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ORIGINAL PAPER

The Narial Anatomy of Extinct and Extant Sloths (Xenarthra, Folivora): Osteological Anomalies in the Extant Two-Toed Sloth *Choloepus*

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Abstract

The skeletal anatomy of the anterior narial region in mammals is complex, comprised of several bony and cartilaginous elements. Because it includes many cartilaginous components, preservation of this area in extant and extinct specimens is often incomplete. This, along with its complexity, means that this region of the cranium is generally understudied, with the exception of humans and a few select mammal species. The present study began with a cranial specimen of the extant Hoffmann's two-toed sloth, *Choloepus hoffmanni* (Xenarthra, Folivora, Megalonychidae), that possessed several unusual well-preserved narial anomalies. In order to determine whether such features are present in other extant sloths, and if so, how frequently, we examined two- and three-toed sloth specimens from a variety of museum collections. Additionally, we examined museum specimens of extinct sloths known to possess unusual osseous narial structures, with the goal of better understanding the anatomy of the anterior opening of the nasal cavity in all sloths, living and extinct. A diverse series of unusual narial elements were found, including an internasal bone, an ossified anterior nasal septum, an os nariale, an ossified processus lateralis ventralis of the nasal capsule, and an internarial bar of varying composition and completeness. All of these features are present in *Choloepus*, although they are preserved in museum skulls infrequently, but none were found to be present in the three-toed sloth, *Bradypus.* An internarial bar, anteriorly elongated ossified nasal septum, and ossified processus lateralis ventralis were observed in several species of extinct mylodontid and megatheriid sloths, and an os nariale was recorded in the extant vermilinguan anteaters *Cyclopes* and *Tamandua.* It is not known how much of the variation we document in these features is genuine and how much is due to preservation issues. Given such uncertainty, it is difficult to assess the phylogenetic or functional significance of these features. We believe, however, that this is an area of the skull in Pilosa (sloths and anteaters) that merits further study.

Keywords Cranial anatomy · Nasal cavity · Nasal septum · Internarial bar · Internasal bone · Os nariale

Introduction

The skeletal anatomy of the anterior narial region in mammals is complex (DeBeer 1937; Pick and Howden 1977; Moore 1981; Novacek 1993; Evans and De Lahunta 2012). It is comprised of several bony elements derived from the dermatocranium as well as chondrocranial ossifications, including an ossified nasal septum and the complex, often scrolled or branched ossified nasal turbinates. It also incorporates several cartilaginous components (DeBeer 1937; Pick and Howden 1977; Moore 1981; Novacek 1993; Evans and De Lahunta 2012). Because of the latter, the preservation of this region is often incomplete, even in macerated museum specimens of recent mammal species, but especially in fossils. That, along with its complexity, means that this region of the

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skull is often poorly studied and not well understood with the exception of humans, animals used in veterinary anatomy, and a limited number of extant mammal species (e.g., *Tachyglossus*, Kuhn 1971; *Tupaia*, Zeller 1993; *Solenodon*, Wible 2008; *Didelphis* and other marsupials, Macrini 2012).

The present study arose from the discovery of a cranial specimen of *Choloepus hoffmanni* (Figs. 1, 2) from the Lincoln Park Zoo (Chicago, IL) that possesses an unusually well-preserved nasal region displaying several remarkable structural features that have not been previously described. We determined to investigate whether such features were preserved in other museum specimens of two-toed sloths. The two-toed sloths include two living species from Central and South America, *Choloepus hoffmanni* and *C. didactylus* (Wetzel 1985; Adam 1999; Gardner 2007; Hayssen 2011). We examined specimens from the Field Museum of Natural History, the Carnegie Museum of Natural History, and University of Tennessee at Chattanooga Natural History Museum. In order to determine whether the features are more broadly distributed among sloths, we examined the other genus of extant sloths, *Bradypus*, the three-toed sloths (Bradypodidae). The two species of *Bradypus* that were available to us were *B. variegatus* and *B. tridactylus,* which also live in Central and South America (Wetzel 1985; Gardner 2007; Hayssen 2009, 2010).

Fossil sloths are known to possess unusual osseous nasal structures as well, particularly among members of the clades Mylodontidae and Megatheriidae (Bargo et al. 2006). These would include the presence of an anteriorly elongated ossified nasal septum and, even more remarkably, a partial or complete ossified internarial bar. The internarial bar is a narrow, median arch of bone that divides the external narial opening in half. It is present in non-mammalian cynodonts and the earliest and most primitive mammaliaformes, but is lost in most mammaliaform lineages (an exception being the meridiolestidan *Necrolestes* [Wible and Rougier 2017]) and in all living mammals (Wible et al. 1990; Kielan-Jaworowska et al. 2004). In these mammalian forebears, the internarial bar is formed largely by the premaxillae, with small contributions from the nasals, and it generally lies well anterior and is unconnected to the osseous median nasal septum.

The goal of the present study is to describe the anatomy of unusual bony structures in and around the anterior opening of the nasal cavity in extant and extinct sloths. In so doing, we may clarify the homology of these structures, which have been interpreted in various ways by previous authors. Ultimately, this may yield insights into the evolution of the nasal cavity in sloths.

Materials and Methods

Institutional Abbreviations: AMNH, American Museum of Natural History, New York, NY, USA; BMNH, Natural History Museum, London, UK; CM, Carnegie Museum of Natural History, Pittsburgh, PA, USA; CN, Zoological Museum, Copenhagen, Denmark; DU EA, Duke University Evolutionary Anthropology, Durham, NC, USA; EPN, Escuela Politécnica Nacional, Quito, Ecuador; FMNH, Field Museum, Chicago, IL, USA; MACN, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires, Argentina; MACNC Pv, Colección Paleontología Vertebrados del Museo de Antropología y Ciencias Naturales de Concordia, Concordia, Argentina; MLP, Museo de La Plata, La Plata, Argentina; MNHN, Muséum National d'Histoire Naturelle, Paris, France; MNHN-Bol-V, Museo Nacional de Historia Natural, La Paz, Bolivia; UTCM, University of Tennessee at Chattanooga Museum of Natural History, University of Tennessee at Chattanooga, Chattanooga, TN, USA.

The original specimen of *Choloepus hoffmanni* (UTCM 1912; Figs. 1a-d, 2) with the unusual nasal features was compared to other museum specimens of the same species, as well as the related species *Choloepus didactylus* (Fig. 1e-h) and specimens of extant three-toed sloths in the species *Bradypus variegatus* and *B. tridactylus* from the UTCM and CM collections, to determine whether other modern sloths possess any of these unusual features. A large number of specimens from the FMNH were examined in previous studies by TJG (Patterson et al. 1992). Only one of the recorded specimens preserved unusual nasal structures, but it was also included in our comparisons. All the specimens of extant and extinct sloths examined in the present study are listed in Table 1.

We examined numerous specimens of extinct mylodontid and megatheriid sloths known to possess unusual nasal structures such as an internarial bar (Reinhardt 1879; Woodward 1900; Weber 1928; McDonald 1987; Brandoni et al. 2008). We utilized unpublished observations made by one of us (TJG) in past studies, as well as photographs kindly supplied by colleagues, especially F. Pujos and A. Boscaini. Species examined (see Table 1) from these observations and pictures included *Scelidotherium leptocephalum, Mylodon darwinii* and its relative, *Glossotherium wegneri,* as well as *Megatherium americanum* and its relative *Megatherium tarijense*. In addition to these unpublished observations, we also consulted published descriptions of *Scelidotherium leptocephalum* (McDonald 1987; Bargo et al. 2006), *Mylodon darwinii* (Reinhardt 1879; Woodward 1900; Kraglievich 1934), *Glossotherium wegneri* (Hoffstetter 1952), and *Megatherium americanum* (Bargo 2001; Bargo et al. 2006; Brandoni et el. 2008).

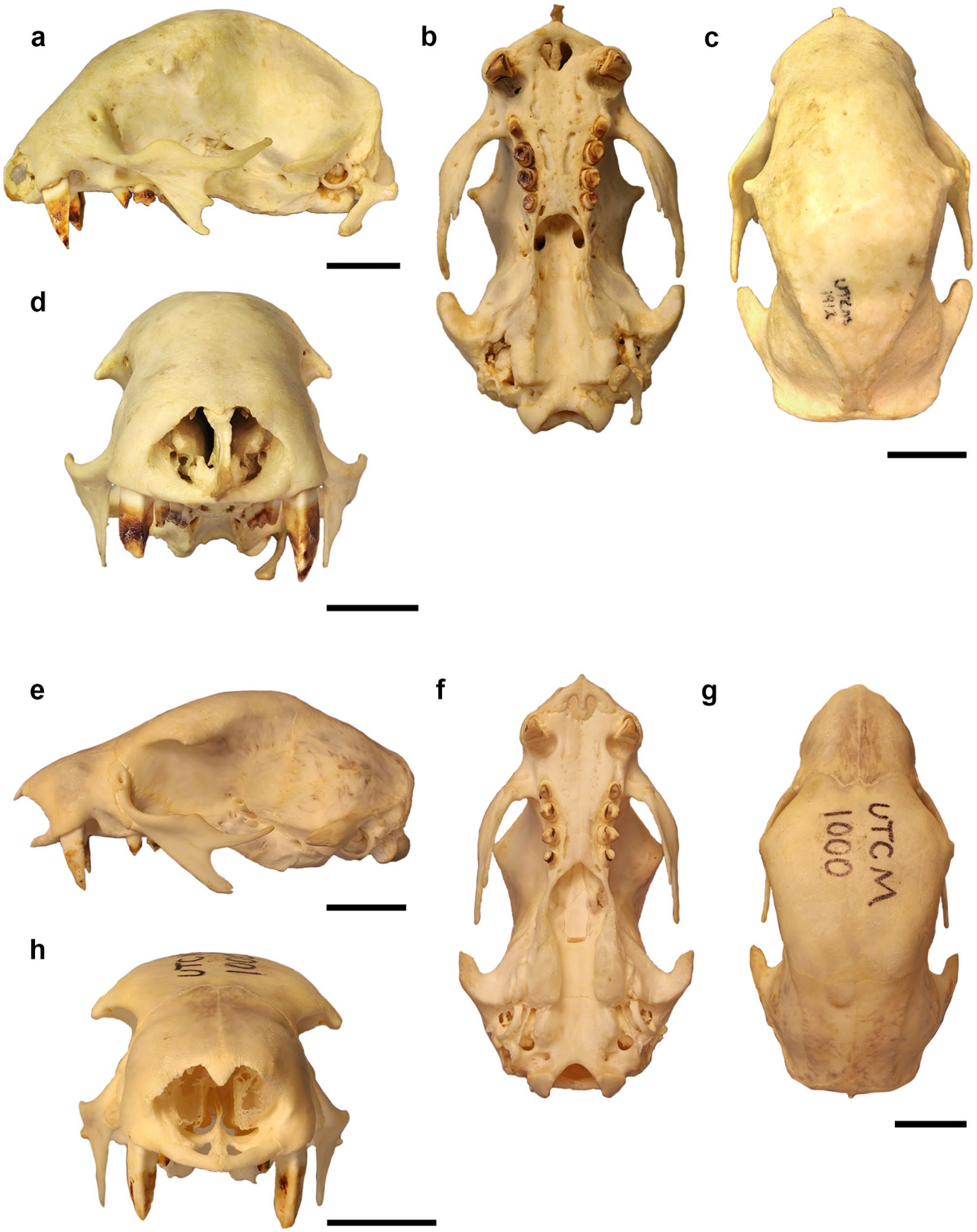

Fig. 1 Skull of *Choloepus hoffmanni* UTCM 1912. **a.** left lateral view; **b.** ventral view; **c.** dorsal view; **d.** anterior view. Skull of *Choloepus didactylus* UTCM 1000. **e.** left lateral view; **f.** ventral view; **g.** dorsal view; **h.** anterior view. Scale bars equal 2 cm

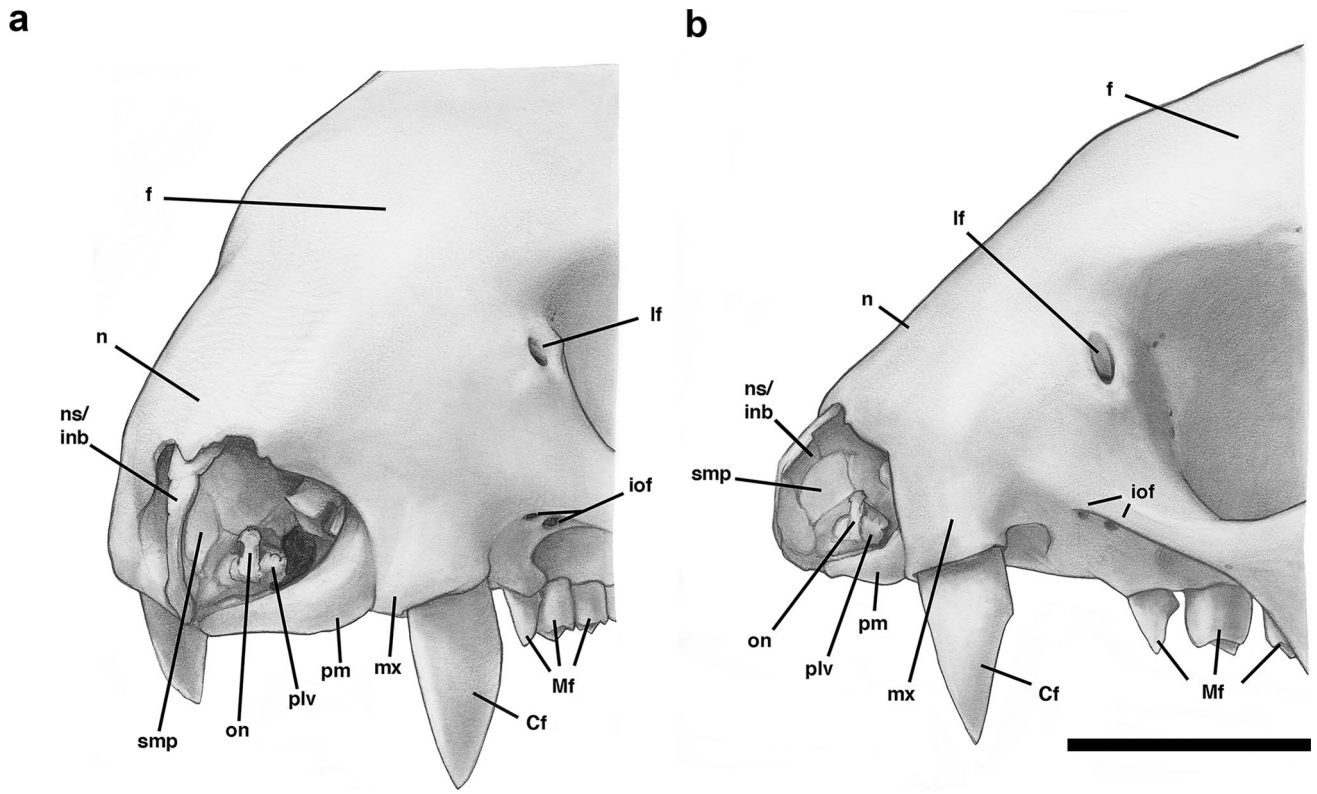

Fig. 2 Skull of *Choloepus hoffmanni* UTCM 1912 depicting unusual narial features. **a.** anterolateral view; **b.** lateral view. Abbreviations: *Cf* caniniform tooth, *f* frontal, *iof* infraorbital foramina, *lf* lacrimal foramen, *Mf* molariform tooth, *mx* maxilla, *n* nasal, *ns/inb* nasal septum and internarial bar, *on* os nariale, *plv* ossified processus lateralis ventralis of the nasal capsule, *pm* premaxilla, *smp* septal membranous perforation. Scale bar equals 2 cm

Results

The nasal bones of *Choloepus hoffmanni* (UTCM 1912; Figs. 1a-d, 2) form the dorsal edge of the external nasal aperture and have three anterior projections separated by two anteriorly concave edges. The maxilla is fused to the nasal dorsomedially in *C. hoffmanni* UTCM 1912 and in *C. didactylus* FMNH 41207, but in other specimens of *Choloepus* (e.g., *C. hoffmanni* CM 3883 [a subadult specimen], *C. hoffmanni* CM 1805, *C. didactylus* UTCM 1000), the nasal has a laterally concave suture with the maxilla. The anterior edge of the maxilla is concave posteriorly and forms the lateral edges of the external nasal aperture. The maxilla broadens transversely immediately behind this

Table 1 Extant and extinct specimens examined

Species	Specimen numbers
Choloepus hoffmanni	CM 1353, CM 1570, CM 1805, CM 3883, CM 22557, CM 22558, UTCM 1912
Choloepus didactylus	FMNH 41207, UTCM 1000
Choloepus sp.	DU EA 167
Bradypus variegatus	CM 1365, CM 1491, CM 1492, CM 2169, CM 2179, CM 2180, CM 2551, CM 3617, CM 3782, CM 4457, CM 22552, CM 22553, CM 22554, CM 22555
Bradypus tridactylus	CM 64, CM461
Scelidotherium leptocephalum	AMNH 45910, FMNH 14274, MLP 3–671,
Mylodon darwinii	BMNH 8722, CM 43, MACN 5080, MACNC Pv 2334, MLP 3–762, MLP 3–763, MLP 3–764, MLP 36-VII-12–1, MLP 3–122, MNHN-Bol-V-006470
Glossotherium wegneri	EPN V107, EPN V120
Megatherium americanum	BMNH 19953, MACN 1000, MACN 5002, MLP 2–64, MLP 2–73, MNHN PAM 276
Megatherium tarijense	MNHN-Bol-V-000671

edge to accommodate the root of the caniniform tooth. The ventromedial edges of the maxilla are sutured to the premaxillae, which create the floor of the external nasal aperture. The suture between the maxilla and premaxilla is partially fused in *C. hoffmanni* UTCM 1912 and CM 1805, and in *C. didactylus* FMNH 41207, but in other specimens of *Choloepus* (e.g., *C. hoffmanni* CM 3883, *C. didactylus* UTCM 1000) it remains distinct, with the lateral ramus of the premaxilla fitting into an anterior concavity in the maxilla, as in other megalonychids (Lyon et al. 2016).

The premaxillae are comprised of two "V"-shaped bones that are typically sutured medially in *Choloepus* (Lyon et al. 2016; e.g., *C. hoffmanni* CM 3883, *C. didactylus* UTCM 1000); however, the median suture is fused in *C. hoffmanni* UTCM 1912. These bones form the anterior border of two large kidney-shaped holes in the anterior reaches of the hard palate, the incisive foramina (Lyon et al. 2016). The margins of the incisive foramina are formed by the lateral and medial rami of the premaxilla anteriorly (for description of medial and lateral rami in sloths, see Lyon et al. 2016) and the maxilla posteriorly.

The anterior edge of the nasal bone is marked by a small, anteriorly pointed median projection, as noted above, that is somewhat ventrally deflected (Figs. 1a-d, 2). In *C. didactylus* UTCM 1000, FMNH 41207, and *Choloepus* sp. DU EA 167, the projection is formed by a diamond-shaped element that is separated from the nasals by a suture (Fig. 3). This bone has been called the "os internasale" bone by Weber (1928). Although Grassé (1955) referred to this same element as the "os nariale," he also used the term "os nariale" to refer to the element often designated as a "septomaxilla" in xenarthrans (Wible et al. 1990; Zeller et al. 1993; Wible and Gaudin 2004). Given Grassé's (1955) inconsistency and Wible and Rougier's (2017) recent use of "os nariale" for the xenarthran "septomaxilla," we follow Weber's (1928) usage of the "os internasale" for the bone in question in the two-toed sloth. The internasal in *C. didactylus* UTCM 1000 (Fig. 3b) has a maximum anteroposterior length of 5.5 mm and a maximum transverse width of 4.4 mm. The bone is fused to the nasal in *C. hoffmanni* UTCM 1912, but an unpaired internasal suturally separate from the nasal has been recorded in both *C. hoffmanni* and *C. didactylus* (*Choloepus* sp. DU EA 167, *C. didactylus* UTCM 1000, *C. didactylus* FMNH 41207; *C. hoffmanni* CM 1570, 1805, and 3883 have a facet for the internasal but the bone itself is not preserved; see also Weber 1928; Grassé 1955). We did not observe a separate internasal in our examination of several specimens of *Bradypus variegatus* or *B. tridactylus* (see Table 1) ranging from juvenile to adult ages. The anterior edge of the nasals in *Bradypus* is generally straight or anteriorly concave, lacking an anterior median process (Gaudin 2004). However, Weber (1928) and Grassé (1955) noted that a paired internasal element has been reported in *Bradypus*. Among extinct species of sloths, most have a median process on the anterior edge of the nasal (Gaudin 2004), but there is no evidence of a separate internasal so far as we are aware.

The nasal septum appears to be thickened and heavily ossified in *C. hoffmanni* UTCM 1912 (Figs. 1a-d, 2). It forms the anterior-most protrusion on the skull, extending forward as an anteriorly convex arch that spans the height

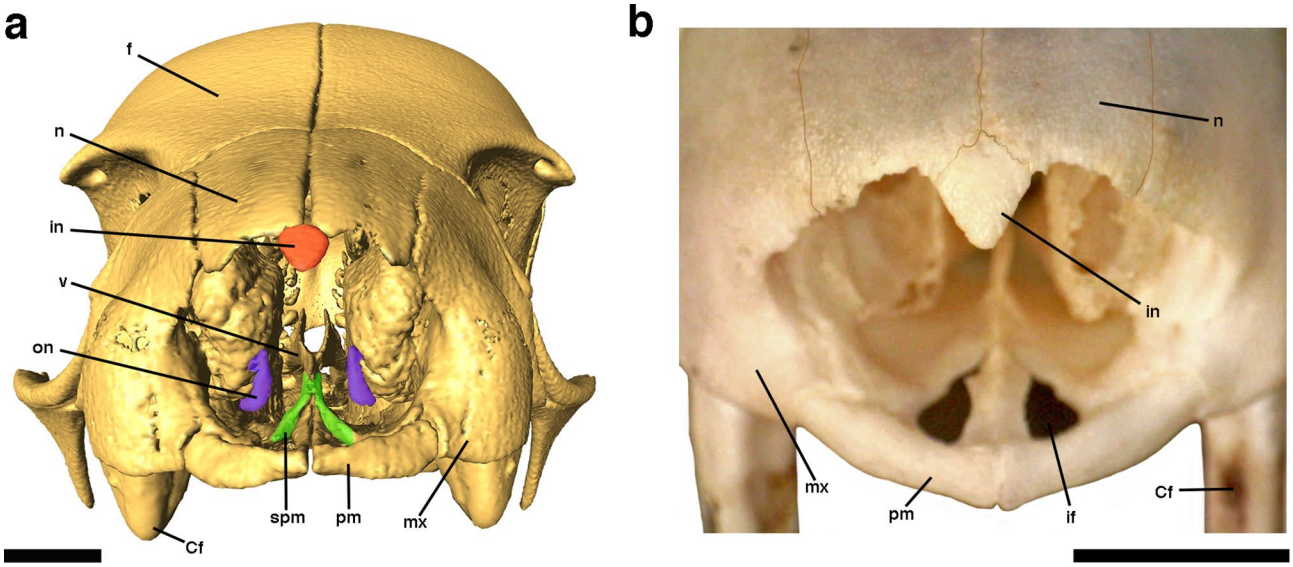

Fig. 3 **a.** CT scan of juvenile *Choloepus* sp. DU EA 167 in anterior view showing internasal and os nariale (morphosource.org); **b.** *Choloepus didactylus* UTCM 1000, close-up of skull in anterodorsal view showing internasal; sutures digitally enhanced. Abbreviations: *Cf* caniniform tooth, *f* frontal, *if* incisive foramen, *in* internasal, *mx* maxilla, *n* nasal, *on* os nariale, *pm* premaxilla, *spm* septal process of maxilla, *v* vomer. Scale bar equals 0.5 cm in **a**, 1 cm in **b**

of the narial opening, from immediately below the nasal and internasal dorsally to immediately above the premaxilla ventrally. The septum is pierced by a large, irregularly shaped perforation behind its anterior edge. This perforation ranges from 2.2 mm to 3.5 mm behind the anterior-most edge of the septum and is covered by a thin membrane. The perforation itself ranges in size from 4.2 mm to 5.7 mm in diameter. The perforation creates an anterior internarial bar in the nasal septum of this specimen, resembling the internarial bar of several extinct sloths (Figs. 1a-d, 2, 4c-d). A similarly positioned membranous gap in the cartilaginous nasal septum is observed in the domestic dog *Canis familiaris*, where it connects the immovable caudal part of the septum with the mobile rostral part (Evans and De Lahunta 2012). In *Canis*, the nasal septum is continuous below this gap, but is broadly interrupted above it. It is possible that the septal perforation seen in sloths is analogous to the membranous gap in dogs and that the anterior part of the nasal septum may have been mobile in sloths, although the ossified nature of the septum in *C. hoffmanni* UTCM 1912 may cast doubt on such an interpretation.

In *C. didactylus* UTCM 1000, the ossified nasal septum is located far back within the nasal cavity and the cartilaginous nasal septum is not preserved. The ossified part was presumably formed largely by the presphenoid, as xenarthrans lack a mesethmoid septum (Parker 1885; Broom 1927; DeBeer 1937; Novacek 1993; but see Ferigolo 1981). In *C. didactylus* FMNH 41207 (Fig. 5), however, the ossified nasal septum extends farther anteriorly than that of *C. didactylus* UTCM 1000, though not as far as that of *C. hoffmanni* UTCM 1912.

An ossified nasal septum and partial or complete internarial bar have also been observed in extinct Pleistocene sloth species from two different families, Mylodontidae and Megatheriidae. These structures have been recorded in the scelidotheriine mylodontid *Scelidotherium leptocephalum* (FMNH 14274, MLP 3–671, AMNH 45910; McDonald 1987; Bargo et al. 2006; T. Gaudin unpublished data) and in several mylodontine mylodontids including *Mylodon darwinii* (CN 43, BMNH 8722 [cited as M8722 by Woodward 1900], MLP 3–122, MLP 3–764, MACN 5080, MNHN-Bol-V-006470, MLP 3–762, and MLP 3–763; Reinhardt 1879; Woodward 1900; Kraglievich 1934; T. Gaudin unpublished data) and *Glossotherium wegneri* (EPN V120 and EPN V107; Hoffstetter 1952). Similar structures have also been recorded in *Megatherium americanum* (MNHN PAM 276, MLP 2–73, MACN 5002, MACN 1000, MLP 2–64; Bargo 2001; Bargo et al. 2006; Brandoni et al. 2008; T. Gaudin unpublished data) and *Megatherium tarijense* (MNHN-Bol-V-000671).

Scelidotherium leptocephalum was described by Bargo et al. (2006) as lacking an internarial bar or anteriorly elongated ossified nasal septum, but McDonald (1987: fig. 6) observed and illustrated a complete internarial bar and a nasal septum in at least one specimen. The internarial bar in *S. leptocephalum* FMNH 14274 is described as partially bifurcated ventrally, arising separately at the tip of each premaxilla and conjoining to form an arc that curves and stretches posterodorsally to contact the nasals (McDonald 1987). The upper portion of the bar is narrow and cylindrical in cross-section. Due to its partially paired nature, this structure may have a compound origin, with the paired portions of the internarial bar arising from the premaxillae and the unpaired portion arising from the nasal septum. An elongated, ossified nasal septum is present in *S. leptocephalum* MLP 3–671, AMNH 45910, and in a specimen illustrated by Bargo et al. (2006: fig. 2I-J) but these specimens lack the internarial bar (Fig. 4a–b). The nasal septum in all three specimens is visible in lateral view, extending under the nasal bone. *Scelidotherium leptocephalum* MLP 3–671 has a small anterior gap between the nasal and the nasal septum, and the septum appears to contact the premaxillae, whereas *S. leptocephalum* AMNH 45910 has a larger gap between the nasal septum and the premaxillae. The ossified anterior portion of the septum in this specimen is triangular in lateral view, bordered posteriorly by a sizeable dorsal indentation. The nasal septum in this specimen does not contact the premaxilla.

Several specimens of *My. darwinii* possess an ossified internarial bar (Reinhardt 1879; Woodward 1900; Kraglievich 1934; T. Gaudin unpublished data; Fig. 6a–d). The bar has a flattened anterior surface and is broader transversely than that of *S. leptocephalum,* and it is never bifurcated like that of the latter taxon. However, the morphology of this region in *My. darwinii* is highly variable. Reinhardt (1879), Woodward (1900), and Brandoni et al. (2008) described specimens of *My. darwinii* (CN 43, BMNH 8722, and MACNC Pv 2334, respectively) that possess a complete internarial bar. A complete internarial bar is also present in *My. darwinii* MLP 3–122. There is a median suture on the anterior surface of the nasal septum of *My. darwinii* BMNH 8722 (Fig. 6b; Woodward 1900: pl. V, fig. 3a), a feature not observed in the other specimens of *My. darwinii* with a complete internarial bar. Multiple specimens of *My. darwinii*, however, lack a complete, fully preserved ossified internarial bar. In these specimens, only the ventral portion of the bar is present, separated by a gap of varying size from the nasals (McDonald 1987). This is the case in *My. darwinii* MLP 3–764 (Fig. 6c) and MACN 5080; both specimens have partially paired projections that extend dorsally from the premaxillae but do not reach the nasals. A partial internarial bar is also observed in *My. darwinii* MNHN-Bol-V-006470 (Fig. 6d). In this specimen, the narial bar is nearly complete due to a dramatic anterior elongation of the nasals (T. Gaudin unpublished data). Kraglievich (1934) described two specimens of *My. darwinii* (MLP 3–762, MLP 3–763) with an anterior extension of the nasals but no dorsal process arising from the

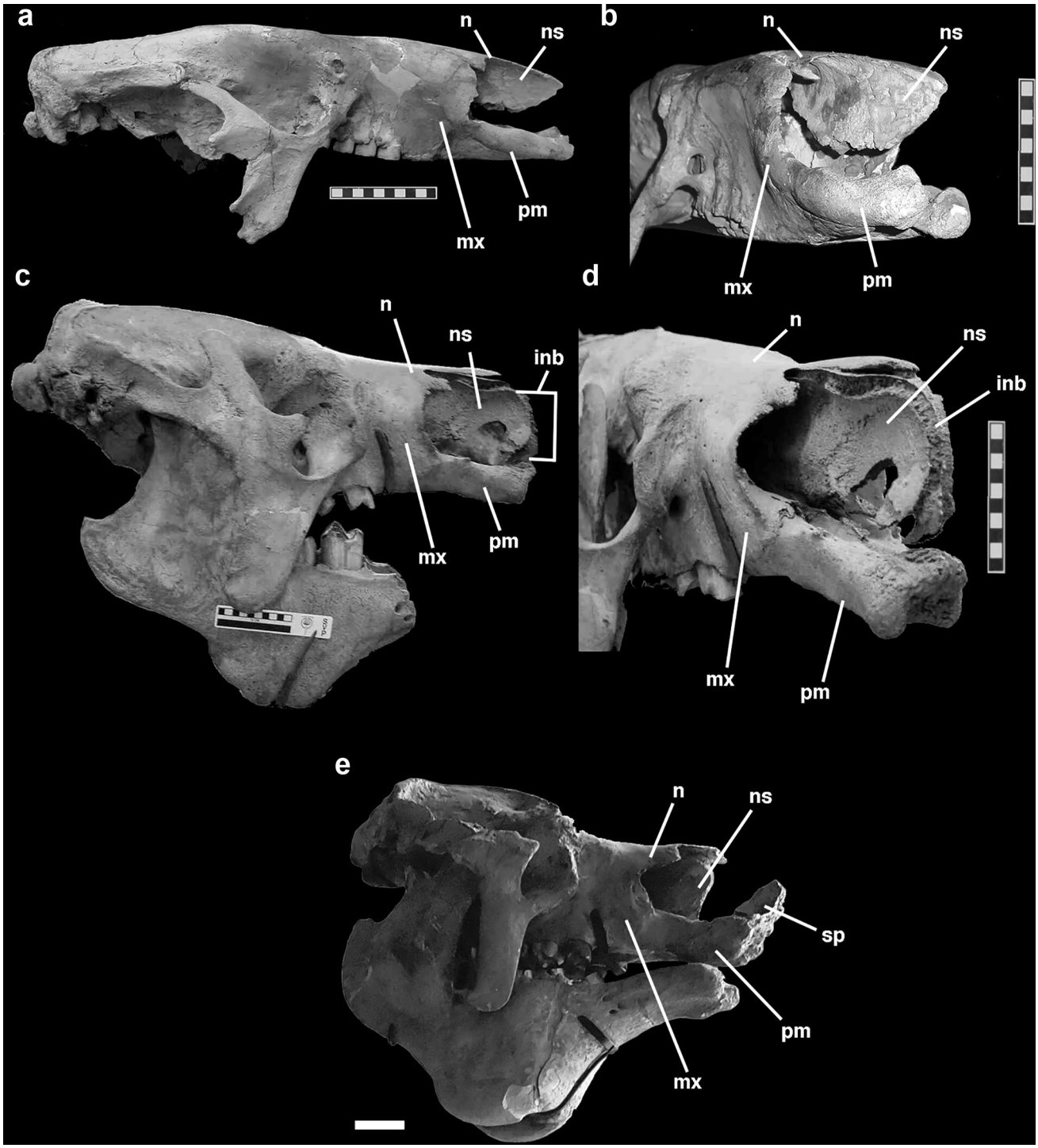

Fig. 4 Skull of *Scelidotherium leptocephalum* MLP 3–671, showing elongated ossified nasal septum. **a.** lateral view; **b.** anterolateral view. Skull of *Megatherium americanum* MNHN PAM 276 showing elongated ossified nasal septum. **c.** lateral view; **d.** anterolateral view. Skull of *Megatherium americanum* (MACN 1000), showing elongated ossified nasal septum and septal process of premaxilla. **e.** lateral view. Images **a-d** modified from Bargo et al. (2006). Abbreviations: *inb* internarial bar, *mx* maxilla, *n* nasal, *ns* nasal septum, *pm* premaxilla, *sp* septal process of premaxilla. Scale bars equal 10 cm

premaxillae, and hence no real vestige of an internarial bar, although it is unclear whether this absence is due to poor preservation in these specimens.

An elongated ossified nasal septum is present in *Glossotherium wegneri* (Fig. 5b, EPN V 107 and EPN V 120; Hoffstetter 1952) as well. The anteriorly extended ossified nasal septum is

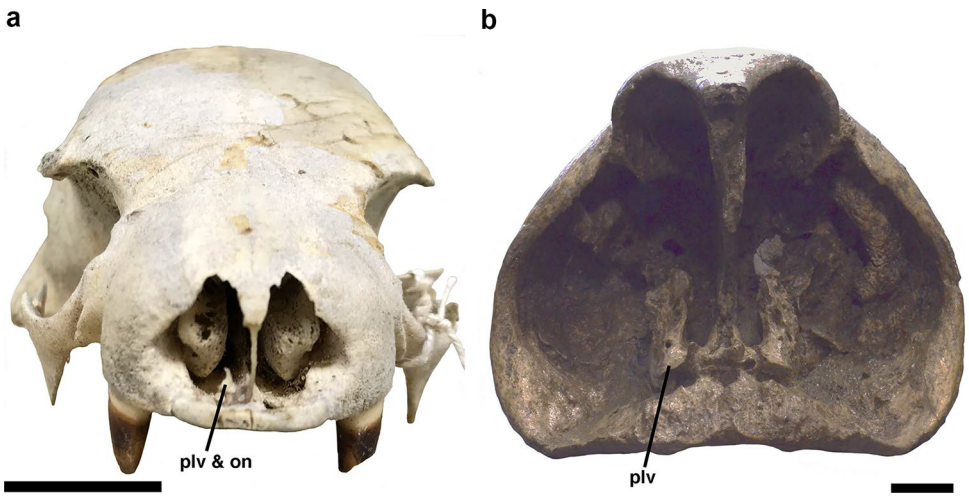

Fig. 5 Skull of *Choloepus didactylus* FMNH 41207. **a.** anterior view. Skull of *Oreomylodon wegneri* EPN V 107. **b.** anterior view. Abbreviations: *on* os nariale, *plv* ossified processus lateralis ventralis of the nasal capsule. Scale bars equal 2 cm

visible in lateral view in both specimens, but that of *G. wegneri* EPN V 107 extends much farther anteriorly, to the end of the nasals. Neither specimen has an internarial bar, but *G. wegneri* EPN V 107 has an anterior extension from the nasals like some *Mylodon* specimens. The nasal extension of *G. wegneri* EPN V 107 looks to be unpaired.

Megatherium americanum MNHN PAM 276 preserves a well-developed and completely ossified nasal septum extending to the tip of the premaxillae (Fig. 4c–d, Bargo et al. 2006). A similar anteriorly extended septum is observed in *Me. americanum* MACN 1000 (Fig. 4e) and MLP 2–64 (Bargo 2001), and in *Me. tarijense* MNHN-Bol-V-000671, although the ossified nasal septum in these specimens extends only to the tip of the nasal, failing to reach the end of the more anteriorly extended premaxillae. In two other *Me. americanum* specimens, MACN P5002 and MLP 2–73, the ossified nasal septum extends beyond the nasals, but does not reach the anterior end of the premaxillae, ending roughly one-third of the distance to the end of the premaxilla. Many *Me. americanum* specimens (including BMNH 19953, MLP 2–73, MACN P5002, and MACN 1000) with an elongated, ossified nasal septum have a pair of crests visible on the anterior edge of the septum. These crests outline a fossa that presumably housed the proximal end of the cartilaginous nasal septum (Owen 1856).

Another pattern evident in *Me. americanum* is the presence of a perforation in the nasal septum some distance behind the anterior edge of the ossified septum (Fig. 4c-d), similar to that described above for *C. hoffmanni* UTCM 1912 (Figs. 1a-d, 2). It has been observed in two specimens (MNHN PAM 276 (Bargo et al. 2006), and MLP 2–73). In *Me. americanum* MNHN PAM 276 (Fig. 4c-d), the

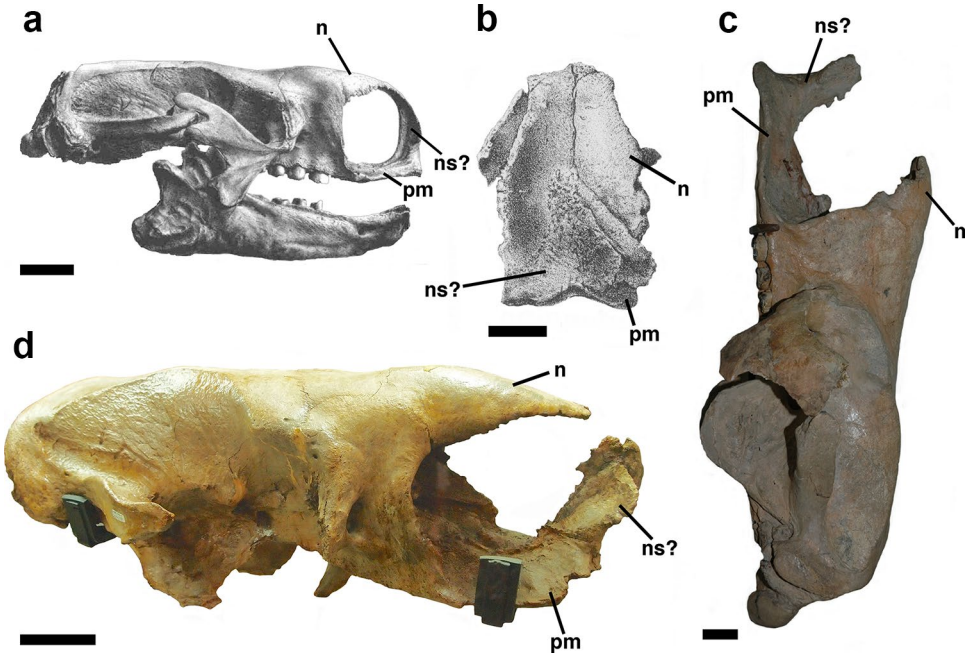

Fig. 6 Skulls of *Mylodon darwinii* showing partial and full internarial bars. **a.** CN 43 in lateral view, from Bargo et al. (2006); **b.** BMNH 8722 in anterior view, from Woodward (1900); **c.** MLP 3–764 in lateral view; **d.** MNHN-Bol-V-006470 in lateral view. Abbreviations: *n* nasal, *ns* nasal septum, *pm* premaxilla. Scale bars equal 5 cm except **b,** in which scale bar equals 2 cm

perforation contacts the ventral edge of the nasal septum and opens into its margin. In *Me. americanum* MLP 2–73, the opposite is true; the perforation is located dorsally, also opening into the margin of the nasal septum (much like the condition in *Canis* described above, and in Evans and De Lahunta 2012). This differs from the condition in *C. hoffmanni* UTCM 1912, where the perforation is located centrally and is surrounded on all sides by ossifications (Figs. 1a-d, 2). Moreover, the perforations in *Me. americanum* are far removed from the anterior end of the septum but still visible in lateral view, again in contrast to the condition in *C. hoffmanni* UTCM 1912. Lastly, the perforations in these *Megatherium* specimens are small relative to the size of that present in *C. hoffmanni* UTCM 1912.

A final structure worth noting in the context of the present study is an anterodorsal process extending from the anterior tip of the premaxillae in two specimens of *Me. americanum* (MLP 2–64 (Bargo 2001: fig. 1a) and MACN 1000 [Fig. 4e]). This process, which may represent a septal process of the premaxilla, is quite small relative to that observed in the specimens of *Mylodon* described above and lacks any osseous connections to other elements.

Just inside of the narial opening of *C. hoffmanni* UTCM 1912 is what we identify as the os nariale (terminology following Wible and Rougier 2017) connected posteroventrally to what appears to be an ossified processus lateralis ventralis of the cartilaginous nasal capsule (Fig. 2; Zeller et al. 1993; Wible 2008). The top of the os nariale is freestanding, but its base is outlined by an elevated margin that is distinct from the irregularly shaped mass of the processus lateralis ventralis. The os nariale is rectangular in shape and is elongated dorsoventrally with laterally concave indentations on its medial and lateral edges. The same structure is present in a juvenile *Choloepus* sp., DU EA 167 (Fig. 3a), an adult *C. didactylus*, FMNH 41207 (Fig. 5a), and is described by Wegner (1950) in an adult specimen of *Choloepus* sp. Zeller et al. (1993) also described an os nariale in a fetal specimen of *C. hoffmanni*. Like our specimen of *C. hoffmanni* (UTCM 1912), the os nariale observed in other specimens is also elongated dorsoventrally and in the same position with respect to the processus lateralis ventralis. Lastly, it should be noted that there is one specimen of *Glossotherium wegneri* (EPN V 107) that has an ossified processus lateralis ventralis like that seen in *Choloepus* although no os nariale is present (Fig. 5b).

Discussion

The presence of ossified elements in and around the external nasal aperture beyond those normally present in other placental mammals (i.e., nasal, premaxilla, and maxilla; DeBeer 1937; Moore 1981; Novacek 1993) is a regular but not universal feature of the extant two-toed sloth species *C. hoffmanni* and *C. didactylus,* as well as a number of extinct sloths in the families Megatheriidae and Mylodontidae. A diversity of such elements has been observed, including an internasal bone, an ossified anterior nasal septum, an os nariale, an ossified processus lateralis ventralis of the nasal capsule, and an internarial bar of varying completeness and composition.

A suturally distinct, unpaired median internasal bone has been observed in specimens of both extant two-toed sloth species (*C. hoffmanni* and *C. didactylus*; Figs. 1, 2, 4a), a feature noted briefly by both Weber (1928) and Grassé (1955). Our sample is not extensive enough to ascertain how frequently such an element appears in *Choloepus* skulls, though we think this is a matter that bears further investigation. The ontogeny of the element is also of some interest. Zeller et al. (1993: 32) noted the presence of "ossa praenasalia" anterior to the nasal in other placentals (the domestic pig *Sus*, and the mole *Talpa*), but stated that these are endochondral elements that form late in ontogeny and hence "are not members of the exoskeleton." There are also multiple ossifications immediately anterior to the nasals in the elephant shrew *Rhynchocyon* (Wible and Rougier 2017). The presence of the internasal in a CT-scanned fetal specimen of *Choloepus* (*Choloepus* sp. DU EA 167; Fig. 3a) may suggest an earlier, dermal origin for this element in two-toed sloths. It also remains to be seen whether the internasal has a broader distribution among sloths as a whole. As noted above, we know of no records of the bone in fossil sloths, and we found no evidence of the bone in our sample of *Bradypus.* Weber (1928) and Grassé (1955) indicate the putative presence of a paired internasal in three-toed sloths, but the appearance of such an element could simply be the result of postmortem damage to the anterior edge of the paired nasals. We believe that acceptance of a paired internasal in *Bradypus* requires further confirmation, ideally from both fetal and adult specimens.

The os nariale has been described in juvenile and adult specimens of *C. hoffmanni* and *C. didactylus* (Figs. 1, 2a, 4a). Zeller et al. (1993) also described an os nariale in a fetal specimen of the anteater *Tamandua tetradactyla* that is shaped similarly to that of the fetal *C. hoffmanni* and occupies a similar position (although oriented more horizontally). Wegner (1950: fig. 3b) described and illustrated an os nariale in an adult specimen of *Tamandua* sp.; however, he did not provide enough information to determine the precise shape of the bone. In addition, we have observed an adult specimen of *Cyclopes* (Gaudin and Branham 1998: fig. 3a) with an os nariale similar to that of the *Tamandua* specimen described by Wegner (1950). The element has not yet been recorded in any fossil pilosans. We encountered one fossil sloth (*Glossotherium wegneri*, as noted above), though, that possessed

an ossified processus lateralis ventralis, the portion of the nasal capsule that the os nariale rests upon. This suggests that there may exist some particularly well-preserved fossil pilosan taxa in which the os nariale is preserved but has not yet been recognized. Given the small size of the element, it may require CT scanning to identify the bone in a fossil specimen. We accept Wible and Gaudin's (2004) and Wible and Rougier's (2017) hypothesis that the os nariale is not homologous to the septomaxilla of monotremes and basal mammaliaformes and is therefore a synapomorphy of Xenarthra. This bone has a rectangular shape in pilosans and becomes branched and expanded in cingulates (Wegner 1950; Wible et al. 1990; Zeller et al. 1993; Wible and Gaudin 2004; Gaudin and Wible 2006; Wible and Rougier 2017).

No consensus exists regarding the homology of the internarial bar in ground sloths. Woodward (1900) asserted that the internarial bar of a specimen of *My. darwinii* (BMNH 8722; Fig. 6b) descends from the nasals and contacts the premaxillae. In this specimen, the internarial bar itself has a median suture dorsally but is unpaired and thickened ventrally. On the other hand, Reinhardt (1879) described the same bone in another specimen of *My. darwinii* (CN 43; Fig. 6a) as an ascending branch of the premaxilla, much like in primitive mammaliamorphs and non-mammalian cynodonts (Wible et al. 1990; Kielan-Jaworowska et al. 2004). Reinhardt (1879) documented a midline division on the posterior surface of the lower internarial bar, but not on its anterior surface. Moreover, he stated that there is a clear suture between the internarial bar and the nasals, but not between the internarial bar and the premaxillae. In neither case does the premaxilla or nasal appear to form the entire bar. The presence of both a ventral process rising from the premaxilla and an anterior elongation of the nasal bones in *My. darwinii* MNHN-Bol-V-006470 (Fig. 6d) suggests both bones may play a role in forming this structure, but the gap in this specimen, and the larger gap in two additional specimens (MLP 3–764 [Fig. 6c] and MACN 5080) might imply that the nasal septum also contributes to the internarial bar of *My. darwinii.* Unfortunately, without more ontogenetic information it is very difficult to be certain which bones are involved in forming the bar, and indeed whether there may be intraspecific variation in this regard.

McDonald (1987) reported on a singular specimen of the scelidotherine mylodontid, *Scelidotherium leptocephalum* (FMNH 14274), and suggested that its internarial bar is also derived mostly from premaxilla. He described the internarial bar as arising from the tip of each premaxilla and joining its partner to form an arc that curves posterodorsally to contact the anterior tips of the nasals. However, there are no sutures evident on the internarial bar, and only the lower portion is paired, so it is possible that the upper portion may be derived from the nasal or the nasal septum rather than the premaxilla. In our specimen of *C. hoffmanni* (UTCM 1912), the internarial bar is unpaired and is clearly formed by an ossified nasal septum that abuts but is separate from both the nasals above and the premaxillae below (Figs. 1a-d, 2). This also appears to be the case in one specimen of *Me. americanum* (MNHN PAM 276; Fig. 4c-d) in which the nasal septum forms a partial internarial bar, though at least two other specimens of *Me. americanum* (MLP 2–64 and MACN 1000 [Fig. 4e]) have a small dorsal process arising from the tip of the premaxilla that might represent either an ossified bit of nasal septum or a septal process of the premaxilla itself. The presence of anteriorly elongated, ossified nasal septae in a number of mylodontid taxa (*S. leptocephalum* MLP 3–671, AMNH 45910, and in specimens illustrated by Bargo et al. (2006); *Glossotherium wegneri* EPN V 107 and EPN V 120) and in many specimens of *Megatherium* (BMNH 19953; MACN 1000, 5002; MLP 2–64, 2–73) may lend credence to the idea that ossifications in the nasal septum could contribute to the internarial bar not only in *Choloepus* and *Megatherium* but in other fossil sloths as well. However, as asserted above, such homology issues are difficult to resolve without better ontogenetic data. It is also noteworthy that the anteriorly elongated ossified nasal septum in both *Choloepus* and *Megatherium* is perforated by membranous gaps that, at least in the former, are filled by membrane. A similar membranous gap in the cartilaginous nasal septum is known to occur in *Canis* (Evans and De Lahunta 2012), and we were able to find at least one other instance of this feature, in the saiga antelope (*Saiga tartarica*, Clifford and Witmer 2004). However, it is unclear how widespread such a feature is among placental mammals in general. We attribute this to the poor state of knowledge of the skeletal tissues of the anterior nasal region among both living and extinct mammals, and believe it serves as an indication of the need for further study of this region.

It seems highly unlikely, whatever its composition, that the internarial bar in sloths is truly homologous to that of non-mammalian cynodonts and basal mammaliaformes (Wible et al. 1990; Kielan-Jaworowska et al. 2004), i.e., that it is truly a retained primitive feature. And yet, it adds to a still growing list of features found in some or all xenarthrans that are reminiscent of more archaic anatomies. These would include the os nariale, which has been homologized by some authors with the septomaxilla of monotremes and more basal taxa (Wible et al. 1990; Zeller et al. 1993), as well as the presence of separate elements in the manubria of some subadult sloths (Buchholtz et al. 2020), a primitive pattern of epaxial muscles (Gaudin and Nyakatura 2018), the presence of separate coracoid elements in the shoulder girdle of pilosans (Rose and Emry 1993), a columelliform stapes (Gaudin et al. 1996), and a list of additional features suggested by McKenna (1975) in his original formulation of the Epitheria hypothesis (i.e., ossified sternal ribs, poorly

differentiated uterus and vagina, low body temperature, and poor thermoregulatory capabilities). Although most of these features have been explained away as neomorphs that just happen to resemble archaic conditions, as features whose phylogenetic distributions have been misinterpreted, or as consequences of the peculiar biology of xenarthrans (e.g., their myrmecophagous or folivorous diets – see Rose and Emry 1993; Gaudin et al. 1996; McDonald 2003), it remains striking how many of these "pseudo-atavisms" turn up in Xenarthra, and how rarely such features are encountered in other placentals. McKenna's Epitheria hypothesis, i.e., that Xenarthra represents the sister group to all other placental mammals (a clade he called Epitheria), has received only lukewarm support from molecular-based analyses of placental phylogeny, while a compelling resolution to the relationship among Xenarthra, Afrotheria, and Boreoeutheria has remained elusive (e.g., Springer et al. 2019; Upham et al. 2019). However, the most recent combined molecule and morphology-based analysis of placental phylogeny did yield a Xenarthra/Epitheria dichotomy (O'Leary et al. 2013). Perhaps the presence of so many primitive looking patterns among xenarthrans suggests that this hypothesis requires further careful consideration.

Conclusion

We have documented several unusual narial features in multiple specimens of extinct and extant Xenarthra. Such features include: the presence of a separate, median, unpaired internasal (although there are reports of a paired internasal); an ossified anterior nasal septum; an ossified processus lateralis ventralis of the nasal capsule; an os nariale; and an internarial bar. We have also documented variation in these elements, including the variable presence of an internasal in *Choloepus* and the os nariale in *Choloepus* and other pilosans; variation in the length and shape of the ossified anterior nasal septum in *Choloepus* and various extinct sloths; and variations in the composition and the degree of completeness of the internarial bar in *Choloepus* and various other extinct sloths. It is not known how much of this variation documented in these features is due to preservation issues and how much is genuine variability. Given this uncertainty, it is difficult to assess the phylogenetic or functional significance of these features. However, we believe that this is an area that merits further investigation from morphologists and paleontologists, in order to better elucidate the homology of the features involved, and their implications for the evolution of the anterior nasal cavity in sloths.

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TJG: I want to begin this personal acknowledgement by stating what an honor it is to participate in this festschrift honoring my colleague and co-author, Dr. John Wible. Let me also make clear that John was unaware he was contributing to his own festschrift, a fact for which I hope he will forgive me. After some discussion with the other co-editors of this volume, we decided that his participation in this paper, and hence, in this volume, was appropriate. Certainly this is the kind of paper for which he is justifiably well-known – one that describes in detail novel aspects of mammalian cranial anatomy, interpreting it in the light of John's vast knowledge of the subject. I also want to affirm how appropriate it is that John is being honored with this festschrift. His work with the *Journal of Mammalian Evolution* has been transformative, and he is personally responsible for its success to a remarkable degree. For myself, it has been my privilege to work with John for many years. I have not always been the best collaborator, often weighed down by teaching and administrative duties, but his understanding and support have been critical to whatever research success I have achieved. I am grateful for all he has taught me, but moreso, for the years of friendship we have enjoyed!

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