THE BASICRANIUM AND ORBITAL REGION OF THE EARLY MIOCENE *EUCHOLOEOPS INGENS* AMEGHINO, (XENARTHRA, PILOSA, MEGALONYCHIDAE)

TIMOTHY J. GAUDIN1, GERARDO DE IULIIS2, NESTOR TOLEDO3, AND FRANÇOIS PUJOS4

1Department of Biological and Environmental Sciences (Department 2653), University of Tennessee at Chattanooga, 615 McCallie Avenue, Chattanooga, TN 37403-2598, USA. timothy-gaudin@utc.edu
2Department of Ecology and Evolutionary Biology, University of Toronto, 25 Harbord Street, Toronto, ON, Canada M5S 3G5 and Section of Palaeobiology, Department of Natural History, Royal Ontario Museum, 100 Queen’s Park Crescent, Toronto, ON, Canada M5S 2C6. gerry.deiuliis@utoronto.ca
3División Paleontología de Vertebrados, Museo de La Plata, Paseo del Bosque s/n, B1900FWA La Plata, Argentina; CONICET, Consejo Nacional de Investigaciones Científicas y Técnicas, Argentina. ntoledo@fcnym.unlp.edu.ar
4Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales (IANIGLA), CCT-CONICET - Mendoza, Avenida Ruiz Leal s/n, Parque General San Martín, 5500 Mendoza, Argentina; Institut Français d’Etudes Andines (IFEA), UMIFRE 17 CNRS MAE USR 3337, Casilla 18-1217, Av. Arequipa 4595, Lima 18, Perú. fpujos@mendoza-conicet.gov.ar

Abstract. New, exceptionally well preserved skulls of the basal megalonychid ground sloth *Eucholoeops ingens* Ameghino have been recovered through recent field work in the late early Miocene Santa Cruz Formation of southern Argentina (Patagonia, Santacrucian SALMA). These specimens have permitted detailed description of the anatomy of the basicranium, endocranium, and orbital wall, including descriptions of the morphology and sutural relationships of the bones from this portion of the skull, and their associated cranial foramina. Comparisons are made to other megalonychid and megatherioid sloths, including the extant two-toed sloth *Choloepus* Illiger (Megalonychidae). As the descriptions are based on multiple specimens of *E. ingens*, we have been able to examine intraspecific variation in the features described, and have found marked differences among individual specimens in sutural patterns (e.g., the bones that surround the foramen ovale aperture), cranial foramina (e.g., the presence/absence of a postglenoid foramen), and bony morphology (e.g., fusion of the alae of the vomer). The basicrinal and orbital morphology of *Eucholoeops ingens* is shown to possess numerous plesiomorphic aspects, including the presence of a descending lamina of the pterygoid that is hemispherical in outline, and the absence of an alisphenoid/parietal contact, no doubt due to its position as the oldest megalonychid known from relatively complete material. The presence of distinct grooves on the promontorial surface directed toward the fenestra ovalis suggest that *Eucholoeops ingens* may be the only known xenarthran to have retained a functional stapedial artery into adulthood.


Resumen. EL BASICRÁNEO Y REGIÓN ORBITAL DE *EUCHOLOEOPS INGENS* AMEGHINO, (XENARTHRA, PILOSA, MEGALONYCHIDAE) DEL MIOCENO TEMPRANO. Nuevos cráneos excepcionalmente bien conservados del megaloniquido basal *Eucholoeops ingens* Ameghino han sido recuperados, en recientes trabajos de campo, en niveles del Miocene temprano de la Formación Santa Cruz (Patagonia Argentina, edad-mamífero Santacrucense). El estudio de estos especímenes ha permitido realizar descripciones anatómicas detalladas del basicraneo, endocraneo y de la pared orbital, incluyendo también descripciones de la morfología y relaciones suturales existentes entre los huesos de esta región del cráneo y de los trabajos craneales asociados. Se realizaron comparaciones con otros megaloniquidos (incluyendo el actual perizoso de dos dedos *Choloepus* Illiger) y con perezosos megaterioides. Al analizar varios especímenes de *E. ingens*, hemos sido capaces de examinar la variación intraspecifica en las estructuras descritas, reconociéndose importantes diferencias en los individuos a nivel de los patrones suturales (e.g., delimitación del foramen ovale), de los forámenes craneales (e.g., presencia/ausencia del foramen postglenoideo) y de la morfología ósea (e.g., fusión de las alae del vomer). La morfología del basicraneo y de la órbita de *Eucholoeops ingens* presenta varios aspectos plesiomórficos, incluyendo la presencia en el pterigoideo de una lámina descendente de contorno semiesférica y la ausencia de un contacto alisfenoido/parietal, sin duda debido a su posición como el más antiguo megaloniquido conocido con material relativamente completo. Por último, la presencia de surcos distintos en la superficie del promontorio y dirigidos hacia la fenestra ovalis sugiere que *Eucholoeops ingens* podría ser el único Xenarthra conocido que ha retenido una arteria estapedial funcional en la edad adulta.

LIVING Xenarthra comprise a relatively small though diverse clade of some 31 species distributed primarily in South and Central America (Aguiar and Fonseca, 2008; Vizcaíno and Loughry, 2008). The abundant xenarthran fossil record, however, documents a much richer history and reveals that xenarthrans were among the more characteristic faunal elements of the South American Cenozoic and successfully invaded North America and the West Indies (McDonald and De Iuliis, 2008). They comprise one of the major clades of placental mammals (Asher and Helgen, 2011; O’Leary et al., 2013) and include Pilosa (sloths and anteaters) and Cingulata ( armored xenarthrans, including extant and extinct armadillos and their extinct kin, the pangolins and glyptodonts). The sloths or Tardigrada (= Phyllophaga = Folivora; see Vizcaíno and Loughry, 2008) are represented today only by the tree sloths Choloepus illigeri, 1811, and Bradypus Linnaeus, 1758, small and almost entirely arboreal leaf-eaters restricted to northern South America and Central America. In contrast, their fossil kin were much more widespread and exhibit considerable diversity, encompassing a wide range of body size, dietary habits, and locomotory abilities (e.g., White, 1993; Bargo and Vizcaíno, 2008; McDonald and De Iuliis, 2008; Vizcaíno et al., 2008; Bargo et al., 2012; Pujo et al., 2012; Toledo et al., 2013, 2014; Amson et al., 2014).

The sloths from the richly fossiliferous Santa Cruz Formation (Vizcaíno et al., 2012) of late early Miocene Age (~19 to 14 Ma; see Marshall, 1976; Fleagle et al., 2012; Perkins et al., 2012) in southern Argentine Patagonia have been known for more than a century, beginning with the work of Ameghino (e.g., 1887, 1889, 1891, 1894), Mercerat (1891), Lydekker (1894), and Scott (1903, 1904). However, the taxonomy and systematics of these mammals has been in a chaotic state since their first descriptions (see De Iuliis et al., 2014). The sustained and ongoing collecting efforts, from 2003 to the present, by a team of researchers led by the Museo de La Plata (MLP) and Duke University (DU), have recovered abundant well-preserved remains of numerous vertebrates, including sloths, that permit a clearer understanding of their systematics and paleobiology (e.g., Bargo et al., 2009, 2012; Vizcaíno et al., 2012; Toledo et al., 2013; De Iuliis et al., 2014).

Among the taxa requiring revision is the basal megahyrid (Gaudin, 2004) Eucholoeops Ameghino, 1887. De Iuliis et al. (2014) analyzed the morphological and metric variation among several specimens recently recovered by the MLP-DU expeditions (belonging to the MPM-PV but currently housed for study at the MLP) and those from the classical collections housed in the AMNH, FMNH, MACN-A, MLP, and YPM-VPPU (see below for abbreviations). They used these data to clarify the concept of the species Eucholoeops ingens Ameghino, 1887, but deferred study of the basicranial, endocranial, and orbital regions. This report analyzes and describes these regions in Eucholoeops ingens based mainly on the recently recovered MPM remains, which provide a wealth of information that compliments earlier studies (e.g., Guth, 1961; Patterson et al., 1992; Gaudin, 1995, 2004) and enhances our knowledge of these parts of the skull.

Institutional abbreviations. AMNH, American Museum of Natural History, New York, USA; DU, Duke University, Durham, North Carolina, USA; FMNH, Field Museum of Natural History, Chicago, Illinois, USA; MACN-A, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Colección Nacional Ameghino, CABA, Argentina; MLP, Museo de La Plata, La Plata, Buenos Aires, Argentina; MPM-PV, Museo Regional Provincial Padre M. J. Molina, Río Gallegos, Santa Cruz, Argentina; UTCM, University of Tennessee at Chattanooga Natural History Museum, Chattanooga, Tennessee, USA; YPM-VPPU, Yale Peabody Museum of Natural History, Vertebrate Paleontology, Princeton University Collection, New Haven, Connecticut, USA.

Anatomical and other abbreviations. C-/c-, upper/lower caniniform tooth; L, left; R, right; M-/m-, upper/lower molariform tooth; SALMA, South American Land Mammal Age.

MATERIALS

Listed below are the cranial remains of the specimens upon which this report is mainly based. For fuller descriptions, refer to De Iuliis et al. (2014).

Specimens of Eucholoeops ingens considered in this study

MPM-PV 3401. The neotype of the species (see De Iuliis et al., 2014) includes a complete skull, including isolated premaxillae, L zygomatic, and R C1; molariform teeth present and well preserved. Ectotympanics, R zygomatic, and R pterygoid blade missing; skull relatively undeformed, par-
particularly anteriorly, but with dorsoventral compression of braincase region and rostral roof, lateral deflection of L pterygoid blade, and slight damage to L orbitofrontal region.

Locality and stratigraphy: Puesto Estancia La Costa; FL (following Tauber, 1997) 7.2, Estancia La Costa Member, Santa Cruz Formation.

**MPPM-PV 3451.** Nearly complete and undistorted skull, missing ectotympanics, premaxillae and zygomatics; pterygoid laminae incomplete, but L lamina is sufficiently preserved to indicate its outline (Figs. 1–2). Locality and stratigraphy: Puesto Estancia La Costa; FL (following Tauber, 1997) 5.3, Estancia La Costa Member, Santa Cruz Formation.

**MPPM-PV 3452.** Skull (Figs. 3–4), missing calavarium, dorsal part of occiput, premaxillae, all teeth but L M4, R zygomatic, ectotympanics, and pterygoid blades; L zygomatic incomplete; maxillae, palate, including alveoli, and basicranium well preserved (Fig. 3). Locality and stratigraphy: Campo Barranca; Estancia La Costa Member, Santa Cruz Formation.

**MPPM-PV 15046.** Nearly complete skull, with some damage to L side and central portion of skull roof compressed ventrally; missing premaxillae, pterygoid blades, zygomatics, and ectotympanics. Palatal region preserves all teeth except R C1; pterygoid laminae complete and relatively undistorted; L C1 distorted. Locality and stratigraphy: Monte Tigre; Estancia La Costa Member, Santa Cruz Formation.

**FMNH P13139.** Nearly complete skull, with slight medial compression of R side; missing L C1 but other teeth well preserved; missing premaxillae, zygomatics, as well as zygomatic process of squamosals, occipital condyles, and R occiput and auditory region; L auditory region largely preserved, including stapes (described by Patterson et al., 1992), but missing ectotympanic and part of entotympanic. Locality and stratigraphy: Santa Cruz Formation, 12 miles north of Cape Fairweather.

**SYSTEMATIC PALEONTOLOGY**

**XENARTHRA** Cope, 1889

**TARDIGRADA** Latham and Davies in Forster, 1795

(= **PHYLLOPHAGA** Owen, 1842 = **FOLIVORA** Delsuc et al., Catzeflis, Stanhope and Douzery 2001)

**MEGALONYCHIDAE** Gervais, 1855

**Genus Eucholoeops** Ameghino, 1887

Type species. **Eucholoeops ingens** Ameghino, 1887; original designation.

**Stratigraphic and geographic occurrence.** Santacrucian SALMA (late early Miocene), Santa Cruz Province, Argentine Patagonia.

**Eucholoeops ingens** Ameghino, 1887

Figures 1–4

Neotype. MPM-PV 3401 (see De luliis et al., 2014).

**Description and comparison**

As noted by De luliis et al. (2014), the occipital condyles of **Eucholoeops ingens** are larger and more prominently projecting compared to those of **Hapalops** Ameghino, 1887, **Mionothropus** De luliis et al., 2011, **Acratocnus** Anthony, 1916, and **Choloepus** Illiger, 1811. The basioccipital and the condyles are at about the same level as the alveolar margins of the palate in **E. ingens** (Fig. 1.1–2), as in **Hapalops** and **Choloepus**. In **Mionothropus** and **Acratocnus** the basioccipital lies more dorsally. The occipital condyles extend considerably ventral to the external auditory meatus in **E. ingens**, but slightly less so in **Hapalops** and **Mionothropus**, and they are directly posterior to the meatus in **Choloepus** and **Acratocnus**. The entotympanic is preserved (see below, Fig. 1.1–2) but the ectotympanic is not, so far as we are aware, present in any specimen of **E. ingens**, in contrast to the

**Figure 1.** **Eucholoeops ingens** MPM–PV 3451 in left lateral view (anterior towards left, dorsal towards top); 1–2, complete skull; 1, photograph; 2, drawing; 3, drawing of orbital wall. Abbreviations: as, alisphenoid; bo, basioccipital; C, upper caniniform tooth; cpf, caudal palatine foramen; eam, external auditory meatus; ent, entotympanic; ethf, ethmoid foramen; f, frontal; fo, foramen ovale; fr, foramen rotundum; iof, infraorbital foramen; l, lacrimal; lf, lacrimal foramen; M–, upper molariform teeth; max, maxilla; mf, maxillary foramen; n, nasal; oc, occipital condyle; pof, optic foramen; p, parietal; pa, palatine; pt, pterygoid; ptc, pterygoid canal; sphi, sphenopalatine foramen; sphi, sphenorbital fissure; so, supraoccipital; sq, squamosal; zpsq, zygomatic process of the squamosal. Scale bars= 20 mm.
The roof of the nasopharynx is dominated by a large, roughly trapezoidal exposure of the presphenoid (Fig. 2.2). The presphenoid has a short, straight suture with the basisphenoid posteriorly, and then expands anteriorly. It has lateral sutures with the pterygoids and palatines, the boundaries between which cannot be determined because of breaks in the area. The suture with the palatine more anteriorly is deeply interdigitated. Anteriorly, there are clear sutures with the alae (= wings) of the vomer. The alae are broadly fan shaped posteriorly, strongly tapering anteriorly, and separated in the midline by a narrow strip of bone which undoubtedly represents the ventral edge of the nasal septum, though it is unclear whether this portion of the septum is formed by presphenoid or mesethmoid. The groove for the vidian nerve (= nerve of the pterygoid canal) is not visible at the edges of the nasopharyngeal roof, where it is found in other megahonychids (e.g., Neocnus; see Gaudin, 2011). It may lie within the pterygoid bone in Eucholoeops, as it does in Choloepus (Gaudin, 2011).

Several foramina, as usual, pierce the orbital wall of Eucholoeops ingens (Fig. 1.3). The sphenopalatine opening is a large, well-defined, and nearly circular opening into which the sphenopalatine foramen opens dorsally and the caudal palatine foramen opens ventrally. Dorsal and posterior to it is a similarly sized though oval opening, the common aperture for the sphenorbital fissure/optic foramen. Gaudin (2004, p. 294) described the condition in nearly all sloths including Eucholoeops, as “optic foramen empties into sphenorbital canal, two foramina share common external aperture”. In MPM-PV 3451 the small ethmoid foramen is preserved just ventral to the dorsal rim of the common aperture for the sphenorbital fissure/optic foramen, and the slightly larger opening of the pterygoid canal lies just ventral to the aperture. Posterior and ventral to the common aperture (thus almost at the same level as the sphenopalatine opening and pterygoid canal) lies the foramen rotundum and then, farther posteriorly, the foramen ovale.

The orbital wall is well preserved in MPM-PV 3451, and the foramina and sutures are evident (Fig. 1.3). The sutures differ somewhat on the left and right sides of the skull. For example, on the left side the alisphenoid has a posterior extension between the squamosal and pterygoid, nearly reaching the back of the descending lamina, which completely encompasses the foramen ovale, excluding both the squamosal and pterygoid from its margins. On the right, the posterior edge of the alisphenoid lies not far posterior to the foramen rotundum, and the squamosal/pterygoid suture extends from the area in front of the foramen ovale posteriorly to the back edge of the descending lamina. Therefore, the external margins of the foramen ovale are formed by the squamosal dorsally and pterygoid ventrally. In addition, there is a small orbitosphenoid exposure in the floor of the common aperture for the sphenorbital fissure/optic foramen on the right side that is apparently absent on the left.

The orbital wall mosaic is comprised of the squamosal, alisphenoid, pterygoid, palatine, maxilla, orbitosphenoid, frontal, lacrimal, and jugal (Fig. 1). The squamosal forms the posterodorsal portion of the orbital wall, contacting the frontal and parietal anteriorly and dorsally and the alisphenoid and pterygoid anteriorly and ventrally. As noted above,
Figure 2. Eucholoeops ingens MPM-PV 3451; 1, skull in ventral view; 2, palate and ear regions in ventral view (anterior towards left, left lateral towards top). Abbreviations: bo, basioccipital; bs, basisphenoid; cf, carotid foramen; epir, epitympanic recess (exposed); f, frontal; fec, fenestra cochleae; feo, fenestra ovalis; fm, foramen magnum; gf, glenoid fossa; gvn, groove for vidian nerve/nerve of pterygoid canal; hf, hypoglossal foramen;jf, jugular foramen; oc, occipital condyle; pa, palatine; prp, promontorium of petrosal; ps, presphenoid; pt, pterygoid; stas, stapedial artery sulcus; stf, stylomastoid foramen; stfo, stylohyal fossa (broken); zpsq, zygomatic process of the squamosal. Scale bars=20 mm.
the length of the squamosal/pterygoid suture, as it emerges from the tympanic cavity, varies on the right and left sides of the skull. The squamosal is crossed by a prominent infratemporal crest that extends from the medial margin of the glenoid cavity, across the dorsal portion of the alisphenoid to end in large, blunt orbital process on the frontal bone. This process is similar to that described in *Mionathrus* by De Iuliis *et al.* (2011), and lies in a similar position, immediately dorsal and lateral to the common aperture for the sphenoidal fissure/optic foramen.

The pterygoid forms the posteroventral portion of the orbital wall. As in other sloths (Gaudin, 1995, 2004, 2011; De Iuliis *et al.*, 2011), it forms the major part of a large descending lamina that is hemispherical in outline and serves as a lateral wall to the nasopharynx. The lateral surface of the pterygoid is marked by large muscular depressions for the medial pterygoid muscle anteriorly; and, along its posterior margin, a deep narrow groove for the tensor veli palatini muscle, the latter a feature that is present in many posterior margin, a deep narrow groove for the tensor veli palatini muscle, the latter a feature that is present in many species of sloth. In the ventral region of the skull, the pterygoid forms the posteroventral portion of the squamosal forming part of the floor of the middle cranial fossa, housing a deep depression that serves as the lateral wall of the middle cranial fossa. The pterygoid is marked by large muscular depressions for the medial pterygoid muscle anteriorly; and, along its posterior margin, a deep narrow groove for the tensor veli palatini muscle, the latter a feature that is present in many species of sloth.

The alisphenoid lies between the pterygoid and squamosal on the left side of the skull, but not the right. On both sides it appears to fully encompass the external margin of the foramen rotundum and form the lateral wall of the common aperture for the sphenoidal fissure/optic foramen. It has an anterior contact with the palatine, the ventral extent of which is obscured by breaks. The small external aperture for the pterygoid canal sits on this suture. The alisphenoid extends dorsally between the frontal and squamosal, but does not reach the parietal, due at least in part to the small size of the anteroventral process of the latter bone. In many sloths, the anteroventral process of the parietal is longer and contacts the alisphenoid (Gaudin, 2004; De Iuliis *et al.*, 2011). The alisphenoid/squamosal suture is gone, except for that portion posterior to the foramen ovale.

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The palatine has an apparently somewhat rectangular exposure in the anteroventral region of the orbital wall, the exposure being substantially taller than it is broad anteroposteriorly (Fig. 1). It has contacts with the maxilla anteriorly and frontal dorsally, the suture with the latter lying roughly at the ventral margin of the common aperture for the sphenoidal fissure/optic foramen. Near the palatine/frontal suture, but well in advance of the common aperture for the sphenoidal fissure/optic foramen (in contrast to the condition in *Neocnus*; Gaudin, 2011), the palatine has the large circular depression, noted above, that houses the sphenopalatine foramen and caudal palatine foramen.

The frontal forms the bulk of the dorsal and anterior orbital wall, contacting the parietal posteriorly, the squamosal, alisphenoid, palatine, and, on the left, the orbitosphenoid ventrally, and the maxilla, jugal, and lacrimal anteriorly (Fig. 1.1–2). It forms the medial wall, and, on the left side, the floor to a common aperture for the sphenoidal fissure/optic foramen. The groove emerging anteriorly from the opening has a small ethmoid foramen present in its medial wall. At the anteriormost reaches of the orbit, there is a large orbital exposure of the jugal which separates the orbital portion of the lacrimal from the orbital exposure of the maxilla, a feature that is also known to occur in scelidotherines, *Bradypterus*, nothrotheriids, basal megatherioids, and some megalonychids (e.g., *Megalonyx* Harlan, 1825; Gaudin, 2004). At the top of the orbital wall is a relatively prominent postorbital process that, in lateral view, lies just posterior to the position of the maxillary foramen, in contrast with the FMNH specimens, in which the postorbital process is even with the maxillary foramen (Gaudin, 2004).

The skull roof of MPM-PV 3452 is broken open, allowing detailed examination of the internal anatomy of the braincase (Fig. 3). The internal openings to the optic foramen, sphenoidal fissure, foramen rotundum, and foramen ovale are clearly visible. The last two open into an anteroposteriorly elongated cavum epipetricum (for the trigeminal ganglion) that lies immediately lateral to a well-defined sulcus for the internal carotid artery, the two separated by a strong ridge. These foramina are situated within the confines of the alisphenoid bone, the alisphenoid/squamosal suture extending clearly lateral to the cavum epipetricum, with the squamosal forming part of the floor of the middle cranial fossa, housing a deep depression that serves as the lateral wall of the middle cranial fossa.
and ventral walls for the temporal lobe of the cerebrum, as in the extinct pangolin *Patriomantis* Emry, 1970 (see Gaudin and Wible, 1999; Gaudin et al., 2009). The sphenobrain fissure lies between the alisphenoid, which forms its ventral floor, and the orbitosphenoid, which forms its dorsal roof. This leaves the optic foramen, as in most mammals (*e.g.*, *Canis* Linnaeus, 1758; Evans and de Lahunta, 2012), within the orbitosphenoid. The latter has a large internal contact with the squamosal, which is somewhat unexpected given the small size of the external orbitosphenoid exposure in most sloths (see Gaudin, 2004, 2011; De Iuliis et al., 2011). The skull is broken just anterior to the anterior clinoid eminence, so that the cribriform plate is missing and it cannot be determined if a distinct orbitosphenoid/mesethmoid suture was present.

The internal carotid sulcus itself extends from the carotid foramen posteriorly, an aperture that lies at the anteromedial pole of the petrosal, toward its ill-defined anterior terminus medial to the orbital foramina and lateral to the prominent midline anterior clinoid eminence (Fig. 3). The carotid sulcus in turn lies lateral to the clearly marked hypophyseal fossa on the roof of the basisphenoid. The hypophyseal fossa ends anteriorly at the anterior clinoid eminence. It is possible that this sulcus, which is quite large, carries not just the internal carotid artery, but branches of the trigeminal nerve as well, in particular the ophthalmic

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**Figure 3.** *Eucholoeops ingens* MPM-PV 3452, cephalic cavity (inner braincase and ear region) in dorsal view (anterior towards top, right lateral towards right). Abbreviations: *as-sq s*, alisphenoid-squamosal suture; *av*, aqueductus vestibuli (for endolymphatic duct); *caep*, cavum epipterygium; *clp*, clinoid process; *fm*, foramen magnum; *fo*, foramen ovale; *fr*, foramen rotundum; *gss*, groove for sigmoid sinus; *hyf*, hypophyseal fossa; *iam*, internal acoustic meatus (for auditory nerve, CN VIII + facial nerve, CN VII); *icf*, internal carotid foramen; *jf*, jugular foramen; *pe*, petrosal; *sica*, sulcus for internal carotid artery; *sphfi + opf*, sphenorbital fissure and optic foramen; *sq-pe s*, squamosal-petrosal suture; *subf*, subarcuate fossa. Scale bar = 10 mm.
branch (cranial nerve V1), given the terminus of the sulcus near the internal aperture of the sphenorbital fissure. The presence of a large lateral ridge separating the sulcus from the cavum epiptericum, however, mitigates against such an interpretation.

The internal or dorsal surface of the petrosal, roughly pentagonal in shape, is readily observable in this specimen (Fig. 3). The petrosal is sutured to the basioccipital ventrally and medially, the alisphenoid and/or basisphenoid at its anteroventromedial corner, the squamosal anteriorly, dorsally and laterally, and the occipital posteriorly, dorsally and laterally. It is marked near its geometric center by a deep internal acoustic meatus, which, as is the case in most sloths (Patterson et al., 1992), lacks a readily observable division into acoustic foramina (for the auditory nerve) and a facial foramen (for the facial nerve). The internal auditory meatus lies immediately posterior to a bulbous eminence that presumably represents the prefacial commissure (see Wible, 2010). Along its ventromedial edge, the petrosal participates in two openings: at its anterior end, the internal carotid foramen, which lies between the petrosal medially and posteriorly, and the alisphenoid and/or basisphenoid anteriorly and laterally; at its posterior end, the much larger jugular foramen, which forms a deep indentation in the lateral wall and a portion of the roof of the internal carotid artery sulcus, but does not form a medial wall to the sulcus as it does in other megalonychids (e.g., Choloepus, Acratocnus, and some Neocnus; Gaudin, 2011), the medial shelf of the entotympanic is reduced, so that it forms the lateral wall and a portion of the roof of the internal carotid artery sulcus, but does not form a medial wall to the sulcus as it does in other megalonychids (e.g., Pliomorphus, Megalonyx, and some Neocnus; Gaudin, 2011; this feature is also coded as being present in the FMNH specimens of Eucholoeeops in Gaudin, 2004). The petrosal bears a large anteroventral process of the tegmen tympani (= processus crista facialis of Patterson et al., 1992) medial to the facet for the anterior crus of the ectotympanic, much like the condition described in Neocnus (Gaudin, 2011). As in the Antillean form, the process likely had an anteromedial contact with the entotympanic, and perhaps with the pterygoid as well.

The ear region (minus the ectotympanics) is also preserved in MPM-PV 3451, although some parts are damaged, e.g., the anteroventral processes of the tegmen tympani (= processus crista facialis of Patterson et al., 1992) are broken on both sides (Figs. 1–2). Among the notable features of this specimen, the entotympanics are less well developed anterodorsally than in MPM-PV 3452, so that the contact between this element and the anteroventral processes of the tegmen tympani is probably missing (though its presence cannot be completely ruled out because of the bilateral damage to the anteroventral processes). In addition, there is no carotid canal through the entotympanic in MPM-PV 3451, as there is in MPM-PV 3452.

Perhaps the most remarkable feature of the ear region of Eucholoeeops ingens is that there appears to be a small groove for the stapedial artery. It is in an unusual position for a stapedial sulcus, passing anterolaterally from the ven-
tromedial margin of the fenestra cochleae (= aperture for cochlear fossula, see Gaudin, 2011), to the anteroventral rim of the fenestra ovalis (Fig. 1.3). There are other examples, however, of mammals with a stapedial sulcus in a very posterior position like this, e.g., the early eutherian Zalambdalestes Gregory and Simpson, 1926 (Wible et al., 2004), the

Figure 4. Eucholoeops ingens MPM-PV 3452 close up left auditory region in ventrolateral view (anterior towards top, lateral towards right). 1, stereophotographs; 2, labeled drawing. Abbreviations: aptt, anteroventral process of tegmen tempani; cf, carotid foramen; epis, epitympanic sinus; fec, fenestra cochleae; feo, fenestra ovalis; fs, facial sulcus; gvn, groove for vidian nerve; hf, hypoglossal foramen; icas, internal carotid artery sulcus; jf, jugular foramen; pgf, postglenoid foramen; prp, promontorium of petrosal; pt, pterygoid; sq, squamosal; stas, stapedial artery sulcus; stmf, stylomastoid foramen; th, tympanohyal; unk, sulcus of unknown function.
Eocene rodent Exmus (Wible et al., 2005), and the metace- 
romyid palaeanodont Palaeanodon Matthew, 1918 (Pa-
tterson et al., 1992). It is also conceivable that this groove 
accommodated the tympanic nerve, a branch of the glos-
ospharyngeal nerve (CN IX) that forms the tympanic plexus 
servicing the promontorial surface of the petrosal in other 
prehensiles (e.g., Canis [Evans and de Lahunta, 2012]; humans 
[Clemente, 1985]). Indeed, the course of part of the nerve 
is very similar in Canis to that of the sulcus described here. 
However, there is no bony sulcus in Canis for the nerve, and 
it is apparently rare among placentals for the tympanic 
nerve to incise grooves on the promontorium itself (though 
an opening behind the promontorium for the nerve, termed 
the tympanic canaliculus, is common enough; see, e.g., Sole-
odon Brandt, 1833 [Wible, 2008] and tree shrews [Wible, 
2011]). In examining specimens and literature representing 
fourteen different orders of placentals mammals across all 
four of the major supraordinal clades, as well as several 
Cretaceous euthérians and the generalized early Cenozoic 
taxon Leptictis Leidy, 1868b, we found only two taxa in which 
sulci for the tympanic nerves could be documented – in hu-
mans, where the grooves differ markedly from Eucholoeops 
in orientation and position, e.g., lying anterior to the fenest-
ra ovalis (Saban, 1963; Clemente, 1985); and in the artio-
dactyl Bos Linnaeus, 1758, where O’Leary (2010) cites older 
descriptions of such a groove, though she did not find the 
sulci in her specimens of that taxon. This groove is best 
represented in MPM-PV 3451, but is apparent though less 
well defined, presumably due to differential preservation, 
in the other MPM-PV remains. For example, in MPM-PV 
15046, its direction differs slightly, passing slightly an-
teroventrally to the fenestra cochleae, whereas in the other 
specimens it approaches the fenestra cochleae rather 
more closely. The stapedial artery is generally thought to be 
absent in xenarthrans (Bugge, 1979; Wible, 1987), though 
Schneider (1955) described a rudimentary stapedial artery 
in fetal specimens of Bradypus, and Patterson et al. (1992) 
described and illustrated what appears to be a dried rem-
nant of the stapedial artery in a juvenile specimen of Cholo-
epus. If a substantial stapedial artery were present, its course 
beyond the stapes is unclear, though it is conceivable that a 
ramus inferior or its branches, like Leptictis (Novacek, 1986), 
passed out through the auditory bulla, which likely had a 
substantial membranous portion as in Choloepus and Ha-
palops (Patterson et al., 1992).

There remains a shallow groove that crosses the pro-
montorium transversely from the region just ventral to the 
fenestra ovalis toward the entotympanic. A similar groove is 
present in some Choloepus hoffmannii Peters, 1858 speci-
mens (e.g., AMNH 18893, 26905, both subadults, and UTCM 
1912, adult), but its function is as yet unknown.

The mastoid exposure of the petrosal is unusual in 
MPM-PV 3451, in that it lacks the mastoid depression 
typically present in sloths (Patterson et al., 1992; Gaudin, 
1995, 2011), the mastoid instead being convex. In addition, 
there is no clear groove for the occipital artery crossing the 
mastoid just posterior to the nuchal crest, although the 
posttemporal foramen is present in this area, as it normally 
is in sloths (Patterson et al., 1992; Gaudin, 1995, 2004, 
2011; De Iuliis et al., 2011). Lastly, this specimen is unusual 
in that it possesses small postglenoid foramina on both 
sides of the skull. The presence of a postglenoid foramen is 

MPM-PV 3401 differs from the previously described 
skulls in a number of features. The skull is crushed dorso-
ventrally and sideways but retains an intact jugal and pre-
maxillae. In the orbit, the foramen ovale lies within the 
alisphenoid internally, but the external aperture lies be-
tween the squamosal and pterygoid, as on the left side of 
MPM-PV 3451. In the nasopharynx, the alae of the vomer 
are fused in the midline, so that the nasal septum is not 
visible in ventral view. In the ear region, the entotympanic 
is somewhat better developed anteriorly, such that a con-
tact between this bone and the anteroventral process of 
the tegmen tympani is clearly present (despite the fact that 
the process is broken), but the bone still lacks a carotid 
canal, as in MPM-PV 3451 but in contrast to MPM-PV 3452. 
This specimen resembles the latter rather than the former, 
however, in the presence of a groove on the mastoid sur-
face of the petrosal just posterior to the nuchal crest. This 
groove connects dorsally with the posttemporal foramen.

DISCUSSION AND CONCLUSIONS

Wible and Gaudin (2004) noted that intraspecific and 
even intraindividual variation for many of the features used 
in morphology-based phylogenetic analyses are rarely 
assessed, despite the fact that variation in, for example, su-
tural patterns or foramina number and position in verte-
brate skulls is not uncommon. Indeed, De Iuliis et al. (2014) described just such morphological (as well as metric) variation among small (fewer than 10 individuals) samples drawn from single, contemporaneous populations of the extant sloths *Choloepus didactylus* (Linnaeus, 1758) and *C. hoffmanni*, and McAfee and Naples (2012) documented similar variability in the presence of supernumerary teeth in the two extant *Choloepus* species. Although work on fossil material necessarily limits the ability to investigate such differences, documentation of this phenomenon is important when sample sizes are adequate to address the issue.

In this light, it is not surprising that the sample of multiple skulls from the extinct, Santacrucian (late early Miocene) sloth *Eucholoeops ingens* described in this report has revealed significant variability in certain cranial features. For example, in the anterior roof of the nasopharynx, the alae of the vomer are unfused in MPM-PV 3451 (Fig. 2) and in the FMNH specimens (Gaudin, 2004), exposing the nasal septum in ventral view, whereas these alae are fused in MPM-PV 3401. Distinct postglenoid foramina are present in MPM-PV 3451 (Fig. 2.2), but not in the other specimens. In the ear region, the entotympanic bears a ridge that forms the medial wall to the sulcus for the internal carotid artery in FMNH P13140 (Gaudin, 1995, 2004), exposing the nasal septum in ventral view, whereas these alae are fused in MPM-PV 3401. Distinct postglenoid foramina are present in MPM-PV 3451 (Fig. 2.2), but not in the other specimens. In the ear region, the entotympanic bears a ridge that forms the medial wall to the sulcus for the internal carotid artery in FMNH P13140 (Gaudin, 1995, 2004), exposing the nasal septum in ventral view, whereas these alae are fused in MPM-PV 3401. Distinct postglenoid foramina are present in MPM-PV 3451 (Fig. 2.2), but not in the other specimens.

In part from the position of the basicranium in *Eucholoeops*, which is at the level of the toothrow as in *Hapalops*, whereas in derived megalonychids (*e.g.*, *Acratocnus*, *Megalocnus*, *Megalonyx*, and to a lesser degree *Neocnus*; Webb, 1985; Gaudin, 2004, 2011) the facial region of the skull is “flexed” downward (Webb’s [1985] terminology), leaving the basicranium elevated above the tooth row. The absence of an alisphenoid/parietal contact and the presence of a large orbital exposure of the jugal interposed between the lacrimal and maxilla are also primitive features of *Eucholoeops* modified in more derived megalonychids (the former in Antillean megalonychids, *Pliomorphus*, and *Megalonyx*, the latter in *Choloepus* and the Antillean taxa but not *Megalonyx*; Gaudin, 2004).

A few of the variable features described above in certain specimens of *E. ingens* appear to foreshadow derived conditions that are more widespread in later megalonychids. For example, the complete enclosure of the foramen ovale within the alisphenoid (Fig. 1.3) is known to occur in both *Acratocnus* and *Neocnus* (Gaudin, 2011). The loss of an entotympanic ridge medial to the internal carotid sulcus is also recorded for *Choloepus*, *Acratocnus*, and some *Neocnus* (Gaudin, 2004, 2011). Given the variable nature of these features within *Eucholoeops* and among sloths in general, however, these are less than compelling links to Megalony-
chidae. One feature that is not known to vary intraspecifically and that may link *Eucholaeops* to other megalonychids is the presence of a large groove, presumably for a venous sinus, passing from the internal aperture of the jugular foramen to the foramen magnum (Fig. 2.2). Although this feature is coded as absent for *Eucholaeops* in Gaudin (2004) based on FMNH 133139, in retrospect it should have been coded as unknown, because the inside of the braincase is not open nor sufficiently well prepared in this specimen to make a definitive assessment for this feature. The foramen magnum “venous” groove is also present in *Acratocnus*, *Megalocnus*, *Pliomorphus*, and *Megalonyx* (Gaudin, 1995, 2004).

The anatomy of the stapedial artery and its branches (or their osteological correlates) has served as an important character in numerous phylogenetic studies of mammalian relationships (e.g., Novacek, 1986, 1993; Wible, 1986, 1987, Diamond, 1991; Wible *et al.*, 2004; Luo and Wible, 2005; O’Leary *et al.*, 2013). It has long been the consensus view among morphologists that the stapedial system is lost early in the history of the xenarthran lineage, and the artery has not been recorded as present in the adult of any living xenarthran (Bugge, 1979; Wible, 1987), although, as noted above, there are records of the artery’s presence in embryonic *Bradytus* (Schneider, 1955) and possibly in a young juvenile specimen of *Choloepus* (Patterson *et al.*, 1992). The specimens examined in this report are all clearly of adult individuals, and in all where it can be determined, there is a clear groove extending anterolaterally toward the ventral rim of the fenestra ovalis from an area near the fenestra cochleae (Fig. 4). Although this is an unusual trajectory for the artery, and there are soft tissue structures other than the stapedial artery in the general vicinity of the fenestra ovalis, such as the tympanic branch of the glossopharyngeal nerve (see discussion above), the facial nerve, and the tendon of the stapedius muscle (Clemente, 1985; Evans and de Lahunta, 2012), none of these actually crosses the fenestra ovalis, and hence none seem likely candidates to have left the indentation described in this report. Therefore, it seems likely that *Eucholaeops* is the first xenarthran known to possess a stapedial artery in the adult. This evidence, coupled with that from the juveniles of extant sloths, suggests that the stapedial system may have been retained in sloths long after it was lost in other xenarthran lineages.

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