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# Muzzle of South American Pleistocene Ground Sloths (Xenarthra, Tardigrada)

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*ABSTRACT* Sloths are among the most characteristic elements of the Cainozoic of South America and are represented, during the Pleistocene, by approximately nine genera of gigantic ground sloths (Megatheriidae and Mylodontidae). A few contributions have described their masticatory apparatus, but almost no attention has been paid to the reconstruction of the muzzle, an important feature to consider in relation to food intake, and particularly relevant in sloths because of the edentulous nature of the muzzle and its varied morphology. The relationship between dietary habits and shape and width of the muzzle is well documented in living herbivores and has been considered an important feature for the inference of alimentary styles in fossils, providing an interesting methodological tool that deserves to be considered for xenarthrans. The goal of this study was to examine models of food intake by reconstructing the appearance and shape of the muzzle in five species of Pleistocene ground sloths (*Megatherium americanum*, *Glossotherium robustum*, *Lestodon armatus*, *Mylodon darwini*, and *Scelidotherium leptocephalum*) using reconstructions of the nasal cartilages and facial muscles involved in food intake. The preservation of the nasal septum, and the scars for muscular attachment in the rostral part of the skulls, allow making a conservative reconstruction of muzzle anatomy in fossil sloths. Wide-muzzled ground sloths (*Glossotherium* and *Lestodon*) had a square, nonprehensile upper lip and were mostly bulk-feeders. The lips, coupled with the tongue, were used to pull out grass and herbaceous plants. Narrow-muzzled sloths (*Mylodon, Scelidotherium*, and *Megatherium*) had a cone-shaped and prehensile lip and were mixed or selective feeders. The prehensile lip was used to select particular plants or plant parts. J. Morphol. 267:248–263, 2006. © 2005 Wiley-Liss, Inc.

KEY WORDS: ground sloths; Xenarthra; Tardigrada; Pleistocene; muzzle; feeding

Tardigrada (sloths) are the most diverse group within the Xenarthra, but at present it is represented only by two genera, the tree sloths *Bradypus* (Linné, 1758) and *Choloepus* (Illiger, 1811). There is general consensus that they cluster together with the Vermilingua (anteaters) in a natural group called Pilosa (Gaudin, 2004). Sloths are among the most characteristic elements of the Cainozoic of South America, but are also well represented in Central and North America (more than 80 genera have been named; see McKenna and Bell, 1997). Gaudin's (2004) analysis corroborates the monophyly of the four ground sloths families (Megatheriidae, Megalonychidae, Nothrotheriidae, and Mylodontidae), and the diphyly of the living tree sloths, with *Bradypus* as the sister-taxon to all other sloths and *Choloepus* allied with members of Megalonychidae (Fig. 1). During the Pleistocene of South America approximately nine genera of gigantic ground sloths (Megatheriidae and Mylodontidae) are recorded. The most conspicuous and better known species are the megatheriid *Megatherium americanum* and the mylodontids *Glossotherium robustum*, *Lestodon armatus*, *Mylodon darwini*, and *Scelidotherium leptocephalum* (Fig. 2).

Extensive descriptions of the skull and mandible of these ground sloths were given by Owen (1842, 1856, 1857), Lydekker (1894), Ameghino (1889), Kraglievich (1922, 1923, 1928, 1934), and more recently by McDonald (1987), De Iuliis (1996), Esteban (1996), and Bargo (2001a,b). The most characteristic features of the masticatory apparatus of extant xenarthrans, and possibly all extinct taxa, are a lack of enamel in the adult dentition, a deciduous dentition, and the cuspation pattern observed in other mammals. Teeth are strongly reduced in number (5/4 in sloths, except in *Mylodon* with 4/4 and the Plio-Pleistocene nothrotheres with 4/3), composed of osteodentine, always hypselodont, and although they can be lobate or bear lophs (mylodontids and megatheriids, respectively), they are usually simple and separated by short diastemata. A predental space (predental spout) is particularly well developed in sloths.

With the exception of the proposition that at least one may have been occasionally carnivorous (Fariña, 1996; Fariña and Blanco, 1996), ground sloths have been largely considered herbivorous, primarily by analogy with living tree sloths. Despite the com-

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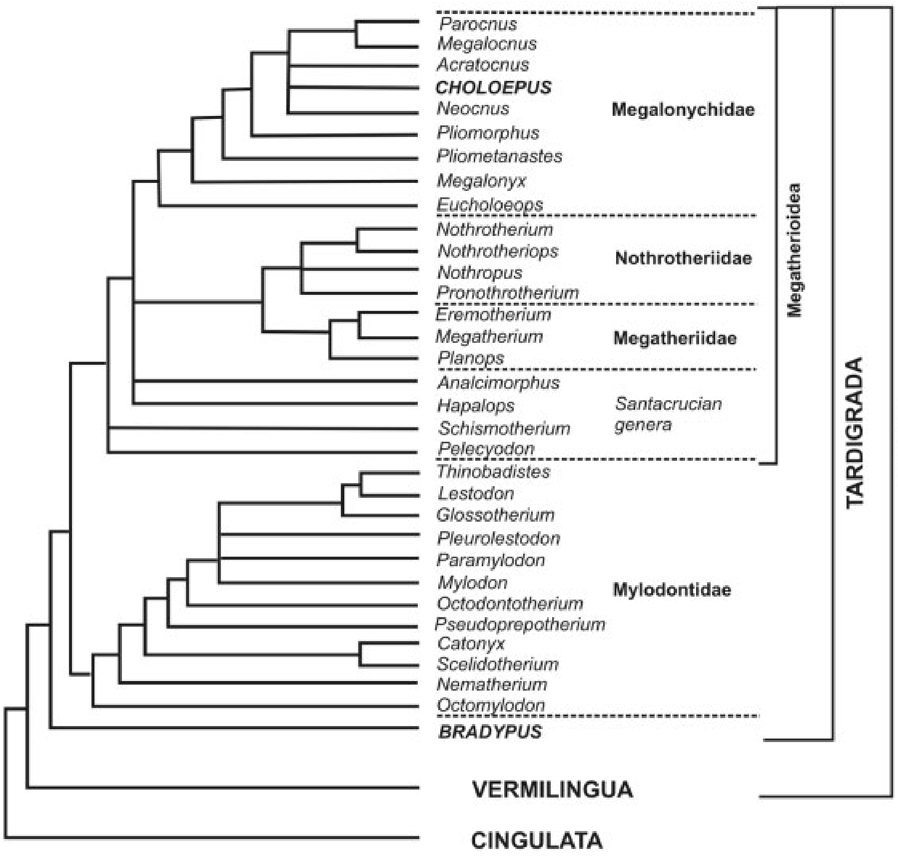

Fig. 1. Phylogeny of Tardigrada (modified from Gaudin, 2004).

mon features mentioned above, the great variation in skull and dental morphology, body size, and proportions among ground sloths suggest that they had diversified to fill a variety of niches (Bargo, 2001a). There are some fairly detailed morphofunctional analyses of the masticatory apparatus of both North American and South American Pleistocene ground sloths (McDonald, 1987, 1995, 1997; Naples 1987, 1989; Bargo, 2001a,b). However, almost no attention has been paid to the reconstruction of the muzzle. The latter is an important feature to consider in relation to food intake, and is particularly relevant in sloths, as well as in almost remaining xenarthrans, because of the edentulous nature of the muzzle and its varied morphology.

Several authors have studied the relationship between dietary habits and shape and width of the muzzle in herbivores, particularly in ungulates (see Janis and Ehrhardt, 1988, and references therein). This feature has been considered important for the inference of alimentary styles in fossil herbivores (Solounias et al., 1988; Solounias and Moelleken, 1993a,b; Janis, 1995), providing an interesting methodological tool that deserves to be considered for xenarthrans.

Here we examine models of food intake by reconstructing the appearance and shape of the muzzle in the five South American Pleistocene giant ground sloths: *Megatherium americanum, Glossotherium robustum, Lestodon armatus, Mylodon darwini*, and *Scelidotherium leptocephalum*.

## Muzzle Musculature and Nasal Cartilages in Living Pilosa

Very few works have dealt with the anatomy of the facial musculature of living Pilosa. Windle and Parson (1899) and Uekermann (1912) speculated on the supposedly primitive condition of the facial musculature in sloths and vermilinguas. Saban (1971) described or mentioned some specific muscles in different xenarthrans. The most complete contribution on facial musculature in both tardigrades (*Bradypus* and *Choloepus*) and vermilinguas (*Myrmecophaga, Tamandua*, and *Cyclopes*) is that by Naples (1985), who made detailed descriptions of the muscles through dissections of adult specimens.

Recently, a series of insightful contributions considered the narial anatomy of living ungulates (Witmer et al., 1999; Clifford and Witmer, 2004a,b) and have been very useful in the reconstruction of fossil taxa (e.g., Mihlbachler and Solounias, 2004). Witmer et al. (1999) and Clifford and Witmer (2004a,b) standardized the nomenclature of the anatomical structures following veterinary anatomy texts and the *Nomima Anatomica Veterinaria* (NAV, 1994).

The following is a summary of the muscles described in living Pilosa by Naples (1985), who fol-

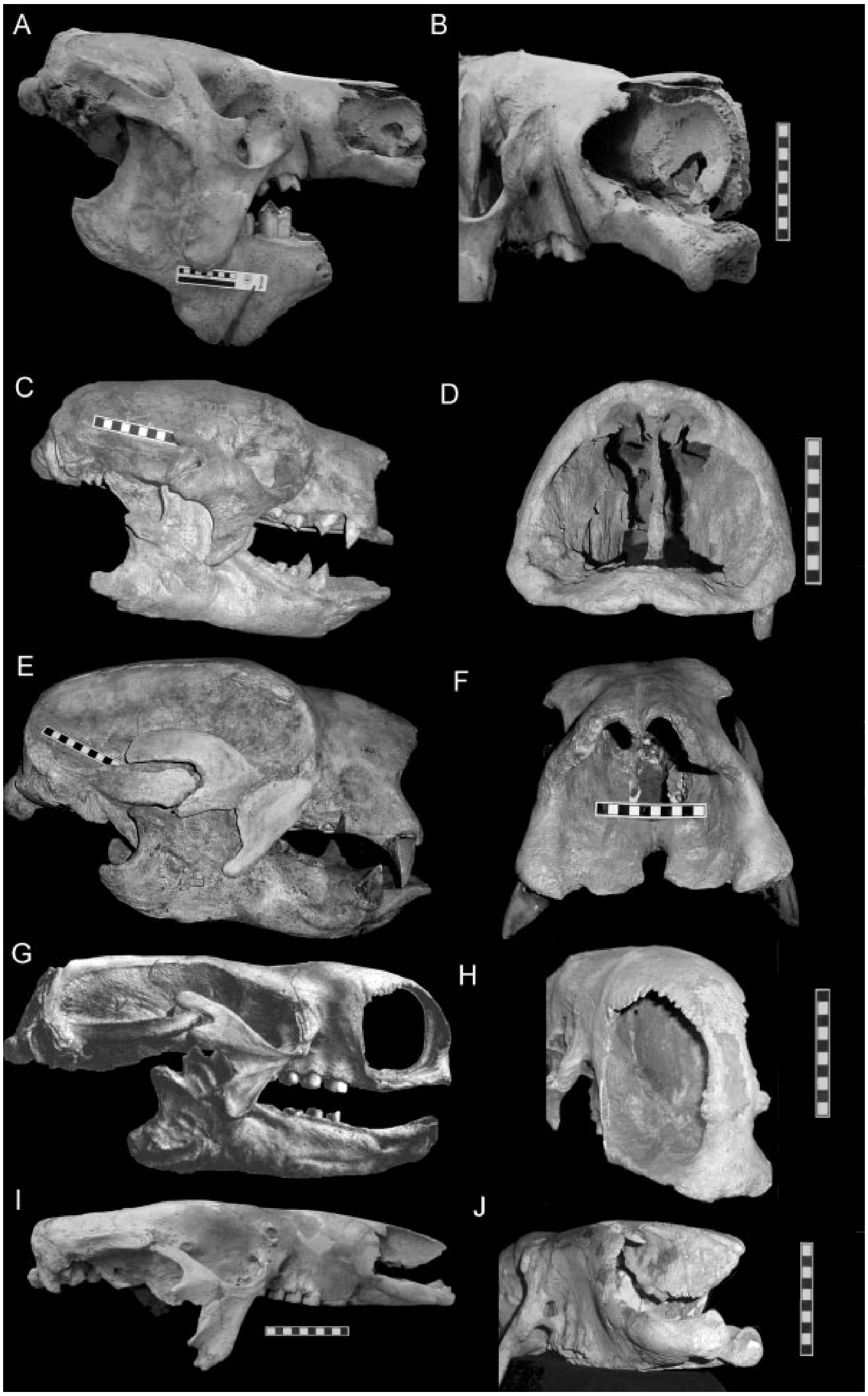

Fig. 2. **A:** Skull of *Megatherium americanum* in lateral view, and (**B**) muzzle frontolateral view. **C:** Skull of *Glossotherium robustum* in lateral view and (**D**) muzzle frontal view. **E:** Skull of *Lestodon armatus* in lateral view and (**F**) muzzle frontal view. **G:** Skull of *Mylodon darwini* in lateral view and (**H**) muzzle frontolateral view. **I:** Skull of *Scelidotherium leptocephalum* in lateral view and (**J**) muzzle frontolateral view.

lowed the terminology of Rinker (1954). In this section we mention only some muscles of the *pars intermedia* and *oris* of the *sphincter colli profundus* in living sloths that are relevant for the reconstruction of muzzle anatomy in fossil sloths. When possible, references to other xenarthrans (Dasypodidae) are provided. We include in parentheses the anatomical equivalent in living ungulates following Witmer et al. (1999) and Clifford and Witmer (2004a) (see Table 1).

*TABLE 1. Muscle nomenclature and homologies, and facial muscles described for the living sloths by Naples (1985)*

| Naples, 1985 | Boas and Paulli, 1908 | Witmer et al., 1999; Clifford and Witmer, 2004a, b | *Choloepus* | *Bradypus* |
|---|---|---|---|---|
| *Zygomaticolabialis* | *Zygomaticus platismatis* | *Zygomaticus* | + | – |
| *Nasolabialis* | *Nasolabialis* | *Levator nasolabialis* | + | + |
| *Dilatator nasi* | *Maxilolabialis superior* | *Levator labii superioris* | + | + |
| *Nasolabialis profundus* | *Nasalis* | *Lateralis nasi?* | | |
| *Pars interna* | *Lateralis nasi* | *Dilatator naris apicalis?* | – | – |
| *Pars media superior* | — | — | – | – |
| *Pars media inferior* | — | — | – | – |
| *Pars mediana* | *Transversus nasi* | *Dilatator naris apicalis?* | – | – |
| *Pars anterior* | — | — | + | – |
| *Pars maxillaris superficialis* | — | — | + | + |
| *Pars maxillaris profunda* | — | — | + | + |
| *Maxillolabialis* | *Maxillolabialis inferior* | *Caninus* | – | – |
| *Buccinator* | *Buccinatorius* | *Buccinator* | + | + |
| *Pars orbicularis oris* | *Pars rimana* | *Orbicularis oris* | + | + |
| *Pars intermaxillaris* | *Pars supralabialis* | *Incisivus superior* | + | + |

+, present and –, absent.

### 1. Pars Intermedia

***M. zygomaticolabialis* (= *zygomaticus*).** It is present only in *Choloepus* as a thin sheet of fibers, arising on the fascia anterior of the ear, inserting on to the fascial covering of the posterior projection of the zygomatic arch.

***M. nasolabialis* (= *levator naso-labialis*).** It is present in *Bradypus*, *Choloepus*, *Myrmecophaga*, and *Tamandua*, but absent in *Cyclopes*. In sloths it arises from the supraorbital ridge anterior to the postorbital prominence and inserts into the fibrous pad on the lateral surface of the maxilla. It elevates the upper lip in its caudal portion.

### 2. Pars Oris

***M. maxillo-labialis* (= *caninus*).** Although Naples (1985) indicates that it is absent in sloths and anteaters, Saban (1971) mentions its presence in *Bradypus, Tamandua*, and the dasypodids *Dasypus* and *Euphractus*, comprising dorsal and ventral fascicles. It attaches on the base of the zygomatic arch and inserts on the upper lip and outline of the naris, topographically equivalent to the *nasolabialis profundus pars maxillaris superficialis* and *pars maxillaris profundus* of Naples (1985) (see below). This muscle retracts the nostrils caudally.

***M. dilatator nasi* (=*levator labii superioris*).** It is present in all genera of sloths and anteaters. In *Choloepus* and *Bradypus* it arises from the ventral portion of the anterior border of the zygomatic plate, deep to the origin of the *m. nasolabialis profundus pars maxillaris superficialis*. The anterior half is composed of a flat tendon that inserts into the dorsolateral border of the rhinarium. In vermilinguas the origin and insertion follow the same pattern as in sloths. Saban (1971) also describes it for *Dasypus*. This muscle elevates and everts the upper lip.

***Nasolabialis profundus* (= *lateralis nasi*).** Following Naples (1985) this muscle is reduced or simplified in Pilosa, including three parts in sloths, and five parts in vermilinguas. Some of them do not have bony attachments.

i) *Pars interna* (= *dilatator naris apicalis?, transversus nasi*). It is present only in *Tamandua* and *Myrmecophaga* (Saban, 1971; Naples, 1985). It arises deep to the skin over the nasal bones, and inserts into the notch at the anterior corner of the naris. Some fibers pass laterally and ventrally to insert dorsal to the fat pad above the upper lip.

ii) *Pars media superioris.* It is absent in sloths but present in vermilinguas. It arises from the bridge of the rostrum with fibers passing ventrally, deep to the tendon of *m. dilatator nasi* and inserting into the fibers of *m. orbicularis oris*.

iii) *Pars anterior.* It is absent in *Bradypus* and *Myrmecophaga*, but present in *Choloepus*, *Tamandua*, and *Cyclopes*. In *Choloepus* it arises from the nasal cartilage, on the dorsolateral margin of the naris and inserts into the fat pad and connective tissue of the upper lip.

iv) *Pars anterior profunda.* It is only present in *Tamandua*.

v) *Pars maxillaris* (= *caninus*?). It is divided into *pars superficialis* and *pars profunda*, and is present in the five genera of Pilosa. In *Choloepus* the *pars superficialis* arises via a short aponeurosis on the ventral portion of the anterior border of the zygomatic plate, but does not extend onto the maxillary bone. It inserts by a tendon, which gives off a number of branches into the fibers of *m. nasolabialis pars orbicularis oris* on the upper lip. The condition is similar in *Bradypus*. The *pars profunda* arises from a thin aponeurosis on the anterior side of the zygomatic plate, dorsally to the origin of *pars maxillaris superficialis*.

***M. buccinator* (= *buccinator*).** It is present in all five genera. In sloths it arises from the lateral surface of the maxilla above the row of cheek teeth, terminating directly posterior to the last tooth. It forms the cheek, as in other mammals. This muscle inserts into the lateral surface of the mandible, dorsal to the roots of the cheek teeth. Following Naples (1985), the *pars orbicularis oris* and *pars intermaxillaris* are part of the *buccinator*. The first acts as a sphincter of the mouth. The second is not clearly differentiated from other parts of the *m. buccinator* in sloths, but it could be a synonym of the *incisivus superior* of Clifford and Witmer (2004a) (see Discussion), the principal action of which is to elevate and retract the upper lip.

Although a detailed reconstruction of the nasal cartilages is not the goal of this work, some general aspects of these structures, necessary for the muzzle reconstruction, can be inferred from features of the nasal cavity. The nasal capsule of the chondrocranium of *Choloepus* and *Tamandua* was described and illustrated by Zeller et al. (1993). The chondrocranial anatomy of the *rostrum nasi* (the anterior end of the nasal capsule) of *Choloepus* resembles that of a generalized eutherian more than that of *Tamandua*. In *Choloepus*, the *tectum nasi* is broadly continuous with the *cartilago cupularis*. A *processus cupularis* (= *processus alaris inferioris*) extends laterally from the rostroventral edge of the *septum nasi*. Laterally, the *paries nasi* is separated from the tectum by an expanded fenestra *nasi superior*. A *processus lateralis ventralis* completes the capsule ventrally. A *processus alaris superioris* protects the external nasal aperture. A septomaxilla lies superficially at the posterior corner of the fenestra narina. Although Wegner (1950) reported this bone for some specimens, Zeller et al. (1993) did not find it in macerated skulls of either *Tamandua* or *Choloepus*.

# MATERIALS AND METHODS

## Acronyms

CN: Zoological Museum, Copenhagen, Denmark. MACN: Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina. MLP: Museo de La Plata, La Plata, Argentina. MMP: Museo Municipal de Ciencias Naturales, Mar del Plata, Argentina. MNHN-BOL: Museo Nacional de Historia Natural, La Paz, Bolivia. MNHNP: Muséum National d' Histoire Naturelle, Paris, France.

Skulls of the following specimens were analyzed and measured for this study: *Megatherium americanum* Cuvier, 1796. MACN 5002, MACN 15154, MACN 6 P, MACN 2832, MLP 2-64, MNHN PAM 276. *Glossotherium robustum* (Owen, 1842). MACN 11769, MLP 3-136, MLP 3-137, MLP 3-138, MLP 3-140, MMP 1489-M, MMP 1490-M. *Mylodon darwini* Owen, 1839. CN 43, MACN 15348, MLP 3-762, MLP 3-764, MNHN-BOL-V 006470. *Lestodon armatus* Gervais, 1855. MLP 3-3, MLP 3-29, MLP 3-30, MMP 47-S. *Scelidotherium leptocephalum* Owen, 1840. MLP 3-671, MLP 3-401, MLP 3-402, MMP 9-S, MMP 31-S, MMP 127-S, MMP 157-S, MMP 458-S, MMP 549-S, MMP 614-M, MMP 1155-M.

## Reconstruction of Musculature and Nasal Cartilages

The attachment sites of the musculature are usually well indicated in mammals by features of the skull and jaws, such as roughened surfaces, scar lines, ridges, and crests. These features are usually very conspicuous in fossils, but it depends on the size and the degree of preservation. The areas of origin and insertion of the musculature were reconstructed based on features of the skull, the patterns of musculature in modern mammals (Maynard Smith and Savage, 1959; Turnbull, 1970), particularly those in tree sloths *Bradypus* and *Choloepus* (Macalister, 1869; Windle and Parson, 1899; Edgeworth, 1935; Sicher, 1944; Naples, 1982, 1985), and the narial anatomy of *Tapirus* (Perissodactyla, Tapiridae), *Alces* (Artiodactyla, Cervidae), and *Saiga* (Artiodactyla, Bovidae) (Witmer et al., 1999; Clifford and Witmer, 2004a,b, respectively). The nomenclature follows Naples' (1985) scheme with changes and additions after Witmer et al. (1999) and Clifford and Witmer (2004a).

Uncertainty regarding the interpretation of the shape and development of the nasal cartilages is greater than that for the muscular reconstruction. For the fossils, we made the most conservative graphic reconstruction based on the described anatomy of immature specimens of the closest living relative, the tree sloth *Choloepus* by Zeller et al. (1993). We looked for evidence on the *septum nasi* (when preserved), general morphology of the area, and the scars that could not be attributed to muscular or ligament attachments, and could correspond topographically to cartilages.

## Relative Width and Shape of the Muzzle

As mentioned above, there is a relationship between dietary habit, shape, and width of the muzzle in ungulates. Following Janis and Ehrhardt (1988), the width of the palate could represent a measure of the rate of food ingestion, which reflects a high correlation with body mass. These authors calculated the relative muzzle width as palatal width divided by muzzle width. High values of this ratio indicate selective feeders with narrow muzzles. The muzzle width in ungulates was measured at the premaxillo-maxillary suture, and the palatal width is the distance between the M2 protocones (Janis and Ehrhardt, 1988; Janis, 1990).

Because the premaxillae are reduced in sloths, the maximum muzzle width (MMW) is generally on the maxilla and these measurements were conveniently modified for the ground sloths. The palatal width (PW) was measured as a mean of the anterior and posterior width, since in some mylodontids the palate is wider anteriorly. Therefore, the index of relative muzzle width for the ground sloths is given as RMW = PW/MMW. The values obtained cannot be directly compared with those for ungulates, but provide a framework for comparison among ground sloths.

Dietary categories (browsers, grazers, and mixed feeders) were differentiated also in extant ruminants through analysis of premaxillary shape (Solounias et al., 1988) and applied to their extinct relatives (Solounias and Moelleken, 1993a). Following this approach, browsers have pointed premaxillae, grazers have square premaxillae, and mixed feeders have an intermediate condition between the first two. As the premaxillae are reduced in ground sloths, the muzzle is formed mainly by the maxillae, and includes an edentulous predental space formed by the premaxillae and maxillae (Fig. 3). The shape of the muzzles was evaluated graphically, superimposing outlines of the premaxillae and anterior part of the maxilla, standardized at the width at the first molariform.

The feeding categories mentioned above are based on field observations, analyses of stomach contents and structure, and fecal studies (see Hofmann and Stewart, 1972; Hofmann, 1973, 1989; Jarman, 1974). However, these terms are imprecise, and have been used to refer to the mode of food acquisition as well as the type of food ingested, i.e., browsing may refer to selective feeding of any food type, as well as eating dicot material, whereas grazing denotes grass eating, but is used to mean eating of forbs as well, or may refer to a nonselective feeding. As it is clear that the form (i.e., shape and size) of the muzzle imposes physical constraints to the size and amount of food that can be taken with each bite, we adopt a morphofunctional criterion classifying dietary habits in a gradation from highly selective to highly nonselective or bulk feeders.

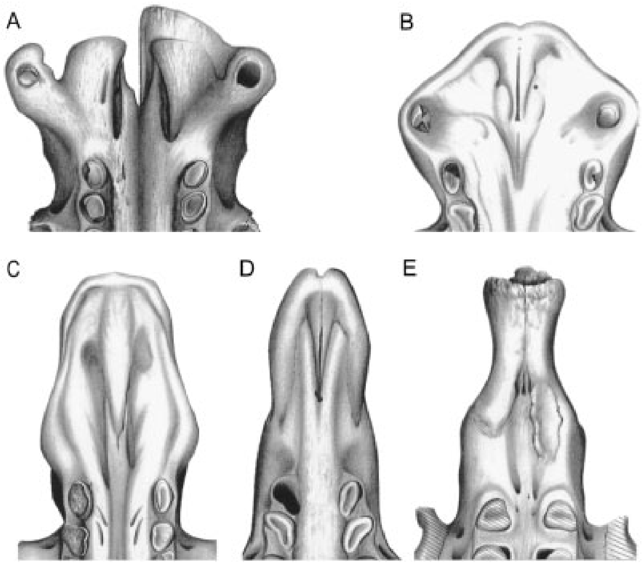

Fig. 3. Muzzle palatal views of the five species of ground sloths. **A:** *Lestodon armatus*. **B:** *Glossotherium robustum*. **C:** *Mylodon darwini*. **D:** *Scelidotherium leptocephalum*. **E:** *Megatherium americanum*.

## RESULTS

### Muzzle Muscular Attachments and Nasal Cartilages

The facial muscles reconstructed in ground sloths are listed in Table 2, which also includes those described for the tree sloths. As mentioned above, the features of the skull and jaws (roughened surfaces, scar lines, ridges, crests) are very conspicuous in fossil ground sloths. On the contrary, the attachment areas of the muscles of living sloths can be observed through dissections, but do not always show rugose surfaces or scars in the corresponding bones. Such difference must be certainly explained by allometry, since the fossils are two or three orders of magnitude larger than the living ones. Differences are also expected because the different habits of the fossil forms, which require stronger muscles.

***Megatherium americanum*** **(Fig. 4).** Most skulls of *Megatherium americanum* either lack the *septum nasi* or preserve only its proximal portion. Nevertheless, the preserved proximal portion of the *septum* indicates that this structure is quite robust. An exceptional specimen exhibited at the MNHN (MNHN PAM 276) completely preserves a well-developed and ossified *septum nasi* (see Fig. 2A,B), which allows us to confirm the robustness of this structure and to infer some morphological features. The *septum* shows two deep grooves that run on both sides of its dorsal edge, continuing ventrally until the level of the premaxilla. These grooves present lateral flanges in their proximal portions, adjacent to the nasoincisive notch, which could be interpreted as insertion areas for the nasal cartilage.

The distal edges of the maxilla, forming the narial aperture are very rugose, possibly for insertion of nasal cartilages. The distal ends of the premaxillae show very distinctive, concave, roughened surfaces that are slightly ventrally directed. They could be interpreted as the origin area of the bilateral retractor muscle of the upper lip (*M. buccinator pars intermaxillaris = incisivus superior*). Above the distal end of the premaxillae there is a robust ascending process, the area of insertion for the *septum nasi*. This process is rugose anteriorly, and could also be part of the origin area of the *incisivus superior*.

The anteromedial border of the orbit, dorsal to the infraorbital foramen, has a roughened and depressed area that could indicate the origin of *m.*

*TABLE 2. Facial muscles described for the ground sloths*

| Facial muscles | *Choloepus* | *Bradypus* | *Megatherium* | *Scelidotherium* | *Mylodon* | *Glossotherium* | *Lestodon* |
|---|---|---|---|---|---|---|---|
| *Zygomaticolabialis (=zygomaticus)* | + | – | NF | NF | NF | NF | NF |
| *Nasolabialis (=levator nasolabialis)* | + | + | P | P | P | P | P |
| *Dilatator nasi (=levator labii superioris)* | + | + | P | NF | P | P | NF |
| *Nasolabialis profundus* | | | | | | | |
| *Pars interna* | – | – | NF | NF | NF | NF | NF |
| *Pars media superior* | – | – | NF | NF | NF | NF | NF |
| *Pars media inferior* | – | – | NF | NF | NF | NF | NF |
| *Pars mediana* | – | – | NF | NF | NF | NF | NF |
| *Pars anterior* | + | – | NB | NB | NB | NB | NB |
| *Pars maxillaris superficialis* | + | + | NF | NF | NF | NF | NF |
| *Pars maxillaris profunda* | + | + | NF | NF | NF | NF | NF |
| *Maxillolabialis (=caninus)* | – | – | P | NF | P | P | NF |
| *Buccinator* | + | + | | | | | |
| *Pars orbicularis oris (=orbicularis oris)* | + | + | NB | NB | NB | NB | NB |
| *Pars intermaxillaris (=incisivus superior)* | | + | P | P | P | P | P |

P, present; NF, not found or absent; NB, no bony attachment; +, present, –, absent.

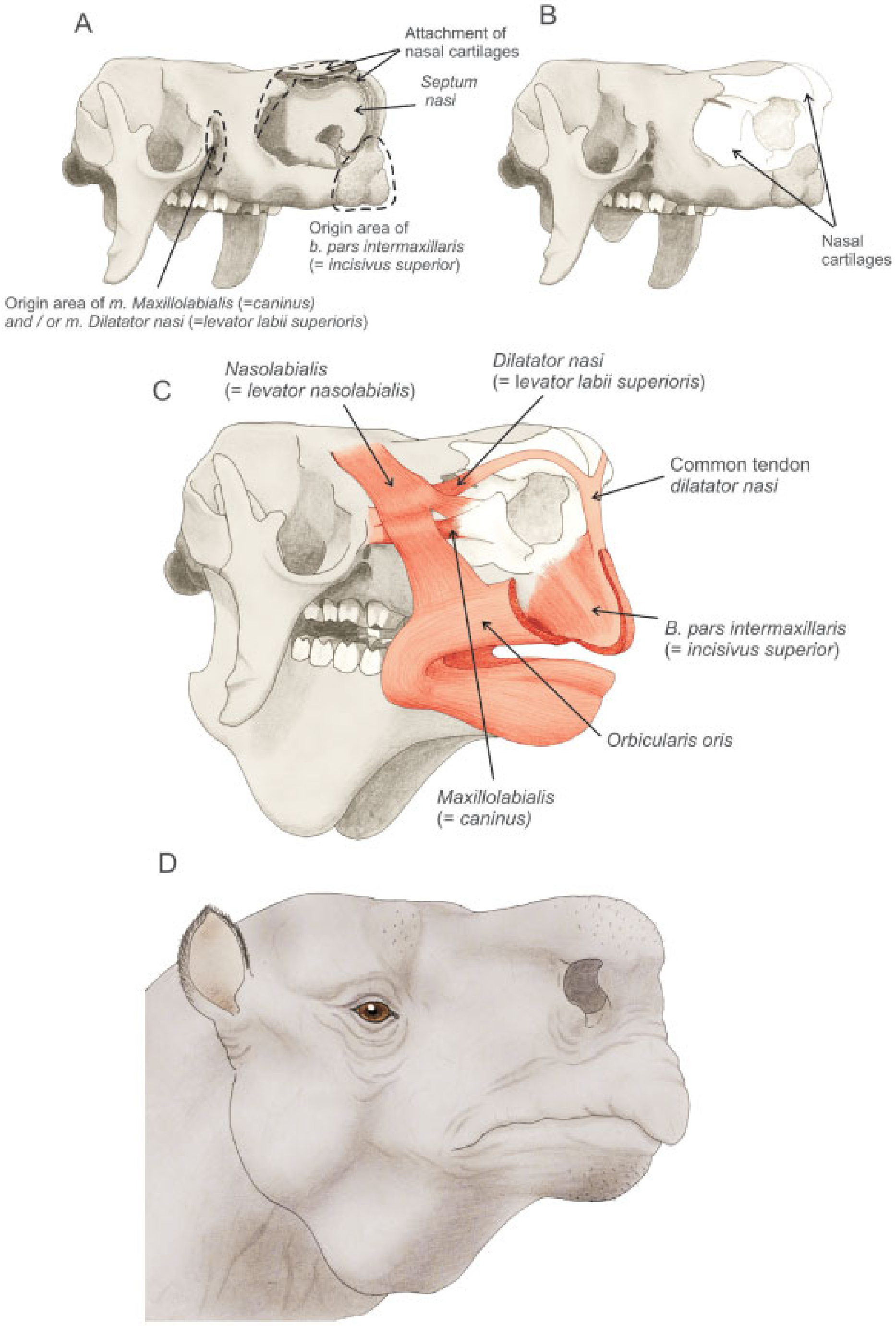

Fig. 4. *Megatherium americanum*. Skull showing (**A**) main attachments areas of muscles and cartilages, (**B**) reconstruction of nasal cartilages, (**C**) reconstruction of muscles, and (**D**) reconstruction of external appearance.

*maxillo-labialis* (= *caninus*) and/or *m. dilatator nasi* (= *levator labii superioris*). The prominent postorbital processes, with obvious scarlines on their dorsolateral surfaces, indicate the origin area for the postorbital ligament closing the orbit caudally. On both sides of the skull the area of the fronto-nasomaxillary suture shows a surface with fine scarlines that could be the origin area for *m. nasolabialis*.

***Glossotherium robustum*** **(Fig. 5).** The *septum nasi* is incomplete, as in most of the ground sloths skulls analyzed, but based on the small preserved parts it seems to be thin, in contrast to *Megatherium americanum* and *Mylodon darwini* (see below).

Distally, the end of the premaxillae form a slightly rugose flange, indicating the origin of *m. incisivus superior*. The dorsal surface of each premaxilla bears a short ascending process that fuses at the midline with that of the opposite side to form a small, triangular, anterodorsally oriented projection. Posterior to the projection there is a roughened, depressed, triangular, and well-marked area, continuing inside of the nasal cavity. It could be the

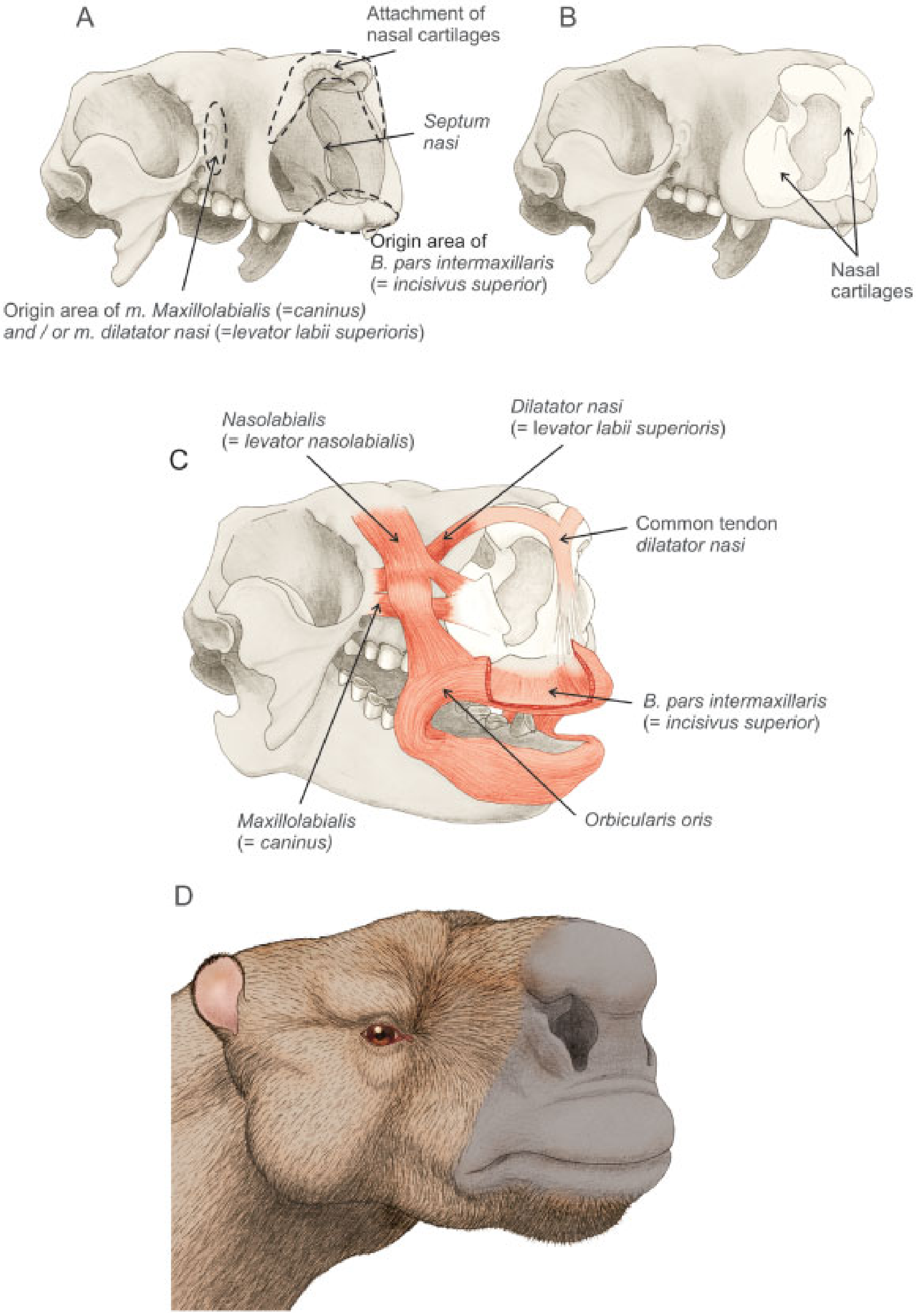

Fig. 5. *Glossotherium robustum*. Skull showing (**A**) main attachments areas of muscles and cartilages, (**B**) reconstruction of nasal cartilages, (**C**) reconstruction of muscles, and (**D**) reconstruction of external appearance.

attachment area for the cartilaginous floor of the nares (*processus lateralis ventralis*?). The borders of the nasal opening (maxillae and nasals) are rugose, but this feature is more accentuated at the edge of nasals.

In the anteromedial edge of the orbit, dorsal to the infraorbital foramen, there is a rugose, depressed, and well-defined area indicating the origin of *m. maxillo-labialis* (= *caninus*) and/or *m. dilatator nasi* (= *levator labii superioris*). At the fronto-naso-maxillary suture, on both sides of the skull, there is slightly depressed surface, which could be the origin of *m. nasolabialis*.

***Lestodon armatus.*** Although clearly larger than *Glossotherium robustum*, the shape of the muzzle of this species clearly constitutes a common morphotype with it, so we refer to Figure 5 for the muscle reconstructions. The *septum nasi* is lost in the specimens studied. Some remains in the floor and roof of the nasal cavity indicate that the *septum* was thin and weak, as in *G. robustum*. The broad anterior edges of the nasals are very rugose, probably indi-

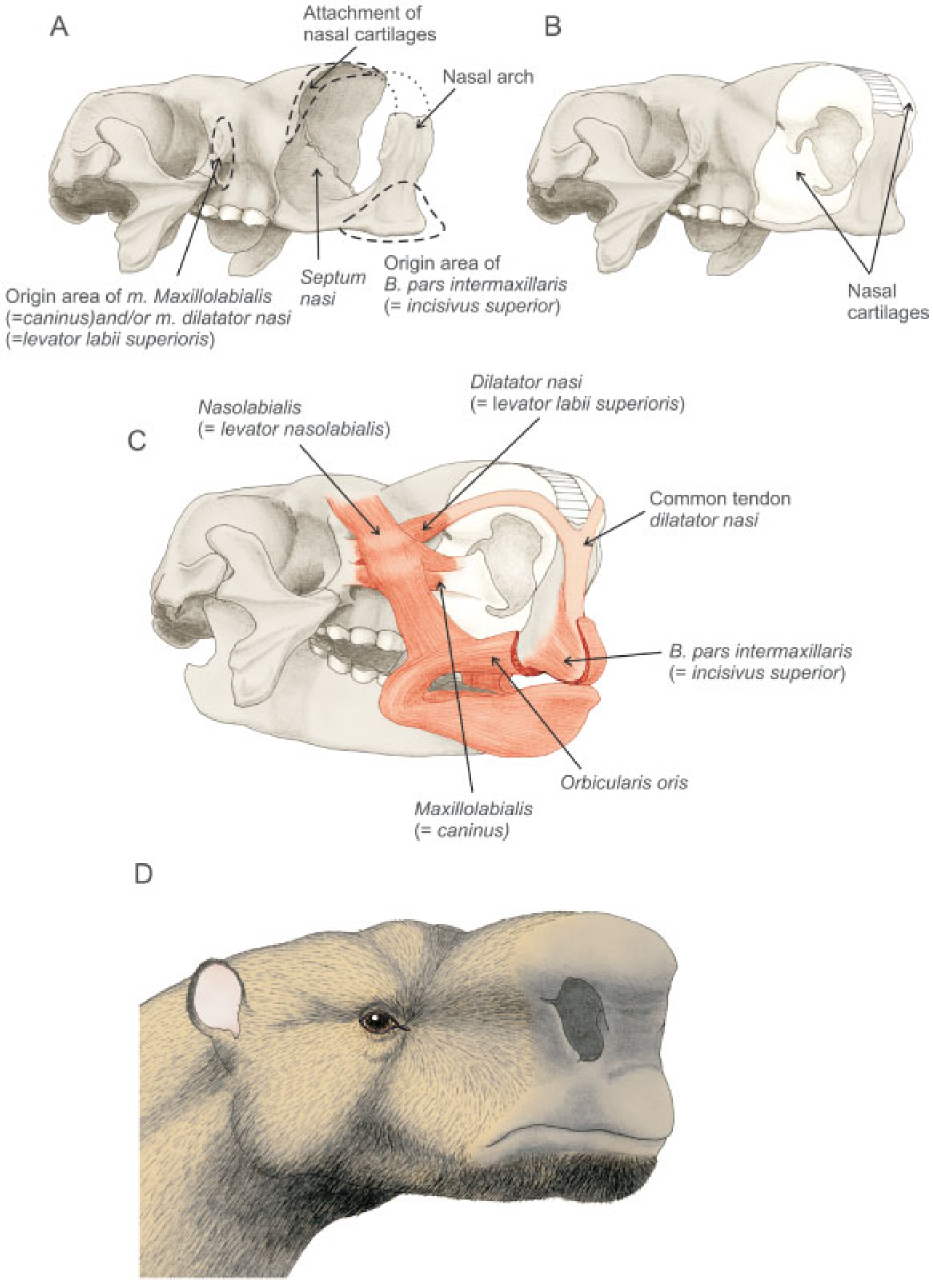

Fig. 6. *Mylodon darwini*. Skull showing (**A**) main attachments areas of muscles and cartilages, (**B**) reconstruction of nasal cartilages, (**C**) reconstruction of muscles, and (**D**) reconstruction of external appearance.

cating a robust *cartilago cupularis*. As in the other ground sloths, the premaxillae have their anteromedial edge broadly roughened, showing the origin of *m. incisivus superior*.

The origin areas of *m. maxillo-labialis* (= *caninus*) and *m. dilatator nasi* (= *levator labii superioris*) are not visible, and that of *m. nasolabialis* is not well defined.

***Mylodon darwini* (Fig. 6).** The *septum nasi* is broken in the skulls of *Mylodon darwini* examined, but the preserved proximal part indicates that it was robust. In the collections of the CN there is an excellent skull (CN 43), with the complete nasal arch preserved (Fig. 2G,H) that was figured by Reindhart (1879). The end of the premaxillae form a thick, slightly roughened flange. A robust ascending process fuses to the nasals, forming a nasal arch. This arch is nearly complete in two or three specimens. The lower part of the anterior face of the arch is also rugose. The retractor muscle of the upper lip (*incisivus superior*) probably originated in this area, i.e., end of the premaxillae and ascending process, as in *Megatherium americanum*.

On the anterior edge of the orbit, dorsal to the infraorbital foramen, there is a depressed rugose area which could be the origin for *m. dilatator nasi* (= *levator labii superioris*) and/or *m. maxillo labialis* (= *caninus*), as observed in *Megatherium america-*

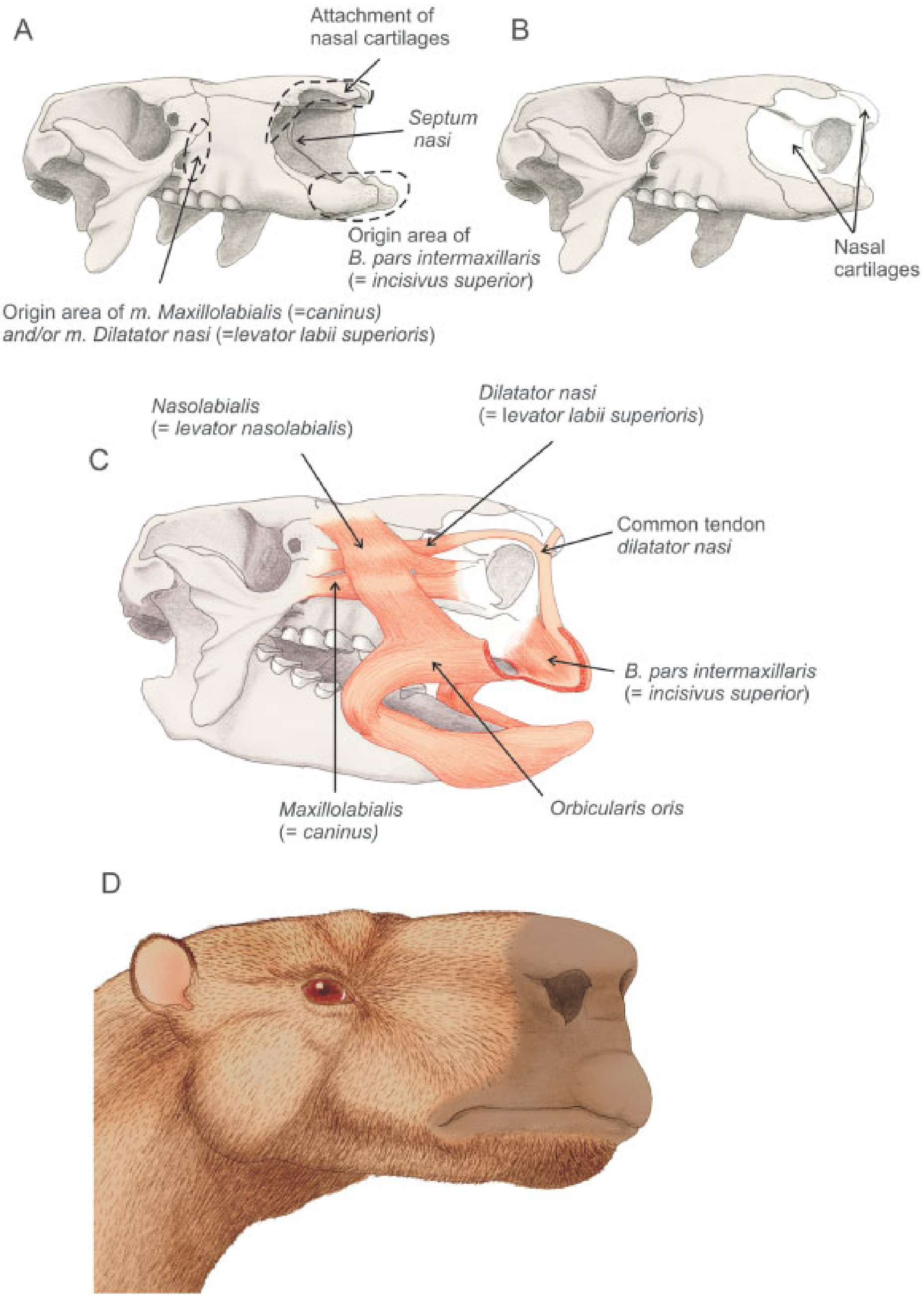

Fig. 7. *Scelidotherium leptocephalum*. Skull showing (**A**) main attachments areas of muscles and cartilages, (**B**) reconstruction of nasal cartilages, (**C**) reconstruction of muscles, and (**D**) reconstruction of external appearance.

*num*. Ventral and anterior to the infraorbital foramen there is an oval and depressed area that extends anteriorly and ventrally to the ventral edge of the maxilla at the level of the nasal opening. It could be interpreted as the attachment area for the *m. buccinator*. The distal edges of the maxillae are not rugose. The nasal opening shows a constriction producing a figure-8 outline in frontal view; the anterior borders of the nasals are clearly roughened.

The descending process of the zygomatic arch has a smooth depression on its lateral surface that could be the origin area of *m. nasolabialis profundus pars maxillaris* or *m. zygomatico labialis* (= *zygomaticus*). Above the orbits, on the fronto-naso-maxillary suture area, there are two depressed and well-delimited surfaces, indicating the origin of *m. nasolabialis*.

***Scelidotherium leptocephalum*** **(Fig. 7).** Most of the *Scelidotherium leptocephalum* specimens observed lack the *septum nasi*. The distal ends of the premaxillae are slightly rugose, not as accentuated as in *Megatherium americanum*, indicating the possible origin areas for the retractor muscle of the upper lip (*m. incisivus superior*). The dorsal faces of the premaxillae present a short ascending process, indicating the distal end of the *septum nasi*. The distal ends of the nasal bones are roughened, probably for insertion of the nasal cartilage.

The attachment area for the origin of *m. maxillolabialis* (= *caninus*) and/or *m. dilatator nasi* (= *levator labii superioris*) in the anteromedial edge of the orbit is not as marked as in *Megatherium americanum*. The area on the nasomaxillary suture possesses two slightly depressed surfaces, anterior to the orbits, that would indicate the origin of *m. nasolabialis*.

Some remarks about the skulls of the five species of ground sloth that summarize the results presented above:

1) The origin areas for *m. nasolabialis*, *m. maxillolabialis*, *m. dilatator nasi*, and *m. incisivus superior* are clearly defined.
2) The rugose surfaces observed in the borders of the nasal opening could be related to the attachment of soft tissues forming the outer nasal cartilages. Alternatively, they could represent the origin of the *m. nasolabialis profundus pars interna*.
3) The rugose distal ends of premaxillae in most ground sloths could indicate the origin of an individual muscle of the upper lip, the *m. buccinator pars intermaxillaris* (= *m. incisivus superior*), that complements the function of *m. dilatator nasi* and *m. nasolabialis* retracting the lip.

## Relative Width and Shape of the Muzzle

Table 3 includes values of relative muzzle width (RMW = PW/MMW) for different specimens and mean values for each species. The figures have a comparative value among xenarthrans and are not quantitatively comparable with ungulates. In ungulates the palate is generally broader than the muzzle; thus, the relative width value is larger than 1. In ground sloths the palate is always narrower than the muzzle, and the relative muzzle width is always less than 1. *Lestodon armatus* shows the lowest value and *Megatherium americanum* the highest. Within the mylodontines, *Glossotherium robustum* has the second lowest value after *Lestodon armatus*, and *Mylodon darwini* has the highest. The scelidotherine *Scelidotherium leptocephalum* shows intermediate values between *M. darwini* and *G. robustum*.

Following Janis and Ehrhardt (1988), a relatively narrow muzzle is important for those species that feed selectively on certain plants or parts of plants. In contrast, bulk-feeders have relatively wider muzzles. Application of this pattern to the ground sloths suggests that the wide-muzzled *Lestodon armatus* and *Glossotherium robustum* have morphologies consistent with bulk-feeding, while the muzzles of *Scelidotherium leptocephalum* and *Mylodon darwini* are more consistent with selective-feeding. The megatheriine *Megatherium americanum*, with the narrowest muzzle, would represent the most selective-feeder.

*TABLE 3. Relative muzzle width of ground sloths*

| Taxa | PW | MMW | RMW |
|---|---|---|---|
| *Glossotherium robustum* | | | |
| MLP 3-136 | 59.5 | 148 | 0.40 |
| MLP 3-137 | 70.5 | 166 | 0.42 |
| MLP 3-138 | 54 | 160 | 0.34 |
| MLP 3-140 | 76 | 175 | 0.43 |
| MACN 11769 | 79 | 157 | 0.50 |
| MMP 1489-M | 84.5 | 170 | 0.49 |
| MMP 1490-M | 70.5 | 175 | 0.40 |
| | | | X = 0.42 |
| *Lestodon armatus* | | | |
| MLP 3-29 | 64 | 210 | 0.30 |
| MLP 3-30 | 69 | 250 | 0.27 |
| MLP 3-3 | 73 | 250 | 0.29 |
| MMP 47-S | 62 | 245 | 0.25 |
| | | | X = 0.27 |
| *Mylodon darwini* | | | |
| MLP 3-764 | 79 | 157 | 0.50 |
| MLP 3-762 | 85 | 122 | 0.69 |
| MACN 15348 | 44 | 124 | 0.35 |
| MNHN-BOL-V 006470 | 68 | 89 | 0.76 |
| | | | X = 0.57 |
| *Scelidotherium leptocephalum* | | | |
| MLP 3-671 | 33.5 | 65.5 | 0.51 |
| MMP 9-S | 26 | 55 | 0.47 |
| MMP 31-S | 36.5 | 81 | 0.45 |
| MMP 127-S | 36 | 69 | 0.52 |
| MMP 157-S | 33 | 64 | 0.52 |
| MMP 458-S | 26 | 54 | 0.48 |
| MMP 549-S | 39 | 67 | 0.58 |
| MMP 614-M | 32 | 65.5 | 0.49 |
| MMP 1155-M | 33 | 79 | 0.42 |
| | | | X = 0.49 |
| *Megatherium americanum* | | | |
| MLP 2-64 | 60 | 89 | 0.67 |
| MACN 5002 | 54.5 | 60 | 0.90 |
| MACN 15154 | 60 | 65 | 0.92 |
| MACN 6 P | 52.5 | 54 | 0.97 |
| MACN 2832 | 61 | 80 | 0.76 |
| | | | X = 0.84 |

PW, palatal width. MMW, maximum muzzle width. RMW, relative muzzle width. X, mean.

Our analyses of muzzle shape following Solounias et al. (1988) and Solounias and Moelleken (1993a) complement the information given above on the possible dietary categories (Fig. 8). *Lestodon armatus* has the widest muzzle, followed by *Glossotherium robustum*, suggestive of less selective feeding ecologies. With their narrower muzzles, *Scelidotherium leptocephalum* and *Mylodon darwini* are more likely to have been selective feeders. With the narrowest muzzle of all, *Megatherium americanum* may have been the most selective feeder.

# DISCUSSION

## Muzzle Reconstruction

The homology of some of the muscles studied is not clear. One case is that of the *M. buccinator*. Naples (1985) based her nomenclature on the work of Rinker (1954), who in turn used that of Meinertz (1935), among others. Saban (1971) considered that Meinertz's *M. buccinator pars intermaxillaris* was a

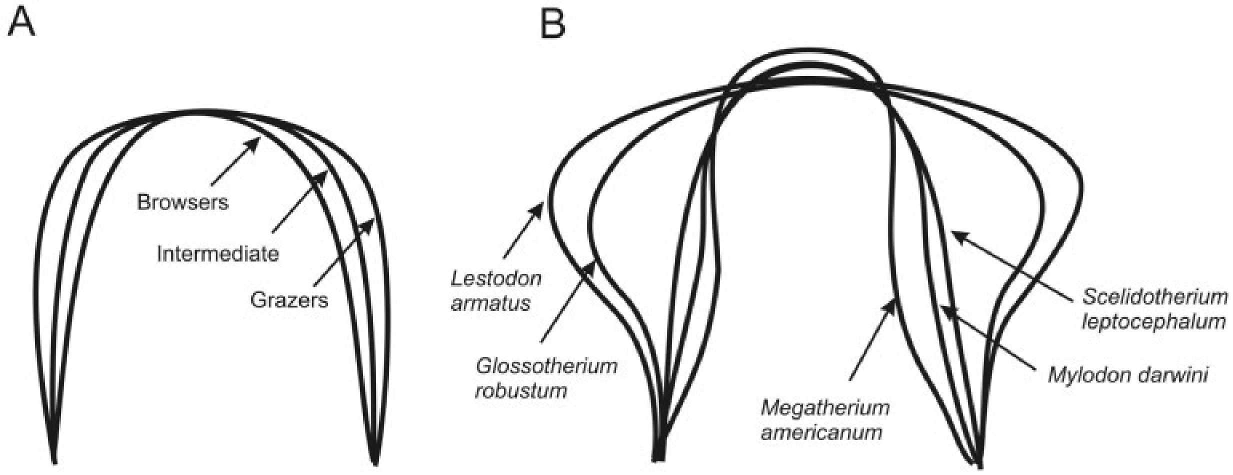

Fig. 8. **A:** Dietary categories of ungulates as inferred from the shape of the muzzle following Solounias and Moelleken (1993a, fig. 1). **B:** Shape of the muzzles of ground sloths.

synonym of the *M. buccinator pars supralabialis* of Boas and Paulli (1908). On the other hand, Clifford and Witmer (2004a) consider the *m. incisivus superior* as homologous with the *M. buccinator pars supralabialis* of Boas and Paulli (1908), indicating homology with Naples' *M. buccinator pars intermaxillaris*, a muscle she could not identify in living sloths, probably because they lack it as a specialization. Following Clifford and Witmer (2004a,b), in ungulates the *m. incisivus superior* is a fan-like muscle arising from the rostral part of the premaxillae, inserting on the upper lip and on the underside of the rhinarium that acts in elevating and/or everting the upper lip and retracting the muzzle. The homology of some other muscles described for ungulates by Witmer et al. (1999) and Clifford and Witmer (2004a,b), such as the *malaris*, *depresor labii superioris* and *nasalis*, remains uncertain to us, and they could not be reconstructed following Naples' (1985) descriptions. Another example is the *nasolabialis profundus* (= *lateralis nasi*?), which following Naples (1985) is reduced or simplified in Pilosa, including three parts in sloths and five parts in vermilinguas, but is described by Witmer et al. (1999) and Clifford and Witmer (2004a,b) as a single muscle. Other muscles described by Naples (1985) as absent in living sloths, but present in living vermilinguas (*m. nasolabialis profundus pars interna* and *pars media superior*) cannot be reconstructed in ground sloths with confidence. The reconstruction of some muscles with no bony attachments such as the *m. orbicularis oris* is highly speculative. The *m. nasolabialis profundus pars anterior* arises from cartilages and inserts on soft tissues.

The contributions on the masticatory apparatus of two fossil ground sloths of North America *Nothrotheriops shastense* and *Paramylodon harlani* (see Naples, 1987, 1989, respectively) paid partial attention to the muzzle reconstruction. That author proposed the presence of large nasal cartilages and abundant soft tissue extending beyond the premaxillae, as suggested by the large nasal openings and the long predental spout, and the presence of a flexible upper lip in both ground sloths to aid in food manipulation, but did not consider the relevant musculature.

The shape and size of the narial aperture in ground sloths are limited by the *cartilago cupularis, processus cupularis*, and *processus alaris superior*. These elements usually extend beyond the bony nasal cavity and their reconstructions are very speculative. However, our interpretations were conservative; i.e., they do not surpass the projected outlines of the distal margins of the nasals, maxillae, and premaxillae (see Figs. 4B, 5B, 6B, 7B).

A phylogenetically important feature of the xenarthran muzzle is the septomaxilla. Whether or not this bone is homologous with that of monotremes, and other Mesozoic mammals (see Wible et al., 1990, Zeller et al., 1993, for further discussion), its presence in both *Tamandua* and *Choloepus* suggests that it was present in the common ancestor of Tardigrada and Vermilingua, and that its absence in *Bradypus*, the sister taxon of all the remaining Tardigrada, is derived within Xenarthra (Zeller et al., 1993; Gaudin, 2004). Consequently, it would be expected to be present in all the taxa studied here. However, it is unknown in the few well-preserved fossil Tardigrada and Vermilingua skulls known, probably due to the small size of this bone and the apparent lack of sutures with other bones (Zeller et al., 1993). Moreover, its function (if any) is unknown, and its reconstruction would be not only speculative but also irrelevant.

## Muzzle and Feeding Behavior in Pleistocene Ground Sloths

Some authors have inferred the feeding habits for South American fossil tardigrades, including some of the species considered here. Based on the morphology of the calcaneum, Scillato-Yané (1977) suggested that grasses were the basis of the diet of both Megatheriinae and Mylodontidae, but without any morphofunctional or ecomorphological analysis of the masticatory apparatus. The only direct evidence is from late Pleistocene fossil dung preserved with skeletal and skin remains at Mylodon Cave, Southern Chile. From this it has been inferred that the diet of *Mylodon darwini* at that specific time, geographic region, and season the remains were deposited comprised mostly grasses (Gramineae) and sedges (Cyperaceae) (Moore, 1978). McDonald (1987) indicated that the Plio-Pleistocene Scelidotheriinae were selective feeders because the long and narrow muzzle was appropriate for selecting plant parts. He proposed that *Scelidotherium leptocephalum* probably searched for underground food with the help of its forelimbs, although feeding on other plant material above, but near the ground level, was also possible. Biomechanical analysis of the forelimbs of this species by Bargo et al. (2000) and Vizcaíno et al. (2001) indicates clear adaptations to digging, and the degree of hypsodonty suggests an abundance of grit in the food (Bargo et al., in press), which is in accordance with its provenance from below or near ground level in relatively open environments. Bargo (2001a) concluded that *Glossotherium robustum* and *Lestodon armatus* were bulk feeders, *Mylodon darwini* was a mixed feeder, and *Scelidotherium leptocephalum* was a selective feeder specialized on succulent plant material, e.g., fruits, buds, and tubers, although it could also browse on bushes and grasses.

Fariña (1996) proposed a singular hypothesis on the basis of a study of the trophic relationships between the South American Lujanian and North American Rancholabrean (both ages being Late Pleistocene/Early Holocene) megamammals, on the basis of body size and its ecological implications. That author proposed that ground sloths, especially *Megatherium*, were opportunistically carrion eaters. Biomechanical and morphofunctional evidence provided by Bargo (2001b) indicates that *M. americanum* would have been a generalized selective feeder, capable of consuming tough items, i.e., browsing for small branches, leaves, and fruits, while meat (carrion?) cannot be discounted. Wroe et al. (2004) suggested that there was an apparent lack of large mammalian omnivores in both Australia and pre-GABI South America, which might indirectly support the contention that some xenarthrans were more opportunistic feeders than previously supposed.

The reconstruction of the muzzle in fossil mammals can be crucial in understanding food intake styles, and hence insightful in interpreting feeding habits and defining niches in a paleoecologic context. However, this subject has rarely been considered in paleobiological reconstruction. Only a few articles have devoted attention to the muzzle reconstruction in fossil mammals, using phylogenetically closely related living forms as models for comparison (e.g., Solounias et al., 1988; Solounias and Moelleken, 1993a,b). This sort of approach may be particularly important when dealing with extinct animals that have no clear analogs among living relatives, as is the case for the ground sloths.

As mentioned above, although data on muzzle shape and width in ungulates cannot be directly compared with values obtained for ground sloths, they provide a framework for tentatively assigning them to certain dietary categories. Following the idea proposed by Owen-Smith (1982), and applied to living and extinct ungulates (Solounias et al., 1988; Solounias and Moelleken, 1993a), that narrow muzzles are important for animals that feed selectively on certain plants or parts of plants, in each lineage narrower muzzles could be related to selective feeding, and wider muzzles with bulk feeding. An analogy occurs even among ungulates: equids are less selective feeders than grazing ruminants; however, their relative muzzle width is smaller, suggesting that direct comparisons must be limited to within lineages (Janis and Ehrhardt, 1988). The same concept has been applied to sloths (see Vizcaíno and De Iuliis, 2003; Vizcaíno et al., in press, for a discussion on phylogenetic constraints in xenarthrans). Based on the shape and proportions of the predental spout of the mandible and premaxillae, McDonald (1997) proposed that Early Miocene sloths were browsers, and that wider muzzles begin to develop in the post-Miocene mylodontids, reaching its maximum expression with the Pleistocene ground sloths, in relation to a change to more grazer forms and/or more open environments. Following this criterion, and according with our analysis, within the mylodontid ground sloths *Glossotherium robustum* and *Lestodon armatus* would be bulk-feeders, while *Scelidotherum leptocephalum* and *Mylodon darwini* would be mixed or selective feeders. The megatheriid *Megatherium americanum* would be the most selective feeder ground sloth.

The shape of the muzzle of ground sloths is also reflected in the shape of the predental spout (symphysis) of the mandible, so even an isolated jaw could be used to identify dietary categories. The mandibular symphysis forms a rigid and stout structure in adult ground sloths (it fuses early during ontogeny), so it should be considered when analyzing the modes of food procurement (see below).

In the wide-muzzled ground sloths, *Glossotherium robustum* and *Lestodon armatus*, the premaxillae are weakly articulated to the maxillae, so they are usually lost, and there is no trace of the presence of an arch or ossified nasal cartilage. In the narrow-muzzled *Mylodon darwini*, *Scelidotherium leptocephalum*, and *Megatherium americanum*, the premaxillae are completely fused to the maxillae. Even more, in *M. darwini* the premaxillae form a strong anterior ascending process that fused with a descending process of the nasals, forming an unusual complete arch, which was extensively described by Kraglievich (1934). *Scelidotherium leptocephalum* also possesses an ascending process on the premaxillae, apparently supporting the nasal cartilage. In one specimen the nasal cartilage was ossified, forming a structure analogous to that of *M. darwini* (McDonald, 1987). A similar condition occurs in aged individuals of *M. americanum*, in which the distal ends of the premaxillae develop ascending processes, but which do not reach the nasals.

These different morphologies may be related to differences in the way food was taken into the oral cavity. In narrow-muzzled forms, like *Mylodon darwini* and, to a lesser extent *Scelidotherium leptocephalum*, the muzzle constituted a robust structure that, combined with the fused symphysis, is consistent with adaptation to resist considerable stress, suggesting that the processing of favored plant materials required significant effort. In *M. darwini* at least, the degree of fusion of the premaxilla and maxilla, the stout nasal arch, and the loss of the first upper tooth suggest the presence of a horny structure on the premaxilla, analogous to the premaxillary pads in bovids, that would aid in clipping or tearing off the food. The muzzle of *Megatherium americanum* is even narrower, particularly compared with the remaining parts of the skull, and very robust. The symphysis is also very stout and the tip is directed downward instead of upward, as in mylodontids. The long predental space suggests that the presence of a strong and movable upper lip, as inferred from the muscle reconstruction, was involved in food intake. The *buccinator pars intermaxillaris* (= *incisivus superior*), a muscle that retracts the upper lip in different ways, depending on the position of the fibers applied, appears to be well developed in the narrow-muzzled ground sloths (Figs. 4C, 6C, 7C), especially in *M. americanum*. This fact could indicate the presence of a thick, cone-shaped, and prehensile upper lip, useful for food intake, as in the black rhinoceros. The prehensile lip of this species enables it to selectively take leaves/twigs, whereas the broad nonprehensile lip of the white rhinoceros is used to crop short grasses and herbaceous plants.

Kraglievich (1921) suggested that, because of the extreme width of their muzzles and shovel-shaped mandibular symphyses, mylodontines (*Glossotheriun* and *Lestodon*) first removed soil with their forelimbs in order to efficiently access grasses and roots. Our analysis clearly indicates that the wide muzzles of *G. robustum* and *L. armatus* allowed them to procure great amounts of food, and demonstrates that, regarding muzzle morphology, they were the best-adapted of all ground sloths to a grazing niche. The upper lip, formed by the *buccinator pars intermaxillaris* (= *incisivus superior*), was probably square-shaped and not prehensile (Fig. 5C), as in the white rhinoceros. This fact, coupled with the absence of incisors, indicates that *G. robustum* and *L. armatus* simply used the upper lip to grasp grass against the lower lip, pulling up to clip it.

Finally, the action of the tongue cannot be neglected when considering food intake. Studies in progress on the hyoid apparatus of several ground sloths reveal that the tongue of forms like *Glossotherium* would have been quite movable and protractile, helping to pull out plants in the manner of cows. This capacity must have been reduced in *Scelidotherium* and, especially, in *Megatherium*. We are unfamiliar with the hyoids of *Lestodon* and *Mylodon*, but judging from the shape of the mandible these are most similar to *Glossotherium* and *Scelidoterium*, respectively.

## CONCLUSIONS

1. The preservation of the nasal septum and scars for muscular attachment in the rostral part of the skull allows conservative reconstruction of the muzzle anatomy in fossil sloths.
2. The most conspicuous feature is the muscular attachment of the *buccinator pars intermaxillaris (= incisivus superior*). The complex function of this muscle complements the action of the *m. dilatator nasi* and *m. nasolabialis* in retracting the lip. In wide-muzzled sloths (*Glossotherium* and *Lestodon*) it forms a squared, nonprehensile upper lip (Fig. 5D), while in the narrow-muzzled (*Megatherium*, *Mylodon*, and *Scelidotherim*) it forms a cone-shaped and prehensile lip (Figs. 4D, 6D, 7D).
3. Our analysis of muzzle anatomy complements previous studies of other oral data, and on these bases we postulate the following models of feeding behavior in fossil sloths:

i) Wide-muzzled sloths (*Glossotherium* and *Lestodon*) were mostly bulk-feeders, and the lips coupled with the tongue were used to pull out grass and herbaceous plants.

ii) Narrow-muzzled sloths (*Mylodon*, *Scelidotherium*, and *Megatherium*) were mixed or selective feeders, with a prehensile lip that was used to select particular plants or plant parts.

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