

Morphology and Function of the Hyoid Apparatus of Fossil Xenarthrans (Mammalia)

Leandro M. Pérez,^{1,2} Néstor Toledo,^{2,3} Gerardo De Iuliis,^{4,5} M. Susana Bargo,^{3,6*} and Sergio F. Vizcaíno^{2,3}

¹División Paleozoología Invertebrados, Museo de La Plata, Paseo del Bosque s/n, B1900FWA, La Plata, Argentina

²CONICET (Consejo Nacional de Investigaciones Científicas y Técnicas)

³División Paleontología de Vertebrados, Museo de La Plata, Paseo del Bosque s/n, B1900FWA, La Plata, Argentina

⁴Faculty of Community Services and Health Sciences, George Brown College, Toronto, Ontario, Canada M5A 1J5

⁵Department of Ecology and Evolutionary Biology, University of Toronto, Toronto, Ontario, Canada M5S 3G5

⁶CIC (Comisión de Investigaciones Científicas Provincia de Buenos Aires)

ABSTRACT The analysis of the hyoid apparatus of fossil xenarthrans provides insight on the form of the tongue and its function in food intake and intraoral processing. The hyoid apparatus of xenarthrans is notable for fusion among its elements. The presence of a V-bone, a complex consisting of fused basihyal and thyrohyal bones, is a consistent and probably synapomorphic feature of xenarthrans. Fusion of other elements is variable in fossil xenarthrans. Most fossil sloths retain independent elements, as in living dasypodids and mammals generally. Among nothrotheriids, the elements are slender and their articular surfaces indicate considerable mobility, and the relatively long and horizontal orientation of the geniohyoid muscle suggests considerable tongue protrusion. Among mylodontines, such as *Paramylodon* and *Glossotherium*, the elements indicate relatively mobile articulations, except between the stylo- and epihyals. The relatively posterior placement of the apparatus and the length and alignment of the geniohyoid muscle indicate considerable capacity for tongue protrusion. *Scelidotherium*, however, had rigidly articulated stylohyal and epihyal, and the apparatus lies farther anteriorly, which together with the elongated, steeply inclined mandibular symphysis, indicates a relatively shorter geniohyoid muscle and thus more limited capacity for tongue protrusion. A similar situation is indicated for *Megatherium*, casting doubt on the classical reconstruction of this sloth as having a long prehensile tongue. Among cingulates *Prozaedius* resembles living dasypodids, indicating considerable tongue protrusion important in food acquisition and intake. More extensive fusion of hyoid elements occurs in the cingulates *Glyptodon* and *Proeutatus*, in which the stylohyal and epihyal at least, are fused into a single element termed the sigmoidhyal. The presence of this element supports recent proposals of a sister-group relationship between glyptodonts and eutatines. The rigidity of the apparatus suggests limited tongue protrusion, but the tongue, in glyptodonts at least, was a powerful structure important for intraoral manipulation of food. *J. Morphol.* 271:1119–1133, 2010. © 2010 Wiley-Liss, Inc.

KEY WORDS: cingulates; tardigrades; hyoid; function; evolution

INTRODUCTION

The mammalian hyoid apparatus consists of an articulated series of skeletal elements located in

the throat region. It functions mainly to control the airway, but also for supporting and maintaining the position of the tongue between the mandibular rami in the procurement, processing, and deglutition of food. It also participates indirectly in the modulation of sounds produced by the vocal cords. The morphology of the apparatus, though generally neglected, provides valuable information on limitations in methods of procuring and processing foods in the oral cavity. Fossilization of the apparatus is rare, although preservation of its isolated elements is more common. While this restricts comparative and integral analyses of its components, there is much to be gained from study of the fossilized remains in some groups.

Xenarthra is a morphologically diverse group of the extant and extinct South American fauna. Recent studies have considered the masticatory apparatus and its possible dietary correlations for several fossil xenarthrans (reviews: Vizcaíno et al., 2008 and Vizcaíno, 2009). Comparative analyses of the hyoid apparatus of living and extinct xenarthrans may provide important information for the determination of feeding behaviors of fossil taxa.

Modern Xenarthra comprise a small clade of placental mammals (about 30 species, all but one neotropical), including the Cingulata (armadillos), the Vermilingua (anteaters) and Tardigrada (=Phyllophaga; tree sloths). The most comprehensive recent morphology-based phylogenetic studies of

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*Correspondence to: M. Susana Bargo, División Paleontología de Vertebrados, Museo de La Plata, Paseo del Bosque s/n, B1900FWA, La Plata, Argentina. E-mail: msbargo@fcnym.unlp.edu.ar

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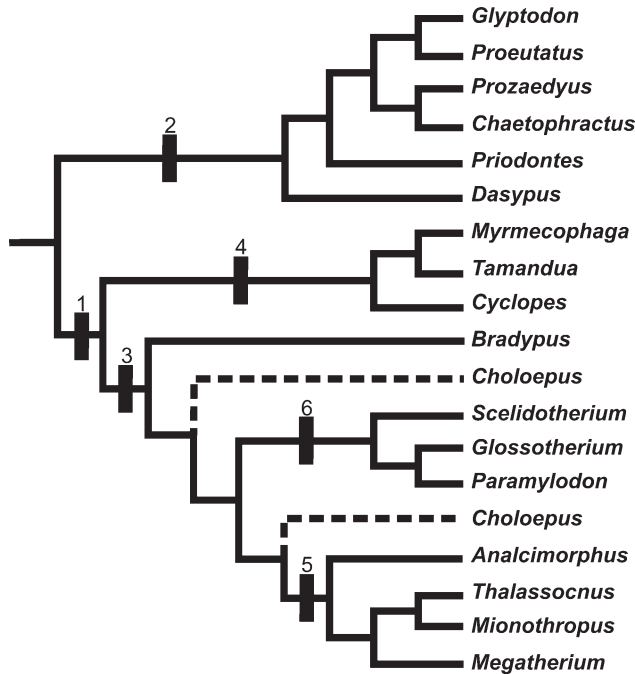


Fig. 1. Phylogeny of Xenarthra showing taxa included in the analysis. Modified from Gaudin (2004) (From Gaudin, *Zool J Linn Soc Lond*, 2004, 140, 255–305), Gaudin and Wible (2006) (From Gaudin and Wible, *The Phylogeny of Living and Extinct Armadillos (Mammalia, Xenarthra, Cingulata): A Craniodental Analysis*, 2006, 153–198, University of Chicago Press), Pujos et al. (2007) (From Pujos et al., *Zool J Linn Soc Lond*, 2007, 149, 179–235), and Fernicola et al. (2008) (From Fernicola et al., *History of the Knowledge of the Evolution of Armored Xenarthrans and a Phylogeny of Glyptodonts*, 2008, 79–85, University Press of Florida). 1. Pilosa; 2. Cingulata; 3. Tardigrada; 4. Vermilingua; 5. Megatherioidea; 6. Mylodontoidea. Alternative hypothesis for Megalonychidae (represented by *Choloepus*) is depicted.

xenarthrans are those of Gaudin (2004) and Pujos et al. (2007) for the tardigrades, and Gaudin and Wible (2006) and Fernicola et al. (2008) for the cingulates (see Fig. 1). Gaudin (2004) strongly supports the diphyly of the living tree sloths (*Bradypus* and *Choloepus*), positioning *Bradypus* as the sister taxon to all other sloths, and *Choloepus* within Megalonychidae, a clade that includes the extinct Antillean sloths. Although the relationships among tree sloths and ground sloths supported by Gaudin (2004) differs from those advocated in other recent morphological analyses (White and MacPhee, 2001; Pujos et al. 2007), it is notable that all of them support the diphyly of tree sloths. Gaudin's (2004) phylogeny also corroborates the monophyly of the four extinct clades of sloths, the Mylodontidae, Megatheriidae, Nothrotheriidae, and Megalonychidae. Gaudin and Wible (2006) provided evidence that several extant genera of armadillos (including *Dasypus* and *Priodontes*) may form a paraphyletic group at the base of Cingulata, that euphractines (*Chaetophractus* and others) constitute a monophyletic group, and that eutatines (*Proeutatus* and others) represent the sister taxon to pampatheres and glyptodonts.

The morphological diversity among fossil xenarthrans is considerably more striking (over 150 genera; McKenna and Bell, 1997), and includes some of the more bizarre mammalian body plans ever evolved, such as glyptodonts and giant ground sloths. Despite the wide ecological differentiation among living and fossil xenarthrans, the elements of the hyoid apparatus display a characteristic and singular arrangement. The morphology and function of the hyoid apparatus are the focus of the current report.

Although fossil preservation of the hyoid complex is rare, well-preserved specimens of the tardigrades *Nothrotherium*, *Thalassocnus*, Nothrotheriidae gen. et sp. nov., *Paramylodon*, *Scelidotherium*, *Glossotherium* (Mylodontidae) and *Analcimorphus*, *Megatherium* (Megatheriidae), and the cingulates *Glyptodon* (Glyptodontidae), *Prozaedyus* and *Proeutatus* (Dasypodidae) are known. These specimens are described and compared here with those of the extant *Bradypus* (sister taxon to all other sloths), *Myrmecophaga* (Myrmecophagidae), and *Chaetophractus*, *Dasypus* and *Priodontes* (Dasypodidae). There are few detailed descriptions of the hyoid apparatus of fossil xenarthrans in the older literature, i.e., the ground sloths *Paramylodon* (Stock, 1925) and *Megatherium* (Owen, 1856), and the glyptodont *Glyptodon* (Burmeister, 1874). After these, a few contributions include at least partial descriptions of the hyoid elements if they were associated with other remains. It has been only recently that functional studies on the hyoid apparatus have been conducted in both living and fossil species of xenarthrans (Naples, 1986, 1999; Pérez et al., 2000a,b; Pérez, 2001). They allow the formulation of hypotheses on the form of the tongue and its function in food intake and intraoral processing.

The Generalized Hyoid Apparatus in Mammals

The mammalian hyoid apparatus is generally composed of 10 bony elements and two associated cartilages (tympanohyal and chondrohyal). In adults, there are four paired bones (stylohyals, epihyals, ceratohyals, and thyrohyals) and an unpaired hyoid body or basihyal, i.e., a transverse bar formed by fusion of left and right basihyals. A median lingual process may project anteriorly from the body, particularly among ruminants and equids, and serves to anchor the tongue. The posterior cornua (=greater cornua of humans) of the hyoid, formed on each side by the thyrohyal, extend posteriorly from the basihyal and contact the thyroid and cricoid cartilages of the larynx. The anterior cornua (=lesser cornua of humans) extend anteriorly and dorsally to contact the basicranium. Each anterior cornu is formed by a chain of ossicles articulated in the following order from the body: ceratohyal, epihyal, and stylohyal. The latter articulates with the basicranium, specifically

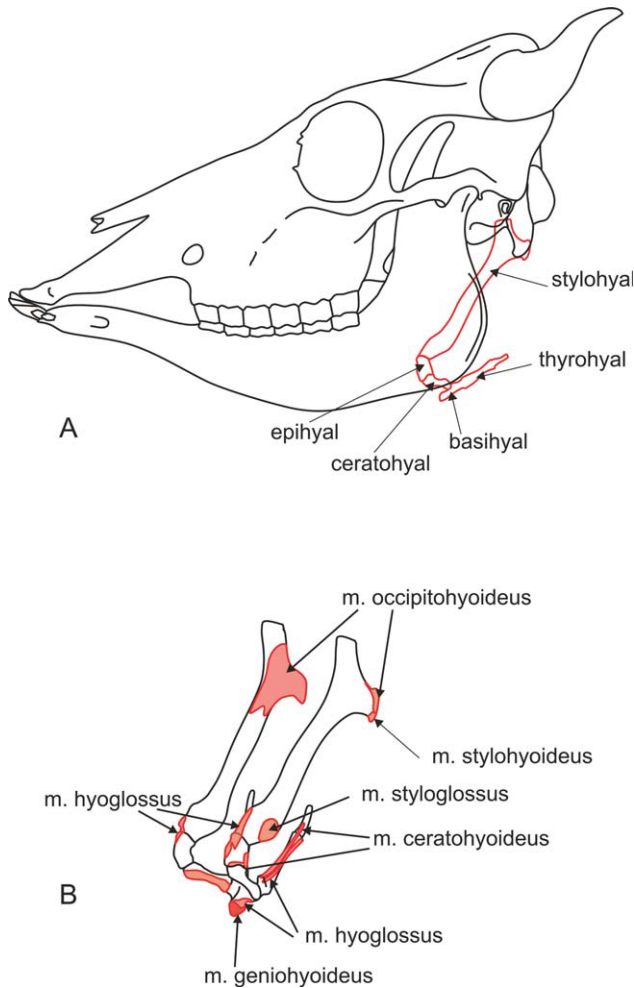


Fig. 2. (A) Skull of *Bos taurus* with the hyoid apparatus. (B) Areas of origin and insertion of the muscles. Modified from Barone (1976) (From Barone, *Anatomie Comparée des Mammifères Domestiques*. Tome Premier Osteologie, 1976, 162). [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

the petrous part of the temporal, via the tympanohyal ligament or cartilage. The articulation with the basicranium varies; sometimes there is a shallow depression that receives the stylohyal. This general form occurs in large herbivores, such as the cow (*Bos taurus*; Fig. 2), and is used as the comparative standard for morphological interpretations of the hyoid apparatus of xenarthrans.

Xenarthrans (Figs. 3 and 4) differ markedly from this generalized condition in that there is fusion among the individual elements. In particular, the thyrohyals and basihyals are fused to form a median basithyrohyal (V-shaped bone of Leidy, 1855; Allen, 1913; Pérez et al., 2000b), which is referred to here as a “V-bone,” an element that is known from fossils at least since the early Miocene (Santacrucian age). As this element is diagnostic for Xenarthra, it is described in detail and generic differences in morphology are noted.

Musculature of the Hyoid Apparatus and Tongue in Mammals

The hyoid apparatus in mammals is typically associated with one unpaired (m. hyoid transversus) and seven paired (m. mylohyoideus, m. geniohyoideus, m. stylohyoideus, m. occipitohyoideus, m. ceratohyoideus, m. styloglossus, and m. hyoglossus) muscles (Fig. 2B). Their functions are related to movements of the tongue, larynx and pharynx. The size and action of these muscles influence the procurement of food and its intra- and extraoral processing. The sternothyrohyoid muscle, properly a muscle of the larynx, is beyond the scope of this article and is therefore not considered here.

The transverse hyoid muscle, the only unpaired muscle, extends transversely between the ceratohyals and elevates the base or root of the tongue. The mylohyoid muscle arises on each side from a longitudinal ridge on the ventrolingual surface of the dentary. It inserts mainly on a fibrous median raphe, as far as the mandibular symphysis, and on the lingual process of the basihyal or, in its absence, the body of the basihyal. It functions to raise the tongue, hyoid apparatus, and floor of the oral cavity. The geniohyoid muscle arises from the lingual surface of the dentary near the symphysis and inserts on the body of the basihyal or, if present, its lingual process. The geniohyoid muscle extends parallel and dorsal to the mylohyoid muscle and ventral to the base of the tongue. Its action is to draw the tongue and hyoid anteriorly. The stylohyoid muscle arises from the muscular angle of the stylohyal and inserts on the thyrohyal near its articulation with the basihyal. Its action is to draw the base of the tongue back and up. The occipitohyoid muscle originates from the lateral surface of the jugular process of the occipital and inserts on the posterior edge of the muscular angle of the stylohyal. It is a thick and strong muscle that acts in directing the muscular angle of the stylohyal posteriorly and the anterior end ventrolaterally. The ceratohyoid muscle arises from the posterior margin of the ceratohyal and adjacent part of the thyrohyal. It inserts on the dorsal surface of the thyrohyal and may (in ruminants) have an attachment to the epihyal. Its action is to raise the thyrohyal and in ruminants, it draws the larynx anterodorsally. The styloglossus and hyoglossus muscles are tongue muscles that attach to the hyoid apparatus and affect the tongue. The former arises laterally on the stylohyal near its articulation with the ceratohyal and inserts on the anterior tip of the tongue. Its action is to retract the tongue, or if acting unilaterally, to draw the tongue laterally. The hyoglossus muscle arises from the basihyal, including its lingual process, and the thyrohyal, and inserts into the tongue, acting to retract and depress it. In some of the studied materials the insertion zones and location of some of these muscles can be easily determined. These areas show evident differences among the groups of the clade.

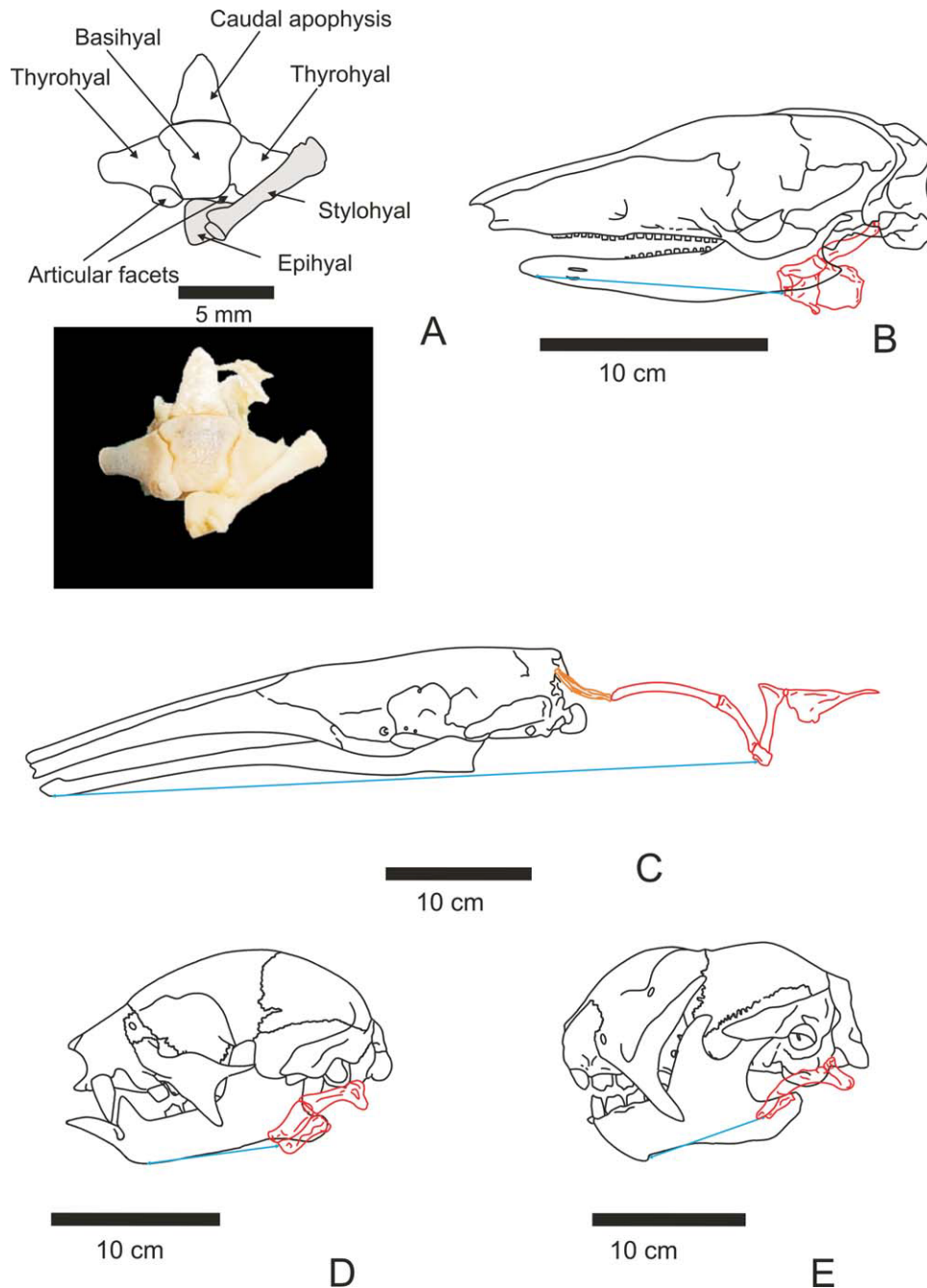


Fig. 3. Skulls with hyoid apparatus of living xenarthrans. (A) *Dasyurus novemcinctus* (MPL 2.III.00.4; juvenile), showing unfused elements of the V-bone in ventral view. (B) *Priodontes maximus*. (C) *Myrmecophaga tridactyla*. (D) *Choloepus hoffmanni*. (E) *Bradypus variegatus*. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

MATERIALS

Acronyms

CB, Colección Botet, Museo de Ciencias Naturales, Ayuntamiento de Valencia, Valencia, Spain; LACM, Los Angeles County Museum, Los Angeles, CA, USA; LACMHC, Los Angeles County Museum Hancock Collection, Los Angeles, CA, USA; MACN, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires,

Argentina; MHM-P, Museo Histórico Municipal Alfredo Múlgura, General Belgrano, Argentina; MMP, Museo Municipal de Ciencias Naturales Lorenzo Scaglia, Mar del Plata, Argentina; MNHN, Muséum National d'histoire Naturelle, Paris, France; MLP, Museo de La Plata, La Plata, Argentina; MPM-PV, Museo Padre Molina, Río Gallegos, Santa Cruz, Argentina; MCA, Museo Carlos Ameghino, Mercedes, Argentina; ROM, Royal Ontario Museum, Ontario, Canada; UNRC PV, Universidad Nacional de Río Cuarto, Córdoba, Ar-

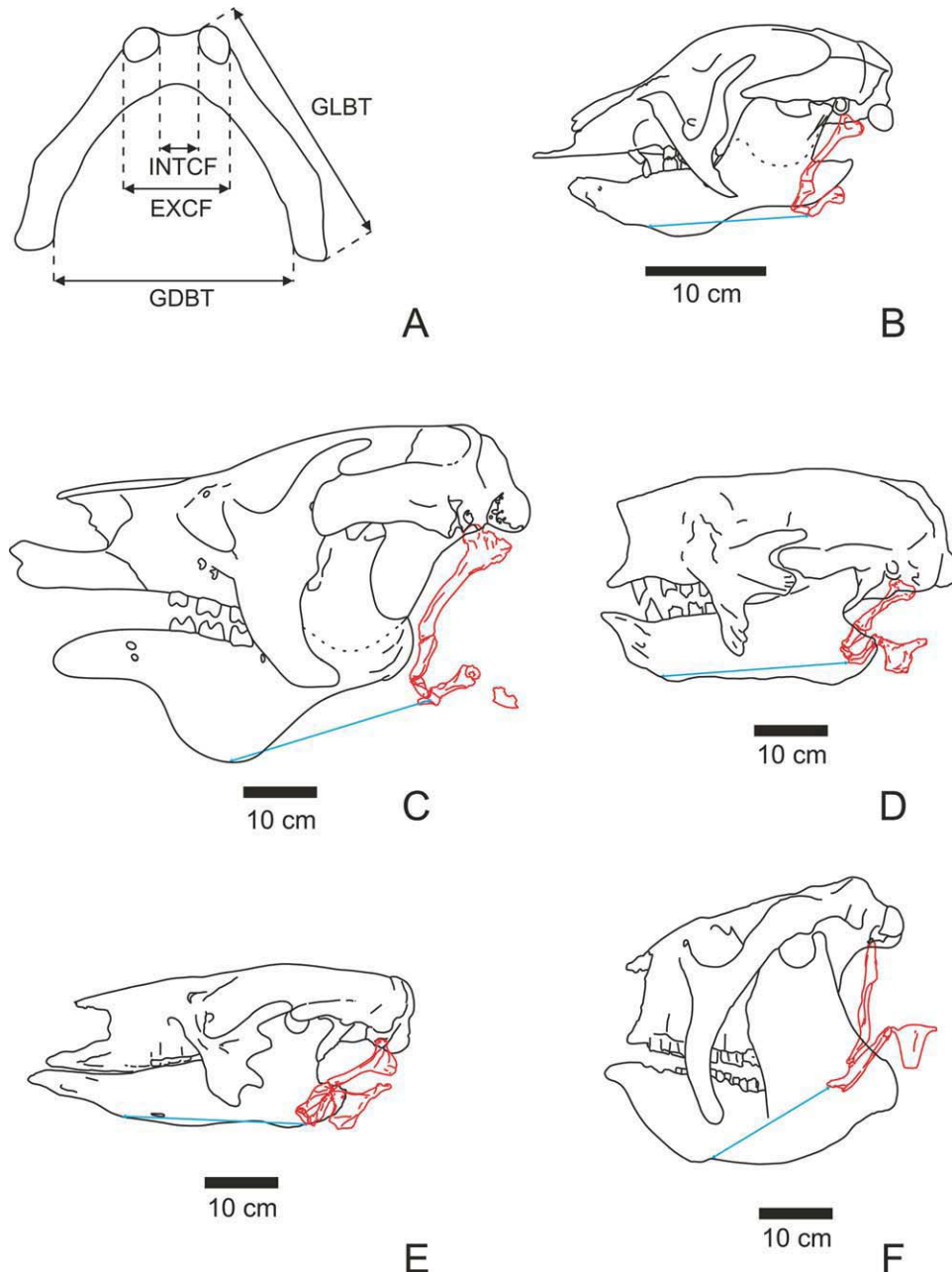


Fig. 4. Skulls with hyoid apparatus of fossil xenarthrans: (A) V-bone of a mylodontid in ventral view showing measurements used in Table 1 available as online Supporting Information. Tardigrades: (B) *Nothrotheriidae* gen. et sp. nov. (De Iuliis et al., in press). (C) *Megatherium americanum*. (D) *Glossotherium robustum*. (E) *Scelidothorium leptocephalum*. Cingulates: (F) *Glyptodon clavipes*. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

gentina; YPM PU, Yale Peabody Museum, Princeton University Collection, New Haven, CT, USA. The following specimens were examined and measured for this study.

Fossil Specimens

Tardigrada, Megatheriidae. *Megatherium americanum* (Cuvier, 1796). CB 64-1a. Skull and mandible, including hyoid apparatus (lacking ceratohyals), and nearly complete skeleton. Provenance: unknown.

MACN 11933. Stylohyal of a juvenile specimen. Provenance: unknown. MLP 2-64. Skull and mandible, with part of the hyoid apparatus (both stylohyals and V-bone), complete skull and partial postcranium. Provenance: "Pampean," Buenos Aires Province, Argentina. MNHN PAM 297. Complete hyoid apparatus with part of the thyroid cartilage. Provenance: unknown.

Tardigrada, Nothrotheriidae. *Thalassocnus natans* (Muizon and McDonald, 1995). MNHN SAS 734 (Holotype). Skull with hyoid apparatus, mandible and partial skeleton. Provenance: Pisco Formation (latest Miocene), Sud-Sacaco, Arequipa Department, Peru.

Nothrotheriidae gen. et sp. nov. De Iuliis et al. (in press). LACM 4609/117533 (Holotype). Nearly complete skeleton, including complete hyoid apparatus and possibly part of ossified thyroid cartilage. Provenience: Ñapari Formation, Member A (late Miocene), Río Acre, Peru.

Tardigrada, Basal Megatherioid. *Analcimorphus giganteus* (Ameghino, 1894). YPM PU 15163. Skull with both stylohyals. Provenience: Santa Cruz Formation (early-middle Miocene), 20 miles South of Coy Inlet, Santa Cruz province, Argentina.

Tardigrada, Mylodontidae. *Scelidotherium leptcephalum* (Owen 1840). MLP 3-671. Skull and mandible with complete hyoid apparatus, lacking ceratohyals. Provenience: "Pampean," Olavarría, Buenos Aires Province, Argentina. MMP s/n. Complete skull with nearly complete hyoid apparatus, including ossified cartilagenous thyrohyoid. Provenience: Centinela del Mar (late Pleistocene) Mar del Plata County. UNRC PV 001. Nearly complete skull and hyoid apparatus. Provenience: La Invernada Formation, late Pleistocene-early Holocene, Elena, Río Cuarto, Córdoba, Argentina.

Scelidotherium sp. MACN 13649. Nearly complete hyoid apparatus with stylohyals, epihyal, V-bone and ossified thyroid cartilage. Provenience: unknown. MACN 5001. An almost complete skeleton, both stylohyals and partial ossified thyroid cartilage. Provenience: unknown. MACN 18118. An isolated V-bone. Provenience: Ciudadela, Buenos Aires, Ensenadan Age (late Pleistocene).

Glossotherium robustum (Owen, 1842). MCA 2014. Skull, mandible with complete hyoid apparatus and nearly complete skeleton. Provenience: late Pleistocene, Mercedes, Buenos Aires Province.

Paramylodon harlani (Owen, 1843). LACMHC 1717-32. Skull and mandible with complete hyoid apparatus. Provenience: Rancho Labrean (late Pleistocene).

MACN 12097. Complete right stylohyal bone. Provenience: Olivera, Buenos Aires. Lujanian (late Pleistocene) lacustrine sediments.

Cingulata, Glyptodontidae. *Glyptodon* cf. *G. clavipes* (Owen, 1838). MHM-P 34. Complete skull, partial hyoid apparatus, including part of the ossified thyroid cartilage, partial postcranial skeleton, and several marginal carapace osteoderms. Provenience: Río Salado cliffs, Lujanian (late Pleistocene-early Holocene), General Belgrano, Buenos Aires Province, Argentina.

Cingulata, Dasypodidae. *Proeutatus* sp. MPM-PV 3415. Stylohyal associated with skull, and partial skeleton. Provenience: Puesto Estancia La Costa (=Corrighuen Aike), Santa Cruz Formation (early Miocene), Ea. La Costa Member, Santa Cruz province, Argentina.

Prozaedyus sp. MPM-PV 3423 A pair of complete stylohyals, associated V-bone and ossified thyroid cartilage in life position, together with nearly complete skull. Provenience: Puesto Estancia La Costa (=Corrighuen Aike), Santa Cruz Formation (early Miocene), Ea. La Costa Member, Santa Cruz province, Argentina.

Extant Specimens

Tardigrada. *Bradypus* sp. Without catalog number. Skull including the hyoid apparatus and complete skeleton.

Vermilingua. *Myrmecophaga tridactyla* (Linnaeus, 1758). MLP 8.X.01.9. Skull with nearly complete hyoid apparatus and skeleton.

Cingulata. *Priodontes maximus* (Kerr, 1792). MLP 1218. Skull with complete hyoid apparatus. Provenience: Chaco austral, Argentina. *Chaetophractus villosus* (Desmarest, 1804). MLP 821. Skull with epihyals, V-bone and thyroid cartilage. Provenience: Río Colorado, Argentina. *Chaetophractus vellerosus* (Gray, 1865). MLP 16.V.00.7. Skull, mandible and hyoid apparatus. Provenience: Chascomus, Buenos Aires Province, Argentina. *Dasypus novemcinctus* (Linnaeus, 1758). MLP 2.III.00.4. Skull with and almost complete hyoid apparatus of a juvenile. Provenience: Iguazú, Misiones Province, Argentina.

RESULTS

The hyoid apparatus of the giant *Megatherium* (Figs. 4C and 5B–D) has the most peculiar form and arrangement among the fossil sloths analyzed here. The stylohyal is markedly elongated, with an extremely expanded and robust muscular angle, which bears several ridges and crests, in contrast to the smooth, lobate and mediolaterally compressed element of *Glossotherium* and *Scelidotherium* (Figs. 4D,E and 6A,B). The proximal articular facet is more massive and differentiated than in mylodontids, forming a head that articulates in a deep stylohyal fossa on the basicranium. Owen (1856: 574) noted the distal widening of the bar-like body of the stylohyal of *Megatherium*, but incorrectly interpreted this element as articulating with the ceratohyal. In all specimens available for study the stylohyal contacts, as is usual, the epihyal. The articulation between these elements is similar to that of *Scelidotherium*, suggesting limited mobility. In MNHN PAM 297 (Fig. 5C,D) the two elements of the left side are fused, suggesting a pathological condition. In that specimen the two elements combined form a sigmoid shape, resembling the homologous element in glyptodonts (see below; Pérez et al. 2000b), although in *Megatherium* the individual components are still recognizable. The ceratohyal is relatively large and subtriangular in section, in contrast to the mediolaterally compressed form of pilosans described above. Both ends bear prominent articular facets, suggesting considerable mobility with both the epihyal and V-bone. As in the other pilosans, the V-bone lacks a lingual process, but bears prominent projections for articulation with the ceratohyals, in contrast to the slight projections in other Pilosa. These projections may represent separate ossification centers that generally fuse in adults, much as in the young specimen of *D. novemcinctus* described above. In a specimen of *M. americanum*, CB 64-1a, the V-bone presents evidence for such separate centers of ossification: on one side of CB 64-1a it is clear that the projection is a center of ossification, while on the other side, it is fused to the basihyal (Fig. 5B). The projections are larger than in MNHN PAM 297 and MLP 2-63. The thyrohyal rami of CB-64 are widely separated. Only portions of the ossified thyroid cartilage are known.

The hyoid apparatus of *Glossotherium* (Figs. 4D and 6A) strongly resembles that of *Paramylodon* in arrangement of the hyoid elements, with minor differences in their form and relative proportions. The stylohyal is robust, as in *Paramylodon*, and proximally bears a strong, rounded area that articulates with the stylohyal fossa. The muscular angle is well-developed, flattened, and lobate. Its articulation with the subtriangularly shaped epihyal is a well-developed, convex facet like in *Paramylodon*. The ceratohyal, similar in form but relatively longer than that of *Paramylodon*, has a con-

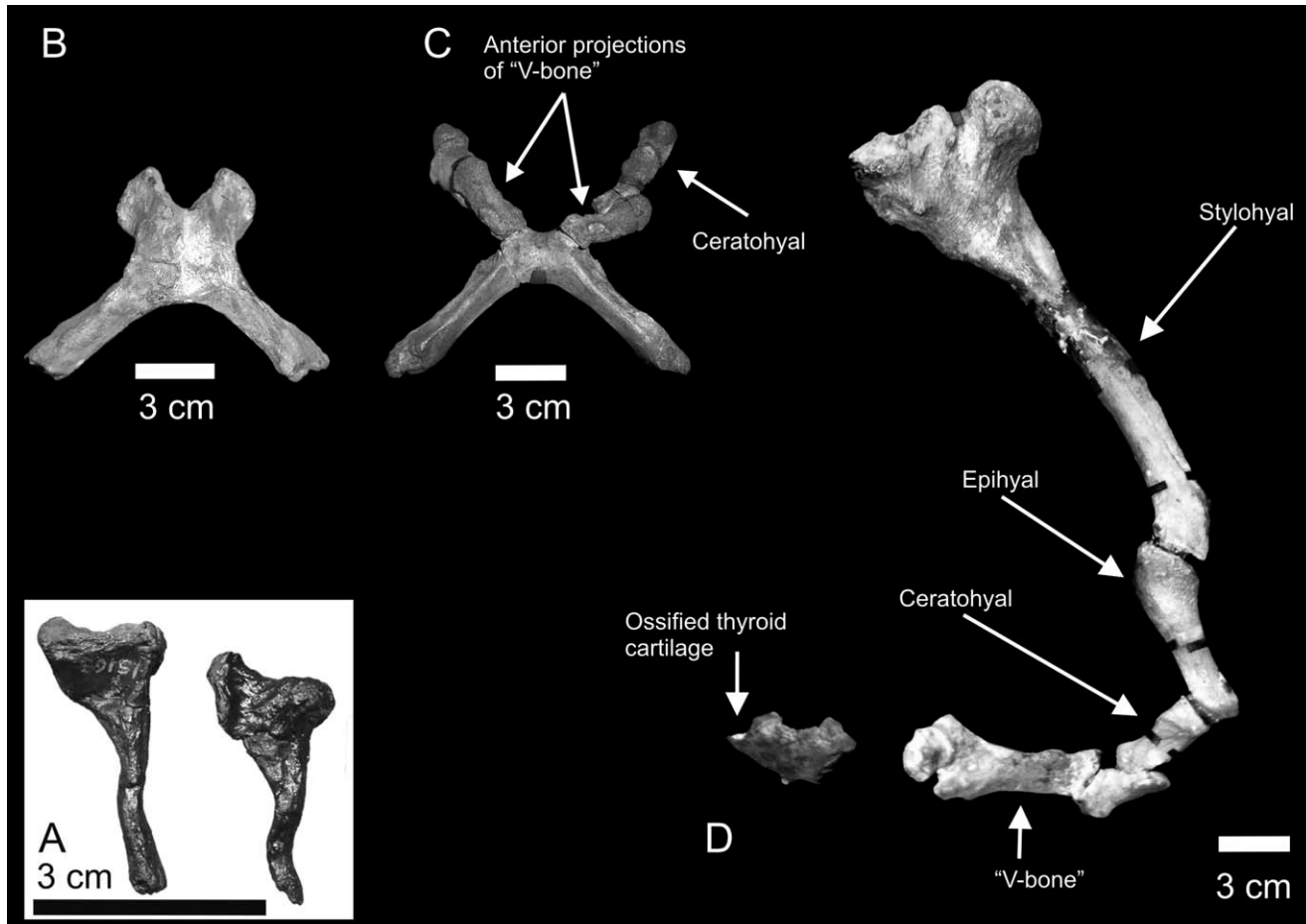


Fig. 5. Hyoid apparatus of megatherioids. (A) Stylohyals of *Analcimorphus* (YPM-PU 15163). (B) V-bone of *Megatherium americanum* (CB 64-1a) in ventral view. (C) Hyoid apparatus of *Megatherium americanum* (MNHN PAM 297) in ventral view, and (D) in right lateral view.

cave distal facet for articulation with the V-bone. The V-bone is U-shaped and, as in *Paramylodon*, it lacks a lingual apophysis. The thyroid cartilage is well ossified.

Scelidotherium, though similar in pattern to mylodontines (*Paramylodon* and *Glossotherium*), presents minor differences in form and articular relationships of the hyoid elements (Figs. 4E and 6B). The stylohyal is a gracile element with a smaller attachment area to the basicranium. Its flattened muscular angle is prominent and lobate, although more slender than in mylodontines. The body of the stylohyal forms a rod that widens slightly toward the epihyal. The latter is somewhat wider anteroposteriorly and compressed mediolaterally. Its articular surface for the stylohyal is flat suggesting little or no movement. The small ceratohyal bears well developed articular facets for the epihyal and the V-bone. The V-bone is relatively small, but otherwise appears unmodified compared to those of other xenarthrans, although it is more V-shaped. Nearly complete, well ossified thyroid cartilages are known from

several individuals. The cartilage is subtriangular and bears a midsagittal ventral process.

In living armadillos (Cingulata), such as *Chaetophractus*, *Dasypos*, and *Priontodes*, the V-bone (Fig. 3A,B) is composed by fused thyrohyals and basihyals, as mentioned above, and is flattened dorsoventrally, producing an elliptical section. The morphology of the other elements, including the paired stylohyals, epihyals, and ceratohyals, is generalized. The thyroid cartilage is partially ossified. In some members of the group (i.e., *Cabassous*, *Dasypos novemcinctus*) the V-bone bears a median posteriorly directed process, the caudal apophysis of the basihyal.

In a young specimen of *D. novemcinctus* (MLP 2.III.00.4) the V-bone is composed of six parts (Fig. 3A). An unpaired, subtrapezoidal element forms the center of the V-bone, and corresponds to the basihyal. Laterally, there are two subtriangular, elongated and dorsoposteriorly oriented elements: the thyrohyals. Posteriorly a triangular element forms the posterior apophysis of the basihyal (see above). Finally, anterior to the base of each

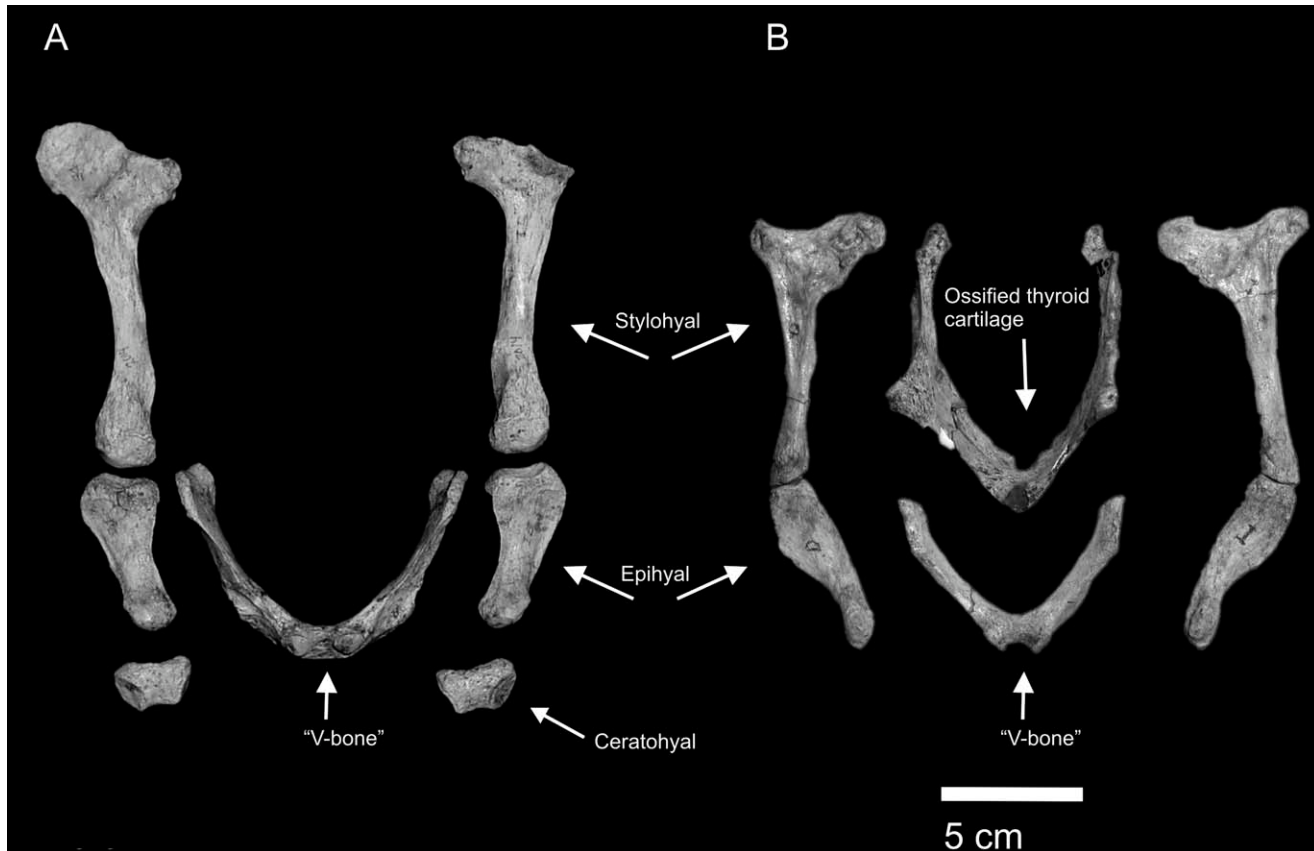


Fig. 6. Hyoid apparatus of mylodontids. (A) *Glossotherium robustum* (MCA 2014). (B) *Scelidotherium leptocephalum* (MLP 3-671).

thyrohyal, there is a small, rounded element articulating with the ceratohyal. In *Priodontes maximus* (Fig. 3B), partial fusion between the stylohyal and epihyal produces a bony bar, although the individual elements are easily distinguishable.

Among fossil armadillos, new material includes that of *Proeutatus* (MPM-PV 3415) and *Prozaedyus* (MPM-PV 3423). The element of *Proeutatus* consists of a single piece, found articulated with the basicranium (Fig. 7A). It is very large, compared with that of living armadillos, and slender. The hyoid apparatus of *Prozaedyus* (MPM 3423) was found articulated with the skull and includes both stylohyals, an epihyal, a V-bone and the ossified thyroid cartilage (Fig. 7B). The stylohyal is a long, slender and curved element as in *Dasypus* and *Chaetophractus*, without a recognizable muscular angle or proximal articular facet, and the proximal end is wider. The epihyal is shorter and broader than the stylohyal, slightly flattened, and also bears few discernable crests or tuberosities. The V-bone is slender; the thyrohyals are flattened, straight and strongly divergent. Anteriorly are clearly defined and rounded articular facets for the articulation with the ceratohyals. Unlike the condition in *Dasypus*, it lacks a posterior median process. The thyroid cartilage has

flat and straight lateral walls, with a shape coincident with the caudal aspect of the V-bone; the posterior bars are absent or broken, and the ventral surface is smooth.

DISCUSSION

Anatomy

Pronounced modifications of the hyoid elements occur among Pilosa. Although there are no records of hyoid bones of fossil Vermilingua, the hyoid apparatus of the living giant anteater *Mirmecophaga tridactyla* (Fig. 3C) is large and elongated (Naples, 1999). Its spatial disposition is modified into a nearly anteroposterior orientation, with well-developed synovial articulations between several of its elements. The thyrohyals and basihyals are fused (V-bone) and project posterodorsally, as is usual. The stylohyal, epihyal, and ceratohyal (anterior cornua) are oriented anteriorly. The stylohyal has lost its articulation with the basicranium via the tympanohyal cartilage, and attaches instead via the long, slender stylo-occipital muscle to an occipital protuberance. These modifications permit a great freedom of movement that aids in the remarkable extraoral protrusion of its highly special-

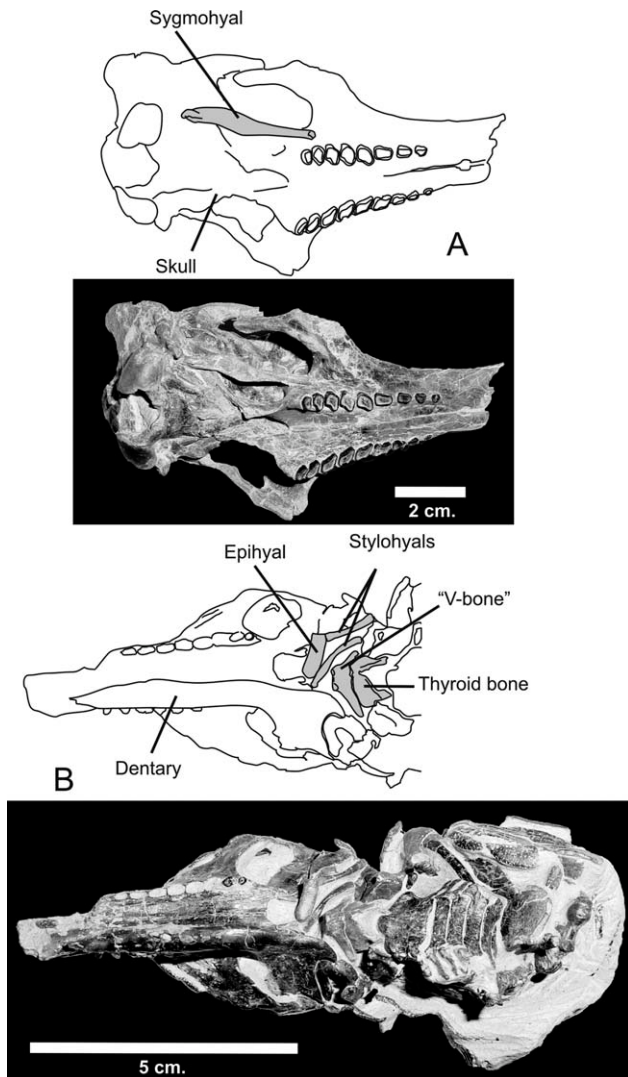


Fig. 7. Skull and hyoid elements of dasypodids. (A) *Proeutatus* sp. (MPM-PV 3415). (B) *Prozaedyus* sp. (MPM-PV 3423). [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

ized tongue (Naples, 1999). The hyoid apparatus of *Tamandua tetradactyla* (Linnaeus, 1758) is robust and well ossified. Although resembling that of *Myrmecophaga*, it differs in that the anterior cornua is longer than in *Myrmecophaga* and consists of two segments: the elongated proximal segment is the stylohyal, and the distal segment formed by the fused epihyal and ceratohyal; unusually, the proximal ends of the epihyals move freely on the basihyal (Reiss, 1997: Fig. 2). Finally, the hyoid apparatus of *Cyclopes* (Gray, 1821) resembles that of the other two genera, but the stylohyal, ceratohyal, and epihyal are individual elements (Reiss, 1997).

The hyoid apparatus of the tree sloths, *Bradypus* and *Choloepus*, is large and robust and extensive fusion between its elements occurs with

age (Naples, 1986). In addition to the typical fusion of the basihyal and thyrohyal, the epihyal and ceratohyal are solidly fused (as in *Tamandua*) to form a robust bony bar. The ventral ends articulate with the basihyal medially and are solidly fused to the thyrohyal posteriorly (Naples, 1986). The stylohyal also fuses to the epihyal–ceratohyal bone and is relatively shorter in *Choloepus* (Fig. 3D) than in *Bradypus* (Fig. 3E). A singular feature of the tree sloths is that the anterior and posterior cornua are folded up against and fused to each other. A notable difference between *Choloepus* and *Bradypus* is that the hyoid elements tend to be relatively shorter and stockier in the former. Also, though fused to the epihyal–ceratohyal bar, the stylohyal is distinguishable as a separate element in *Choloepus*, whereas in *Bradypus* (more elongated and curved) it appears continuous with the epihyal–ceratohyal bar (see Naples, 1986: Fig. 2A,C). Naples (1986) noted that fusion among its elements and attachment to the skull results in relatively restricted movements of the apparatus although the tongue is relatively large and mobile compared to that of many other mammals. The peculiar feeding mode of tree sloths probably accounts for much of the singular morphology of the apparatus: extensive fusion and rearrangement of the elements might be due partly to “the frequency with which they feed or reach for food items from an upside down position” (Naples, 1986: 720).

The hyoid elements other than the V-bone generally retain their primitive condition of being separate elements in fossil sloths. In addition to this general condition of the main elements, it is worth noting that other centers of ossification are possible in the hyoid apparatus, as described in the “Results” for the young specimen of *D. novemcinctus*. The similar presence of such ossifications was noted for *M. americanum*. Indeed, their presence is not restricted to these xenarthrans: Sisson (1982), for example, described a separate ossification center between the thyrohyal and basihyal that articulates with the ceratohyal in *Equus*, precisely as reported in the “Results” for *M. americanum*.

Scott (1903–1905) described part of the hyoid apparatus of the Miocene megatherioid *Analcimorphus*. It includes both stylohyals (Fig. 5A), similar in shape to that of the Pleistocene ground sloth and living tree sloth. These bones are described as hammer like, with the proximal end anteroposteriorly expanded and laterally compressed, and bearing a small anterior tubercle for the attachment to the skull. The stylohyal is slender, subcylindrical in cross-section and slightly sigmoid.

Cartelle and Fonseca (1983) described an almost complete hyoid apparatus of *Nothrotherium maquinense* (Lund, 1839). The stylohyal is a straight, slender element, with its proximal third laterally expanded, and bearing distally a flat,

slightly medially directed articular facet. The proximal condyle that articulates with the skull is relatively flat, especially when compared with that of *Megatherium* (see below). The epihyal is wider proximally than distally, and bears a slightly laterally directed distal articular facet for the ceratohyal, which is described as a minute cube-like element. Finally, the V-bone is formed by the coossification of the basihyal and the proximal portion of both thyrohyals, and bears two condyles that articulate with the ceratohyals.

De Iuliis et al. (in press) described the hyoid apparatus of *Nothrotheriidae* gen. et sp. nov. which includes all the elements and possibly a scrap representing the ossified thyroid cartilage (Fig. 4B). The proximal end of the stylohyal bears a well-developed and convex surface for articulation with the skull, suggesting considerable movement at this joint, even though the condyle and fossa arrangement of *Megatherium* (see below) is not present. In contrast to the condition in the latter, the muscular angle extends posterior to the articulation (the pivot), producing a marked moment arm of the occipitohyoid in the new taxon. Distally, the stylohyal bears a well-developed oval and convex surface for articulation with the concave proximal surface of the epihyal. The two elements are clearly independent, in contrast with the condition in *Megatherium*, and produce a highly mobile joint. Just beyond its proximal articular surface, the epihyal bears a prominent muscular attachment site, possibly for the styloglossus, that is not evident in the epihyal of *Megatherium*, perhaps reflecting nonfunctionality of this muscle in this genus. Distally, the epihyal bears a convex oval surface for articulation with the ceratohyal, with which it apparently formed a highly mobile articulation. The ceratohyal, a small element, has a small, oval and flattened proximal surface, oblique to the long axis of the bone, and a circular, shallowly concave distal surface, reflecting a mobile articulation with the V-bone. The latter element, similar in shape to that of other sloths described here, appears to have been similar to that of *Paramylodon* and *Scelidotherium* in being relatively more vertically oriented with respect to the long axis of the skull, compared to a less vertically oriented V-bone in *Megatherium*.

McDonald and de Muizon (2002) described the nothrotheriid *T. natans* Muizon and McDonald, 1995 based on a specimen that includes two stylohyals, a ceratohyal, a V-bone, and a fragmentary ossified thyroid cartilage. The stylohyal is elongated, and resembles that of *Nothrotherium*. In lateral view its surface appears rough and the articular facet for the epihyal is poorly differentiated. The ceratohyal is a small, triangular and mediolaterally compressed element, with concave medial surface. The V-bone is described as U-shaped in dorsal view, and bears a small postero-

ventral tubercle, similar to the ventral roughened process described for *Glyptodon* (Pérez et al., 2000b). The ossified thyroid cartilage is fragmentary and T-shaped, with two laterally expanded processes. The articular facets in the thyrohyal arms for the thyroid cartilage suggest a subvertical orientation for the V-bone. Stock (1925) described a partial hyoid apparatus of the nothrotheriid *Nothrotheriops* and compared it with that of the mylodontid *Paramylodon* and the megalonychid *Megalonyx*. The material consists of a stylohyal, more slender than that of *Paramylodon*, and a V-bone, described by Stock as a basihyal with both thyrohyals ankylosed to it. The portion corresponding to the basihyal was described as proportionally smaller than in *Megalonyx* and with more widely separated articular facets for the ceratohyal.

Among mylodontid sloths, the hyoid apparatus of *Paramylodon* was described and figured by Stock (1925). In this genus, the arrangement of the elements is more generalized than in its living relatives. The articulations, particularly between the epihyal and ceratohyal, are mobile. The stylohyal is robust, with a subtriangular muscular angle, and articulates with the epihyal by way of a well-developed, convex facet. The shorter, more robust epihyal tapers distally. The ceratohyal is short and rounded. The V-bone is formed, as usual, by fusion of the thyrohyals and basihyals, and has two anterior expansions for the articulation with the ceratohyals. A lingual process is absent, and the thyroid cartilage is well-ossified and anteriorly bears facets for the articulation with the posterior facets of the V-bone, as occurs in the other ground sloths described. Stock (1925) described a specimen with the epihyal fused with the stylohyal. Not surprisingly, the hyoid apparatus of the phylogenetically closely related *Paramylodon* and *Glossotherium* are similar morphologically and in the presence of mobile articulations between the elements. The relationship of the hyoid to the skull, including its position in the throat, the well-formed articular facets and the line of action of the geniohyoid, aligned with the direction of tongue protrusion, suggests that relatively agile movements of the tongue were possible in these taxa. *Scelidotherium* differs from these genera in having more restrictive protrusive capabilities. This is suggested by the barely mobile articulations between elements of the apparatus, restricting freedom of movement, and the relatively reduced distance between the mentonian spine and the apparatus in situ, indicating a relatively short geniohyoid muscle. Although the skull of *Scelidotherium* is long and tubular, its form apparently does not reflect a highly mobile and protrusible tongue, in contrast to *Myrmecophaga* and *Tamandua*.

In *Nothrotherium*, the nature of the articulation between the epi- and stylohyal, and between the epi-

and ceratohyal suggests mobile articulations, whereas the relatively flat stylohyal condyle for articulation with the stylohyal fossa suggests a more limited mobility. In *Nothrotherium*, the more horizontal orientation of the geniohyoid suggests greater protrusion of the tongue than in *Megatherium*. In *Nothrotheriidae* gen. et sp. nov., the overall morphology of the hyoid apparatus suggests it was quite mobile, being more similar to the condition observed in *Nothrotherium* than of *Megatherium*, in spite of displaying considerable morphological similarity with both genera. The relatively horizontal orientation of the geniohyoid suggests, as for *Nothrotherium*, greater protrusion of the tongue than in *Megatherium*.

Megatherium similarly displays evidence of limited tongue protrusion. For example, movement among the apparatus' elements was limited, restricting its overall degree of freedom, and the distance between the mandibular symphysis and apparatus is quite short, indicating a short geniohyoid muscle capable of providing limited lingual protrusion. Also, the orientation of this muscle's line of action was markedly oblique to the direction of lingual protrusion, and thus was far from optimizing the line of action for protrusion. These features suggest that the tongue of *Megatherium*, as in *Scelidotherium*, was not highly protrusible, which throws doubt on the classical reconstruction of this sloth as having a long prehensile tongue used to grasp and draw branches and leaves to its mouth. Recent reconstructions of the snout musculature of *M. americanum* suggest that it had a prehensile upper lip comparable to that of the black rhinoceros (Bargo et al., 2006). Among the fossil sloths considered here, those with a shorter preorbital region of the skull (e.g., *Glossotherium*, *Paramylodon*) have a shorter symphysis and greater hyoid mobility. They are wide-muzzled sloths with short and wide lips. On the other hand, fossil sloths with longer preorbital regions (e.g., *Scelidotherium* and *Megatherium*) seem to have relatively less tongue protrusion (less efficient hyoid movement), with longer, narrow and prehensile upper lips (see Bargo et al., 2006).

Among cingulates, none of the armadillos approach the extreme specializations of the masticatory apparatus, including the hyoid apparatus, of glyptodonts (see below). *Priodontes* represents the opposite extreme in specialization (excluding, of course, the pilosan anteaters), with its elongated, untelescoped skull and very low mandible as adaptations to a myrmecophagous diet (Vizcaíno, 1994, 1997). Further adaptations are that the elements of the hyoid apparatus have relatively mobile articulations, the mentonian spine is not developed, and the mandibular symphysis is short and displaced far anterior with respect to the hyoid apparatus (thus, the latter two features allow for a relatively long geniohyoid). In this

armadillo the tongue is critical for food intake, performing quick, agile movements and capable of protruding considerably beyond the entrance of the oral cavity.

The record of the hyoid apparatus among fossil cingulates is less complete than among pilosans. The earliest descriptions of the glyptodont hyoid apparatus are for *Glyptodon* and *Panochthus* by Burmeister (1864) (227, Pl. VIII, Fig. 6; Burmeister, 1874: 283, Pl. I, Fig. 4 and Pl. XXX, Figs. 3 and 4), who compared them with living armadillos. He recognized the V-bone (greater cornua *sensu* Burmeister), and two lateral, elongated rods (lesser cornua *sensu* Burmeister), which he considered the result of loss of some of the hyoid elements, and described differences between *Glyptodon* and *Panochthus*: a greater ventral tubercle of the V-bone in the former, and a more laterally compressed, less pointed lingual apophysis in the latter. In a recent morphofunctional analysis of *Glyptodon*, Pérez et al. (2000b: Fig. 2A) proposed fusion (in contrast to Burmeister's view of loss of elements) among the stylohyal, epihyal and, probably, ceratohyal to produce the robust vertical rod, which bears extremely prominent areas for muscular attachment (Fig. 4F). The element was termed the sigmohyal bone by these authors. Re-evaluation of the evidence based on the comparison with the morphology of the stylohyal and epihyal of pilosans suggests that only these two bones participate in the formation of the sigmohyal, with the ceratohyal so far unknown or, as suggested partly by Burmeister (1864), lost in glyptodonts. Proximally the sigmohyal displays ankylosis to the basi-cranium. The V-bone differs notably from that of Pilosa in the presence of a lingual process, suggesting increased development of the tongue and associated musculature compared to other xenarthrans. On the dorsal surface of the lingual process there is a slight depression bearing a conspicuous oval foramen. On the ventral surface there is a prominent descending process. *Glyptodon* and other derived glyptodonts in general are also notable for peculiar modifications of the skull in which the facial portion, including the masticatory apparatus, has migrated posteroventrally to lie beneath the cranium (Fariña 1985; Fariña and Vizcaíno, 2001).

Among fossil armadillos, Scott (1903–1905) described the hyoid morphology of *Proeutatus* and compared it with that of the living *Chaetophractus*. This author recognized a long slender proximal element (probably a fusion between the stylohyal and epihyal; see above), a very short subcylindrical ceratohyal articulating loosely with the V-bone, which bears a short medial posterior projection, and an ossified thyroid cartilage. Unfortunately, this material was not available for study at the YPM PU collections. The element of this taxon (MPM 3415), described in the "Results," allows complementation of Scott's assessment. Its large and slender nature

suggests that it is a sigmoidal, formed by the fusion of stylohyal and epihyal, as in glyptodonts (Pérez et al., 2000b).

Phylogenetic Implications

Within Xenarthra a primary dichotomy between the Cingulata (armadillos and glyptodonts) and Pilosa (sloths and anteaters; Fig. 1) is widely accepted (Engelmann, 1985; Delsuc et al. 2001; Delsuc and Douzery, 2008; Gaudin and McDonald, 2008). The V-bone, represented by the fusion of basihyal and thyrohyal, can be recognized in the earliest known hyoid elements of *Proeutatus* from the early Miocene (Scott, 1903–1905: Plate 31). In addition to the taxa discussed here, it is also present in *Megalonyx jeffersonii* (Desmarest, 1822) (Leidy, 1855; McDonald, 1977) and *Nothrotheriops shastensis* (Sinclair, 1905) (McDonald, 1977). All xenarthrans studied exhibit fusion of the basihyal and thyrohyals into a composite V-shaped element. This suggests that the character state was present in the common ancestor of all clades of the group, and thus is a synapomorphy of Xenarthra. Detailed study of the remaining living xenarthrans and discovery of hyoid elements of other fossil xenarthrans are required to test this hypothesis. Fusion of these two elements is known to occur occasionally in other mammalian clades, such as the cetacean *Mesoplodon*, the lagomorph *Lepus*, as well as among suids and anthropoid primates, including humans, and the coossified element may even be V-shaped. The sporadic occurrence of this element and the phylogenetic relationships already established among these clades suggest that coossification was independently acquired. Clearly, a comprehensive phylogenetic evaluation of this character is beyond the scope of the current article.

Among cingulates the epihyal, ceratohyal, and stylohyal are separate elements in armadillos, whereas in glyptodonts (at least in the Pleistocene), fusion among these elements produces a single bony element, the sigmoidal. Engelmann (1985) proposed that eutatines are the sister-group of glyptodonts. The inclusion of eutatines within Engelmann's Glyptodonta was considered feasible by Vizcaíno and Bargo (1998). Recently, Gaudin and Wible (2006) supported this hypothesis in their cladistic analysis of Cingulata. In this context, the presence of a sigmoidal in *Proeutatus* and glyptodonts may be synapomorphic for a eutatine–glyptodontid clade, providing additional support for the phylogenetic hypothesis of these authors.

Functional Interpretation

The hyoid apparatus of *Nothrotherium* resembles that of *Megatherium* but the slenderness of its

elements suggests a more mobile apparatus, specifically in the articulation between the epi- and stylohyal, and between the epi- and ceratohyal. The stylohyal condyle (relatively flat) for articulation with the stylohyal fossa suggests less mobility than in *Megatherium*, which has a more rounded condyle that articulates in the fossa. The relatively horizontal orientation of the geniohyoid compared with that of *Megatherium* suggests greater protrusion of the tongue. The same articular pattern is present in *Thalassocnus*, suggesting mobility as in *Megatherium*. The distal end of the stylohyal bears a facet like that of *Nothrotherium*, but the epihyals are not preserved, precluding further functional inferences. In *Nothrotheriidae* gen. et sp. nov. (De Iuliis et al., in press), the hyoid elements as a whole were apparently fairly mobile, in contrast to the condition in *Megatherium* in which the articulation between the stylohyal and epihyal indicates restricted movement, as does (though to a lesser extent) that between the ceratohyal and V-bone.

The robust hyoid apparatus of the mylodontines *Paramylodon* and *Glossotherium*, with relatively mobile articulations between its elements, lies posteriorly beneath the skull, almost completely behind the mandible. The mandibular symphysis is elongated and steeply inclined, so that the origin of the geniohyoid lies ventral to the level of m1, far from the anterior margin of the lower jaw. This conformation would have placed the geniohyoid nearly parallel to the alveolar margins of the jaws, so that its line of action would have been coincident with protrusion of the tongue out of the oral cavity.

The skull and mandible of *Scelidotherium* differs in shape from those of the preceding genera, as do the shape, position, and mobility of the hyoid apparatus. In *Scelidotherium* the stylohyal and epihyal were rigidly articulated, suggesting a single functional unit that would have constrained movement. The position of the apparatus differs in that its ventral end lies farther anteriorly, between the angular processes of the dentaries. Together with the elongated, steeply inclined mandibular symphysis this indicates a relatively shorter geniohyoid, suggesting a more limited capacity for tongue protrusion.

The hyoid apparatus of *Megatherium* is highly modified with respect to relative length of its elements, changes that may be related to its relatively high and short skull. The distance between the posterior border of the symphysis (i.e., origin of geniohyoid) and the apparatus' position in the throat differ from that of other Pilosa, which have lower, more tubular skulls. Due to the high postorbital region of the skull of *Megatherium*, the distance between the basicranium, where the hyoid articulates, and the putative setting of the larynx is longer than that observed in the other sloth genera. The posterior end of the symphysis extends posteriorly to about the level of m2 and the dentaries are very close together anteriorly,

indicating a shorter geniohyoid than in the other ground sloths described. Also, the posterior border of the symphysis is considerably lower than the hyoid, indicating a steep orientation for the geniohyoid, markedly oblique from the direction of tongue protrusion. The short length and steep orientation indicates little capacity for tongue protrusion.

In *Glyptodon*, the telescoping process that displaced the masticatory apparatus beneath the cranium (Fariña and Parietti, 1983; Vizcaíno et al., 1998; Fariña and Vizcaíno, 2001) also affected the hyoid apparatus. The elements of the greater cornu are in almost vertical sequence, nearly at a right angle to the basicranium (Pérez et al., 2000b). As a consequence of the fusion of its elements into a sigmohyal, the nature of its articulation to the skull, and the surrounding skull elements indicates severely restricted movement of the sigmohyal, so that it comes to resemble a splinter bar, with the V-bone pivoting at its articulation with the sigmohyal mainly through the action of the ceratohyoid and geniohyoid muscles. The former draws the thyrohyal rami anterodorsally, retracting and depressing the tongue. The geniohyoid draws the lingual process anteriorly, protracting and slightly raising the tongue. Pérez et al. (2000b) suggested that the hyoid apparatus of *Glyptodon* was well suited for powerful movements of the tongue, based on its general robustness, fusion of its elements, and the marked development of the anchoring structures of the tongue musculature, such as the lingual process, the mid-ventral process of the basihyoid, and the mentonian spine of the mandible. The oral cavity was a relatively large space, resembling a longitudinal tube defined by the high mandible and transversely concave palate, suggesting an extremely thick tongue. The mentonian spine, at about the level of m4, is relatively far back in relation to the anterior end of the symphysis. As a consequence, the contraction of the geniohyoid could not have produced extensive anterior displacement of the tongue and hyoid apparatus.

As mentioned above, the hyoid apparatus of *Proeutatus* possesses a sigmohyal, similar in morphology to that of glyptodonts. However, the lack of other elements of the apparatus of the new specimen studied preclude functional interpretations.

The hyoid apparatus of *Prozaedyus* is very similar in morphology and arrangement to that of living dasypodids *Dasyus* and *Chaetophractus*, with a subvertical V-bone, and a long and anteroposteriorly directed geniohyoid. This suggests that the functional features were comparable to the modern forms.

In both glyptodonts and ground sloths, the absence of front teeth has been traditionally interpreted as indicating that the tongue played an important role in food intake. The highly modified apparatus of *Glyptodon* apparently occurred in

response to the migration of the masticatory apparatus below the cranium that occurred over the evolutionary history of glyptodonts (Fariña and Parietti, 1983). The hyoid apparatus and musculature in this group indicates powerful movements of a short, strong tongue (Pérez et al., 2000b; Fariña and Vizcaíno, 2001) that was not particularly well-suited for lingual protrusion. This may indicate that the tongue was probably more important for intraoral food manipulation and processing than in obtaining and drawing food into the oral cavity.

The form and disposition of the hyoid apparatuses of fossil xenarthrans analyzed here are apparently related to the shape of the skull. In those taxa with high skulls (i.e., *Megatherium* and *Glyptodon*) the apparatus tends to form elongated and nearly perpendicularly oriented descending bars, whereas in taxa with lower, more tubular skulls (i.e., mylodontids), the apparatus tends to have shorter elements, with marked angles between them, and with subparallel or oblique orientation to the anteroposterior axis of the oral cavity.

CONCLUSIONS

The form of the hyoid apparatus as a whole, mobility among its elements, and its anatomical position and relationship to other skeletal features provide insight on procurement and processing of foods in the oral cavity. Among the smaller sloths (nothrotheriids), the hyoid elements are slender and their articular surfaces indicate considerable mobility. The relatively long and horizontal orientation of the geniohyoid suggests considerable tongue protrusion. Among mylodontines, the elements indicate relatively mobile articulations, except between the stylo- and epihyals, which may have functioned as a single unit. Nonetheless, the relatively posterior placement of the apparatus and the length and alignment of the geniohyoid (nearly parallel to the mandibular alveolar margin) indicate considerable capacity for tongue protrusion. *Scelidotherium*, on the other hand, had rigidly articulated stylohyal and epihyal, and the apparatus lies farther anteriorly, which together with the elongated, steeply inclined mandibular symphysis, indicates a relatively shorter geniohyoid and thus more limited capacity for tongue protrusion.

A similar situation is indicated for *Megatherium*: movement among the elements was limited and the distance between the mandibular symphysis and apparatus is short, indicating a short geniohyoid muscle. Also, the orientation of this muscle's line of action was markedly oblique to the direction of lingual protrusion. Together these features indicate limited lingual protrusion, casting doubt on the classical reconstruction of this sloth as hav-

ing a long prehensile tongue used for grasping and drawing food to its mouth, but supporting recent interpretations of the presence instead of a long prehensile upper lip, as was also apparently true of *Scelidotherium*. In general, the main conclusions for these larger sloths is that taxa with shorter preorbital regions (e.g., *Glossotherium*, *Paramylodon*) have considerably mobile tongues and are wide-muzzled sloths with short and wide lips. Those with longer preorbital regions (e.g., *Scelidotherium* and *Megatherium*) seem to have relatively less tongue protrusion, with longer, narrower and prehensile upper lips.

Among cingulates *Prozaedus* resembles living dasypodids, with a subvertical V-bone and a long and anteroposteriorly directed geniohyoid. Its lingual capabilities were thus similar: the tongue was capable of protruding considerably beyond the oral cavity and important in food acquisition and intake. Conversely, in *Proeutatus* and (Pleistocene, at least) glyptodonts, the rigidity, particularly in the latter, of the apparatus suggests limited tongue protrusion. In glyptodonts the tongue was a powerful structure, based on the general robustness of the hyoid elements, the marked development of the anchoring structures of the tongue musculature, and form of the oral cavity, and its important role in intraoral manipulation of food is clearly evident.

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