

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

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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 basicranial 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.

Key words. *Eucholoeops*. Megalonychidae. Skull. Morphology. Basicranium.

Resumen. EL BASICRÁNEO Y REGIÓN ORBITAL DE *EUCHOLOEOPS INGENS* AMEGHINO, (XENARTHRA, PILOSA, MEGALONYCHIDAE) DEL MIOCENO TEMPRANO. Nuevos cráneos excepcionalmente bien conservados del megaloníquido basal *Eucholoeops ingens* Ameghino han sido recuperados, en recientes trabajos de campo, en niveles del Mioceno temprano de la Formación Santa Cruz (Patagonia Argentina, edad-mamífero Santacrucense). El estudio de estos especímenes ha permitido realizar descripciones anatómicas detalladas del basicráneo, endocráneo 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 forámenes craneales asociados. Se realizaron comparaciones con otros megaloníquidos (incluyendo el actual perezoso de dos dedos *Choloepus Illiger*) y también con perezosos megaterioideos. Al analizar varios especímenes de *E. ingens*, hemos sido capaces de examinar la variación intraespecífica 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 vómer). La morfología del basicráneo 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 alisenoideo/parietal, sin duda debido a su posición como el más antiguo megaloníquido 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.

Palabras clave. *Eucholoeops*. Megalonychidae. Cráneo. Morfología. Basicráneo.

LIVING Xenarthra comprise a relatively small though diverse clade of some 31 species distributed primarily in South and Central America (Aguar 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 pampatheres and glyptodonts). The sloths or Tardigrada (= Phyllophaga = Folivora; see Vizcaíno and Loughry, 2008) are represented today only by the tree sloths *Choloepus* Illiger, 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; Pujos *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 megalonychid (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-

ticularly 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.

MPM-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.

MPM-PV 3452. Skull (Figs. 3–4), missing calvarium, 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.

MPM-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.*,
Catzefflis, 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 Iuliis *et al.*, 2014).

Description and comparison

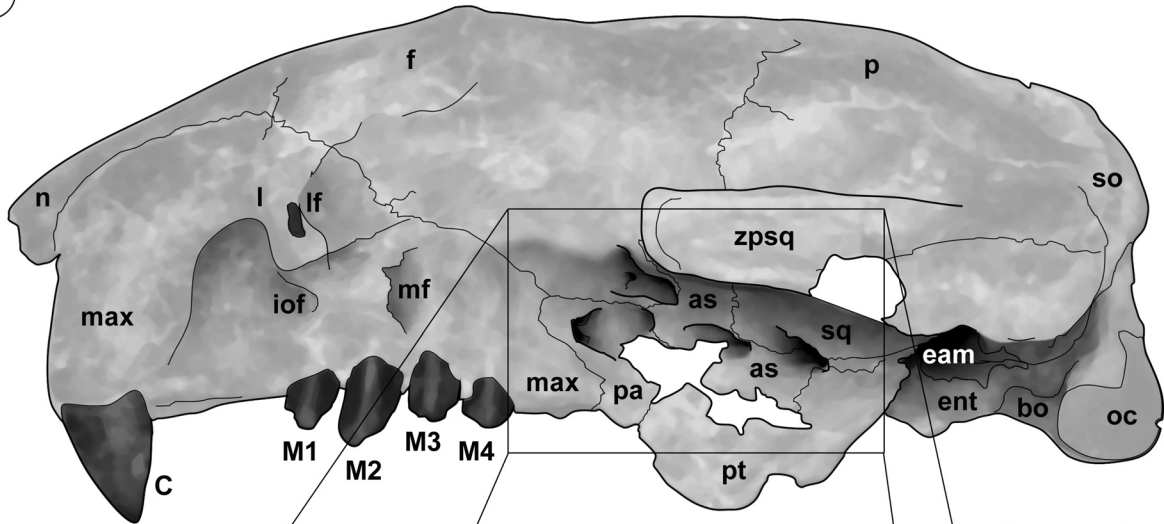
As noted by De Iuliis *et al.* (2014), the occipital condyles of *Eucholoeops ingens* are larger and more prominently projecting compared to those of *Hapalops* Ameghino, 1887, *Mionothropus* De Iuliis *et al.*, 2011, *Acrotocnus* Anthony, 1916, and *Choloepus* Illiger, 1811. The basioccipital and the 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 *Acrotocnus* 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 *Acrotocnus*. 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; **opf**, optic foramen; **p**, parietal; **pa**, palatine; **pt**, pterygoid; **ptc**, pterygoid canal; **sphf**, sphenopalatine foramen; **sphfi**, sphenorbital fissure; **so**, supraoccipital; **sq**, squamosal; **zpsq**, zygomatic process of the squamosal. Scale bars= 20 mm.

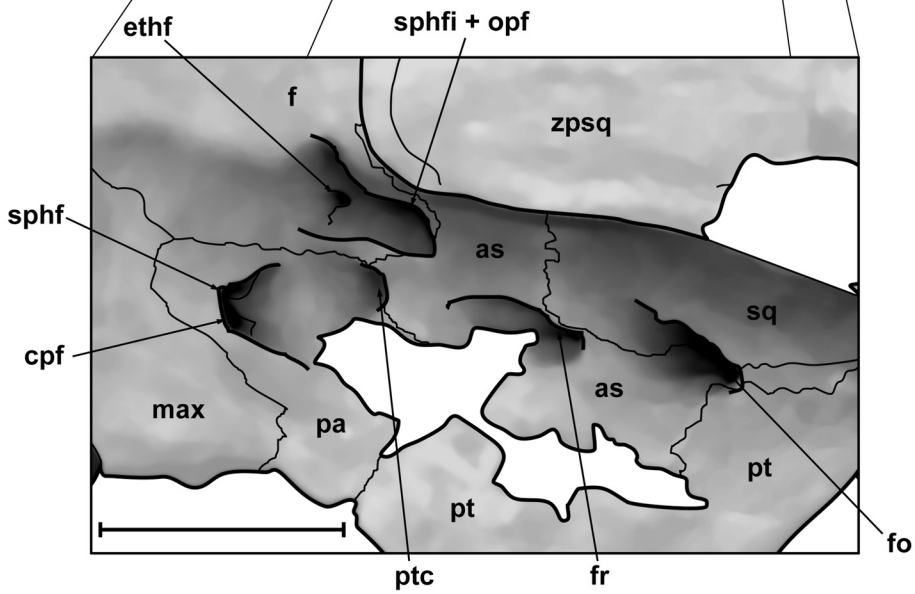
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2



3



common preservation of this element in *Hapalops* and some other Santacrucian sloths, suggesting that it was only loosely attached to the skull in *E. ingens*.

MPM-PV 3451 (Figs. 1–2) is a beautiful, undistorted skull, with sutures and foramina plainly evident, and many features preserved that are oftentimes not evident in fossil sloths. For example, much of the left and right ear regions are preserved, although not the ectotympanics; the pterygoid descending laminae are nearly intact; the roof to the nasopharynx is well preserved; and a complete zygomatic process is present on the right squamosal. The pterygoid laminae of *E. ingens* are well developed and similar to those of *Hapalops* in that the anterior and posterior margins are about equal in length and of similar, though reversed, slope (Fig. 1). This contrasts with the condition in *Acratocnus*, *Mionothropus*, and *Nothrotheriops* Hoffstetter, 1954, in which the posterior margin is longer, which is probably a reflection of the more dorsal position of the basicranium in these taxa. *Neocnus* Arredondo, 1961 (Gaudin, 2011) appears to more closely resemble the condition in *E. ingens* and *Hapalops*, though the posterior margin may be slightly longer. This corresponds to a basicranium that is more elevated than in *E. ingens* and *Hapalops*, but less than in *Acratocnus*, *Mionothropus*, and *Nothrotheriops*. In *Choloepus*, in which the basicranium is at about the same level as the alveolar margin, the anterior margin of the descending lamina is longer and more gently sloped.

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 megalonychids (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,

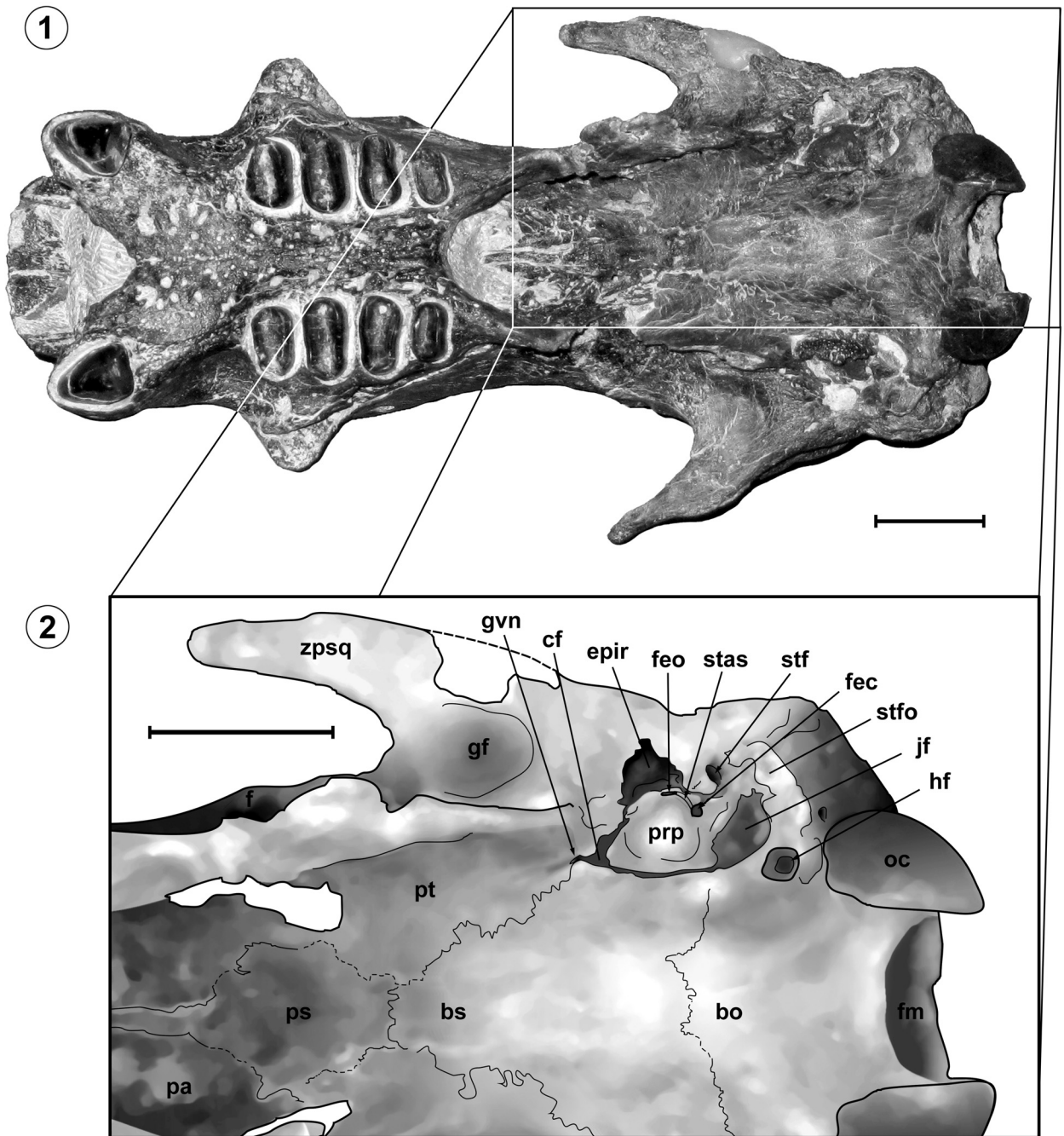


Figure 2. *Eucholoeps ingens* MPM-PV 3451; 1, skull in ventral view; 2, palate and ear regions in ventral view (anterior towards left, left lateral towards top). Abbreviations: **bo**, basioccipital; **bs**, basisphenoid; **cf**, carotid foramen; **epir**, epitympanic recess (exposed); **f**, frontal; **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**, stapedia 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 *Mionthropus* by De Iuliis *et al.* (2011), and lies in a similar position, immediately dorsal and lateral to the common aperture for the sphenorbital 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 (*e.g.*, *Bradypus*, nothrotheriids, megatheriids, *Hapalops*, and *Neocnus*) but not all sloth taxa (see Patterson *et al.*, 1992; Gaudin, 1995, 2004, 2011; McDonald and Muizon, 2002; De Iuliis *et al.*, 2011). The dorsal margin of the pterygoid is either obscured by matrix or obliterated by breakage, so that only a small, ventral portion of the pterygoid/palatine suture is preserved, extending posterodorsally from a point roughly $\frac{3}{4}$ of the way along the ventral margin of the descending lamina, and most of the alisphenoid/pterygoid suture is gone, except for that portion posterior to the foramen ovale.

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 sphenorbital 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 palatine has an apparently somewhat rectangular exposure in the anteroventral region of the orbital wall, the exposure being substantially taller than it is broad antero-posteriorly (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 sphenorbital fissure/optic foramen. Near the palatine/frontal suture, but well in advance of the common aperture for the sphenorbital 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 sphenorbital 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 scelidotheriines, *Bradypus*, 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, sphenorbital fissure, foramen rotundum, and foramen ovale are clearly visible. The last two open into an anteroposteriorly elongated cavum epiptericum (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 epiptericum, with the squamosal forming part of the floor of the middle cranial fossa, housing a deep depression that serves as the lateral

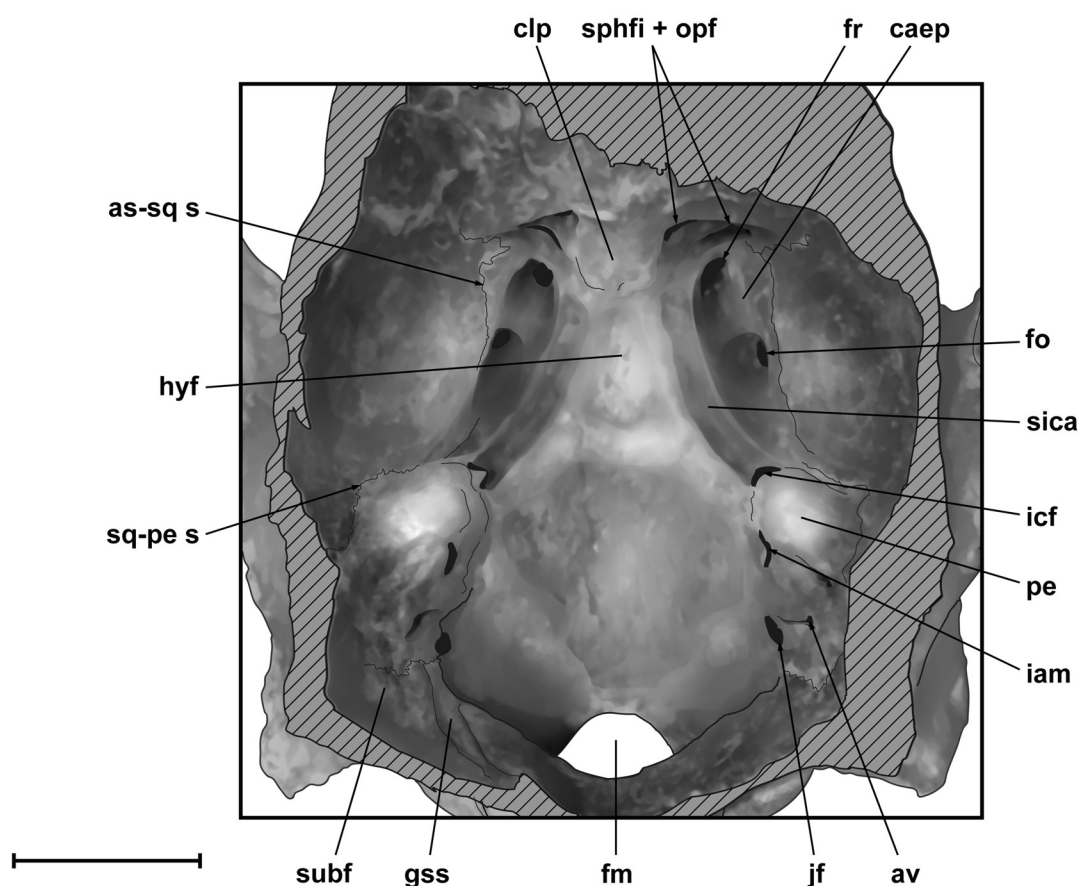


Figure 3. *Eucholoeops ingens* MPM-PV 3452, cephalic cavity (inner braincase and ear region) in dorsal view (anterior towards top, right lateral towards right). Abbreviations: **as-sq s**, alisphenoid-squamosal suture; **av**, aqueductus vestibuli (for endolymphatic duct); **caep**, cavum epiptericum; **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.

and ventral walls for the temporal lobe of the cerebrum, as in the extinct pangolin *Patriomanis* Emry, 1970 (see Gaudin and Wible, 1999; Gaudin *et al.*, 2009). The sphenorbital 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

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 posteroventromedial margin of the petrosal. The jugular foramen itself is framed by the petrosal anteriorly, dorsally, and laterally, and the basioccipital posteriorly, ventrally and medially. The posterodorsal corner of the petrosal is impressed by a broad, shallow subarcuate fossa, which extends posteriorly onto the occipital bone, strongly reminiscent of the condition described in *Dasypus* Linnaeus, 1758 by Wible (2010). In contrast to *Dasypus*, however, the subarcuate fossa bears a small, ventrally directed foramen in its anteroventral quadrant. This is the aqueductus vestibuli for the endolymphatic duct (Clemente, 1985; Evans and de Lahunta, 2012).

On the left side of the skull, a large, presumably venous groove can be observed passing from the internal aperture of the jugular foramen to the foramen magnum (Fig. 4). This groove was described in other sloths (*e.g.*, *Myiodon* Owen, 1840; Patterson *et al.*, 1992), and is known to occur in other megalonychids (*e.g.*, *Acratocnus*, *Megalocnus* Leidy, 1868a, *Pliomorphus* Ameghino, 1885, and *Megalonyx*; Gaudin, 2004), though it is not present in extant forms, so its soft-tissue

correlates are not known (Patterson *et al.*, 1992). The groove is confluent with a small groove for the sigmoid sinus, which crosses the occipital bone posterior to the subarcuate fossa and just lateral to the median depression in the occipital for the vermis of the cerebellum (Fig. 3).

Portions of the ear region in MPM-PV 3452 are preserved in ventral view as well, including the entotympanics and petrosals (Fig. 4). Among the notable features, the entotympanic bears the strong anteroventral process characteristic of megatherioid sloths (Gaudin, 1995, 2004, 2011). In this specimen the base of the process is perforated by a short carotid canal. As in some 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 *Eucholoeps* 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 *Eucholoeps 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 exam-

ples, 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

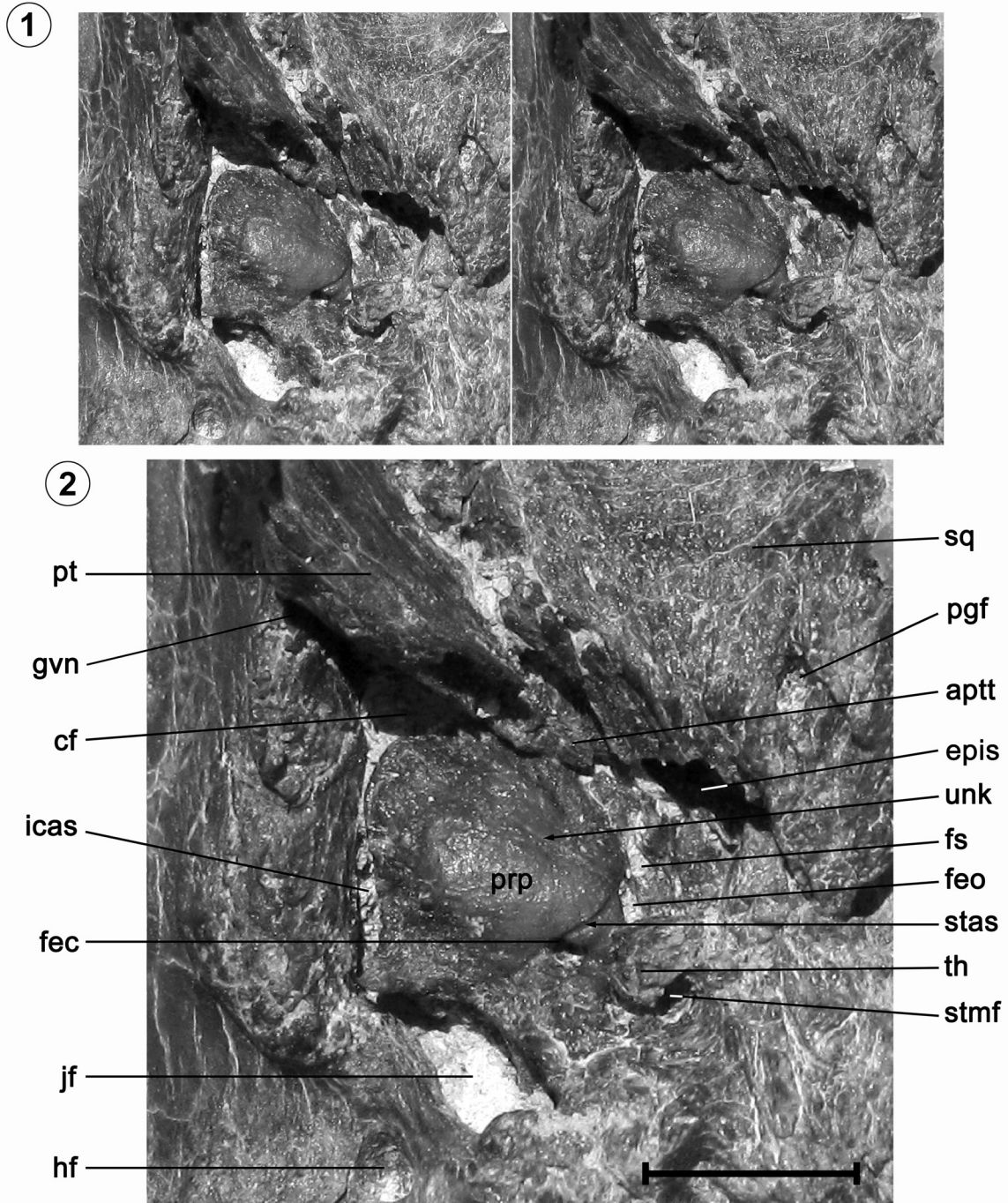


Figure 4. *Eucholoeops ingens* MPM-PV 3452 close up left auditory region in ventrolateral view (anterior towards top, lateral towards right). 1, stereophotographs; 2, labeled drawing. Abbreviations: **aptt**, anteroventral process of tegmen tempani; **cf**, carotid foramen; **epis**, epitympanic sinus; **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 metacheiromyid palaeonodont *Palaeonodon* Matthew, 1918 (Patterson *et al.*, 1992). It is also conceivable that this groove accommodated the tympanic nerve, a branch of the glossopharyngeal nerve (CN IX) that forms the tympanic plexus servicing the promontorial surface of the petrosal in other mammals (*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.*, *Solenodon* Brandt, 1833 [Wible, 2008] and tree shrews [Wible, 2011]). In examining specimens and literature representing fourteen different orders of placental mammals across all four of the major supraordinal clades, as well as several Cretaceous eutherians 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 humans, where the grooves differ markedly from *Euchloeops* in orientation and position, *e.g.*, lying anterior to the fenestra ovalis (Saban, 1963; Clemente, 1985); and in the artiodactyl *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 anteroventral 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 remnant of the stapedial artery in a juvenile specimen of *Choloepus*. 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 promontorium transversely from the region just ventral to the fenestra ovalis toward the entotympanic. A similar groove is present in some *Choloepus hoffmanni* Peters, 1858 specimens (*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 an uncommon feature among sloths (Gaudin, 2004, 2011).

MPM-PV 3401 differs from the previously described skulls in a number of features. The skull is crushed dorsoventrally and sideways but retains an intact jugal and premaxillae. In the orbit, the foramen ovale lies within the alisphenoid internally, but the external aperture lies between 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 contact 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 surface 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, sutural 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), but this ridge is missing in the MPM specimens. The entotympanic also bears a distinct carotid canal in MPM-PV 3452 and FMNH 13139 (Gaudin, 1995, 2004), but this canal is absent in MPM-PV 3451 and MPM-PV 3401. MPM-PV 3451 lacks both the mastoid depression and mastoid groove for the occipital artery found in other *E. ingens* specimens. In the orbit, the postorbital process clearly lies posterior to the maxillary foramen in MPM-PV 3451 (Fig. 1.1–2), but is even with this opening in FMNH 13139 (Gaudin, 2004), and the participation of orbital bones in the margin of the foramen ovale shows three distinct patterns in various *E. ingens* specimens: 1) the foramen lies between the squamosal (dorsal), pterygoid (ventral), and alisphenoid (anterior) in FMNH 13139 (Gaudin, 2004); 2) the foramen lies between the pterygoid and squamosal externally, but is surrounded internally by alisphenoid in MPM-PV 3401 and on the right side of MPM-PV 3451; and 3) the foramen lies entirely within the alisphenoid on the left side of MPM-PV 3451. In addition to the intraindividual variation in the foramen ovale just noted, MPM-PV 3451 also varies in the presence of an

orbitosphenoid exposure in the floor of the common aperture for the sphenorbital fissure/optic foramen.

Without a detailed phylogenetic analysis, it is difficult to ascertain the phylogenetic significance of the features described in this report. Moreover, *Eucholoeops* is one of the oldest undoubted megalonychids (McDonald *et al.*, 2013), and certainly the oldest known from relatively complete skeletal remains. Thus many of the features that appear to have phylogenetic significance are likely plesiomorphies, features retained in *Eucholoeops* but modified or missing in later, more derived megalonychids. These would include the presence of a hemispherical descending lamina of the pterygoid, one in which anterior and posterior edges are of nearly equal length, along with the presence of a distinct groove for the tensor veli palatini muscle on the posterior edge of the descending lamina. This morphology is similar to the condition in the basal megatherioids such as *Hapalops*, but quite different from that of derived megalonychids (Gaudin, 2004). As noted above, the pterygoid morphology derives 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 *Eucholoeops* 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 *Eucholoeops* 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 *Bradypus* (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 *Eucholoeops* 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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REFERENCES

- Aguilar, J.M., and Fonseca, J.A.B. 2008. Conservation status of the Xenarthra. In: S.F. Vizcaíno, and W.J. Loughry (Eds.), *The Biology of the Xenarthra*. University Press of Florida, Gainesville, p. 215–231.
- Ameghino, F. 1885. Nuevos restos de mamíferos fósiles Oligocenos recogidos por el Profesor Pedro Scalabrini y pertenecientes al Museo provincial de la ciudad de Paraná. *Boletín de la Academia Nacional de Ciencias de Córdoba* 8: 5–207.
- Ameghino, F. 1887. Enumeración sistemática de las especies de mamíferos fósiles coleccionados por Carlos Ameghino en los terrenos eocenos de la Patagonia austral y depositados en el Museo de La Plata por Florentino Ameghino. *Boletín del Museo de La Plata* 1: 1–26.
- Ameghino, F. 1889. Contribución al conocimiento de los mamíferos fósiles de la República Argentina. *Actas de la Academia Nacional de Ciencias de Córdoba* 6: 1–1027.
- Ameghino, F. 1891. Nuevos restos de mamíferos fósiles descubiertos por Carlos Ameghino en el Eoceno inferior de la Patagonia austral. Especies nuevas, adiciones y correcciones. *Revista Argentina de Historia Natural* 1: 289–328.
- Ameghino, F. 1894. Énumération synoptique des espèces de Mammifères fossiles des formations éocènes de Patagonie. *Boletín de la Academia Nacional de Ciencias de Córdoba* 13: 259–455.
- Amson, E., Muizon, C. de, Laurin, M., Argot, C., and de Buffrénil, V. 2014. Gradual adaptation of bone structure to aquatic lifestyle in extinct sloths from Peru. *Proceedings of the Royal Society B: Biological Sciences* 281: DOI: 10.1098/rspb.2014.0192.
- Anthony, H.E. 1916. Preliminary report of fossil mammals from Porto Rico. *Annals of the New York Academy of Science* 27: 193–203.
- Arredondo, O. 1961. Descripciones preliminares de dos nuevos géneros y especies de edentados del Pleistoceno cubano. *Boletín del Grupo de Exploraciones Científicas* 1: 19–40.
- Asher, R.J., and Helgen, K.M. 2011. High level Mammalian taxonomy: a response to Hedges. *Zootaxa* 3092: 63–64.
- Bargo, M.S., and Vizcaíno, S.F. 2008. Paleobiology of Pleistocene ground sloths (Xenarthra, Tardigrada): biomechanics, morphology and ecomorphology applied to the masticatory apparatus. *Ameghiniana* 45: 175–196.
- Bargo, M.S., Vizcaíno, S.F., and Kay, R.F. 2009. Predominance of oral masticatory movements in the Early Miocene *Eucholoeops* (Mammalia, Xenarthra, Tardigrada, Megalonychidae) and other Megatherioid sloths. *Journal of Vertebrate Paleontology* 29: 870–880.
- Bargo, M.S., Toledo, N., and Vizcaíno, S.F. 2012. Paleobiology of the Santacrucian sloths and anteaters (Xenarthra, Pilosa). In: S.F. Vizcaíno, R.F. Kay, and M.S. Bargo (Eds.), *Early Miocene Paleo-*

- biology in Patagonia: high-latitude paleocommunities of the Santa Cruz Formation*. Cambridge University Press, Cambridge, p. 216–242.
- Brandt, J.F. 1833. De Solenodonte, novo mammalium insectivorum genere. *Memoires de l'Académie Impériale des Sciences de St. Pétersbourg, séries 6, sciences mathématiques, physiques et naturelles* 2: 459–478.
- Bugge, J. 1979. Cephalic arterial patterns in New World edentates and Old World pangolins with special reference to their phylogenetic relationships and taxonomy. *Acta Anatomica* 105: 37–46.
- Clemente, C.D. 1985. *Gray's Anatomy*. Lea and Febiger, Philadelphia, 416 p.
- Cope, E.D. 1889. The Edentata of North America. *American Naturalist* 23: 657–664.
- De Iuliis, G., Gaudin, T.J., and Vicars, M.J. 2011. A new genus and species of nothrotheriid sloth (Xenarthra, Tardigrada, Nothrotheriidae) from the late Miocene (Huayquerian) of Peru. *Palaeontology* 54: 171–205.
- De Iuliis, G., Pujos, F., Toledo, N., Bargo, M.S., and Vizcaíno, S.F. 2014. *Eucholoeops* Ameghino, 1887 (Xenarthra, Tardigrada, Megalonychidae) from the Santa Cruz Formation, Argentine Patagonia: implications for the systematics of Santacrucian sloths. *Geodiversitas* 36: 209–255.
- Delsuc, F., Catzeflis, F.M., Stanhope, M.J., and Douzery, E.J.P. 2001. The evolution of armadillos, anteaters and sloths depicted by nuclear and mitochondrial phylogenies: Implications for the status of the enigmatic fossil *Eurotamandua*. *Proceedings of the Royal Society of London series B* 268: 1605–1615.
- Diamond, M.K. 1991. Homologies of the stapedia artery in humans, with a reconstruction of the primitive stapedia artery configuration of euprimates. *American Journal of Physical Anthropology* 84: 433–462.
- Emry, R.J. 1970. A North American Oligocene pangolin and other additions to the Pholidota. *Bulletin of the American Museum of Natural History* 142: 459–510.
- Evans, H.E., and de Lahunta, A. 2012. *Miller's Anatomy of the Dog*. W.B. Saunders Company, Philadelphia, 872 p.
- Fleagle, J.G., Perkins, M.E., Heizler, M.T., Nash, B., Bown, T.M., Tauber, A.A., Dozo, M.T., and Tejedor, M.F. 2012. Absolute and relative ages of fossil localities in the Santa Cruz and Pinturas Formations. In: S.F. Vizcaíno, R.F. Kay, and M.S. Bargo (Eds.), *Early Miocene Paleobiology in Patagonia: high-latitude paleocommunities of the Santa Cruz Formation*. Cambridge University Press, Cambridge, p. 41–58.
- Gaudin, T.J. 1995. The ear region of edentates and the phylogeny of the Tardigrada (Mammalia, Xenarthra). *Journal of Vertebrate Paleontology* 15: 672–705.
- Gaudin, T.J. 2004. Phylogenetic relationships among sloths (Mammalia, Xenarthra, Tardigrada): the craniodental evidence. *Zoological Journal of the Linnean Society* 140: 255–305.
- Gaudin, T.J. 2011. On the osteology of the auditory region and orbital wall in the extinct West Indian sloth genus *Neocnus* (Megalonychidae, Xenarthra, Placentalia). *Annals of the Carnegie Museum* 80: 5–28.
- Gaudin, T.J., and Wible, J.R. 1999. The entotympanic of pangolins and the phylogeny of the Pholidota. *Journal of Mammalian Evolution* 6: 39–65.
- Gaudin, T.J., Emry, R.J., and Wible, J.R. 2009. The phylogeny of living and extinct pangolins (Mammalia, Pholidota) and associated taxa: a morphology based analysis. *Journal of Mammalian Evolution* 16: 235–305.
- Gervais, F.L.P. 1855. Mammifères. In: F. de Castelnau (Ed.), *Animaux nouveaux ou rares recueillis pendant l'expédition dans les parties centrales de l'Amérique de Sud. Volume 1, Part 2*. P. Bertrand, Paris, p. 1–116.
- Gregory, W.K., and Simpson, G.G. 1926. Cretaceous mammal skulls from Mongolia. *American Museum Novitates* 225: 1–20.
- Guth, C. 1961. [*La région temporale des Édentés*. PhD Thesis, Université de Paris, Paris, 192 p. Unpublished.].
- Harlan, R. 1825. *Fauna Americana: being a description of the mammiferous animals inhabiting North America*. Philadelphia: Anthony Finley p. 199–203.
- Hoffstetter, R. 1954. Les gravigrades (Édentés, Xénarthres) des caverns de Lagoa Santa. *Annales des Sciences Naturelle, Zoologie* 11: 741–764.
- Illiger, C. 1811. *Prodromus systematis mammalium et avium additis terminis zoographicis utriusque classis*. C. Salfeld, Berlin, 301 p.
- Latham, J., and Davies, H. 1795. Faunula indica. Appendix. In: J.R. Forster (Ed.), *Zoologia Indica*. Secunda, Halle A. S., p. 1–38.
- Leidy, J. 1868a. Notice of some vertebrate remains from the West Indian islands. *Proceedings of the Academy of Natural Sciences, Philadelphia* 20: 178–180.
- Leidy, J. 1868b. Notice of some remains of extinct Insectivora from Dakota. *Proceedings of the Academy of Natural Sciences, Philadelphia* 20: 315–316.
- Linnaeus, C. 1758. *Systema naturæ per regna tria naturæ, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio decima, reformata*. Salvius, Stockholm, 824 p.
- Luo, Z.X., and Wible, J.R. 2005. A Late Jurassic digging mammal and early mammalian diversification. *Science* 308: 103–107.
- Lydekker, R. 1894. Contribuciones al conocimiento de los vertebrados fósiles de la Argentina. Part II. *Anales del Museo de La Plata-Paleontología Argentina* 1: 1–118.
- Marshall, L.G. 1976. Fossil localities for Santacrucian (Early Miocene) mammals, Santa Cruz Province, Southern Patagonia, Argentina. *Journal of Palaeontology* 50: 1129–1142.
- Matthew, W.D. 1918. A revision of the Lower Eocene Wasatch and Wind River Faunas. Part V- Insectivora (continued), Glires, Edentata. *Bulletin of the American Museum of Natural History* 38: 565–657.
- McAfee, R.K., and Naples, V.L. 2012. Notice on the occurrence of supernumerary teeth in the two-toed sloths *Choloepus didactylus* and *C. hoffmanni*. *Mastozoología Neotropical* 19: 339–344.
- McDonald, H.G., and De Iuliis, G. 2008. Fossil history of sloths. In: S.F. Vizcaíno, and W.J. Loughry (Eds.), *The Biology of the Xenarthra*. University Press of Florida, Gainesville, p. 39–55.
- McDonald, H.G., and Muizon, C. de. 2002. The cranial anatomy of *Thalassocnus* (Xenarthra, Mammalia), a derived nothrothere from the Neogene of the Pisco Formation (Peru). *Journal of Vertebrate Paleontology* 22: 349–365.
- McDonald, H.G., Rincón, A., and Gaudin, T.J. 2013. A new genus of megalonychid sloth (Mammalia, Xenarthra) from the late Pleistocene of Sierra de Perijá, Zulia State, Venezuela. *Journal of Vertebrate Paleontology* 33: 1226–1238.
- Merccerat, A. 1891. Datos sobre restos de mamíferos fósiles pertenecientes a los Bruta. *Revista del Museo de La Plata* 2: 1–46.
- Novacek, M.J. 1986. The skull of leptictid insectivorans and the higher-level classification of eutherian mammals. *Bulletin of the American Museum of Natural History* 183: 1–112.
- Novacek, M.J. 1993. Patterns of diversity in the mammalian skull. In: J. Hanken, and B.K. Hall (Eds.), *The Skull, Volume 2, Patterns of Structural and Systematic Diversity*. University of Chicago Press, Chicago, p. 438–545.
- O'Leary, M.A. 2010. An anatomical and phylogenetic study of the

- osteology of the petrosal of extant and extinct artiodactylans (Mammalia) and relatives. *Bulletin of the American Museum of Natural History* 335: 1–206.
- O'Leary, M.A., Bloch, J.I., Flynn, J.J., Gaudin, T.J., Giallombardo, A., Giannini, N.P., Goldberg, S.L., Kraatz, B.P., Luo, Z.X., Meng, J., Ni, X., Novacek, M.J., Perini, F.A., Randall, Z., Rougier, G.W., Sargis, E.J., Silcox, M.T., Simmons, N.B., Spaulding, M., Velasco, P.M., Weksler, M., Wible, J.R., and Cirranello, A.L. 2013. The placental mammal ancestor and the post-KPg radiation of placentals. *Science* 339: 662–667.
- Owen, R. 1840. Fossil Mammalia. In Darwin, C.R. (Ed.) *Zoology of the Voyage of H.M.S Beagle, under the command of Captain Fitzroy, during the years 1832 to 1836*. 1(4): 81–111.
- Owen, R. 1842. *Description of the skeleton of an extinct gigantic sloth, Mylodon robustus, Owen: with observations on the osteology, natural affinities, and probable habits of the megatheriid quadrupeds in general*. R. and J.E. Taylor, London, 176 p.
- Patterson, B., Segall, W., Turbull, W.D., and Gaudin, T.J. 1992. The ear region in xenarthrans (=Edentata: Mammalia). Part II. Pilosa (Sloths, Anteaters), Palaeonodons, and a Miscellany. *Fieldiana, Geology, New Series* 24: 1–79.
- Perkins, M.E., Fleagle, J.G., Heizler, M.T., Nash, B., Bown, T.M., Tauber, A.A., and Dozo, M.T. 2012. Tephrochronology of the Miocene Santa Cruz and Pinturas Formations, Argentina. In: S.F. Vizcaíno, R.F. Kay, and M.S. Bargo (Eds.), *Early Miocene Paleobiology in Patagonia: high-latitude paleocommunities of the Santa Cruz Formation*. Cambridge University Press, Cambridge, p. 23–40.
- Peters, W. 1858. Charakterist eines neuen zweizehigen Faulthiers. *Monatsberichte der Königlich preussischen Akademie der Wissenschaften zu Berlin* 1859: 128.
- Pujos, F., Gaudin, T.J., De Iuliis, G., and Cartelle, C. 2012. Recent advances on variability, morpho-functional adaptations, dental terminology, and evolution of sloths. In: T.J. Gaudin, and F. Pujos (Eds.), *Proceedings of the Symposium Form and Function of the Xenarthra*, *Journal of Mammalian Evolution* 19. p. 159–170.
- Saban, R. 1963. Contribution à l'étude de l'os temporal des Primates. Description chez l'Homme et les Prosimiens. Anatomie comparée et phylogénie. *Mémoires du Musée National d'Histoire Naturelle, Série A, Zoologie* 29: 1–378.
- Schneider, R. 1955. Zur Entwicklung des Chondrocraniums der Gattung *Bradypus*. *Morphologisches Jahrbuch* 95: 209–301.
- Scott, W.B. 1903. Mammalia of the Santa Cruz beds. Part I. Edentata. In: W.B. Scott (Ed.), *Reports of the Princeton University Expeditions to Patagonia 1896–1899. Vol. 5, Paleontology 2*. Princeton University Press, Princeton, p. 1–226.
- Scott, W.B. 1904. Mammalia of the Santa Cruz beds. Part I. Edentata. In: W.B. Scott (Ed.), *Reports of the Princeton University Expeditions to Patagonia 1896–1899. Vol. 5, Paleontology 2*. Princeton University Press, Princeton, p. 227–364.
- Tauber, A.A. 1997. Bioestratigrafía de la Formación Santa Cruz (Mioceno inferior) en el extremo sudeste de la Patagonia. *Ameghiniana* 34: 413–426.
- Toledo, N., Bargo, M.S., and Vizcaíno, S.F. 2013. Muscular reconstruction and functional morphology of the forelimb of Santacrucian (Early Miocene) sloths (Xenarthra, Folivora) of Patagonia. *The Anatomical Record* 296: 305–325.
- Toledo, N., Cassini, G.H., Vizcaíno, S.F., and Bargo, M.S. 2014. Mass estimation in fossil sloths (Xenarthra, Folivora) from the Early Miocene Santa Cruz Formation of Patagonia, Argentina. *Acta Palaeontologica Polonica* 59: 267–280.
- Vizcaíno, S.F., and Loughry, W.J. 2008. *The Biology of the Xenarthra*. University of Florida Press, Gainesville, Florida, 370 p.
- Vizcaíno, S.F., Bargo, M.S., and Fariña, R.A. 2008. Form, function and paleobiology in xenarthrans. In: S.F. Vizcaíno, and W.J. Loughry (Eds.), *The Biology of the Xenarthra*. University Press of Florida. Gainesville, p. 86–99.
- Vizcaíno, S.F., Kay, R.F., and Bargo, M.S. 2012. Background for a paleoecological study of the Santa Cruz Formation (late Early Miocene) on the Atlantic Coast of Patagonia. In: S.F. Vizcaíno, R.F. Kay, and M.S. Bargo (Eds.), *Early Miocene Paleobiology in Patagonia: high-latitude paleocommunities of the Santa Cruz Formation*. Cambridge University Press, Cambridge, p. 1–22.
- Webb, S.D. 1985. The interrelationships of tree sloths and ground sloths. In: G.G. Montgomery (Ed.), *The Ecology and Evolution of Armadillos, Sloths, and Vermilinguas*. Smithsonian Institution Press, Washington, D.C., p. 105–112.
- White, J.L. 1993. Indicators of locomotor habits in Xenarthrans: evidence for locomotor heterogeneity among fossil sloths. *Journal of Vertebrate Paleontology* 13: 230–242.
- Wible, J.R. 1986. Transformations in the extracranial course of the internal carotid artery in mammalian phylogeny. *Journal of Vertebrate Paleontology* 6: 313–325.
- Wible, J.R. 1987. The eutherian stapedial artery: character analysis and implications for superordinal relationships. *Zoological Journal of the Linnean Society* 91: 107–135.
- Wible, J.R. 2008. On the cranial osteology of the Hispaniolan solenodon, *Solenodon paradoxus* Brandt, 1833 (Mammalia, Lipotyphla, Solenodontidae). *Annals of Carnegie Museum* 77: 321–402.
- Wible, J.R. 2010. Petrosal anatomy of the nine-banded armadillo, *Dasypus novemcinctus* Linnaeus, 1758 (Placentalia: Xenarthra: Dasypodidae). *Annals of Carnegie Museum* 79: 1–28.
- Wible, J.R. 2011. On the treeshrew skull (Mammalia, Placentalia, Scandentia). *Annals of Carnegie Museum* 79: 149–230.
- Wible, J.R., and Gaudin, T.J. 2004. On the cranial osteology of the yellow armadillo *Euphractus sexcinctus* (Dasypodidae, Xenarthra, Placentalia). *Annals of the Carnegie Museum* 73: 117–196.
- Wible, J.R., Novacek, M.J., and Rougier, W. 2004. New data on the skull and dentition in the Mongolian Late Cretaceous eutherian mammal *Zalambdalestes*. *Bulletin of the American Museum of Natural History* 281: 1–144.
- Wible, J.R., Wang, Y., Li, C., and Dawson, M.R. 2005. Cranial anatomy and relationships of a new ctenodactyloid (Mammalia, Rodentia) from the early Eocene of Hubei Province, China. *Annals of the Carnegie Museum* 74: 91–150.

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