ON THE OSTEOLOGY OF THE AUDITORY REGION AND ORBITAL WALL IN THE EXTINCT WEST INDIAN SLOTH GENUS *NEOCNUS* ARREDONDO, 1961 (PLACENTALIA, XENARTHRA, MEGALONYCHIDAE)

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ABSTRACT

The present study entails a description of several well-preserved skulls from the diminutive, extinct West Indian megalonychid sloth genus *Neocnus* Arredondo, 1961, recovered from Holocene cave deposits in Haiti and housed in the collections of the Florida Museum of Natural History. Detailed descriptions and illustrations are provided of the external anatomy of the bones in the auditory region and orbital wall, and their sutural connections. The foramina in these regions are also described and illustrated in detail, and their contents reconstructed. The orbitotemporal osteology of *Neocnus* is compared to its purported closest relatives in the subfamily Choloepodinae, the somewhat larger extinct Antillean sloth genus *Acratocnus* Anthony, 1961, and the extant two-toed sloth *Choloepus* Linnaeus, 1758. Contrary to recent phylogenetic hypotheses, which link either *Choloepus and Acratocnus* or *Choloepus and Neocnus* as sister taxa, *Neocnus* and *Acratocnus* exhibit more similarities to one another in the anatomy of their orbitotemporal bones than either does to *Choloepus*. This may be explained in part by the highly autapomorphic anatomy of *Choloepus*. The study highlights the need for further anatomical investigations of Antillean sloths, and for further, more comprehensive phylogenetic investigations of the sloth family Megalonychidae.

KEY WORDS: auditory region, Megalonychidae, *Neocnus*, osteology, sloths, skull, Xenarthra

INTRODUCTION

Whether one chooses to follow traditional taxonomies that treat Xenarthra as an order, or more recent works that consider it a supraordinal level clade (Gardner 2005a, b; see Preface to Vizcaíno and Loughry 2008a, for discussion), the group is widely regarded as one of the primary lineages of placental mammals. This distinction is based largely on recent molecular studies of placental phylogeny (Springer et al. 2005; Delson and Douzery 2008), although at least one recent morphology-based phylogenetic study (Wible et al. 2007) concurs with molecular work in recognizing Xenarthra as the sister-taxon to one of the other four primary placental lineages, the Afrotheria, the two together forming the Gondwanan supraordinal grouping Atlantogenata (Murphy and Eizirik 2009).

In addition to its phylogenetic prominence among placental, Xenarthra represents one of the most characteristic elements of the Neotropical mammalian fauna, both living and extinct. Xenarthra is unusual relative to other placental orders in that its morphologically and ecologically diverse but taxonomically rather modest modern representation (13-14 genera and 31 species of tree sloths, anteaters and armadillos; Gardner 2005a, b; Aguiar and Fonseca 2008) is but a small remnant of a much larger extinct radiation. This extinct radiation includes some of the most important groups of large herbivorous mammals from the Neogene fossil record of South America, including the armored glyptodonts and pampatheres, and well over 90 described genera of extinct “ground sloths” (McKenna and Bell 1997). These animals spread northward into North America at the end of the Miocene (e.g., *Pliometanastes* Hirschfeld and Webb, 1968, and *Thinobadistes* Hay, 1919) and more extensively during the episode known as the “Great American Biotic Interchange” (GABI; Marshall 1988), including (and of particular import for the present study) an endemic radiation of sloths in the West Indies (White and MacPhee 2001), and disappeared with other Western Hemisphere megafauna during the Pleistocene-Holocene extinction event (Kurtén and Anderson 1980; Steadman et al. 2005).

Given the phylogenetic and paleobiological significance of Xenarthra, it is unfortunate that the group historically has been understudied. Other authors have noted the dearth of investigations and investigators for many aspects of xenarthran biology (e.g., Vizcaíno and Loughry 2008b), but Wible and Gaudin (2004) called particular attention to the lack of basic, detailed information on the cranial osteology of xenarthrans. Although the availability of such detailed anatomical information has improved somewhat for the cingulate part of the xenarthran tree with the publication of Wible and Gaudin’s (2004) study of the yellow armadillo, *Euphractus sexcinctus* (Linnaeus, 1758), and Wible’s (2010) more recent description of the petrosal anatomy of the nine-banded armadillo, *Dasypus novemcinctus* Linnaeus, 1758, no such improvement has occurred for the other half of the xenarthran tree, the Pilosa, including the modern anteaters and tree sloths and extinct “ground sloths.” This kind of descriptive data is a key element in attempts to reconstruct the phylogenetic history of Xenarthra, especially considering the fact that so much of the diversity of the group is extinct and therefore not amenable to analysis using molecular phylogenetic techniques. It is worth noting, in this context, that even fewer detailed studies of xenarthran postcranium osteology exist, and that additional well-illustrated descriptions,
though outside the purview of the current report, are sorely needed.

The impetus for the present study was a description of a new Pleistocene megalonychid sloth from Venezuela (McDonald et al. in prep). In the course of conducting a phylogenetic analysis to ascertain the relationships of this new taxon, I had occasion to borrow several skulls of the extinct Antillean megalonychid sloths Neocnus dousman MacPhee et al., 2000, and Neocnus comes (Miller, 1929), from the collections of the Florida Museum of Natural History. These skulls, recovered from cave deposits in Haiti on the island of Hispaniola, are wonderfully well preserved, in part due to the fact that they are likely only 4000-5000 YBP in age (MacPhee et al. 2000; Steadman et al. 2005). Because preservation of these skulls was so extraordinary, I felt that they would serve as an ideal basis for conducting a very detailed descriptive study of the cranial anatomy of a pilosan, and in particular, of the auditory region, petrosal, and orbital wall, areas which have served as rich sources of characters for my own previous cladistic investigations in other placental mammal taxa (e.g., Wible et al. 2009).

Neocnus dousman and the somewhat larger N. comes are two of five currently recognized species in the extinct genus Neocnus (MacPhee et al. 2000; White and MacPhee 2001), which also includes one other, smaller species from Haiti (N. toupit MacPhee et al., 2000), as well two species from Cuba [N. major Arredondo, 1961 and N. gliriformis (Matthew, 1931)—although see discussion in Taboada et al. 2007, who suggest that only one Cuban species, N. gliriformis, is valid, and that several of the Haitian species may not be distinct either]. Neocnus is roughly the size of modern tree sloths, making it the smallest genus among an Antillean radiation of sloths that ranged in stature up to the bear-sized Megalocnus Leidy, 1868 (Matthew and Paula Couto 1959). This radiation of endemic sloths included at least at least ten genera dating back to the Oligocene (McDonald and De Iuliis 2008) and found throughout the Caribbean, but especially on the larger islands of the Greater Antilles (White and MacPhee 2001). MacPhee et al. (2000) and White and MacPhee (2001) placed Neocnus in the monotypic tribe Cubanochnini within the subfamily Choloepodinae, the latter, according to White and MacPhee (2001), also including four species in the extinct genus Acratocnus, known from Puerto Rico, Hispaniola, and Cuba (MacPhee et al. 2000; Rega et al. 2002), the extinct genus Paulocnus Hooijer, 1962, from Curaçao, and the two extant species of two-toed sloths in the genus Choloepus (Gardner and Naples 2007; Aguiar and Fonseca 2008). The inclusion of Choloepus within a subfamily of the family Megalonychidae makes this the only one of the five currently recognized families of sloths (Gaudin 2004; McDonald and De Iuliis 2008) to include both extinct and extant members. The phylogenetic relationships within Megalonychidae are still very much unsettled and in need of more detailed study, so that the current taxonomic assignment of Neocnus should probably be viewed as provisional. The taxonomy of MacPhee et al. (2000) is based upon the phylogeny of White and MacPhee (2001), in which Neocnus is a sister taxon to a clade uniting Choloepus and Acratocnus. However, the broader analysis of sloth phylogeny conducted by Gaudin (2004: fig. 2) leaves these three genera in an unresolved trichotomy at the base of a monophyletic clade of Antillean sloths plus Choloepus. The monophyly of Antillean sloths is not supported by White and MacPhee’s (2001) analysis, and neither Antillean monophyly nor the alliance of Choloepus with Antillean taxa is supported in other recent analyses of megalonychid phylogeny (Carlini et al. 2004; Pujos et al. 2007).

The literature on sloths in general contains relatively few detailed, well-illustrated, bone-by-bone descriptions of cranial osteology. For the two modern genera, there is a study of cranial anatomy in prenatal stages of the living three-toed sloth Bradypus Linnaeus, 1758, by Schneider (1955), and Napoles’ (1982) rather cursory and error-plagued descriptions of both Bradypus and Choloepus. For extinct sloths, the situation is somewhat better, as exemplified in the recent treatments by McDonald and Muizon (2002), Pujos et al. (2007), and De Iuliis et al. (2011). Nevertheless, most published osteological descriptions of the cranium in Antillean sloths are also rather cursory (e.g., Anthony 1918, 1926; Paula Couto 1967; MacPhee et al. 2000; Rega et al. 2002) even in fairly extensive monographic studies (e.g., Matthew and Paula Couto 1959). The works of Fischer (1971) and Mayo (1980) offer more detailed descriptions, including descriptions of skulls from the two Cuban species of Neocnus, but neither is well illustrated. A very recent article by McAfee (2011) describes the anatomy of the jugal in UF specimens of Neocnus, and includes several skull reconstructions, but offers few details on other aspects of cranial anatomy.

In scope, the present study is fashioned after Guth’s (1961) thesis study of the auditory and orbitotemporal anatomy in Xenarthra. Guth described and illustrated the bony anatomy of the ear region and orbital wall in a wide variety of living and extinct xenarthrans. However, his drawings were somewhat stylized, and his descriptions lack the kind of details of petrosal anatomy that are prevalent in more modern descriptions of auditory anatomy in placental mammals (e.g., Giannini et al. 2006; Wible et al. 2009; Wible 2010). Additionally, Guth (1961) described few megalonychid sloths, apart from Choloepus, and did not examine any megalonychid taxa from the Antilles. The present study also complements the work of Patterson et al. (1992), who did describe the bony anatomy of the ear region in several Antillean megalonychids (Acratocnus and Megalocnus), but, as in Guth (1961), concerned themselves largely with the elements surrounding the petrosal rather than providing a detailed description of the petrosal itself, and did not address the osteology of the orbital region. The goal of this analysis, then, is to present the first detailed, carefully illustrated description of the auditory and orbitotemporal osteology of an Antillean megalonychid sloth.
Fig. 1.—Skulls of the extinct Antillean sloth *Neocnus* in dorsal view (left), ventral view (middle), left lateral view (upper right), and right lateral view (lower right). A, *N. dousman* (holotype), UF 76363; B, *N. dousman*, UF 76364; C, *N. comes*, UF 170527. Scale = 10 cm.
Materials and Methods

The descriptions contained in this account are based largely on two specimens of Neocnus dousman, UF 76363 (holotype) and UF 76364 (Figs. 1A–B). Both are extremely well preserved, with nearly intact orbitotemporal regions and basicrania except for the loss of the pterygoid descending laminae. The holotype, recovered from cave deposits in Trouing de la Sciere, Morne la Visite, Département de l’Ouest, Haiti (MacPhee et al. 2000), retains entotympanics and ectotympanics on both sides of the skull, along with a left malleus that is preserved roughly in place. Published photographs of the holotype skull in dorsal, ventral, left and right lateral, and posterior views are available in MacPhee et al. (2000). UF 76364, also from Trouing la Sciere, likewise retains both entotympanics, but is missing the right ectotympanic, exposing much of the ventral surface of the petrosal. An isolated right malleus is preserved with this specimen, and is described and illustrated below. The descriptions of the two specimens of N. dousman are supplemented with information obtained from a third specimen of Neocnus, N. comos (UF 170527, from Trouing Deron #1, Plain Formon, Département du Sud, Haiti; Fig. 1C). This specimen also has a well-preserved orbitotemporal region and basicranium, including a complete left pterygoid, but it lacks both entotympanics and ectotympanics.

In order to provide a comparative perspective, these Neocnus specimens were compared to specimens of the somewhat larger bodied extinct West Indian sloth genus Acratocnus and the extant two-toed sloth Choloepus, following White and MacPhee (2001), who identify these two taxa as the closest relatives of Neocnus. Information on Acratocnus was largely derived from my own pre-existing notes and photographs of Puerto Rican specimens from the American Museum of Natural History (Acratocnus odontrogirus Anthony, 1916, AMNH 17720, 17721, and 17722), as well as a juvenile Haitian specimen of Acratocnus ye MacPhee et al., 2000 (UF 171341), borrowed for this study. The last is a partial cranium, including the basicranium, ventral orbital wall, and posterior palate, of a very young individual, with open sutures still evident. Information on Choloepus was obtained from two specimens housed at the University of Tennessee at Chattanooga (C. didactylus Linnaeus, 1758, UTCM 1000, and an uncataloged specimen of C. hoffmanni Peters, 1858) and a Carnegie Museum of Natural History specimen of C. hoffmanni (CM 3883). Information from these specimens was supplemented with data from Gaudin (2004).

The terminology used in these accounts follows Wible and Gaudin (2004) and Wible (2010). The close-up photographs and stereophotographs of the ear region (Figs. 2–5) in Neocnus dousman (UF 76363 and 76364) were prepared with the assistance of Dr. Stelios Chatzimanolis of the Department of Biological and Environmental Sciences, University of Tennessee at Chattanooga. For each figure, multiple images at different, sequential focal planes were obtained using a Visionary Digital Passport system with a Canon 40D digital SLR camera, and then the images were automontaged into a single photograph using Helicon Focus version 4.2.1 software.

Institutional Abbreviations

AMNH—American Museum of Natural History, New York, New York
CM—Section of Mammals, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania
UF—Florida Museum of Natural History, University of Florida, Gainesville, Florida
UTCM—Mammal Collection, University of Tennessee at Chattanooga Natural History Museum, Chattanooga, Tennessee

DESCRIPTION OF BASICRANIAL AND ORBITOTEMPORAL BONES

Ectotympanic

Both left and right ectotympanic are present in UF 76363, whereas only the left ectotympanic of UF 76364 is preserved (Figs. 1–4). The bone is essentially U-shaped in lateral view (Figs. 3–4), and more elongated dorsoventrally than anteroposteriorly (typical for Xerarthra—see Patterson et al. 1989, 1992; Gaudin 1995). As in most sloths (Patterson et al. 1992), the anterior and posterior crura do not meet dorsally, but are separated by a narrow incisura tympanica. The anterior crus is nearly vertical, whereas the posterior crus is bowed posteriorly, and the bone broadens ventrally. In all these aspects Neocnus more closely resembles Acratocnus than Choloepus (Patterson et al. 1992). The ectotympanic in Choloepus is more circular or horseshoe-shaped in lateral view, with dorsoventral and anteroposterior dimensions roughly equivalent, a slightly bowed anterior crus and strongly bowed posterior crus, and lacking any ventral expansion. The anterior crus of the ectotympanic is sutured to the squamosal dorsally and anteriorly, and the anteroposterior process of the tegmen tympani (= processus crista facialis of Patterson et al. 1992; Gaudin 1995, 2004; Wible and Gaudin 2004—see Wible 2010; the tegmen tympani is an anterolateral projection of the petrosal pars cochlearis that typically contributes to the roof of the tympanic cavity, see Novacek 1993) medially along much of its length. However, like Acratocnus and unlike Choloepus (Patterson et al. 1992), the anterior crus is free along its ventralmost portion, extending below the entoglenoid process of the squamosal. The posterior crus is sutured to the posttympanic process of the squamosal dorsally. It abuts the mastoid and tympanohyal posteriorly and the tympanohyal medially along the greater portion of its length. In Choloepus, the posterior crus of the ectotympanic nearly contacts the paroccipital process (= mastoid process of Patterson et al. 1992; Gaudin 1995) of the
mastoid. However, *Neocnus* more closely resembles *Acratocnus* in this regard, wherein the paroccipital process is situated further posteriorly (Patterson et al. 1992).

Like *Acratocnus*, there is extensive contact between the ectotympanic and the entotympanic. In UF 76363, as in *Acratocnus*, the sutural connection only occurs along the ventral portion of the ectotympanic (Fig. 3A), whereas in UF 76364 the sutural connection is much more extensive, beginning posteriorly at the medial margin of the tympanohyal and ending anteriorly at the back edge of the musculotubal canal (= foramen for the auditory tube, see section entitled “Foramina: Auditory Region” below) (Fig. 2). Contact between ectotympanic and entotympanic is variably developed in *Choloepus* (Patterson et al. 1992). Immediately posterior to the musculotubal canal, the ectotympanic forms a styliform process that extends ventromedially toward its suture with the entotympanic. This styliform process is broad and elongate in UF 76364; it is somewhat smaller in UF 76363. In *Choloepus* there is a weak, free-standing styliform process, but it lies anterior to the musculotubal canal (Patterson et al. 1992). According to Patterson et al. (1992: 19), a “styliform process is not developed” in *Acratocnus*, but Gaudin (1995) notes the presence of a weak styliform process in this taxon, located as in *Neocnus* posterior to the musculotubal canal. The external surface of the ectotympanic is relatively smooth, except along its medial edge where it contacts the entotympanic. Its broad ventral expansion forms a relatively flat surface in UF 76364, but this area is swollen and rounded in UF 76363.

On the medial surface of the ectotympanic, the crista tympanica is weak and rounded and the sulcus tympanicus shallow, resembling the condition in both *Acratocnus* and *Choloepus* (Patterson et al. 1992; Gaudin 1995). Note that this condition is identified as a unique synapomorphy of the last two taxa in Gaudin (1995), although it is also found in the South American megalonychid *Pliomorphus* Ameghino, 1885, according to Gaudin (2004; see also Guth 1961). There is a fairly substantial, bony recessus meatus external to the crista tympanica.

Entotympanic

An entotympanic element is preserved on both sides of UF 76363 and 76364. The entotympanics appear to be completely intact in the former specimen and on the left side of the latter (Figs. 2–3), whereas on the right the ventrolateral edges of the bone have been chipped away, and it is split in two by a transverse crack (Fig. 5). I take this crack as evidence that the single adult entotympanic developed from two centers of ossification in *Neocnus*. This interpretation is based in part on the fact that the single adult entotympanic of *Choloepus* develops from rostral and caudal centers of ossification (Patterson et al. 1992). In addition, the crack occurs in precisely the same position, and has the same orientation, as a similar fissure in an undescribed juvenile specimen of *A. ye* (UF 171341), where it clearly divides the rostral and caudal portions of the entotympanic. Rostral and caudal entotympanics are also known to occur in the other living sloth genus, *Bradypus*, and in other xenarthrans (Patterson et al. 1989, 1992; Wible 2010). The rostral portion of the entotympanic is fused dorsally to the ventral surface of the petrosal promontorium on the right side of both specimens, but a suture is retained in this area on the left.

As in other sloths (Patterson et al. 1992), the entotympanic of *Neocnus* (Figs. 2–3, 5) is dominated by a vertical crest that lies lateral to the course of the internal carotid artery, extending from the anteromedial edge of the jugular foramen (= posterior lacerate foramen of Patterson et al. 1992; Gaudin 1995) to the posterior margin of the carotid foramen (= medial lacerate foramen of Patterson et al. 1992; Gaudin 1995). The crest extends ventrally from the body of the entotympanic, the body itself forming a vertical wall-like area of bone attached to the ventromedial edge of the petrosal promontorium. The ventral edge of the entotympanic extends well ventral to the lower surface of the ectotympanic, resembling *Acratocnus* and in contrast to *Choloepus* (Patterson et al. 1992; Gaudin 1995). In *Neocnus*, this ventral entotympanic edge is extended into the anteroventral process that characterizes megatheriid sloths (Gaudin 1995, 2004). This process is situated somewhat farther posteriorly in *Neocnus* than in other megatherioids, near the middle of the bone, where the strongly anteroventrally sloping posterior half meets the strongly anterodorsally sloping anterior half. These sloped anterior and posterior regions confer on the entotympanic of *Neocnus* an overall shape that is quite distinctive from that of either *Acratocnus* or *Choloepus*. Nevertheless, the entotympanic in this genus shares several of the unusual, derived features of *Acratocnus* and *Choloepus* noted by Gaudin (1995, 2004)—it has a sharp, thin ventral edge on the main (lateral) crest, it has a flat lateral surface, lacking in its anterior portion the deep dorsal depression found in many other sloths (e.g., see illustration of *Mylodon* in Patterson et al. 1992: fig. 1B), and it has a flat dorsal edge (abutting the petrosal promontorium), lacking the curved dorsal edge and strong anterodorsal prong found in other sloths (again, see Patterson et al. 1992: fig. 1B).

Like most sloths, the main body of the entotympanic bears a medial shelf that extends ventromedially from the body of the bone, forming a roof to the sulcus for the internal carotid artery. On the left side of UF 76364, this shelf is weakly developed and separated from the lateral edge of the basioccipital and basiphenoid by a fissure for most of its length (Fig. 2). It forms a suture with the basioccipital tuber at its posteriormost end. However, on the right side of UF 76364 and on both sides of UF 76363, the shelf is much more strongly developed, forming a second, lower vertical crest that serves as a medial wall to the internal carotid artery sulcus (Figs. 3, 5). This medial crest extends forward from the anteroventral process of the entotympanic. Behind the anteroventral process, there is
Fig. 2.—Close up of left auditory region of *Neocnes dousman*, UF 76364, in ventral view: A, stereophotographs; B, labeled drawing. Abbreviations: 

- **bo**: basioccipital
- **bs**: basisphenoid
- **cf**: carotid foramen
- **eam**: external auditory meatus
- **ec**: ectotympanic
- **en**: entotympanic
- **eng**: entoglenoid process
- **fm**: foramen magnum
- **fo**: foramen ovale
- **gf**: glenoid fossa
- **glf**: Glaserian fissure
- **gtv**: groove for m. tensor veli palatini
- **gvn**: groove for the vidian nerve
- **hf**: hypoglossal foramen
- **jf**: jugular foramen
- **mtc**: musculotubal canal
- **oc**: occipital condyle
- **pcp**: paracristal process of exoccipital (=paroccipital process of Patterson et al. 1992)
- **pgf**: postglenoid foramen
- **pop**: paroccipital process of petrosal (= mastoid process of Patterson et al. 1992)
- **shf**: stylohyal fossa
Fig. 3.—Close up of left auditory region of *Neocnus doussan*, UF 76363 (holotype): A, stereophotographs in ventral view; B, photograph in lateral view. Abbreviations: bo, basisphenoid; bs, basisphenoid; ec, ectotympanic; en, entotympanic; eng, entoglenoid process; gf, glenoid fossa; glf, Glaserian fissure; hf, hypoglossal foramen; jf, jugular foramen; man, manubrium of malleus; me, mastoid exposure of petrosal; mtc, musculotubal canal; oc, occipital condyle; pcp, paracondylar process of exoccipital (=paroccipital process of Patterson et al. 1992); pop, paroccipital process of petrosal (= mastoid process of Patterson et al. 1992); pr, promontorium of petrosal; ptc/oa, opening leading to posttemporal canal housing emerging groove for occipital artery; shf, stylohyal fossa; sq, squamosal. Scale = 0.5 cm.
a posteriorly directed prong on the entotympanic. In UF 76363, this is a free-standing process that marks the anterior edge of the jugular foramen, but on the right side of UF 76364, it forms an extensive, fused contact with the basioccipital tuber. The medial shelf on the left entotympanic of UF 76364 resembles the condition in Acratocnus and Choloepus (Patterson et al. 1992; Gaudin 1995, 2004), whereas the stronger medial shelf and crest on the right of UF 76364 and on both sides of UF 76363 are more like the condition in the Pliocene South American megalonychid Pliomorphus (Guth 1961; Gaudin 2004) and the Plio-Pleistocene mainland North American megalonychid Megalonyx Harlan, 1825 (Hirschfeld and Webb 1968; Patterson et al. 1992; Gaudin 1995, 2004).

The entotympanic contacts four to five other bones in the skull. It has an extensive dorsal contact with the promontorium of the petrosal bone. In UF 76363 and on the left side of UF 76364, this takes the form of a relatively flat, straight, anteroventrally directed suture (Fig. 3B). On the right side of UF 76364, the posterior portion of the bone is sutured, but, as noted above, the anterior reaches are fused dorsally to the promontorium. Like Choloepus, there is only a small posterolateral contact with the mastoid portion of the petrosal, between the jugular foramen and stylohyal fossa. In UF 76364, the contact is nearly precluded by the close approximation of the tympanohyal and the paracodylar process of the exoccipital (= paroccipital process of Patterson et al. 1992; Gaudin 1995). The entotympanic/mastoid contact is more extensive in UF 76363, in which the paracodylar process is smaller, and in Acratocnus, in which the paracodylar process is situated farther posteriorly (Patterson et al. 1992). In addition to its mastoid contact between the stylohyal fossa and jugular foramen, the entotympanic also connects to the paroccipital process of the exoccipital in this same vicinity. In UF 76364, there may be a second contact between entotympanic and exoccipital in the medial wall of the jugular foramen. The two bones certainly approach one another, but the sutures in this area are fused, leaving open the possibility that the basioccipital is interposed between the two. In the anteromedial wall of the stylohyal fossa, there is a lateral extension of the entotympanic that contacts the tympanohyal. Such an arrangement is typical for sloths (Gaudin 1995). The last two contacts between entotympanic and the other skull bones were described above—a sutural connection between the lateral edge of the entotympanic and the medial edge of the ectotympanic in both specimens, and a sutured or fused connection between the postero medial portion of the entotympanic and the basioccipital tubera in UF 76364 only. The contact between basioccipital and entotympanic is variably present in Choloepus (Patterson et al. 1992) as well as Neocnus, and is typically present but small in Acratocnus.

Petrosal

Promontorium and tympanohyal.—The petrosal is visible in ventral view on the right side of UF 76364 (N. dousman) because of the missing ectotympanic (Fig. 5), and on both the right and left sides of UF 170527 (N. comes) because of the missing ecto- and entotympanics (Fig. 1C). The promontorium is the dominant feature on the ventral surface of the bone. In N. dousman (UF 76364), it is rounded posteriorly with a more flattened lateral surface anteriorly. It is also slightly elongated anteromedially and ventrally. This shape is similar to that of most other sloths, including Acratocnus, but differs from Choloepus, in which the promontorium is more globose (Patterson et al. 1992; Gaudin 1995, 2004). Neocnus comes (UF 170527) has a more globose promontorium like that of Choloepus.

Posterior to the promontorium is the aperture for the cochlear fossula (i.e., the aperture for the region housing the recessed fenestra cochleae. The fenestra cochleae itself is obscured by matrix and the tympanohyal behind it, and cannot be directly observed—the aperture for the cochlear fossula is treated as equivalent to the fenestra cochleae in Patterson et al. 1992 and Gaudin 1995, 2004). The aperture faces mainly posteriorly and slightly ventrally, although it also has a slightly lateral orientation and is plainly visible in lateral view, as is the case in Choloepus and in other West Indian megalonychids (Gaudin 1995, 2004). The petrosal forms a small bony shelf extending posterodorsally from the dorsal edge of this opening. This shelf forms the roof of the post-promontorial tympanic sinus, a space that is much smaller in megalonychid sloths than in armadillos (Wible and Gaudin 2004; Wible 2010) due to the impinging medial, posterior, and lateral walls formed by tympanohyal and entotympanic.

On the lateral surface of the petrosal, the posterior edge of the promontorium is marked by a strong crista interfrenstraalis separating the fenestra vestibuli from the aperture for the cochlear fossula. The crista is somewhat broader than the comparable structure in Choloepus. The fenestra vestibuli itself is deeply recessed, the recess being larger anterior to the opening. The opening is ovate, facing laterally and slightly anteriorly, with a stapedial ratio (length/width, Segall 1970) of 1.5. This is a smaller ratio than that reported for living armadillos (1.9–2.0 in Euphractus sexcinctus, Wible and Gaudin 2004; 1.9–2.1 in Dasypus novemcinctus, Wible 2010), but is similar to the ratio in living sloths (1.62 in Bradypus tridactylus Linnaeus, 1758, see Fleischer 1973; 1.46 in Choloepus didactylus, UTCM 1000). Posterior to the fenestra vestibuli, and hidden from lateral view by the tympanohyal, is a deep fossa for the stapedius muscle. This fossa is somewhat deeper dorsoventrally in UF 170527 than the equivalent depression in Choloepus. Just dorsal to the fenestra vestibuli is the deep facial sulcus, the groove that accommodates cranial nerve VII. It is bounded laterally by a strong crista parotica that extends posteriorly from the secondary facial foramen to reach the base of the tympanohyal.
The tympanohyal looks very much like that of other sloths—it is shaped like a “golf tee,” narrow at the base and broadening distally toward a circular head. It is directed strongly ventrally and slightly posteriorly, as in *Acratocnus* and *Choloepus*, so that its head comes to line up almost directly posterior (though well ventral) to the aperture for the cochlear fossula in ventral view. The circular head forms the bulk of the stylohyal fossa, an articular surface for the stylohyal characteristic of all sloths except *Bradypus* (Patterson et al. 1992; Gaudin 1995, 2004). As in other sloths, the stylohyal fossa also includes contributions from the entotympanic (anteromedially), the exoccipital (posteromedially—not preserved in *N. dousman*, UF 76363), and the mastoid region of the petrosal (posterolaterally). The stylohyal fossa is circular (*N. dousman*, UF 76363, Fig. 3) or ovate (*N. dousman*, UF 76364, Fig. 2; *N. comes*, UF 170527) in *Neocnus*, and intermediate in size between the small stylohyal fossa of *Choloepus* and the very large stylohyal fossa of *Acratocnus* (Patterson et al. 1992; Gaudin 1995, 2004). In addition, the stylohyal fossa faces ventrally as in *Acratocnus*, whereas it is tilted laterally in *Choloepus* (Patterson et al. 1992; Gaudin 1995).

At its anterior end, the crista parotica [a crest that emerges from the lateral side of the auditory capsule and, in mammals, forms a ridge lateral to the sulcus for the facial nerve (cranial nerve VII) and serves as the attachment point for the hyoid arch, i.e., the tympanohyal—see De Beer 1937; Wible 2010] contacts a very large process, the anteroventral process of the tegmen tympani (= processus crista facialis of Patterson et al. 1992; Gaudin 1995, 2004; Wible and Gaudin 2004), a feature noted above. This process extends anteriorly, medially, and ventrally along the lateral edge of the promontorium (Fig. 5). It appears to abut or be sutured to the promontorium in UF 170527, but in UF 76364 there is a narrow groove separating the two. This groove presumably housed the greater petrosal nerve, a branch of cranial nerve VII (see Wible 2010: fig. 3), though the process obscures the hiatal foramen where this nerve would presumably emerge from the cavium supra-cochleare. Therefore, the process forms a ventral floor to the cavium supracochleare and encloses a secondary facial foramen. The anteroventral process of the tegmen tympani has a very rugose surface and is roughly oval in outline in UF 76364, with two well-marked concavities on its ventral surface—one is more anterior and lateral, and serves as the contact surface for the ectotympanic; the second is larger, more posterior and medial in position, and is comparable to the concavity present on this process in many xenarthrans, including *Choloepus* and *Acratocnus* (Patterson et al., 1989, 1992; Gaudin 1995, 2004; Wible and Gaudin 2004; Wible 2010). The process enjoys its largest contact with the entotympanic process of the squamosal, along its entire anterolateral edge. It also contacts the ectotympanic ventrally and laterally, and the pterygoid at its anteroventralmedial tip (the latter contact does not occur in UF 76363). In contrast to some *Choloepus* (Patterson et al. 1992), there is no contact with the entotympanic. The anteroventral process of the tegmen tympani is much smaller in UF 170527. It lacks the anterolateral concavity that serves as the contact surface for the ectotympanic, and it comes nowhere near contacting the pterygoid, extending only one-half to one-third as far in the anteroventromedial direction when compared to UF 76364. The process may be broken in UF 170527—this view is supported by the presence of a hollow on the posterior side of the entotemnoid process, which is in the appropriate position to abut against a larger process. It is also suggested by the presence of a larger process in both *N. dousman* specimens (the process is partially visible in UF 76363 despite the presence of the ectotympanic), as well as in other megahyoids, including *Choloepus* and *Acratocnus* (Patterson et al. 1992; Gaudin 1995, 2004). If this is true, however, the process in UF 170527 is broken bilaterally.

Dorsal and lateral to the crista parotica is a large epitympanic sinus that extends upward deep into the squamosal bone (Fig. 5). A well-developed epitympanic sinus is a feature of megatheriod sloths, though it also occurs in *Bradypus* and various other xenarthrans (Patterson et al. 1989, 1992; Gaudin 1995, 2004; Wible and Gaudin 2004). There is a clear suture on both sides of UF 170527 showing that the petrosal forms only a small ventral portion of the medial wall of the sinus, the remainder lying within the squamosal. The posteriormost portion of this petrosal contribution to the wall of the epitympanic sinus is marked by a deep fossa on its lateral surface. This fossa, the fossa incudis, extends onto the squamosal as well, occupying nearly the entirety of the posteroverental wall of the epitympanic sinus. This arrangement is also characteristic of *Bradypus* and megatheriod sloths (Patterson et al. 1992; Gaudin 1995, 2004).

Because of the absence of the entotympans, the region of the petrosal medial to the promontorium is visible in UF 170527 in ventral view. This region is marked by a well-developed medial transverse flange. This flange is separated from the basioccipital medially by a patent basicochlear fissure. The flange is perforated by two small foramina—anteriorly, the cochlear canaliculus, the small opening for the perilymphatic duct; and, posteriorly, the aqueductus vestibuli for the endolymphatic duct. The lateral opening is the larger of the two.

**Mastoid.** *Neocnus*, like other sloths (Patterson et al. 1992), is characterized by a prominent exposure of the pars mastoidea of the petrosal on the posterolateral corner of the skull. This exposure has a roughly triangular shape, with its apex dorsally. It lies between the nuchal crest of the squamosal bone anterolaterally, and the exoccipital crest
At its ventral end, the pars mastoidea is marked by two strong projections (Figs. 2–5). The more ventral and medial of these is the mastoid contribution to the stylohyal fossa. The more lateral is the paroccipital process (sensu Wible and Gaudin 2004; = mastoid process of Patterson et al. 1992; Gaudin 1995, 2004). In Chloeocephus, the paroccipital process is small, and the paroccipital process at the end of the exoccipital crest is very large, giving the mastoid depression a more lateral orientation (Patterson et al. 1992; Gaudin 1995). In Acratocnus, the paroccipital process is variably developed, but generally smaller than that of Chloeocephus, whereas the paroccipital process is much larger, hiding much of the mastoid exposure laterally (Patterson et al. 1992; Gaudin 1995). Neocnus has a paroccipital process that is intermediate in size between that of Acratocnus and Chloeocephus, and a paroccipital process that is smaller than in either genus. In UF 76363 (N. dousman) and UF 170527 (N. comes), this leads to an intermediate degree of mastoid exposure laterally. In UF 76364, the situation is complicated by a highly unusual posterior extension of the nuchal crest immediately dorsal to the pars mastoidea. This draws the pars mastoidea out much farther posteriorly in this specimen, increasing its visibility in lateral view. Both specimens of N. dousman are unusual in that the lateral surface of the paroccipital process is not convex, as is typical for sloths, but instead bears a strong concavity.

The pars mastoidea is perforated by two prominent foramina. The more anterior and ventral of these is the stylomastoid foramen (Figs. 3B, 4B). The stylomastoid foramen, for the exit of cranial nerve VII, lies immediately posterior to the mastoid bridge, a prominent lateral ridge on the mastoid that extends from the head of the tympanohyal ventrally to the posttemporal process of the squamosal dorsally. This mastoid bridge forms an attachment surface for the posterior crus of the ectotympanic in all sloths (Gaudin 1995), excluding the ectotympanic from the margins of the stylomastoid foramen, and from posterolateral contact with the tympanohyal. In N. comes (UF 170527), a thin bar of bone extends posteriorly from the mastoid bridge, dividing the stylomastoid foramen into a smaller upper opening and a larger lower opening. This feature is absent in both specimens of N. dousman. The stylomastoid foramen is bordered by the paroccipital process dorsally and laterally, and the head of the tympanohyal ventrally and medially, as in Acratocnus and Chloeocephus (Patterson et al. 1992). The more dorsal and posterior of the openings in the mastoid is the posttemporal foramen (Figs. 3, 5), the posterior entrance into the posttemporal canal that accommodates the arteria diploëtica magna (Wible 1984, 2010; Patterson et al. 1992; Wible and Gaudin 2004). The posttemporal foramen lies near the dorsal end of the pars mastoidea, just posterior to the nuchal crest. It is connected ventrally to the stylomastoid foramen by a strong, open groove that passes under the paroccipital process and presumably accommodated the occipital artery (Wible 1984, 2010; Patterson et al. 1992; Wible and Gaudin 2004).
Fig. 5.—Close up of right auditory region of *Neocnus dousman*, UF 76364, in ventrolateral view: A, stereophotographs; B, labeled drawing. Abbreviations: **aptt**, anteroventral process of tegmen tympani (= processus crista facialis of Patterson et al. 1992); **bo**, basioccipital; **bs**, basisphenoid; **cf**, carotid foramen; **en**, entotympanic; **eng**, entoglenoid process; **eps**, epitympanic sinus; **fas**, facial sulus; **fc**, aperture of cochlear fossula, housing the fenestra cochleae; **fm**, foramen magnum; **fo**, foramen ovale; **fv**, fenestra vestibuli; **gf**, glenoid fossa; **gtv**, groove for m. tensor veli palatini; **hf**, hypoglossal foramen; **jf**, jugular foramen; **me**, mastoid exposure of petrosal; **mtc**, musculotubal canal; **oc**, occipital condyle; **pcp**, paracondylar process of exoccipital (= paroccipital process of Patterson et al. 1992); **pgf**, postglenoid foramen; **pop**, paroccipital process of petrosal (= mastoid process of Patterson et al. 1992); **pr**, promontorium of petrosal; **pt**, pterygoid; **ptc**, posttemporal canal; **shf**, stylohyal fossa; **stmf**, stylomastoid foramen; **th**, tympanohyal.
morphology of this groove is very similar to the condition in *Acratocnus* and *Choloepus*, but differs from that of other megalonychids, in which the groove may be partially or fully enclosed to form a canal (Patterson et al. 1992; Gaudin 1995, 2004). The posttemporal foramen is covered posterolaterally by the bridge between the nuchal crest and mastoid ridge in UF 76363, which creates two additional foramina on the pars mastoidea in this specimen, a ventral foramen at the lower edge of the bridge that provides access for the occipital artery to the posttemporal canal, and an upper opening that admits the occipital artery onto the dorsal surface of the occiput above the posttemporal canal. An upper opening that admits the occipital artery to the posttemporal canal, and an upper opening that admits the occipital artery onto the dorsal surface of the occiput above the posttemporal canal. In all three *Neocnus* specimens, the groove for the occipital bridge continues dorsally past the posttemporal foramen onto the occiput. A similar morphology has been described in the armadillos *Euphractus sexcinctus* (Wible and Gaudin 2004) and *Dasypus novemcinctus* (Wible 2010).

**Malleus**

On the right side of the skull in UF 76364, the malleus was preserved within the epitympanic sinus. The bone has been extricated, and is nearly complete, missing only the distal tip of the manubrium and perhaps part of the lamina and anterior process (Fig. 6). A malleus is also preserved in situ on the left side of UF 76363 (Fig. 3B), but it is largely hidden by the ectotympanic, the anteroventral process of the tegmen tympani, and matrix. The exposed portion, consisting of manubrium and a small part of the mallear neck, does not differ in any significant manner from the isolated malleus of UF 76364, so the following description will be based entirely on the latter specimen.

The malleus is roughly the same size as that from an uncataloged UTC specimen of *Choloepus hoffmanni*, which is not surprising given the close similarity in overall skull length between the two specimens. The maximum anteroposterior length of the mallear head in UF 76364 is 2.16 mm. The same measurement in the uncataloged specimen of *C. hoffmanni* is 2.08 mm. The head in *Neocnus* appears much less elongated in dorsal view than in the specimen of *C. hoffmanni* illustrated in Patterson et al. (1992), largely because it is considerably wider mediolaterally, and hence more ovoid in outline (Fig. 6C). In fact, the mallear head of *Neocnus* has a lower ratio of maximum head length/maximum head width than any of the sloth specimens illustrated in Patterson et al. (1992: fig. 21). The ratio is 1.33 in *Neocnus*, 1.82 in *Choloepus* (measured from Patterson et al. 1992: fig. 21C), 1.58 in the mylodont *Lestodon Gervais*, 1855 (Patterson et al. 1992: fig. 21B), 1.48 in *Bradypus* (Patterson et al. 1992: fig. 21D), and 1.35 in the nothrotheriid *Notherioterius* Hoffstetter, 1954 (Patterson et al. 1992: fig. 21D). It should be noted, however, that Patterson et al. (1992) based their discussions and illustrations on single specimens. In the uncataloged UTC specimen of *Choloepus hoffmanni*, the ratio of mallear head length to width is 1.5, much less than the 1.82 obtained from the specimen of *Choloepus hoffmanni* illustrated in Patterson et al. (1992), suggesting there is more variation at low taxonomic levels than allowed for by these authors.

The head bears two facets for the incus, each facing posteriorly and slightly medially. Like all pilosans (i.e., sloths and anteaters), the upper and lower incudal facets are nearly equivalent in size, and meet at an angle of slightly more than 90°, as in other sloths (Patterson et al. 1992; Gaudin 1995, 2004). On its ventral surface, the mallear head is connected by a thin sheet of bone, the lamina, to an elongate anterior process. Both the anterior process and lamina are smaller than the equivalent structures in *Choloepus* (Patterson et al. 1992), although in both cases this could be due to postmortem breakage. The anterior process is oriented at a right angle to the neck of the malleus, and diverges from the manubrium distally, whereas in *Choloepus*, the anterior process forms roughly a 110° angle with the neck, and extends nearly parallel to the manubrium. The last feature also appears to characterize *Acratocnus*, based on the illustration of an in situ malleus in this taxon by Patterson et al. (1992: fig. 5B). As in *Choloepus* and in contrast to *Bradypus* (Patterson et al. 1992), the lateral process that forms at the junction of the mallear neck and manubrium in *Neocnus* is relatively small. Patterson et al. (1992) reported that the manubrium of *Choloepus* forms a 110° angle to the mallear neck in lateral view (in the uncataloged UTC specimen, the angle is somewhat greater, ~120°), whereas in *Bradypus* the two are aligned and form a 180° angle. *Neocnus* is intermediate in this respect, with the manubrium forming an angle of approximately 135° with the neck.
Squamosal

The sutures are almost entirely closed in UF 76364 (*N. dousman*) and UF 170527 (*N. comes*), but in UF 76363 all the sutures on the braincase remain visible, as are most of those in the posterior orbital wall, including nearly the entire outline of the squamosal (Figs. 1A, 7). The bone appears to have had the normal contacts found in other sloths (and indeed in most other placental mammals)—parietal dorsally, alisphenoid anteromedially, ectotympanic ventrally and laterally, and petrosal ventrally, including a more posterior and lateral contact with the pars mastoidea of the petrosal and a more medial contact with the pars cochlearis of the petrosal. There is a dorsal contact between the supraoccipital and squamosal in the posteriormost portion of the lateral wall of the squamosal. Contact between the anterior portion of the squamosal and frontal, like that occurring in *Choloepus* (Patterson et al. 1992: fig. 4B; Gaudin 2004: fig. 11), is precluded by a short sutural link between the dorsal edge of the alisphenoid and a blunt anteroverentral process of the parietal. In this respect, *Neocnus* closely resembles the condition in *Acratocnus*.

The zygomatic process of the squamosal is heavily damaged in both *N. dousman* specimens and on the left side of UF 170527 (*N. comes*), but the right zygomatic process of UF 170527 is mostly intact, except for its anterior extremity (Figs. 1C, 8). The sharp dorsal edge of the zygomatic process is continuous with a ridge on the braincase marking the posterior limit of the temporal fossa. In the two *N. dousman* specimens (Figs. 1A–B, 4), this ridge is also present, and passes well anterior to the nuchal crest, as in the large West Indian megalonychid *Megalotus* (Matthew and Paula Couto 1959; Gaudin 2004). In *N. comes* (UF 170527), this ridge is continuous with the nuchal crest posterodorsally, as it is in *Choloepus, Acratocnus*, and many other megalonychids (Patterson et al. 1992; Gaudin 2004). The zygomatic process is deep dorsoventrally, not as much as in *Acratocnus* (Anthony 1918, 1926; Paula Couto 1967; Patterson et al. 1992), but more than in *Choloepus* (Naples 1982; Patterson et al. 1992). It is directed somewhat ventrally in lateral view, as in *Choloepus*. On its ventral surface it bears the fossa for the glenoid articulation with the mandibular condyle. Like other megalonychids (Patterson et al. 1992; Gaudin 1995, 2004), the glenoid fossa is elongated transversely, its mediolateral width greatly exceeding its anteroposterior length. The glenoid is roughly boomerang-shaped in ventral view. It is very strongly concave transversely, with its medial edge extending farther ventrally than its lateral edge, but is only very slightly concave in the anteroposterior plane. As in other megalonychids, the glenoid is bordered by two prominent crests—the “posterior shelf” (see Patterson et al. 1992; Gaudin 1995) that extends along its posterolateral margin, and the entoglenoid process along its posteroomedial edge. The entoglenoid process of the squamosal is well developed in most megalonychid sloths (Gaudin 1995, 2004). There is also a weak, rounded eminence marking the anteromedial edge of the glenoid fossa. In lateral view, the glenoid lies only slightly ventral to the level of the supercicies meatus (i.e., the groove on the squamosal immediately lateral and dorsal to the dorsal attachment of the ectotympanic), resembling *Acratocnus* rather than the more ventrally displaced glenoid of *Choloepus* (Patterson et al. 1992). Similarly, in ventral view the glenoid lies somewhat forward of the porous acusticus of the ectotympanic, as in *Acratocnus*, and not immediately anterior to this opening, as in *Choloepus* (Patterson et al. 1992; Gaudin 1995, 2004). A surprising feature of the glenoid region in *Neocnus* is the presence (in all three specimens—Figs. 2–3, 5, 8) of a well-developed postglenoid foramen, lying posterior to the midpoint of the glenoid fossa and somewhat dorsal to its surface. Although not unheard of in sloths, the postglenoid foramen is generally rudimentary or absent in the Pilosa (Patterson et al. 1992; Gaudin 1995, 2004). The postglenoid foramen has been reported present in the West Indian megalonychid *Parocnus* (Fischer 1971: fig. 9) and in a few other unrelated sloth taxa (*Megatherium* G. Cuvier, 1796, *Nematotherium* Ameghino, 1887, *Analcimorphus* Ameghino, 1891; see Gaudin 2004; *Mionothropus*, De Iuliis et al., 2011, see De Iuliis et al. 2011).

In UF 170527 (Fig. 1C), the lateral surface of the squamosal’s zygomatic process carries a distinct depression that occupies the entire depth and length of the process as preserved, ending posteriorly at the level of the supercicies meatus. Just posterior to this depression, and indeed, posterior to the zygomatic process itself, lies a second, even deeper fossa. The second fossa is triangular in shape, with its apex dorsally. Its base is formed by the supercicies meatus/posttympanic process of the squamosal; its overhanging anterodorsal border is formed by the crest marking the posterior limit of the temporal fossa, and its vertical posterior border is formed by the nuchal crest. This second fossa is also present in UF 76363, but is enlarged in UF 76364, in part because the crest marking the edge of the temporal fossa is situated much farther forward in *N. dousman*, and in part because (as was noted previously) the nuchal crest in this area forms a triangular posterior extension. This posterior extension is likely an individual anomaly, as it not present in UF 76363, and it has not been observed, described, or illustrated in other specimens of *Neocnus* (Fischer 1971; Mayo 1980; MacPhee et al. 2000). The function of both of the lateral depressions on the squamosal, if any, is unknown, although the more anterior depression could serve as an attachment site for part of the platysma, as in the armadillo *Euphractus sexcinctus* (Wible and Gaudin 2004). The posterior depression occurs in both *Choloepus* and *Acratocnus* (Patterson et al. 1992).

As noted in the preceding descriptions, the squamosal participates in the formation of the auditory region in several respects. It serves as the dorsolateral boundary for the tympanic cavity, where its supercicies meatus and posttympanic process bear facets for the anterior and posterior crura of the ectotympanic. The two crura are separated by a narrow stretch of squamosal, the incisura tympanica. The
entoglenoid process abuts the anterior crus of the ectotympanic and the anteroventral process of the tegmen tympani, forming part of the anterolateral boundary of the tympanic cavity. Finally, the squamosal largely encompasses the capacious epitympanic sinus, forming its entire lateral wall, and parts of the posterior, anterior, and medial walls. This sinus, as in other xerarthrans (Patterson et al. 1992; Gaudin 1995), extends not only dorsally above the ear ossicles, but also anteriorly into the root of the zygoma.

**Exoccipital**

The exoccipital bone carries the occipital condyles at the back of the skull, but also participates in the auditory region along its ventral and lateral edges. In all three specimens, the sutures surrounding the exoccipital are largely fused, with the exception of the exoccipital/mastoid suture and a small part of the exoccipital/supraoccipital suture on the right side of UF 170527 and on both sides of UF 76363. The exoccipital contacts the supraoccipital dorsally on the occipital surface of the skull, its dorsal extent roughly equivalent to that of the pars mastoidea of the petrosal. It has a vertical lateral boundary with the pars mastoidea, which is marked along nearly its entire extent by a raised crest, labeled the exoccipital crest by Gaudin (1995). The exoccipital crest terminates ventrally in a very low, bulbous paracondylar process (Figs. 2–5) that is considerably larger in Acratocnus, and larger still in Choloepus (Patterson et al. 1992; Gaudin 1995). The exoccipital normally contacts the basioccipital anteroventromedially, along the basicranial surface, in the vicinity of the jugular foramen. There remains no trace of this suture, apart from some low ridges along the medial wall of the jugular fora-amina that may mark the lateralmost edge of the contact. Based on the position of these ridges, it can be inferred that the exoccipital forms the entire posterior wall of the jugular foramen, extending anteriorly a short distance along the lateral wall to contact the entotympanic. It appears to extend even farther anteriorly along the medial wall of the jugular foramen, approaching the entotympanic in UF 76364, but as noted previously, without sutures the pattern of bony contacts cannot be confirmed.

The exoccipital is perforated by numerous foraamina. There is a deep dorsal condylid fossa along the dorso-medial edge of the occipital condyle, perforated by at least four small nutrient foraamina at its base in UF 76364. A similar number of nutrient foraamina are likely present in UF 76363 and UF 170527, though only two are exposed in each specimen, the remainder covered by matrix. There is also a large ventral condylid fossa situated just anterior to the lateral edge of the condyle in ventral view. In UF 76363, this fossa is deep, and contains one large and one small foramen at its base. On the right side of UF 76364, the ventral condylid fossa is perforated by one large and four small vascular foraamina. On the left, there is one large and three small foraamina, along with several large nutrient foraamina in the exoccipital medial to the ventral condylid fossa and anterior to the condyle. In UF 170527, the ventral condylid fossa is more medially situated and contains only two openings, but again there are other small nutrient foraamina in the area immediately anterior to the condyles. These nutrient foraamina are smaller, less numerous, and may even be lacking in Choloepus (e.g., they are missing on the left side of C. hoffmanni, CM 3883 and C. didactylus, UTCM 1000) and Acratocnus. The largest opening in the exoccipital is the hypoglossal foraamen. Like Choloepus and some Acratocnus specimens, there is a single hypoglossal foraamen for cranial nerve XII (in some Acratocnus, there are two foraamina—see Patterson et al. 1992: fig. 5A). In N. dousman, the hypoglossal foramen is situated very close to the posteromedial edge of the jugular foramen (Figs. 2–3, 5), so that the two are separated by only a narrow ridge of bone, much like the condition in Megalonyx (Patterson et al. 1992; Gaudin 1995, 2004). Neocnus comes (UF 170527) resembles Choloepus and Acratocnus (Patterson et al. 1992; Gaudin 1995, 2004) in having a wider separation between the hypoglossal and jugular foraamina.

**Basioccipital/Basisphenoid**

The basioccipital and basisphenoid elements form the floor of the basicranium. They are fused together in all three specimens, with little indication of where the suture between them lies. There are some faint ridges and grooves in UF 76364 that may indicate this suture near the posterior margin of the carotid foramen, anterior to the basioccaipital tubera. This would be slightly posterior to the position of this suture in Choloepus (Patterson et al. 1992; Gaudin 2004), but similar to the position in A. ye (based on juvenile specimen UF 17131).

The basioccipital in most mammals forms the anteroventral rim of the foramen magnum (e.g., see Choloepus in Patterson et al. 1992: fig. 4A). It has a posterolateral contact with the exoccipital. Laterally, the basioccaipital of Neocnus forms the medial wall to the basicochlear fissure, approaching (but not contacting) the petrosal. It may also, as noted above, contact the entotympanic laterally, as in UF 76364. The ventral surface of the basioccipital is marked by a pair of large basioccaipital tubera. There is some variation in the size of these tubera among the various Neocnus specimens (Fig. 1). For example, in UF 76364, the tubera are relatively small, and do not extend as far ventrally as the ventral edge of the entotympanic, whereas in UF 76363, they are much larger, extending well ventral to the entotympanic. In general, however, the basioccaipital tubera in Neocnus are similar in size to those of Acratocnus, differing dramatically from the hypertrophied, pneumaticized basioccaipital tubera of Choloepus (Patterson et al. 1992). In N. comes (UF 170527), but not in N. dousman (UF 76363 and 76364), there are two distinct pairs of depressions in close proximity to the
basioccipital tuba. The first pair lies at the posteromedial base of the tubera. These depressions are round in the back, but become narrow and shallower as they extend anteroventromedially along the margin of the tubera. These depressions are fossae for the insertion of the rectus capitis muscle (Gaudin 2004). The second pair of depressions is round, shallow, and lies on the posterolateral surfaces of the tubera. The function of this second pair of fossae is uncertain. It is possible that they represent attachment points for the longus capitis muscles, but in domestic dogs these muscles insert further forward on the basisphenoid (Evans and Christensen 1979).

The margins of the basisphenoid cannot be determined in the available specimens, as all its sutural contacts have closed. It certainly contacted the pterygoid laterally, and it likely formed part of the medial wall of the basicochlear fissure and the carotid foramen.

Pterygoid

The pterygoid bones are broken through their base in both *N. dousman* specimens and on the right side of the *N. comes* (UF 170527) specimen, but the left pterygoid of UF 170527 is completely intact (Fig. 1C), including the thin, semicircular flange that descends along the sidewall of the nasopharynx as in other sloths, the so-called pterygoid “descending lamina” (Gaudin 1995, 2004). As in *Acratocnus* and in strong contrast to *Choloepus*, the pterygoids are largely uninflated. Breaks in all three specimens, however, reveal that there were small, presumably air-filled spaces in the posterocondal reaches of the bone. Once again, because of sutural closure it is impossible to be sure about many of the boundaries of the pterygoid, especially those with the palatine anteriorly (Fig. 7) and basisphenoidal medially. However, the pterygoid clearly participates in the antero-lateral margin of the carotid foramen in *Neocnus*, and may form part of the anterocondal margin. As in *Choloepus* but unlike *Acratocnus*, the pterygoid does not appear to participate in the walls of the tympanic cavity proper, lying just anteroventrally to this chamber. In UF 76364 it is excluded by the enlarged anteroventral process of the tegmen tympani, which it contacts posterocondal laterally.

There are two prominent grooves along the posterodorsal margins of the pterygoid and the area where the pterygoid meets the basisphenoid and carotid foramen (Figs. 2, 5). The more lateral groove lies along the posterocondalateral rim of the pterygoid lamina, extending anteroventrally from the lateral edge of the carotid foramen to a point well ventral to the plane of the basioccipitic/roof of the nasopharynx. In *N. comes* (UF 170527), this groove is shallow and poorly marked, but in *N. dousman* (UF 76363 and UF 76364), it is deep, bounded by strong medial and lateral ridges. The lateral ridge is formed by the entoglenoid process of the squamosal in UF 76363, and by a ridge of the pterygoid in UF 76364. The medial ridge is formed in both specimens by the anteroventral process of the tegmen tympani dorsally, and by a strong lateral flange of the pterygoid ventrally. In UF 76364, the medial and lateral ridges actually meet dorsally to form an enclosed tube. The groove that emerges thusly from between the petrosal, squamosal, and pterygoid onto the lateral surface of the pterygoid descending lamina resembles a similar groove found in *Bradyus* and many megatherioid sloths, where it is hypothesized to have housed the tensor veli palatini muscle (Patterson et al. 1992; Gaudin 1995, 2004; McDonald and Muizon 2002). This groove does not occur in *Choloepus*, *Acratocnus*, or other megatheroids (Gaudin 1995, 2004).

In UF 76364, there is a smaller additional lateral groove traversing the area of the region of the pterygoid/alisphenoid/squamosal boundary, posterior to the foramen ovale, which emerges from a foramen formed by contact between the more lateral of the two pterygoid ridges and the entoglenoid process of the squamosal. Its function is unknown.

The more medial of the two main grooves in the pterygoid region extends anteroventromedially from the carotid foramen. It is bounded laterally by the descending lamina of the pterygoid, and medially by a strong crest on the basioccipital surface, extending forward toward the roof of the nasopharynx, in the region where the pterygoid/basisphenoid contact would be expected to occur. This groove housed the vidian nerve (or nerve of the pterygoid canal; Fig. 2B), a rostral continuation of the greater petrosal nerve that eventually attaches to the pterygopatine ganglion in the orbit (see below). In *N. comes* (UF 170527), the medial crest marking this groove is strong (nearly contacting the pterygoid descending lamina on the left side of the skull) but short antero-posteriorly, and lies immediately anterior to a gentle concavity that presumably housed the cartilage of the auditory tube. In UF 76364, the ridge is much longer posteriorly. On the left side of UF 76364, the ridge extends back almost to the area where the basioccipital/basisphenoid contact is likely situated. On the right side of UF 76364 and on both sides of UF 76363, the morphology is even more unusual. Along its ventral edge, this ridge contacts the lateral flange of the pterygoid that was mentioned above, enclosing the groove for the tensor veli palatini. This pterygoid flange is greatly enlarged in UF 76364 and on the right side of UF 76364. It expands anteroventromedially and is hollow internally. Its contact with the medial crest encloses the proximal portions of the vidian nerve in a short canal. On its posteroventrolateral surface, the flange bears a strongly concave groove that almost certainly cradled the auditory tube as it emerged from the tympanic cavity (Figs. 3, 5). The morphology of the groove for the vidian nerve in UF 170527 resembles that of *Acratocnus*. In *Choloepus*, the vidian nerve travels in a canal within the pterygoid, and so it lacks any external groove, but the inflated pterygoid does house a weak groove for the auditory tube reminiscent of that found in UF 76363 and on the right side of UF 76364.
In UF 76363, the sutures along the dorsal edge of the left alisphenoid are preserved nearly in their entirety, but the anterior and ventral sutures are either fused or missing because of damage to the pterygoid region (Fig. 7). The alisphenoid contacts the squamosal along its posterodorsal margin. As noted above, it has a short connection with the parietal that leads anteriorly into a horizontal suture between the alisphenoid and frontal. This suture disappears as it enters a shallow fossa situated immediately dorsal to the opening of the sphenorbital fissure/optic foramen (see description below). This is likely near the actual anterior limit of the alisphenoid; as in most xenarthrans the alisphenoid forms the lateral wall to the sphenorbital fissure, but does not extend anterior to the opening (Guth 1961; Gaudin and Branhman 1998; Wible and Gaudin 2004). From its posterior inception near the anterior margins of the tympanic cavity, the squamosal/alisphenoid suture passes anteroventrally along the medial edge of the squamosal’s entoglenoid process. It then turns at the anterior terminus of that process to travel in an anterodorsal direction, passing clearly dorsal and lateral to the foramen ovale as it does so. Because of breakages or fusion in this area, it cannot be determined from the available specimens whether the foramen ovale is completely within the alisphenoid, as it is in the undescribed juvenile specimen of *A. ye* (UF 171341), or between the alisphenoid and pterygoid, as is known to occur in other sloths (e.g., *Megalonyx*, Gaudin et al. 1996; Gaudin 2004). However, both MacPhee et al.’s (2000: figs. 9B, 12C) illustrations of the holotype specimen of *N. toujiti* and Mayo’s (1980) photograph of *N. major* show a clear alisphenoid/pterygoid suture ventral to the foramen, suggesting that *Neocnus* resembles the condition in *A. ye*, and so I have reconstructed the suture in this position (Fig. 7). In *Choloepus*, the alisphenoid typically forms the internal aperture of the foramen ovale in the braincase, but the external aperture on the orbital wall may lies between the alisphenoid, squamosal and pterygoid, or just the squamosal and pterygoid (Gaudin et al. 1996; Gaudin 2004).

In *N. comes* (UF 170527), there is a lappet of bone in the anterodorsal wall of the tympanic cavity, between the entoglenoid process and the promontorium, that may be formed in part by the alisphenoid. The lack of sutures here also leaves open the possibility that it is formed in whole or in part by the pterygoid or the squamosal. In *N. dousman*, the alisphenoid is excluded from the tympanic cavity by contact between the large anteroventral process of the tegmen tympani and the entoglenoid process.
DESCRIPTION OF AUDITORY AND ORBITAL FORAMINA

The Neocnus specimens that form the basis of this study preserve not only their auditory region anatomy in unusual detail, but also the orbital foramina. The course of these foramina can be traced into the braincase, in part because they have been cleaned of matrix, but also in part because there are large breaks in the skull roof of UF 76364 that allow their internal apertures to be observed (Fig. 1B). This allows these foramina to be positively identified and their contents reconstructed. Therefore, a description of the orbital foramina was thought to be a valuable addition to the present study. Along with the orbital foramina, a brief discussion is included of the foramina from the auditory region that were not discussed in detail above. There are few published, detailed descriptions of the orbital foramina available for other sloths. Guth (1961) briefly describes this region in both Bradypus and Cholopeus as well as a variety of fossil sloths, but he focused more on the auditory region than the orbit, and as noted above, he described few extinct megahystrichid taxa, none from the West Indies. The descriptions of the cranial osteology of Bradypus and Cholopeus by Naples (1982) are unreliable, particularly in the orbitotemporal region, where numerous foramina are unlabeled or mislabeled, orbital bones are unlabeled, and several sutures are missing or inaccurately drawn. For comparative purposes, then, I have relied on my own personal observations of specimens of Acratocnus and Cholopeus (see Materials and Methods above) and data from Gaudin (2004).

Foramina: Auditory Region

Fissura Glaseri.—The fissura Glaseri, or Glaserian fissure, is the term applied to the opening that transmits the chorda tympani nerve anteriorly from the tympanic cavity. In UF 76364, there are two openings that might represent the Glaserian fissure (Fig. 4A). The first is between the dorsal end of the entotympanic’s anterior crus and the squamosal, posterior to the medial portion of the glenoid fossa. The second is much more ventral, in front of the lower end of the anterior crus, just medial to the entogle- noid process of the squamosal (Fig. 2). In UF 76363, the upper opening appears to be present on the left (Fig. 3B), the lower on the right. This lower foramen is identified as the Glaserian fissure in Neocnus, because it resembles the condition in Cholopeus and Acratocnus, and because with one exception (a juvenile specimen of the basal megatheri- oid sloth Hapalops elongatus Ameghino, 1891, described by Patterson et al. 1992), in all xenarthrans in which the Glaserian fissure has been described, it is medial to the en- togleenoid process (Patterson et al. 1992; Wible and Gaudin 2004; Wible 2010).

Carotid foramen.—As discussed by Wible and Gaudin (2004), there is some confusion surrounding this term. It has been used both for the opening on either side of the carotid canal for those taxa with a peribullar course of the internal carotid artery (peribullar referring to a condition wherein the artery travels within or perforates the medial wall of the auditory bulla; see Wible 1986), as well as for the opening that admits the internal carotid artery into the braincase. Wible and Gaudin (2004) use the term in the last sense, and I follow them in doing so here, although it is worthy of note that many sloths, including some specimens of Cholopeus, have a short carotid canal (Patterson et al. 1992; Gaudin 1995), and that the latter two papers use the term “carotid foramen” to refer to the posterior opening of the carotid canal, and the term “median lacerate foramen” or “foramen lacerum medium” to refer to the basicranial opening for the internal carotid.

Neocnus lacks a carotid canal, there being no contact between the anterior part of the entotympanic and the basi- cranium, or between the medial and lateral ridges that flank the internal carotid sulcus on the entotympanic. The carotid foramen (Figs. 2, 5) is a large opening bordered by the basioccipital/basisphenoid medially, the pterygoid anteriorly, the entotympanic posteroventrally, and the epitympanic wing of the petrosal posterosdorsally (the epitympanic wing being much less prominent in N. comes, UF 170527). The opening is clearly visible in ventral view in UF 170527 and on the left side of UF 76364, as it is in Acratocnus (Patterson et al. 1992; Gaudin 1995); on the right side of UF 76364 and on both sides of UF 76363, the opening is obscured by the Eustachian flange of the ptery- goid, resembling the condition in Cholopeus (Patterson et al. 1992; Gaudin 1995).

Musculotubal canal.—The bony opening for the carti- laginous auditory tube, termed the musculotubal canal by Wible and Gaudin (2004, following Evans and Christiansen 1979—in dogs, the cartilaginous auditory tube represents a rostral continuation of the bony musculotubal canal), is immediately posterolateral and ventral to the carotid fora- men. It is bordered by the entotympanic posteromedially, by the pterygoid anteromedially, and by the entotympanic laterally and posteriorly, the posterior margin being formed by the styliform process of the entotympanic (Fig. 2). As noted above, the further course of the auditory tube may be marked by grooves on the pterygoid and/or the basicranium (Fig. 5). This is similar to the morphology in Acratocnus and Cholopeus (Patterson et al. 1992; Gaudin 1995), although the opening is less well defined in both genera, due to the lack of anterior ossification of the entotympanic in the former and the lack of a ventrally expanded ectotympanic in the latter. The musculotubal canal and auditory tube serve to link the tympanic cavity to the nasopharynx (Evans and Christiansen 1979).

Jugular foramen.—The jugular foramen is the large opening that serves as the cranial exit for the ninth, tenth, and eleventh cranial nerves and the internal jugular vein in many mammals, including xenarthrans (Evans and Chris-
the mandibular branch of the trigeminal nerve (Evans and Christiansen 1979; Wible and Gaudin 2004; Wible 2010). The opening is termed the "foramen lacerum posterium" or "posterior lacerate foramen" in Patterson et al. (1992) and Gaudin (1995). It is between the entotympanic and petrosal anteriorly and the exoccipital posteriorly in Neocnus, likely with a small contribution from the basioccipital to the medial wall. It is ovate in shape in UF 170527, UF 76363 (Fig. 3), and on the left side of UF 76364 (Fig. 2), elongated along an anteroposterior axis, but more circular on the right of UF 76364 (Fig. 5). In Acratocnus and Choloepus, the jugular foramen is circular, and has a larger contribution from the basioccipital to the anteromedial wall of the opening, due to a lack of contact between the entotympanic and the basioccipital.

Foramina: Orbital Region

Foramen ovale.—The foramen ovale, which transmits the mandibular branch of the trigeminal nerve (Evans and Christiansen 1979; Wible and Gaudin 2004), is not only the most posterior and ventral of the orbital foramina, but also the largest. It is at the level of the anterior edge of the glenoid, between the entoglenoid process of the squamosal and the pterygoid descending lamina, and, as discussed above, is apparently contained entirely within the alisphenoid bone (Figs. 2, 4–5, 7–8). As in Acratocnus (Patterson et al. 1992), it opens anteroventrally, whereas in Choloepus it has a more lateral tilt and is less visible in ventral view, due no doubt to the sizable inflation of the pterygoid (Patterson et al. 1992).

Foramen rotundum.—A separate opening for the maxillary branch of the trigeminal nerve, the foramen rotundum (Evans and Christiansen 1979; Wible and Gaudin 2004), is present in Neocnus (Figs. 7–8). This opening often fuses with the sphenorbital fissure in sloths, though it is separate in all megatherioid sloths except the derived members of Megatheriidae (Gaudin 2004). It is only variably present in Choloepus (Gaudin 2004; though it is present in all three Choloepus specimens examined in the present study). The opening is anterior and slightly dorsal to the foramen ovale, and faces anteriorly and slightly lateral. It opens into a deep, anteroposteriorly elongate fossa, presumably the pterygopalatine fossa (Evans and Christiansen 1979; Wible and Gaudin 2004), that it shares with the anterior opening of the pterygoid canal, the caudal palatine foramina, and the sphenopalatine foramen (Fig. 8). In N. doumsian, this fossa is partially walled laterally by a bar of bone that covers over the pterygoid canal and appears to separate the caudal palatine foramina and sphenopalatine foramen from the foramen rotundum in lateral view; although the pterygopalatine fossa is continuous medial to the bar of bone. There is no indication of the bar in N. comes (UF 170527). When present as a separate passage, the foramen rotundum in Choloepus is between the alisphenoid posterolaterally and the palatine anteromedially, whereas in A. ye (UF 171341, juvenile) it is entirely within the alisphenoid. Based on MacPhee et al.'s (2000) figures of N. toupi, it would appear that in Neocnus the opening is largely within the alisphenoid, although the palatine/pterygoid may make a small contribution to the ventral-most rim of the foramen (Fig. 8).

Sphenorbital fissure/optic foramen.—Although it is clear from peering through openings in the braincase of UF 76364 that there are separate internal apertures for the optic canal (accommodating the optic nerve, cranial nerve II, and associated vessels) on the one hand, and the nerves and vessels that traverse the sphenorbital fissure on the other (typically cranial nerves III, IV, V1, and VI, and a variety of accompanying veins and arteries; Evans and Christiansen 1979; Wible and Gaudin 2004), these canals merge well before they exit the skull via a common superficial opening. This arrangement is a unique apomorphy of sloths (Gaudin 2004), although in armadillos and anteaters the optic foramen and sphenorbital fissure often open externally into a common fossa (see, e.g., Wible and Gaudin 2004).

The position of this opening is unusual in Neocnus, situated along the posterior edge of a prominent swelling that accommodates the root of the last molariform tooth (Figs. 7–8). This places the opening slightly anterior to the anterior edge of the pterygopalatine fossa, where the sphenopalatine and caudal palatine foramina are located. The opening for the combined optic foramen/sphenorbital fissure is well dorsal to the pterygopalatine fossa as well. It is positioned just dorsal to the level of the anterior edge of the glenoid. This means that the combined sphenorbital fissure/optic foramen is separated by a substantial distance from the foramen rotundum. This stands in contrast to the condition in Choloepus, where the two openings are immediately adjacent to one another, the sphenorbital fissure/optic foramen only slightly dorsal and anterior to the foramen rotundum. Furthermore, in Choloepus the opening for the sphenorbital fissure/optic foramen is well posterior to the sphenopalatine and caudal palatine foramina, which, as in Neocnus, is in close proximity to the root of the last molariform. The position of the opening for the sphenorbital fissure/optic foramen in Acratocnus is nearly identical to that in Neocnus. The alisphenoid appears to form the lateral wall of the opening in Neocnus, as in Acratocnus and Choloepus, but the medial wall is formed either by frontal, orbitosphenoid, or both (Fig. 8; the absence of sutures in this area precluding a more definitive assessment). The medial wall, including the entirety of the optic canal, is formed by orbitosphenoid in the juvenile specimen of A. ye (UF 171341), but by frontal and orbitosphenoid in adult A. odontigrinus (AMNH 17722). The floor, medial wall, and roof of the sphenorbital fissure/optic foramen are formed by a complex interdigitiation of the frontal, orbitosphenoid, and palatine in Choloepus. The Carnegie Museum specimen of C. hoffmanni (CM 3883) is highly unusual in that is has a large bilateral orbitosphenoid exposure forming the dorsal half of the lateral wall of the
sphenorbital fissure/optic canal opening. This exposure then extends posterodorsally between the frontal bone anteriorly and the alisphenoid and squamosal posteriorly. This large orbitosphenoid exposure is quite atypical for xenarthrans in general, in which the orbitosphenoid generally has only a small exposure in the medial wall of the orbit, an exposure that is normally confined to the area immediately anterior and medial to the sphenorbital fissure (see, e.g., description of *Euphractus* in Wible and Gaudin 2004). Whether this is a juvenile condition, or simply an individual anomaly of this specimen, is unclear at present.

In both specimens of *N. dousman* (UF 76363 and 76364), there is an additional foramen between the foramen rotundum and the combined opening of the sphenorbital fissure/optic foramen on the left side of the skull only (Fig. 7). Although this extra foramen is somewhat closer to the foramen rotundum than to the opening for the sphenorbital fissure/optic foramen, by passing a fine wire into the extra foramen and peering through the breaks in the braincase in UF 76364, it can be demonstrated that the extra opening is connected with the internal aperture of the sphenorbital fissure within the braincase. It is not clear which of the nerves and vessels normally passing through the sphenorbital fissure travel through this extra foramen, and the extra foramen is not found in *N. comes* (UF 170527), *Acratocnus*, or *Choloepus*.

**Sphenopalatine foramen.**—The sphenopalatine foramen, which admits the caudal nasal nerve and sphenopalatine artery into the nasal cavity (Evans and Christiansen 1979; Wible and Gaudin 2004), is situated at the anterior end of the pterygopalatine fossa in *Neocnus* (Figs. 7–8). The pterygopalatine fossa is somewhat expanded dorsoventrally at its anterior end, with the sphenopalatine foramen situated at the dorsal margin of this expansion, and the caudal palatine foramina at the ventral edge. As noted above, both are situated slightly behind a prominent swelling that accommodates the root of the last molariform tooth. In *Acratocnus* and *Choloepus*, the sphenopalatine and caudal palatine foramina occupy a position very much like those of *Neocnus*. The foramina open into a circular pterygopalatine fossa in *Acratocnus*, though the foramen rotundum does not open into this fossa; the uncataloged UTC specimen of *C. hoffmanni* lacks a distinct fossa in the medial orbital wall for these foramina, whereas in *C. didactylus* (UTC 1000) and *C. hoffmanni* (CM 3883) the sphenopalatine foramen is a small aperture in the roof of the caudal palatine foramen. The sphenopalatine foramen lays on the suture...
between the maxilla and palate in *C. didactylus* (UTCM 1000) and the juvenile specimen of *Acratocnus ye* (UF 171341), but just behind the maxilla/palatine suture, entirely within the palate, in *Acratocnus odonttrigonus* and *C. hoffmanni* (CM 3883). The sutures are fused in this area in all three *Neocnus* specimens available, but MacPhee et al.'s (2000: figs. 9B, 12C) illustrations of the holotype of *N. toupiti* indicate that the foramen is contained within the palate as in *A. odonttrigonus* and some *Choloepus*.

**Caudal palatine and postpalatal foramina.**—The caudal palatine foramen in the dog is the opening in the orbit that admits the major palatine nerve and artery into the palate canal (Evans and Christiansen 1979). As discussed by Wible and Gaudin (2004), there is a similar but not strictly homologous opening between the maxilla and palate in the armadillo *Euphractus sexcinctus*. The opening, which they also label “caudal palatine foramen,” is not strictly homologous because it transmits not only the major palate nerve and artery servicing the hard palate, but also the minor palatine nerve and artery servicing the soft palate, which in the dog passes through a separate notch in the back of the hard palate. In *Neocnus*, there are two openings in the anteroventral corner of the pterygopalatine fossa. The more medial of these is the opening into the longitudinal palatine canal for the major palatine nerve and artery (described in the armadillo *Euphractus*, Wible and Gaudin 2004). The more lateral opens into a canal that passes ventrally and medially into the postpalatal shelf, a surface found in many sloths that slopes upward and laterally from the back edge of the palate along the insides of the descending laminae of the pterygoids (Gaudin 2004). The postpalatal shelf is in turn perforated by a variable number of postpalatine foramina—one large and three small foramina in UF 76364 (only the left side is preserved); one large and one small foramen on both sides of UF 76363; and two large foramina on the right of UF 170527, five small foramina on the left (Fig. 1). These postpalatine foramina are present in many sloths (e.g., see descriptions in Gaudin 2004; De Iuliis et al. 2011), and are occasionally enlarged to form very large openings (see Stock’s 1925 description of *Nothotheriops*). Based on the anatomy of *Neocnus*, these postpalatine foramina, more properly called postpalatinal foramina because they occur within the palate bone, almost certainly transmit branches of the minor palatine nerve and artery to the soft palate. Thus, the two separate openings in the anteroventral corner of the pterygopalatine fossa accommodate the major and minor palatine nerves and arteries, respectively, and are therefore jointly homologous with the single caudal palatine foramen described in *Euphractus* (Wible and Gaudin 2004). I am therefore designating these two foramina collectively as the caudal palatine foramina.

In *Acratocnus* and *Choloepus*, there is a single caudal palatine foramen that, as in *Euphractus* (Wible and Gaudin 2004), transmits both major and minor palatine nerves and arteries. *Acratocnus* has anywhere from two to four postpalatal foramina on the postpalatal shelf that transmit branches of the minor palatine nerve and artery to the soft palate. In *Choloepus*, there is no postpalatal shelf. The specimens examined in this study, however, possess a large, oval foramen on the back of the hard palate, between the last molariform and the postpalatine notch on the maxilla/palatine suture. Though this foramen opens into the palatine canal passing forward through the palate, there is a short, posteriorly directed groove emerging from its posterior margin, suggesting that it serves at least in part as the opening for the minor palatine nerves and arteries and is at least in part homologous to the postpalatal foramina of the West Indian sloths. Additionally, the CM 3883 specimen of *C. hoffmanni* bears a small foramen on the left palate, posterior to the aforementioned larger opening, that very closely resembles the postpalatal foramina of these extinct sloths. Some specimens of *Choloepus didactylus* lack the enlarged “postpalatal foramen” described here (De Iuliis, personal communication), but do possess smaller posteriorly directed openings in this region of the palate that likely accommodated the minor palatine nerves and arteries.

**Pterygoid canal.**—The nerve of the pterygoid canal typically emerges from the area around the carotid foramen as a rostral continuation of the greater petrosal nerve. It enters a small groove along the lateral margins of the nasopharyngeal roof, and eventually enters into the pterygoid canal proper, passing to an anterior opening in the medial wall of the orbit near the sphenorbital fissure where it then joins the pterygopalatine ganglion (Evans and Christiansen 1979; Wible and Gaudin 2004). The presence of a medial groove or canal passing anteriorly from the carotid foramen of *Neocnus* and carrying the nerve of the pterygoid canal was noted above in the description of the pterygoid bone. This groove or canal is continuous anteriorly with a shallow but clearly marked groove that passes forward along the lateral edge of nasopharyngeal roof for much of the length of the nasopharynx. The posterior entrance to the pterygoid canal is situated at roughly the same position as its anterior opening in the medial wall of the pterygopalatine fossa, midway between the foramen rotundum and the sphenopalatine and caudal palate foramina (Figs. 7–8). This means that the pterygoid canal itself is very short. The anatomy in *Acratocnus* appears similar, though with a smaller pterygopalatine fossa. The anterior opening to the pterygoid canal lies along the back wall of the fossa, within the palate bone (*A. odonttrigonus*) or between the alisphenoid and palate (*A. ye*). Because of the inflation of the pterygoids in *Choloepus*, there is no exposed nasopharyngeal groove for the nerve of the pterygoid canal. Instead, the pterygoid canal is greatly elongated. In *C. didactylus* (UTCM 1000), its posterior opening lies along the posteroventral margin of the pterygoid inflation, at the end of a short groove that emerges anteroventrally from the carotid foramen and traverses the lateral surface of the pterygoid inflation. In *C. hoffmanni* (uncataloged UTC specimen), there is no groove, and the posterior opening for the pterygoid canal
is in the anteroventral edge of the carotid foramen itself, much further dorsally than in *C. didactylus*. There also appears to be a great deal of variability in the position of the anterior opening of the pterygoid canal in *Choloepus*. In *C. didactylus*, it is just anterior to the bar of bone separating the foramen rotundum from the sphenorbital fissure/optic foramen on the left side of the skull, between the palatine and alisphenoid. On the right it is situated below this bar and more posteriorly, actually opening on the medial wall of the foramen rotundum within the palatine bone. The anterior opening is even farther ventral in *C. hoffmanni*, lying just anterior to the lower edge of the foramen rotundum on both sides of the skull in the uncataloged UTC specimen, and in a similar ventral location in CM 3883, albeit well forward of the foramen rotundum, indeed somewhat closer to the sphenopalatine/caudal palatine foramina. The opening is clearly within the palatine in CM 3883, and likely in the former specimen as well, though the orbital sutures are fused in this individual.

**Ethmoidal foramen.**—The ethmoidal foramen or foramina transmit the ethmoidal nerve and ethmoidal vessels, passing through the medial wall of the orbit into the cranial cavity (Evans and Christiansen 1979; Wible and Gaudin 2004). *Neocnus* has a single ethmoidal foramen that lies just anterior to the dorsal edge of the opening for the sphenorbital fissure/optic foramen (Figs. 7–8). *Choloepus* is virtually identical, although on the right side of the one *C. hoffmanni* specimen (UTC uncataloged specimen) there is a lateral bar of bone that divides the external aperture of the ethmoidal foramen in two. *Acratocnus* has two separate ethmoidal foramina. These are roughly in the same position as in *Neocnus* and *Choloepus*, though slightly farther anterior relative to the sphenorbital fissure/optic foramen opening. The opening is completely contained within the frontal in *Acratocnus* and *Choloepus didactylus* (UTC 1000), whereas in *C. hoffmanni* (CM 3883) it is between orbitosphenoid and frontal, a condition known to be present in other xenarthrans (Gaudin and Wible 2006).

**Foramen for frontal diploic vein.**—Many xeranths are characterized by the presence of a prominent foramen at the upper margin of the orbital wall, often just anterior and ventral to the postorbital process of the frontal. This opening has been called the supraorbital foramen, and its presence and position has been used as a character in xenarthran systematics (e.g., Gaudin and Branham 1998; Gaudin 2004). Wible and Gaudin (2004) demonstrated that this foramen transmits the frontal diploic vein in the armadillo *Euphractus sexcinctus*, and labeled it the “foramen for the frontal diploic vein.” That terminology is followed here. The foramen for the frontal diploic vein sits on the orbital rim, immediately anterior and ventral to the postorbital process of the frontal, and opens into an anterioedly directed groove (Figs. 7–8). The postorbital process is very weakly developed in *Neocnus*. *Acratocnus* displays a similar morphology, though the postorbital process itself is much more robust. In *C. didactylus* (UTC 1000), the foramen lies on the undersurface of the broad, shelf-like postorbital process. The foramen occupies a similar position on the right side of *C. hoffmanni* (CM 3883), but on the left side of that specimen and on both sides of *C. hoffmanni* (UTC uncataloged specimen, which has much smaller, more pointed postorbital processes that the other *Choloepus* specimens examined in this study), it is much farther forward, just ventral to the anterior base of the postorbital process.

**DISCUSSION**

In most respects, the basicranial and orbitotemporal anatomy of *Neocnus* more closely resembles that of its fellow extinct Antillean sloth *Acratocnus* than it does that of the extant *Choloepus*. Based on the descriptions above, only a small list of resemblances can be generated that are shared by *Choloepus* and *Neocnus* exclusive of *Acratocnus*—an anteroventrally oriented zygomatic process of the squamosal (in lateral view), the exclusion of the pterygoid from the tympanic cavity, and the presence of a single ethmoidal foramen. Similarly, the number of features linking *Choloepus* and *Acratocnus* exclusive of *Neocnus* is small—a weak stylohyoid process of the ectotympanic, a strong paracorodyl process, the lack of contact between the entotympanic and basioccipital, and the parallel orientation of the manubrium and the anterior process of the malleus in lateral view. In contrast, the list of similarities between *Neocnus* and *Acratocnus* that are not shared by *Choloepus* is lengthy indeed, and would include the following: ectotympanic elongated dorsoventrally (with the anterior crus extending ventral to the entotympanic process) and expanded ventrally, with the stylohyoid process located posterior to the musculotubal canal; entotympanic and entotympanic extensively sutured to one another ventrally; stylohyal fossa facing ventrally; mastoid depression rugose, traversed by numerous grooves and ridges; zygomatic process of the squamosal deep dorsoventrally in lateral view; glenoid fossa separated anteriorly from the porus acusticus of the ectotympanic and roughly at the same level as the superciliary meatus of the squamosal; parietal with short, blunt anteroventral process forming a contact with the alisphenoid; absence of inflated basioccipital tubera, basisphenoid, and pterygoid; foramen ovale rim completely within the alisphenoid, with the foramen facing anteroventrally; foramen rotundum completely within the alisphenoid; sphenorbital fissure/optic foramen located immediately posterior to the root of the last molariform, slightly anterior to the position of the sphenopalatine foramen, separated dorsally from the foramen rotundum; no palatine contribution to the medial wall of the sphenopalatine fissure/optic foramen; and the postpalatal shelf present, perforated by a variable number of small postpalatal foramina.

The close anatomical resemblance in this part of the skull between *Neocnus* and *Acratocnus* would seem to
be inconsistent both with the phylogenetic hypotheses of White and MacPhee (2001), and those of Gaudin (2004). The cladogram of White and MacPhee (2001) links *Choloepus* and *Acratocnus* as sister taxa, with *Neocnus* as the nearest relative of this clade. The consensus tree of Gaudin (2004: fig. 2) places *Neocnus*, *Acratocnus*, and *Choloepus* in an unresolved trichotomy at the base of a monophyletic assemblage that includes the other extinct Antillean sloths. However, the most parsimonious trees on which the consensus tree is based either ally *Choloepus* with *Acratocnus* or with *Neocnus*, but do not yield an *Acratocnus*/*Neocnus* clade, despite the fact that such a clade has intuitive appeal from a temporal and biogeographic standpoint. *Acratocnus* and *Neocnus* are both extinct Quaternary taxa with largely sympatric distributions in Cuba and Hispaniola (Paula Couto 1967; Fischer 1971; Mayo 1980; MacPhee et al. 2000; White and MacPhee 2001; Rega et al. 2002—*Acratocnus* is also known from Puerto Rico; Anthony 1918, 1926; Paula Couto 1967), whereas *Choloepus* is an extant genus with no known fossil record and a geographic range restricted to northern South America and southern Central America (Gardner and Naples 2007; Aguiar and Fonseca 2008).

In the absence of a formal cladistic analysis (which is beyond the scope of the present study), it is not possible to definitively assess the phylogenetic implications of the anatomy described in this report. However, it is worth noting that many of the resemblances between *Neocnus* and *Acratocnus* listed above may represent plesiomorphies. Gaudin (2004) has noted previously that *Choloepus* is in many ways an aberrant megalonychid characterized by a long list of autapomorphies. Some of the features linking *Neocnus* and *Acratocnus* merely represent the absence of these autapomorphies, e.g., the lack of prominent basioccipital, basisphenoid, and pterygoid inflations. Furthermore, it is likely that some features shared by *Neocnus* and *Acratocnus*, such as the ventrally expanded, dorsoventrally elongate ectotympanic that is in broad connection with the entotympanic, are primitive features within Megalonychidae, or at least among the late Miocene–Recent megalonychids, which is to say the more circular, slender, more isolated ectotympanic of *Choloepus* is yet another derived autapomorphy of this taxon (a similar suggestion is made in Gaudin 1995).

There are several specialized auditory features that characterize all three genera, including the weak development of the sulcus and crista tympanica; the sharp ventral edge of the lateral crest of the entotympanic; the flat lateral surface and flat dorsal edge of the entotympanic; and the presence of an open groove connecting the stylomastoid foramen and posttemporal canal. As was noted in the descriptions above, Gaudin (1995) identified all but the last of these features as synapomorphies of *Choloepus* and *Acratocnus*, but they are also clearly present in *Neocnus*. It is possible that they diagnose a monophyletic subfamily Choloepodinae as proposed by White and MacPhee (2001), though their condition is unknown in the poorly preserved genus *Paulocnus* (Hooijer 1962, 1964). It is also possible that some of these features are present in other Antillean megalonychids, but the basi- cranial and orbitotemporal anatomy of most of these taxa is incompletely known. Even in relatively well-known taxa such as *Megalocnus* and *Parocnus* Miller, 1929, there is limited information available. For example, so far as I am aware the only description of an ectotympanic for either taxon is a brief note by Fisher (1971) describing the ectotympanic of both taxa as “slender” and “ring-like,” accompanied by no further anatomical details and only a rather sketchy illustration.

Ultimately, the details provided by the present study should facilitate future investigations of megalonychid cranial anatomy, and may spur further detailed study of some of the wonderful fossil material available for other Antillean sloths in the Florida Museum of Natural History and elsewhere. It is clear that the interpretation of this anatomy, and of cranial evolution in Antillean sloths in particular and megalonychid sloths in general, will require a better understanding of megalonychid phylogeny than is currently available. There is little consensus among most recent studies regarding the shape of phylogenetic relationships within the family. Moreover, these studies are hampered either by limited taxon sampling (e.g., White and MacPhee 2001; Pujos et al. 2007), character sampling (e.g., Gaudin 2004), or both (e.g., Carlini and Scillato-Yáñez 2004). New studies are required that examine a broad range of megalonychid taxa from South America, including early, Santacrucian taxa like *Eucholoepus* Ameghino, 1887, and *Megalonychotherium* Scott, 1904, as well as later forms like *Pliomorphus* (Kraglievich 1923), *Athytherium* Cartelle et al., 2008 (Cartelle et al. 2008), and extant *Choloepus*, alongside taxa from North America and from the West Indies. These studies should include a well-chosen array of relevant outgroups from other sloth families, and should consider anatomical details from all parts of the skeleton. Completion of such studies should help to resolve the current muddled state of megalonychid phylogeny, and would go far to enhancing our understanding of the evolution of this important sloth family and the evolution of sloths and New World mammalian faunas as a whole.

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