The ground sloth *Megatherium americanum*: Skull shape, bite forces, and diet

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Megatherium americanum (late Pleistocene of South America) has traditionally been regarded a herbivore, but its dietary habits have not been considered in terms of a morphofunctional analysis. This study describes and analyses the morphology of the masticatory apparatus in order to interpret the jaw mechanics of *M. americanum*, and thus to infer its diet and behaviour. The results are compared with those for the mylodontid *Glossotherium robustum* and the extant sloth *Bradypus variegatus*. The areas of origin and insertion of the masticatory musculature were reconstructed, and the moment arms generated by this musculature were estimated so that the mechanics of the feeding apparatus might be described. These analyses indicate that *M. americanum* was well adapted for strong and mainly vertical biting. The teeth are extremely hypsodont and bilophodont, and the sagittal section of each loph is triangular with a sharp edge. This suggests that the teeth were used mainly for cutting, rather than grinding, and that hard and fibrous food was not the main dietary component. The diet of *M. americanum* merits more rigorous analysis, but the evidence provided here indicates that it probably had a browsing diet in open habitats, but also could have fed on moderate to soft tough food.

Key words: Xenarthra, Tardigrada, *Megatherium*, biomechanics, mastication, diet.

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Introduction

The first fossil sloth (Xenarthra, Tardigrada) to be discovered was *Megatherium americanum*, in 1788 in Luján, Argentina. Since its description by Cuvier (1796) this giant ground sloth has gained the attention of many palaeontologists. It is the largest of all ground sloths, with an estimated body mass of about 4 tonnes (Casinos 1996; Fariña *et al.* 1998). Other genera of large Pleistocene ground sloths were discovered soon after *M. americanum*, but the latter is undoubtedly the most representative mammal of the Lujanian (late Pleistocene–early Holocene) fauna of the Pampean region.

Traditionally, ground sloths were placed into three families, Megatheriidae, Mylodontidae, and Megalonychidae, which are considered to be monophyletic groups. The Nothrotherinae, including various Santacrucian genera (e.g., *Hapalops*, *Eucholoeops*, *Pelecyodon*) and the Plio-Pleistocene nothrotheres (e.g., *Nothrotherium*, *Nothrotheriops*) have been alternatively considered megatheriids or megalonychids. However, this assemblage has been recognized as paraphyletic. The Plio-Pleistocene taxa form a monophyletic group, for which familial distinction has recently been advanced (the Nothrotheriidae), while the Santacrucian 'nothrotheres' remain as successive outgroups to the other ground sloths. Of the extant tree sloths, *Bradypus* apparently represents the sister-taxon to all other sloths, while *Choloepus* is a megalonychid (see Gaudin 1995, and references therein).

For more than a century general speculations on the dietary preferences of ground sloths have been proposed, but without explanations of how the conclusions were reached. Essentially, they have always been considered herbivorous, primarily by analogy with living tree sloths. Owen (1842, 1851) considered that giant sloths fed on the foliage of trees. Stock (1925) stated that megatheres, together with megalonychids and nothrotheres, were probably browsers, whereas mylodontids were grazers. Winge (1941: p. 364) noted that *Megatherium* 'has progressed farthest in specialisation as a plant feeder' and that it 'must undoubtedly have fed on unusually tough leaves which required much power of mastication.' However, the great variation in skull and dental morphology, body size and proportion among ground sloths suggests that they had diversified to fill a variety of niches.

The marked differences in the skeletal and dental anatomy of ground sloths and other mammalian herbivores, and the lack of recent analogues, makes it difficult to interpret the ecology of ground sloths, particularly of their dietary habits. Even the extant tree sloths are too specialised to provide good models. They are small mammals (less than 10 kilograms) that spend much of their lives suspended from the branches of trees and are barely able to travel on the ground (Mendel 1985).

In a detailed analysis of the dietary preferences and ecology of the Plio-Pleistocene scelidotheres, McDonald (1987) suggested that these ground sloths were probably selective feeders (according to Guthrie's 1984 classification), because the narrow anterior part of the skull was best suited for the selective harvesting of plant parts. Naples' (1987, 1989) studies of the masticatory apparatus of the North American sloths *Nothrotheriops shastense* and *Glossotherium harlani* concluded that the former was a selective browser and the latter a browser-grazer, rather than a strict grazer. McDonald (1995) hypothesized that *Megalonyx* and *Eremotherium* were browsers. The dietary habits of *Megatherium americanum*, however, have not been considered in terms of a detailed morpho-functional analysis of its masticatory apparatus.

This study describes and analyses the morphology of the masticatory apparatus of *M. americanum* in order to interpret jaw mechanics and to infer diet and ecology. The results are compared with those for the mylodontid *Glossotherium robustum* and the extant *Bradypus variegatus*, as Naples (1982, 1985, 1989) has already considered various aspects of the masticatory apparatus for these genera. Further, the comparison is interesting from the phylogenetical perspective because *Glossotherium* is considered a plesiomorphic taxon within the mylodontids (Perea 1992, 1998) and *Bradypus* the sister-taxon to all other sloths (Gaudin 1995).

Abbreviations. — MLP, Museo de La Plata, Argentina; MACN, Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina; MPEG, Museu Paraense Emilio Goeldi, Belém, Brasil; FMNH, Field Museum of Natural History, Chicago, USA; RFTRA, Resistant Fit Theta-Rho Analysis; m., musculus.

Material

Megatherium americanum

MLP 2-64, skull and mandible, with part of the hyoid apparatus. Pampean Formation, Argentina. Figured in Lydekker (1894: pl. 45: 1)

MLP 2-56, complete mandible. Pampean Formation. Argentina. Figured in Lydekker (1894: pl. 45: 1a).

MACN 1000, nearly complete mounted skeleton. Río Salado, Buenos Aires Province, Argentina.

Megatherium gallardoi

MACN 5002 (TYPE), skull and mandible, femur, humerus and ulna. Palermo, Buenos Aires, Argentina. Figured in Ameghino and Kraglievich (1921).

Megatherium sp.

Museo Universitario C. y F. Ameghino, No. 899, nearly complete skull and complete mandible of a juvenile; fragments of postskeleton and caudal vertebrae. Río Carcarañá, La Casilda, Santa Fe Province, Argentina.

Glossotherium robustum

MLP 3-137, skull, mandible, and part of the skeleton. Pampean Formation, Olivera, Buenos Aires Province, Argentina.

MLP 3-138, skull, mandible, and skeleton. Pampean Formation, San Antonio de Areco, Buenos Aires Province, Argentina. Figured in Lydekker (1894: pl. 51).

MLP 3-140, skull, mandible, and skeleton. Pampean Formation, Olivera (Río Luján), Buenos Aires Province, Argentina. Figured in Lydekker (1894: pls. 49, 50: 1, and 52: 1).

Bradypus variegatus

MPEG 21809, skull and mandible. Parque Zoobotânico do Museu Paraense Emilio Goeldi, Belém, Brazil.

Methods

Various studies on extant mammals have demonstrated the correlation between diet and form of the skull, jaws, dentition and musculature (Maynard Smith & Savage 1959; Turnbull 1970; Moore 1981; Smith 1993; Janis 1995). Such studies have been useful in the reconstruction of the masticatory musculature of fossil mammals and provide a framework for the analysis of diet and behaviour in edentates (Naples 1987, 1989; Vizcaíno 1994; Vizcaíno & Fariña 1997; Vizcaíno & Bargo 1998; Vizcaíno *et al.* 1998; De Iuliis *et al.* 2000).

The masticatory muscles of *Megatherium* were reconstructed in order to estimate the moment arms of their lines of action, with the craniomandibular joint as pivot. The occlusal patterns and mandibular movements were determined through study of the craniomandibular joint, the form and arrangement of the dentition, including occlusal

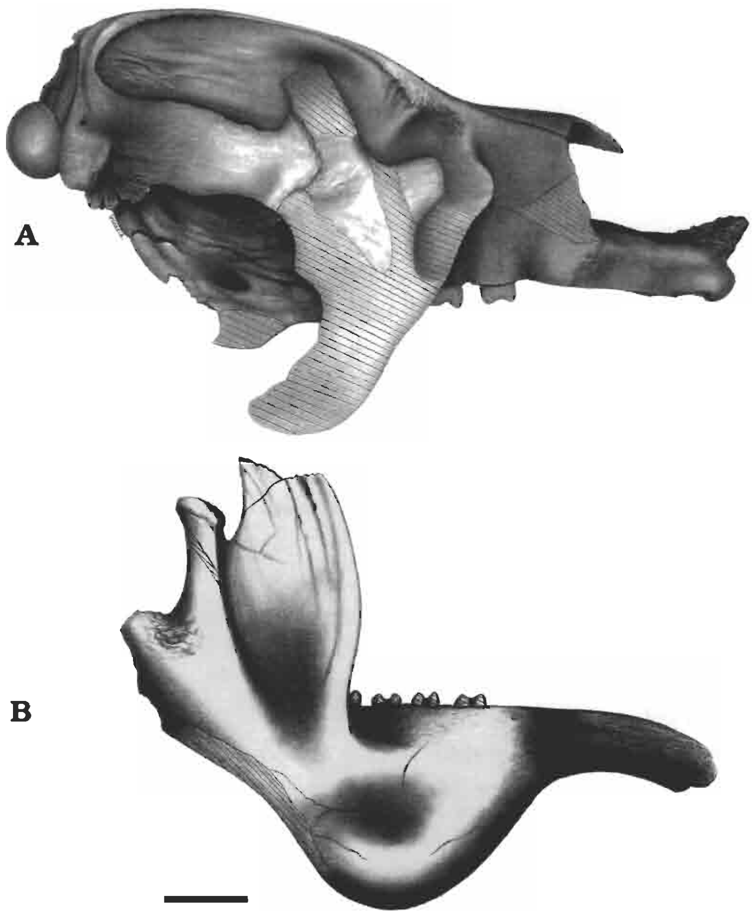

Fig. 1. Skull (**A**) and mandible (**B**) of *Megatherium americanum* (MLP 2-64) in lateral view. Scale bar 10 cm.

wear patterns, and the form and structure of the mandibular symphysis. Morphometric analyses were performed to evaluate differences with *Glossotherium robustum* and *Bradypus variegatus*.

Masticatory musculature. — The estimation of the moment arms requires an interpretation of the form and position of the masticatory musculature. The areas of origin and insertion of the muscles were reconstructed based on features of the skull and mandible (Turnbull 1976; Finch 1982; De Iuliis 1988), following the patterns of musculature in modern mammals (Maynard Smith & Savage 1959; Turnbull 1970), particularly those in the tree sloths *B. variegatus* and *Choloepus* (Sicher 1944; Naples 1985). The attachment sites of the muscles are indicated by features such as muscular scar lines, ridges, and crests. These suggest the attachment of aponeuroses and tendons; the texture of the attachment surfaces indicate fleshy or tendinous origins and insertions. In extinct mammals the position of the muscles is often reasonably clear due to the presence of these features. However, knowledge of the muscular arrangement in the nearest living relatives is essential. The musculature reconstructed for this analysis in-

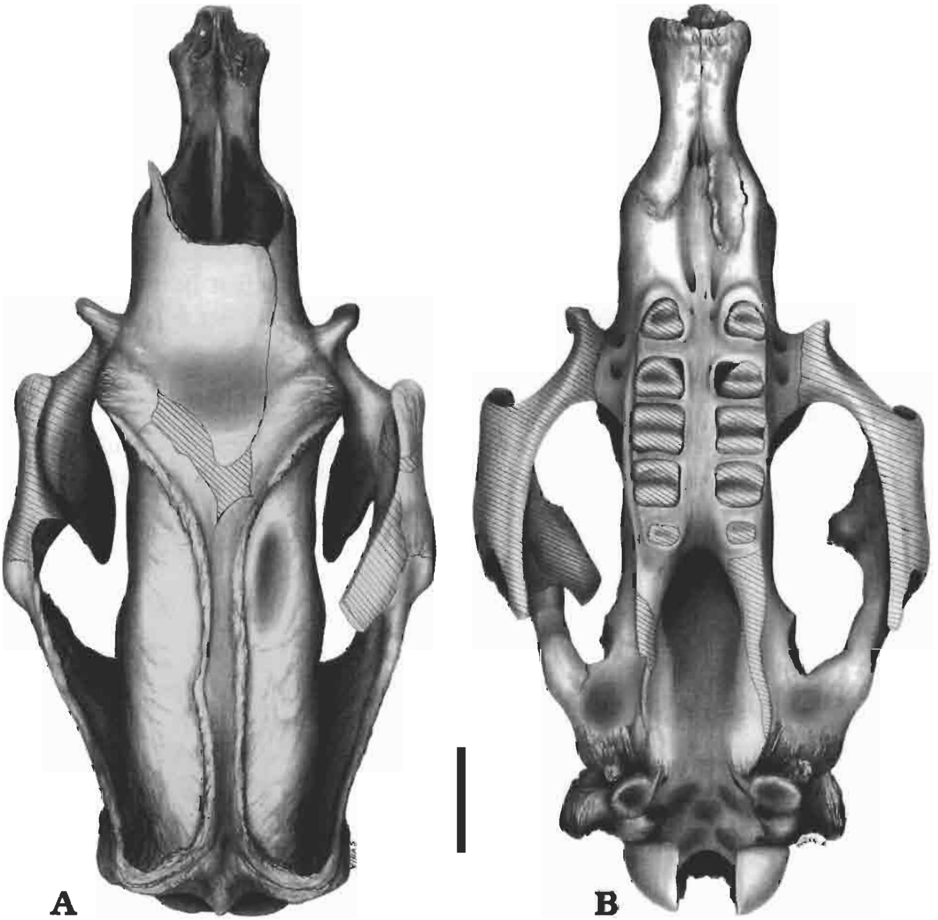

Fig. 2. Skull of *Megatherium americanum* in dorsal (**A**) and ventral (**B**) views (MLP 2-64). Scale bar 10 cm.

cludes the 3 jaw-closing muscles groups: temporalis, massetericus and pterygoideus (Turnbull 1970).

Moment arms. — The moment arms of the lines of action of the temporalis and massetericus muscles were estimated so that the mechanics of the masticatory apparatus of *M. americanum* could be described and compared with those of *G. robustum* and *B. variegatus*. The total lengths of the mandibles were standardised to allow comparison among forms of different sizes. A method proposed by Vizcaíno *et al.* (1998) was used, which allows comparisons between fossil and extant mammals. For the massetericus the lines of action were estimated from the most anterior and posterior positions of the origin and insertion. For the temporalis, they were estimated from the most anterior, middle, and most posterior origins on the skull, and from a single insertion on the coronoid process. In this way average values for the moment arms were obtained independently of the line of action of the muscle. Interpretations on the relationships between bite force and velocity may be made by comparing the proportions of the combined moment arms of the massetericus and temporalis to those of different tooth positions (i.e., the anteriormost, middle, and posteriormost teeth).

Shape analysis. — The shapes of the skull and mandible were analysed using a morphometric procedure that allows the determination of patterns of morphological variability and change. This technique, Resistant Fit Theta-Rho Analysis (RFTRA), analyses changes in shape through the superimposition of one form onto another (base and target specimens respectively) using the position of landmarks (homologous and geometrical points). RFTRA identifies and measures the homologous regions of change in shape by establishing congruence among those that have not changed (Benson *et al.* 1982; for detailed information see Chapman 1990a, b, and references therein). Although RFTRA has been applied especially to identify shape variability in a taxonomical context, it has also been demonstrated as useful in morpho-functional interpretations (Chapman 1990b; Vizcaíno & Bargo 1998; Vizcaíno *et al.* 1998). The skull and lower jaw of *M. americanum* were compared in lateral view with those of *Glossotherium robustum* and *Bradypus variegatus* (as the base specimens).

Results

Cranial morphology

Extensive descriptions of the skull and mandible of *Megatherium americanum* were given by Owen (1856), Lydekker (1894), Ameghino & Kraglievich (1921) and De Iuliis (1996). This section deals with the description of those features of the cranium that are relevant for analysis of the mechanics of the masticatory apparatus.

Skull. — The skull shape of *M. americanum* differs strongly from that of other Pleistocene ground sloths (Figs. 1 and 2). Its general form is approximately cylindrical, but the cranial and rostral regions are narrow. This feature contrasts notably with the slender and elongated skull of *Scelidotherium* (Scelidotheriinae) or the prismatic-rectangular and anteriorly widened skull of *Glossotherium robustum* (Mylodontinae, Fig. 3).

The premaxillae are stout, elongated and quadrangular, although the shape and length vary considerably in different specimens (De Iuliis 1996). They became fused firmly to each other and the maxillae with age, and are thus often preserved with the skull. In *G. robustum* and *Bradypus variegatus* the premaxillae are arrowhead-shaped and loosely fused to the maxillae. This contributes to the frequent loss of these bones in these taxa, as well as in most fossil sloths.

In lateral view, the maxilla of *M. americanum* is approximately trapezoidal, and the alveolar or ventral margin is nearly straight. The edentulous part from M1 to the maxillo-premaxillary suture varies notably in length.

The zygomatic arch of *M. americanum* is large and robust (Fig. 1). The jugal consists of an approximately quadrangular body with five processes. The ascending and descending processes are well developed, and their orientations vary. The ascending process may incline posterodorsally, while the more robust descending process extends posteroventrally. The anterior and posterior parts of the zygomatic arch may be in contact, unlike the condition in many other sloths, but usually are not fused, except in some aged individuals (De Iuliis 1996). In *G. robustum* and some other ground

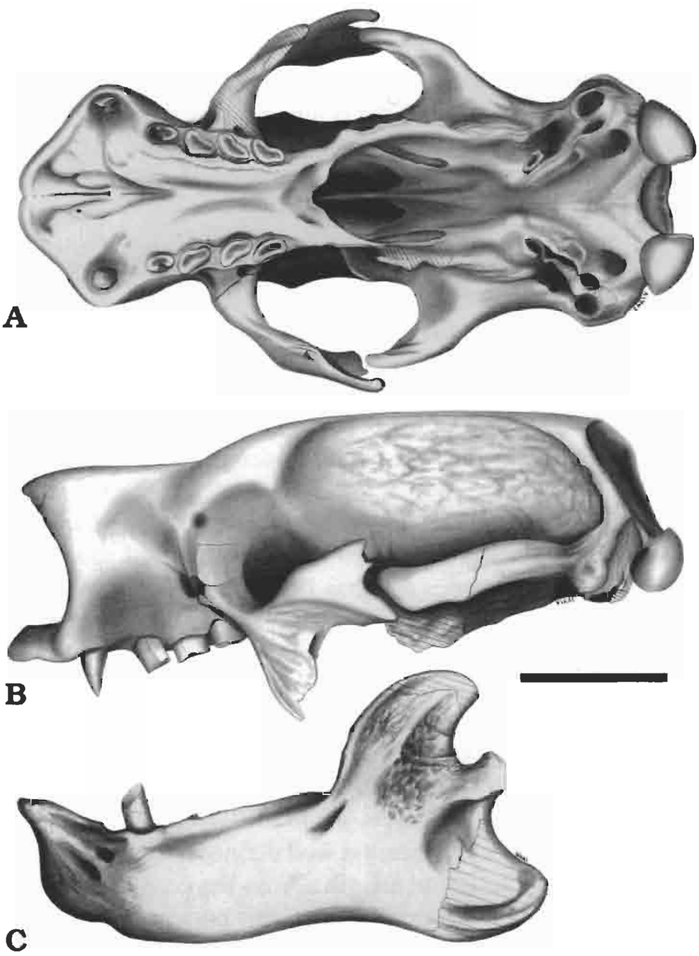

Fig. 3. *Glossotherium robustum* (MLP 3-137). Skull in ventral (**A**) and lateral (**B**) views; mandible in lateral (**C**) view. Scale bar 10 cm.

sloths the anterior and posterior parts of the arch are very close, but never fuse (Fig. 3). Finally, *B. variegatus* (as well as *Choloepus*) has an interrupted zygomatic arch, connected by ligaments (Naples 1982).

The pterygoid in *M. americanum* is prominent and forms a broad blade, as is common in sloths. It varies considerably in shape and size, but does not descend as far ventrally below the alveolar border (De Iuliis 1996). The external surface is roughened, and shows scars for the origin of the pterygoideus muscle. *G. robustum* and *B. variegatus* have a similar pterygoid morphology, with minor changes in size and shape.

Craniomandibular joint (CMJ). — The CMJ in *M. americanum* is located well above the occlusal plane. The glenoid fossa is poorly defined, with a shallow depression on the squamosal process, which allows the mandibular condyle great freedom of motion. The mandibular condyle is also raised well above the occlusal plane, as expected for a herbivorous mammal. It is wider mediolaterally than anteroposteriorly, and projects farther medially than laterally relative to the coronoid process. The CMJ in *Glossotherium robustum* has a similar morphology to that of *Megatherium americanum*, except for its position, which is approximately at the level of the tooth row (see Naples 1989). In *Bradypus variegatus* the condyle is raised above the occlusal plane, so the CMJ is also located dorsal to the level of the tooth row. The glenoid fossa is troughlike, and the articular condyle is single, oval in shape, with the long axis oriented anteroposteriorly (Naples 1982).

Mandible. — The shape of the mandible of *M. americanum* differs considerably from those of *G. robustum* and *B. variegatus*, and, in general, from those of other mylodontids. There are two features which easily distinguish it: the ventral margin forms a prominent bulge and the molariform teeth are functionally similar and form a continuous series, without diastema. The ventral bulge reflects increased hypsodonty in this species (see below). In *G. robustum* and *B. variegatus*, on the contrary, the ventral margin of the mandible is almost straight, with the deepest part at the level of the last molariform tooth.

The robust symphysis is shallow dorsoventrally and fused in *M. americanum*, as in most ground sloths. It extends anteriorly to form an elongated and narrow predental spout. The length of the spout varies and may be greater than the toothrow length (De Iuliis 1996). In *G. robustum* the predental spout is shorter and broader. *B. variegatus*, which has the shortest rostrum, lacks a predental spout.

The coronoid process of the jaw is prominent and vertical in *M. americanum* and raised well above the level of the mandibular condyle. The dorsal part of the process curves posteriorly. In *B. variegatus* the coronoid process is also raised, but only slightly above the condyle. In *G. robustum* it is much lower, and more inclined and curved posteriorly.

In *M. americanum* the angular process is well defined, with the lateral surface convex and the medial concave. Its dorsal margin always lies considerably above the level of the occlusal plane, and the ventral margin inclines posterodorsally. In contrast, the angular process lies below the level of the occlusal plane in *G. robustum* and *B. variegatus*.

Dentition. — The dental morphology of sloths, as well as of other xenarthrans, is sufficiently distinct from that of other mammals that it is difficult to establish tooth homologies (their teeth are called molariforms or caniniforms pending on their location on the jaws, and their shape). Sloths have an open-rooted adult dentition and a reduction in number of teeth (the dental formula is generally 5/4). They lack enamel, a deciduous dentition, and the dental cuspation pattern observed in other mammals. They also reverse the typical mammalian pattern of tooth-alternating occlusion; that is, the maxillary teeth precede the mandibular teeth by half a tooth length (Owen 1842; Stock 1925; Naples 1982, 1989).

The teeth of *M. americanum* are molariform, extremely hypsodont, subequal in size, nearly square in cross section, and bilophodont. The teeth are equidistantly spaced in a continuous series and placed well posteriorly, leaving a long predental space (Figs. 1 and 2). The occlusal surfaces bear two prominent, sharp, and transversely oriented crests separated by a V-shaped valley, so an interlocking occlusion is observed (Fig. 4). In *G. robustum* the mesial tooth is a chisel-shaped caniniform tooth.

Fig. 4. Skull of a juvenile of *Megatherium* sp. showing the interlocking occlusion of the molariform teeth. Scale bar 10 cm.

The remaining molariform teeth are subtriangular to elliptical in section, with lobes of different sizes (Fig. 3). The tooth row is longer, and the predental spout is shorter and broader, than in *M. americanum*. *B. variegatus* has a shortened rostrum. The mesial tooth is peg or chisel-shaped, and less differentiated from the remaining cheek teeth, which are also peglike and oval or subrectangular.

The structure of the *M. americanum* tooth consists of three tissues: an extremely thick layer of cementum, a thin layer of orthodentine, and a modified orthodentine, which has low resistance to abrasion, forming the core (Ferigolo 1985). The cementum and modified orthodentine are easily abraded, leaving the orthodentine, interposed between these two tissues, to form the sharp, transverse crests. The molariform occlusal surfaces of *G. robustum* and *B. variegatus* are concave, due to the central soft dentine basin. The dentine is surrounded by a layer of orthodentine and then by a thin layer of cementum (Ferigolo 1985; Naples 1982). The outer hard dentine forms sharp-edged cutting surfaces. In the tree sloth the wear facets are more prominent and the sharp edges become 'cusps' with age (see Naples 1982, 1989).

The degree of hypsodonty in *M. americanum* (and other ground sloths) was measured (Bargo & De Iuliis 1999) using a hypsodonty index proposed by McDonald (1995). The index is independent of body size and obtained by dividing the maximum depth of the mandible by alveolar length of the tooth row. The results have shown that values for *M. americanum* are greater than for the other ground sloths, including its closest contemporary relative *Eremotherium*.

Masticatory musculature

Windle & Parson (1899), Edgeworth (1935), Urquiola de De Carli & Aramayo (1980) and Sicher (1944) give general descriptions of the masticatory musculature of living tree sloths. Urquiola de De Carli & Aramayo (1980) described also the masticatory musculature of *Megatherium* and *Scelidotherium*. More recently, Naples (1985) described extensively the form and function of the masticatory muscles of *Bradypus* and *Choloepus*. On this basis, Naples (1987, 1989) reconstructed the masticatory musculature in great detail, including the subdivisions of the temporalis, massetericus and pterygoideus, of the fossil species *Nothrotheriops shastense* and *Glossotherium harlani*. The nature and relationships of the skeletal features in *M. americanum* are such that they preclude as confident a reconstruction of the detail that Naples (1987, 1989) was able to achieve for the other fossil sloths. In any event, the scope of this paper does not require that it be reconstructed in such detail. Thus, only those features of the musculature that are relevant for analysis of the lines of action are described here.

M. temporalis. — This muscle is usually divided into superficial and deep portions in most living mammals (see Turnbull 1970), including tree sloths. Features that might indicate a division are ambiguous in *M. americanum*, and the temporalis is thus recognised as a unit. It arose from the scarred surface of the temporal fossa, and covered most of the dorsal and lateral parts of the frontal and parietal bones (Fig. 5). *M. americanum* lacks a sagittal crest, but the dorsal origin of the temporalis is marked by a prominent ridge, which extends anteriorly through the prominent postorbital processes, and posteriorly nearly to the margins of the nuchal crests. The temporalis inserted, probably tendinously as in other mammals (Turnbull 1970), on the roughened lateral, anterior, and medial surfaces of the well-developed coronoid process. In *G. robustum* the temporalis was large and thick relative to that of the tree sloths, and probably undivided (Naples 1989). Its origin and insertion do not differ in general pattern to that of *M. americanum*, but the origin was relatively more elongated than in *B. variegatus*, reflecting the relatively greater length of the skull. In *B. variegatus* the temporalis arose directly behind the orbit, but appears to have originated further anteriorly than in *Choloepus* due to the shortened facial region of *Bradypus* (Naples 1985).

M. massetericus. — The masseteric musculature is complex in nearly all mammals. It is usually subdivided into superficial and deep components and the zygomaticomandibularis. In some forms, such as ungulates and rodents, the massetericus may be further subdivided (see Turnbull 1970). Although the superficial and deep components of the massetericus may be recognised, the subdivisions of the massetericus superficialis cannot be reliably reconstructed in *M. americanum*. The massetericus superficialis arose laterally from the zygomatic arch, as is indicated by the scarred central and lower part of the jugal, and inserted mainly on the lateral surface of the angular process (Fig. 5). The massetericus profundus presumably arose (together with the zygomaticomandibularis) on the antero-medial surface of the descending process of the zygomatic arch, and inserted on the base of the coronoid process, ventral to insertion of the zygomaticomandibularis.

Naples (1985, 1989) recognised and described five subdivisions of the massetericus superficialis in tree sloths and *G. harlani*. The areas of origin and insertion do not differ markedly among these forms. The massetericus profundus of *G. robustum* arose from a smooth depression on the medial surface of descending process of the jugal, and inserted on the lateral surface of the mandibular ramus, anterodorsally to the massetericus superficialis (Naples 1989). In *B. variegatus* the massetericus profundus is

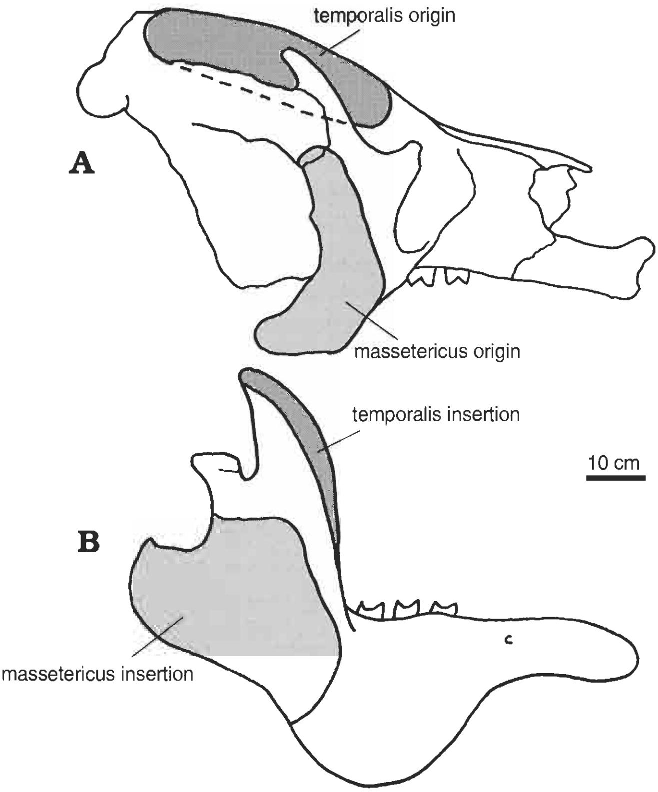

Fig. 5. Skull (**A**) and mandible (**B**) of *Megatherium americanum*. Reconstruction of areas of origin and insertion of the massetericus and temporalis muscles.

larger than in *Choloepus*, probably because the elongated ascending and descending processes of the jugal of the zygomatic arch provide more surface area for muscle fiber origin (Naples 1985).

The zygomaticomandibularis (= m. temporalis superficialis pars zygomaticomandibularis of Naples 1985, 1989) in *M. americanum* was probably relatively as large as those in *G. robustum* and *B. variegatus*. This is reflected in the ascending process of the jugal which is well developed and elongated in these forms, in contrast to *Choloepus* which lacks the elongated ascending process of the jugal. Thus, the zygomaticomandibularis in *M. americanum* probably arose from the scarred anteromedial surface of the dorsal part of the jugal, and inserted on the smooth depression of the masseteric fossa at the base of the coronoid process.

M. pterygoideus. — The pterygoid musculature in sloths is large relative to that of other mammals (Edgeworth 1935; Naples 1985; Turnbull 1970), and is subdivided as m. pterygoideus lateralis and medialis, as typically occurs in other mammals.

In *M. americanum* the medial pterygoideus arose from a depression in the lateroventral surface of the elongated pterygoid flange, and inserted on the concave and prominently scarred medial surface of the large angular process. M. pterygoideus lateralis originated on the lateral surface of the pterygoid hamulus, probably above

m. pterygoideus medialis, as occurs in tree sloths, and inserted in a roughened depression on the anterior edge of the mandibular condyle. This arrangement is very similar to that described by Naples (1985, 1989) for *B. variegatus* and *G. harlani*.

Jaw mechanics

The moment arms of m. massetericus (Mm) and m. temporalis (Mt) of *M. americanum*, *G. robustum* and *B. variegatus* were calculated from the mandibles standardised to 110 mm total lenght. The results are shown in Table 1.

Values for Mm are the same in *M. americanum* and *G. robustum*, while Mt is somewhat higher in *G. robustum*. Comparison between *B. variegatus* and *M. americanum* shows that the former has higher values, and the difference is more marked for the Mm.

The ratios of muscle moments to bite moments were also calculated. In this case, *M. americanum* has the highest values, not only for the posterior part of the mandible, but also for the anterior part.

Table 1. Comparison of the moment arms of the jaw muscles and bite points.

	Mm	Mt	r.Mb_1	r.Mb_2	r.Mb_3
Megatherium americanum	27	19	1.63	1.14	0.89
Glossotherium robustum	27	22	1.04	0.77	0.66
Bradypus variegatus	44	24	1.13	0.89	0.72

Mt, moment arm of temporalis. Mm, moment arm of massetericus. Mb_1, Mb_2 and Mb_3, moment arms of the bite points at the distal, middle and mesial tooth, respectively. r.Mb, ratio of muscle/bite, that is, the combined moment arm of the muscles (Mm + Mt) divided Mb_1, Mb_2, and Mb_3. Values are in milimeters and were calculated from the mandibles standardised to 110mm total lenght.

Shape analysis

RFTRA was used to compare in lateral view the shapes of the skull and mandible of *M. americanum* with those of *G. robustum* and *B. variegatus* as the base specimens. The landmarks used are shown in Fig. 6.

When compared with *G. robustum* the skull of *M. americanum* shows various differences (Fig. 7): the snout is extended anteriorly and slightly depressed dorsoventrally; the basicranium is elevated well above the alveolar plane; and the braincase is shorter. The zygomatic process of the squamosal and the ascending process of the jugal lie further dorsally, while the tip of the descending process of the jugal lies at nearly the same level as in *G. robustum*. Further, the molariform series is displaced posteriorly, leaving a long predental space. In the mandible of *M. americanum* the angular, condylar and coronoid processes are markedly displaced dorsally. The horizontal ramus, except at the well-developed ventral bulge, is shallower. The predental space is longer, due to the more distal tooth row.

The comparison of *M. americanum* with *B. variegatus* (Fig. 8) reveals the same general pattern: longer snout, elevation of the basicranium, shorter braincase, more dorsally positioned zygomatic arch, and molariform teeth displaced distally. In the mandible, the ascending ramus is also elevated but less so in comparison with *G. robustum*; the predental spout and the teeth are extended further mesially and distally respectively.

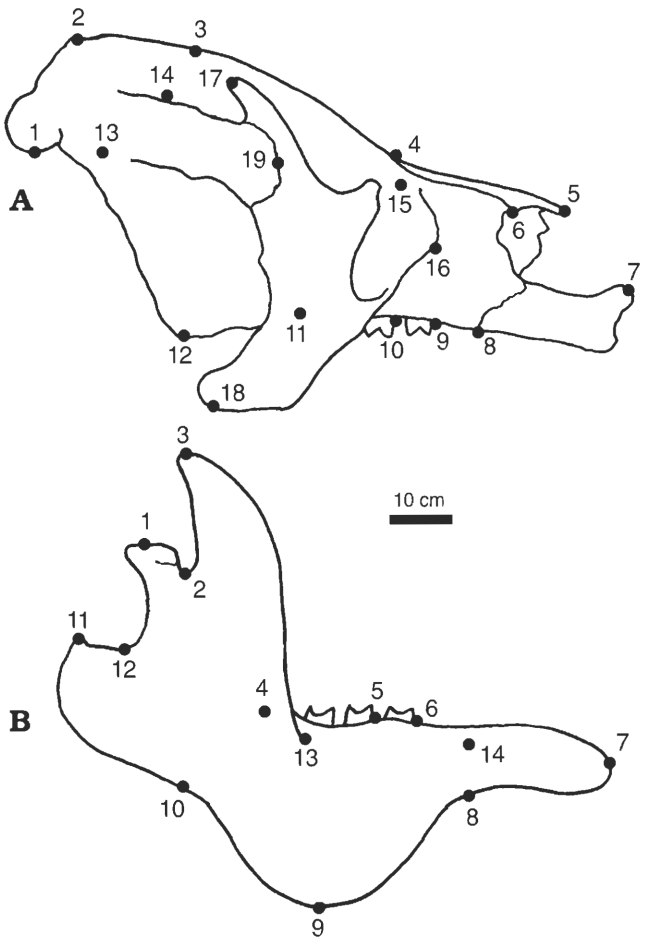

Fig. 6. Skull (**A**) and mandible (**B**) of *Megatherium americanum* showing the landmarks used for RFTRA analysis. Landmarks in **A**: 1, ventral margin of the occipital condyle; 2, dorsal margin of the sagittal crest; 3, parietofrontal suture on the sagittal plane; 4, nasofrontal suture on the sagittal plane; 5, anterior end of the nasal; 6, anterior end of the nasopremaxillary suture; 7, anterior end of the premaxilla; 8, premaxillo-maxillar suture on the ventral margin; 9, mesial margin of first molariform tooth; 10, mesial margin of second molariform tooth; 11, distal margin of the last molariform tooth; 12, ventralmost margin of the pterygoid; 13, auditory foramen; 14, squamoso-parieto-frontal suture; 15, lacrimal foramen; 16, infraorbital foramen; 17, dorsal end of the ascending process of the jugal; 18, ventral end of the descending process of the jugal; 19, anterior end of the squamosal. Landmarks in **B**: 1, dorsal end of the condyle; 2, junction between the condylar and coronoid processes; 3, dorsal tip of the coronoid process; 4, distal margin of the last molariform tooth; 5, mesial margin of the second molariform tooth; 6, mesial margin of the first molariform tooth; 7, anterior symphyseal margin; 8, intersection of the ventral margin of the dentary with the line extending down perpendicularly from the line drawn between landmarks 7 and 11 and at 1/4 the distance between 7 and 11; 9, intersection of the ventral margin of the dentary with the line extending down perpendicularly from the line drawn between landmarks 7 and 11 and at 1/2 the distance between 7 and 11; 10, intersection of the ventral margin of the dentary with the line extending down perpendicularly from the line drawn between landmarks 7 and 11 and at 3/4 the distance between 7 and 11; 11, posterior margin of angular process; 12, junction between the angular process and the condyle; 13, external foramen of the dentary channel; 14, anterior mental foramen.

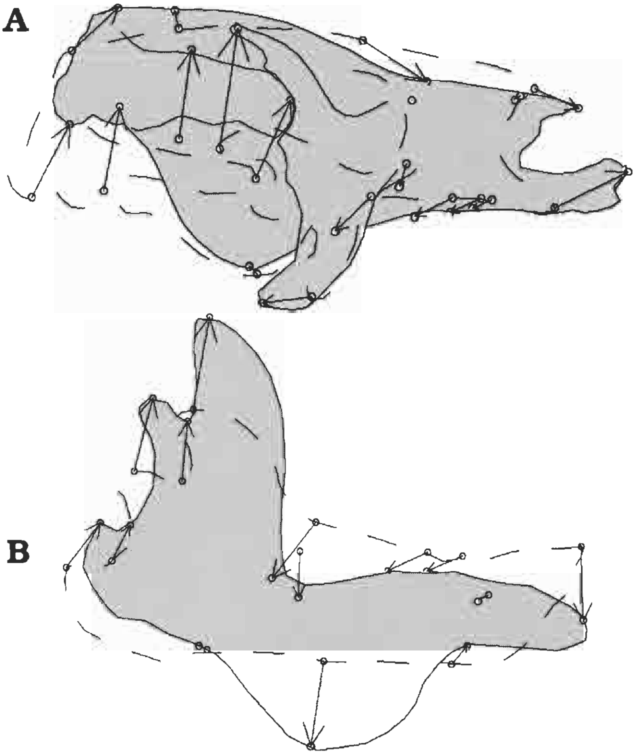

Fig. 7. Results of RFTRA on the skulls (**A**) and mandibles (**B**) of *Glossotherium robustum* (base specimen, broken lines) and *Megatherium americanum* (target specimen, continuous lines and shaded).

Discussion

The tardigrades (sloths) are not a morphologically homogeneous group, but demonstrate a high degree of diversity in shape and size, varying from the less than 10 kg living tree sloth to the 4 tonne *Megatherium americanum*. Sloths also show a great diversity in the combination of their cranial characters, both within the fossil and recent families (Naples 1982). For instance, within mylodontids, there are forms with extremely long tubular skulls (e.g., *Scelidotherium*), and others with a very broad, short rostrum, with very prominent caniniform teeth (e.g., *Lestodon*). The general pattern in megatheriids is a moderately long and narrow rostrum lacking caniniform teeth.

The masticatory apparatus of *M. americanum* is distinct compared to those of *Glossotherium robustum* and *Bradypus variegatus*, particularly in the form of the dentition and mandible, and in the attachment sites of the masseter muscle. De Iuliis (1996) stated that many features characteristic of the mandible of *M. americanum* are due to the increased hypsodonty of this species. The ventral bulge is greater to accommodate the more hypsodont molariform teeth and the hypsodont maxillary molariform teeth require a deeper maxilla. The craniomandibular joint thus lies relatively more dorsally, well above the level of the occlusal plane. The angular process is also displaced dorsally.

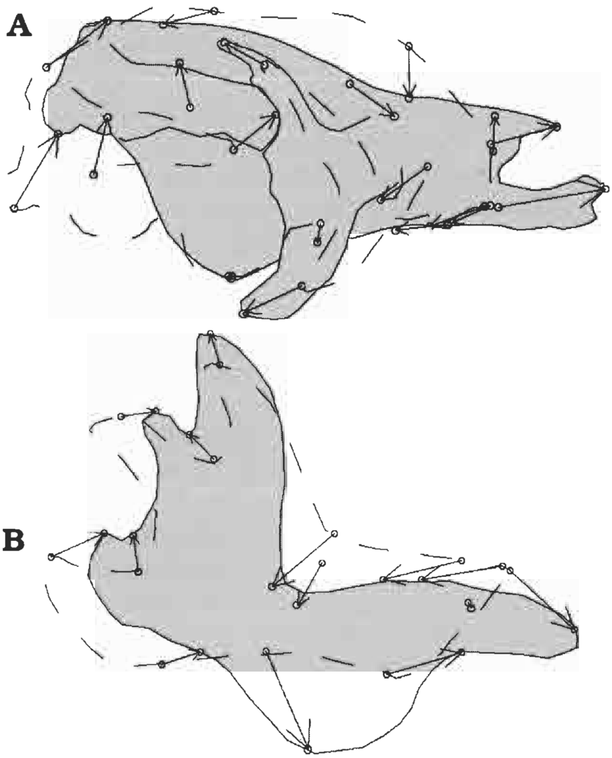

Fig. 8. Results of RFTRA on the skulls (**A**) and mandibles (**B**) of *Bradypus variegatus* (base specimen, broken lines) and *Megatherium americanum* (target specimen, continuous lines and shaded).

It is generally accepted that a high condyle improves the mechanical advantage of the masseter and the medial pterygoideus by increasing the moment arm of the lines of action, as occurs in living ungulates (Maynard Smith & Savage 1959; Turnbull 1970; Naples 1982). However, as noted by De Iuliis (1996), the raising of the angular process in *M. americanum* averts a dramatic rearrangement of the muscular attachment sites and force vectors. RFTRA clearly shows that both the condyle and the angular process are elevated nearly to the same degree in *M. americanum* compared with the mandible of *G. robustum*, and the same is true for the masseteric fossa (Fig. 7). Consequently, the estimated moment arm for the masseter is the same in both forms (Table 1). On the other hand, RFTRA shows that the condyle of *M. americanum* is essentially at the same level as in *B. variegatus*, but that the angular process and the masseteric fossa are raised and anteriorly displaced in the fossil. This explains the lower value obtained for the moment arm of the masseter in *M. americanum* in comparison with the living species.

The condyle and the coronoid process of *M. americanum* and *G. robustum* are separated by more or less the same distance in RFTRA graphics, although both are higher in *M. americanum*. The similar distance produces relatively similar moment arms for the temporalis. The slightly higher value in *G. robustum* is due to its broader coronoid process, which places the insertion of the temporalis further from the pivot. In *M.*

americanum the condyle is also displaced anteriorly in comparison with *Bradypus variegatus*, resulting in a shorter moment arm of the temporalis in *Megatherium americanum*.

RFTRA supports the hypothesis that the mandible is modified to such a different shape to accommodate the highly hypsodont teeth (De Iuliis 1996). The change in shape of the ascending ramus maintains the same relative moment arms of the jaw muscles in *M. americanum* as seen in *Glossotherium robustum*.

The tooth rows are displaced distally in *M. americanum* compared with *G. robustum* and, in particular, with *B. variegatus* (Figs. 7 and 8). This results in shorter moment arms for bite positions throughout the toothrow. The combined moment arms of the temporalis and masseter are larger relative to the bite force throughout the tooth row in *M. americanum*. The ratio of muscle moment to bite moment provides a relative measure of the effective bite force generated by the musculature. Large ratios indicate forceful biting rather than rapid jaw movements. Hence, the masticatory apparatus of *M. americanum* is designed to generate larger bite forces all along the tooth row than those of *G. robustum* and *B. variegatus*.

The condyle is wide and slightly convex, and the glenoid fossa is well defined and shallowly concave. This arrangement probably permitted considerable freedom of motion, but dental and other osteological features apparently restricted movement of the mandible. The interlocking occlusion of the transverse crests and valleys and the great development of the descending process of the zygomatic arch indicate that both anteroposterior and lateral movements were restricted.

The chewing mechanisms of other large bilophodont mammals are probably similar to those with bunodont teeth; jaw movements are predominantly orthal, with emphasis on puncturing and crushing (Janis & Fortelius 1988). Otherwise, the primary lophodont or bunodont morphology would be lost by palinal movements and replaced by a secondary movement, essentially in one occlusal plane, as happens in elephantids and some suid lineages (Fortelius 1985). Thus, in *M. americanum* the well marked bilophodonty would be maintained by performing essentially orthal movements. In addition, Janis & Fortelius (1988) proposed that the bilophodont morphology combined with hypselodonty in *M. americanum* was maintained through the presence of dentine layers of unequal hardness.

The stoutly built zygomatic arch, with its long descending process, leaves only a narrow space between it, the horizontal ramus and, in part, the ascending ramus. This suggests a physical restriction to lateral movements. Moreover, this space would have been occupied by the deep masseter and the zygomaticomandibularis, which probably functioned in mandibular elevation (Naples 1985).

The combination of these morphological features and the moment arm analysis indicates that *M. americanum* was well adapted for strong, predominantly orthal movements. Hiiemae & Crompton (1985) summarised the mechanical principles of tooth design in relation to the nature of the food. They recognised three basic patterns: a mortar and pestle system suitable to crush hard and brittle (e.g., nuts) or turgid (e.g., fruit pulp) food; blades to cut soft but tough food (e.g., muscle and skin); and a serial array of low profile blades acting as a milling machine for tough and fibrous food (e.g., grass). The first two patterns coincide respectively with 'routes' 1 and 2, and the third with 'routes' 3 and 4 of Janis & Fortelius (1988: pp. 224–225). According to these authors, moderately tough and abrasive food such as leaves require reciprocal blades for comminution of food items, a function which is accomplished by orthal chewing with bilophodont teeth ('route' 2). They also stated that bilophodont teeth are common in relatively large mammalian herbivores that, at least in living forms, browse on vegetation of moderate fibre content.

The tooth rows of *M. americanum* essentially represent a battery of high-crested lophs. The sagittal section of each loph is triangular with a sharp blade of hard dentine at the apex. This morphology apparently represents a condition approximately intermediate between the two first patterns proposed by Hiiemae & Crompton (1985), which indicates that hard and brittle or fibrous food did not constitute the most appropriate dietary items of *M. americanum*. Instead, *M. americanum* seems to have been better suited for consuming a variety of turgid or moderate to soft tough items.

As emphasised by Janis & Fortelius (1988), *M. americanum* is a peculiar case in combining hypsodonty with bilophodonty. Janis (1988, 1995) clearly established that an important issue in determining hypsodonty in ungulates is the grit and other abrasive material accumulated on plants. Dust and grit is more abundant in open habitats than in closed habitats. Thus, a high degree of hypsodonty in fossil ungulates is good indicator of open habitat environmental preference rather than solely an indicator of true grazing.

This hypothesis would also be applicable to the late Pleistocene megatheriines in South America, *M. americanum* and *Eremotherium*. Their masticatory apparatuses are very similar in general morphology, but *M. americanum* is considerably more hypsodont (De Iuliis 1996). *M. americanum* generally occurred in the southern part of South America (i.e., Argentina and Uruguay), whereas *Eremotherium* is known from Brazil north through to the southern United States. De Iuliis *et al.* (2000) stated that the particular occurrences of these sloths may be taken as broadly indicative of environmental conditions, with *Megatherium* typically considered more adapted to temperate, arid or semiarid open habitats, and *Eremotherium* to more tropically or semitropically forested habitats. During the last part of the Pleistocene, the Pampa plains (Argentina), the region typically occupied by *M. americanum*, experienced a cool, dry climate (Clapperton 1993; Tonni 1985; Prado *et al.* 1987; Alberdi *et al.* 1989; Iriondo & García 1993, and references therein) similar to that of modern northern Patagonia at about 40° S. Based on analysis of the isotopic composition of the enamel of high-crowned ungulate teeth, MacFadden *et al.* (1996) proposed a mixed grassland/browser ecosystem. Palynological evidence suggests mainly herbaceous psammophytic steppe environments, associated with xerophytic woodland in the southwestern part (Prieto 1996, and references therein). This evidence suggests an environment dominated mainly by hard grasses, with less abundant moderate to soft tough plant material, along the distributional range of *M. americanum*. Paradoxically, the analyses performed here indicate that *M. americanum* was better prepared to consume moderate to soft tough food. This suggests that reconsideration of the traditional concept of *M. americanum* as exclusively herbivorous may not be inappropriate. Fariña (1996) considered an intriguing, and in one sense complementary, possibility. Based on a comprehensive palaeocological approach, he recognized that the Lujanian (late Pleistocene–early Holocene) fauna of Argentina and Uruguay would represent an unbalanced ecosystem compared with modern faunas, if traditional concepts of niche occupation were maintained. Of particular importance is that Fariña (1996) noted a simultaneous existence of an excess of herbivores, given the level of primary producers, and a scarcity of carnivores, given the high number of large herbivores. His explanatory hypothesis for this situation is that there must have been previously unrecognized opportunistic carrion-feeders (accompanying a primarily browsing diet) among the Lujanian fauna. Fariña (1996) considered *M. americanum* among the more likely candidates for this role among the members of this fauna. The evidence provided here on the masticatory apparatus of *M. americanum* combined with the probable scarcity of appropriate vegetation indicates that it probably had mainly a browsing diet in open habitats, but also that it probably fed on other moderate to soft tough food. If the availability of an appropriate vegetation source were indeed a factor, then it is not implausible that this species practised carrion-feeding to supplement its diet. Nevertheless, more evidence (e.g., coprological, isotopic, biochemical, palynological) is required in order to reconstruct a more accurate understanding of the feeding behaviour of this giant ground sloth.

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