ICA existed in toxodontians; however, it is equally likely that toxodontians may have annexed their cranial blood supply from ramifications of the external carotid artery as happens in extant artiodactyls (Sisson, 1975).

REMARKS

This research has clarified and updated Patterson's (1932, 1936) interpretations of the ear region of toxodontians. Detailed examination of the intratympanic anatomy has revealed several new findings, including the presence of an expanded, crenulated medial margin of the petrosal, an intratympanic opening of the canal for the greater petrosal nerve, the position of the tensor tympani fossa on the tegmen, a single, large lacerate foramen incorporating the foramen ovale, median lacerate, and jugular foramina, a very large tegmen that contributes to the medial wall of the temporal sinus, and the presence of an osteologically distinct origin for the tensor veli palatini. Some of these traits, such as the lacerate foramen, are common among ungulates. Others, such as the intratympanic opening of the canal for the greater petrosal

nerve, which toxodontians and other notoungulates share with *Equus* (Gabbert, 1997), appear to have a more limited distribution based on preliminary character analysis. These new data provide a good starting point for systematic analysis of the higher taxonomic affinities of toxodontians and notoungulates.

Patterson (1936) suggested that toxodontians shared with typotherians a compound bulla of ento- and ectotympanic origin based on the presence of a septum in the bulla. In typotherians, the septum fits the criteria defined by Klaauw (1931). Toxodontians do not fit Klaauw's criteria other than the presence of the septum. In addition, entotympanics often form very early in development and fuse completely with the ectotympanic, making it impossible to determine their presence in an adult (Klaauw, 1931; Wible, 1984). The findings of this study suggest a simpler explanation for the presence of the bullar septum in toxodontians, namely that the septum is the result of inflationary development of the ectotympanic bulla. This hypothesis is preferred until ontogenetic sequences are available or the condition can be inferred phylogenetically.

The implied presence and course of the internal carotid artery (ICA) suggested by Patterson are challenged. Presence of the foramina for the intratympanic course of the ICA could not be confirmed, leaving open the question of which arterial system provided intracranial blood supply.

ACKNOWLEDGMENTS

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