CONTRIBUTIONS IN SCIENCE

THE FEEDING MECHANISM IN THE PLEISTOCENE GROUND SLOTH, GLOSSOTHERIUM

VIRGINIA L. NAPLES
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THE FEEDING MECHANISM IN THE
PLEISTOCENE GROUND SLOTH, GLOSSOTHERIUM

VIRGINIA L. NAPLES

ABSTRACT. The masticatory musculature in Glossotherium Owen, 1840, was reconstructed from study of the scars of muscle origin and insertion. Details of muscle architecture and hypotheses of function were deduced through comparison with the extant tree sloths, Bradypus Linnaeus, 1758, and Choloepus Illiger, 1811. Examination of dental wear facets has shown that Glossotherium had an anteromedially directed masticatory power stroke, comparable with most other mammals. As in other sloths, the shape and orientation of the zygomatic arch and its processes suggest a biomechanical advantage for muscles of the masseter complex. Although the anterior caniniform teeth in Glossotherium are short, they require a precise dorsoventral occlusal relationship, facilitated by a craniomandibular joint, at or near the level of the cheek tooth row as seen in Choloepus. The masticatory muscles in Glossotherium show a distribution of primitive and derived characters different from that of tree sloths and Nothrotheriops shastense Sinclair, 1905. A greater number of cranial morphological characters in Glossotherium are more similar to those of Choloepus than to Bradypus, although this probably reflects similar constraints placed upon masticatory architecture by elongate caniniform teeth. Derived characters, including (1) inflated cranial sinuses, (2) elongated uninalveolar prerygoid flanges, and (3) zygomatic arch process size and orientation, do not resemble those of the tree sloths or of Nothrotheriops shastense.

INTRODUCTION

The sloths are divided into three large groups, the mylodontids, the megacholodids, and the megatheres. The genus Glossotherium Owen, 1840, from the Pleistocene of North America is a member of the mylodontids. Of these sloths, the Mylodontidae are most likely to be monophyletic, as suggested by several character complexes that include cranial and mandibular morphology and dentition (Stock, 1925). Engelmann (1985) divided the Mylodontidae into three categories: (1) an unspecialized group that includes two genera, Orophodon Ameghino, 1895, and Pseudopropotherium Hofstetter, 1961; (2) the Schlictherini, a group characterized by having a concave cuboid facet on the distal head of the astragulus and a slender, elongate skull and mandibles; and (3) the Mylodontinae, a group united by loss of the entepicondylar foramen of the distal humerus and by anteriorly broad snouts.

Of the five genera in the Mylodontinae, Lestodon Gervais, 1865, can be separated at the first node of Engelmann's (1985) cladogram, based upon dental characters, and Thinobadistes Hay, 1919, at the second node, based upon cranial and astragalar differences, from the remaining three genera. The genera Mylodon Owen, 1840, Paramylodon Brown, 1903, and Glossotherium have been confused for one another in the literature (Stock, 1925; Hofstetter, 1952). The tendency to lose the upper first tooth in Paramylodon makes assessment of the phylogenetic distance between Paramylodon and Mylodon (which lacks the anterior teeth entirely [Reinhardt, 1879; Stock, 1925]) difficult. Paramylodon has also been included within Glossotherium at some times, giving Paramylodon an unusually wide range of morphologic diversity. Hofstetter (1952) and Engelmann (1985) observe that morphologic differences between Glossotherium and Paramylodon need to be defined to clarify their relationship. Some confusion exists as to the proper generic name for the North American late Pleistocene mylodont, and the use of the name Glossotherium reflects the current convention, following Kurten and Anderson (1980), and is not a taxonomic decision based on the present study.

The purpose of this study is to identify interdependent cranial characters and character complexes among Mylodon, Paramylodon, and Glossotherium by analyzing functional constraints on feeding in Glossotherium. An attempt to ascertain the limits of variability of the components of each cranial morphological complex will also be made. Definition of the interrelationships of characters and character complexes should show the biomechanical constraints upon variation among them, and thus establish physical boundaries that could not be exceeded for the performance of a given function. Any variation beyond these parameters would demonstrate that the function of the character or complex differed from predictions based upon biomechanical principles and, therefore, could be assumed to reflect a different habitus or different selective pressures from those acting upon the rest of the group, and would suggest a more distant relationship within the Mylodontinae.

The present study provides the first step toward

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Table 1. Terminology and abbreviations used in this study.

<table>
<thead>
<tr>
<th>Ligaments</th>
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<tr>
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<td>Zygomatic arch ligament</td>
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<table>
<thead>
<tr>
<th>Joints</th>
<th>Abbreviations</th>
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<tr>
<td>Craniomandibular joint</td>
<td>CMJ</td>
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<table>
<thead>
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<th>Muscles</th>
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<td>M. masseter superficialis, part 1</td>
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<td>M.p.(L).</td>
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<tr>
<td>M. pterygoideus lateralis, lower division</td>
<td>M.p.(L)</td>
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<tr>
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<td>M.p.m.</td>
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</table>

Bones and muscles of function have been tested experimentally (Naples, 1982, 1985a). Although Bradypus and Choloepus are both arboreal, they are probably not closely related; they show many differences in cranial morphology (Sicher, 1944; Naples, 1982, 1985a, 1985b, 1986) and have been aligned with the megatherids and megachirochids, respectively (Patterson and Pascual, 1972; Webb, 1985; Wetzell, 1985). Thus, comparison of Glossothorium, a mylodontid, with members of each of the other two sloth families will show the pattern of the distribution of characters and complexes among the three lineages, and contribute to the determination of primitive or derived status for those characters. Comparison of osteological characters in Glossothorium with those of the extant tree sloths permits a detailed reconstruction of the cranial soft anatomy in the fossils, based upon the assumption that similar features are homologous and are subject to similar functional constraints (Naples, 1987). Accordingly, the cranial musculature in Glossothorium has been reconstructed to be similar in pattern of differentiation and action to that of the tree sloths. Morphological comparison of Glossothorium with Nothrotheriops will increase understanding of the dietary habits, masticatory patterns, and biomechanical constraints on cranial function in Glossothorium. The dietary habits are well known for Nothrotheriops, and its cranial morphology has been reconstructed (Hansen, 1978; Naples, 1987). Nothrotheriops and Glossothorium are both megatherioid ground sloths present in the asphalt seeps at Rancho La Brea.

MATERIALS AND METHODS

Specimens of Glossothorium examined, and the collections in which they are housed, are listed in Table 1. Cranial osteological characters studied include attachment areas of muscles and the position and orientation of cranial sutures. The relative size and shape of the craniomandibular joint and the mental prominence were also considered because of their effects upon the pattern of masticatory movements, and the relative size, structure, and placement of the muscles of mastication. Significant cranial characters and character polarities were determined based upon comparison with the Recent tree sloths, Bradypus and Choloepus, and the megatheriid sloth, Nothrotheriops. Abbreviations of terms used in this study are listed in Table 2.

Dental features were analyzed to determine degree of tooth wear, tooth wear patterns, and the path of mandibular movement, based upon techniques developed by Greaves (1973), Rensberger (1973), and Costa and Greaves (1981). Occlusal relationships were deduced from examination of "cusps" formed by wear according to the path of mandibular motion.

Cranial muscles were reconstructed based upon dissections of tree sloth masticatory muscles (Windle and Parsons, 1899; Sicher, 1944; Naples, 1985a). The muscle terminology used here is consistent with that developed during other studies of Recent and fossil sloths (Naples, 1985a, 1985b, 1986, 1987). Muscle and muscle segment identifications in tree sloths were determined by tracing innervations. Scars located on osteological elements indicating muscle origin and insertion accurately predict the limits of muscle size and general structure in tree sloths;
Table 2. Specimens examined in this study. Specimens belonging to the Hancock Collection (HC) are so designated. The specimen from the American Museum of Natural History is a juvenile.

<table>
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<th>Mandibles</th>
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Museum of Comparative Zoology
8429 skull 8429 mandible

American Museum of Natural History
11270 skull 11270 mandible

therefore, similarly positioned muscles in Glossotherium have been assumed to be identical. Muscles reconstituted in Glossotherium are listed in Table 3.

The distance reflecting maximum gape in Glossotherium was quantified by the method of Herring and Herring (1974). This model allows an estimate of the length to which fibers of the masticatory muscles could be stretched. This length is determined by measuring the distance between the center of the scars of origin and insertion (Table 3). It has been demonstrated that long-fibered muscles (such as most tree sloth masticatory muscles) function under different biomechanical constraints than do short-fibered muscles (Gans and Bock, 1965; Alexander, 1968; Gans, 1982). These features therefore
Table 3. The cranial muscles, divisions, and abbreviations used in this study and the amount of stretch of each muscle segment when the mouth is opened to various degrees of gape. Multipinnate muscles may stretch up to two times their resting length without incurring damage; therefore, only stretch factors over 2.00 would be limiting. For *Glossotherium* the *M. masseter superficialis*, part 5, could then be overstretched at gapes greater than 22 degrees, with the *M. pterygoideus medius* and *M. zygomaticomandibularis* only slightly less limiting. The lowest gape at which a muscle could be overstretched is italicized.

<table>
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<tr>
<th>Muscle</th>
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maximize the accuracy of predictions by this model. Masticatory muscle origin and insertion scars in *Glossotherium* were similar to those of tree sloths, suggesting that this method is also accurate for predicting maximum gape in this extinct species. The distance to which a muscle fiber can stretch without damage is approximately 1.4 times the resting length of the fibers for parallel fibered muscles, and approximately twice the resting length for multipinnate fibered muscles (Carlsöö, 1942). The equation used by Herrig and Herrig (1974) to predict the distance to which a muscle segment must stretch to achieve a given angle of mandibular rotation is:

\[
\frac{L^2}{T} = \frac{a^2 + b^2 - 2ab \cos(\theta + \phi)}{a^2 + b^2 - 2ab \cos \theta - 2c^2 \cos \phi}.
\]

The stretch factor for each muscle (ratio L/T) is the positive square root of the equation. The values of the variables are: a = length from the muscle origin to the crano-mandibular joint (CMJ), b = length from the insertion to the CMJ, \( \phi \) = the angle between a and b, L = length of the muscle with the mandible closed, and I = the length of the muscle with the mandible opened to angle \( \theta \).

RESULTS

CRANIAL OSTEOLOGY

A suite of osteologic characters distinguishes sloth crania from those of other mammals: (1) a reduced edentulous premaxilla loosely bound to the maxilla; (2) lengthy maxillae; (3) a persistently growing adult dentition reduced in tooth number, complexity, lacking enamel, and lacking a deciduous dentition; (4) zygomatic arches often incomplete; (5) elaborated descending and often ascending zygomatic arch processes; (6) pterygoid bones showing elongate flanges and/or inflated sinuses; (7) elaborate frontoparietal sinuses; (8) fused mandibular symphyses; and (9) an elongate predental mandibular spur. All sloths show some of these characters, although none possess all, and the distribution differs among the tree sloth lineages (Mylodontidae, Megalonychidae, and Megatheriidae). Additionally, each character may vary in structure, both within and between sloth groups. Although many authors (Stock, 1925; Winge, 1941; Simpson, 1945; Romer, 1966; Patterson and Pascual, 1972; Engelman, 1985; Webb, 1985) have proposed phylogenetic relationships among sloths, few studies have investigated the functional implications of sloth cranial structure. Only cranial characters that contribute to the understanding of structural-functional complexes and evolutionary relationships in *Glossotherium* have been included here.

Premaxilla and Predental Spout (Fig. 1A, B)

Few specimens of *Glossotherium* have the premaxillae intact. They are arrowhead-shaped, reminiscent of those found in *Bradytopus*. The two elements are fused at the midline posteriorly and are loosely bound to the maxilla. In all large adult specimens a gap is present between the premaxilla-maxilla articulation, except midventrally, where the posteriorly projecting premaxillary process fuses with a V-shaped notch between the left and right maxillae. The body of the premaxilla is thickened by a dorsal ridge running along the "sides" of the arrowhead. Anteriorly, the premaxillae show a transverse groove, probably for attachment of nasal cartilages extending farther anteriorly. The presence of large nasal cartilages is suggested by the large nasal openings and a widely flaring predental spout that projects anteriorly, which is close to the length of the premaxillae (Fig. 1A-C, E). Tree sloths have large nasal cartilages along with thick, flexible upper lips that extend the nasal region anteriorly and slightly beyond the predental spout. A thick, flexible upper lip is postulated for *Glossotherium*.
Postorbital Process

Sloths lack a complete postorbital bar, and typically the postorbital process is small. In *Glossotherium*, the process is broad and thick, inflated by the underlying frontal sinus, and is an elaboration of a ridge continuing posterodorsally from the eminence at the origin of the jugal, consisting of two rounded processes that project laterally. The process which lies more posteriorly is larger and sharper, with a ridge that continues posterodorsally to fade into a broad, flattened area of the frontal that is underlain by the frontal sinus. Both projections may have served as sites of attachment for the postorbital ligament.

Cranial Sinuses

An extensive frontoparietal sinus network is present in *Glossotherium*. Sectioned or partially eroded skulls (Stock, 1925) indicate that the sinuses are divided by bony partitions into chambers of varying size and shape. Both tree sloths have frontal sinuses. These sinuses also extend above the parietal area in *Choloepus*; however, they lack bony partitions (Naples, 1982). The sinuses increase frontal bone surface area and, in *Glossotherium* and *Choloepus*, the parietal area is inflated by distinct parietal sinuses. *Glossotherium* and *Choloepus* lack a sagittal crest; however, cranial sinuses increase the surface area that *M. temporalis* and, in some cases, the neck muscles inserting upon the occiput can occupy. In *Glossotherium*, the parieto-occipital suture is thickened and flares laterally, forming a lambdoidal crest that widens the occiput by approximately one-third. This effectively increases the area for insertion of the head-controlling and postural neck muscles.

Occiput and Occipital Condyles

The lateral occipital protuberance and crest form a narrow raised ridge from the sagittal suture to the foramen magnum. Because the lambdoidal crest is also raised, the occipital plane appears concave. The entire area is rough with dorsoventral ridges. The occiput is slanted, and the occipital condyles project posteriorly. The condyles are widely separated, strongly convex, rounded triangles with a horizontal long axis. The foramen magnum is relatively small and round, and large ventral and lateral openings for the jugular foramina are present.

Structure of the Craniomandibular Joint (CMJ; Fig. 1C–I)

In *Glossotherium*, the glenoid fossa is poorly defined, with a shallow, ventrally facing, mediolateral depression at the condylar articulation on the squamosal process. A round depression occurs on the vertical wall at the thickened pterygoid flange base, ventral to the temporal-pterygoid suture, and receives a distinct medial facet of the mandibular condyle. The mandibular condyle is wider mediolaterally than anteroposteriorly, with a weakly defined dorsal surface that is poorly separated from the condylar notch anteriorly. Laterally, the condyle flares slightly. In addition to the main broad facet, a smaller anterior facet is present, separated by a curved ridge trending posterolaterally. Medially, there is a vertical round face, separate and angled at between 80 and 90 degrees from the horizontal dorsal condylar facet; the condyle projects farther medially than laterally relative to the ascending ramus of the coronoid process. This glenoid fossa and mandibular condyle structure indicates that condylar movement was unrestricted anteroposteriorly and laterally, but strictly limited medially.

In *Choloepus*, the CMJ is generally similar to that of *Glossotherium*, although the articular surfaces are more sharply defined, except for the medial vertical facet. In contrast, the long axis of the CMJ in *Bradytypus* is anteroposteriorly oriented, and the base of the pterygoid flange is somewhat thickened, but lacks a medial face. In *Glossotherium*, which may have short caniniform teeth, the CMJ is approximately the same height as the cheek tooth row. *Choloepus*, which also has long caniniform teeth, has a CMJ level with the cheek tooth row, whereas *Bradytypus*, which lacks elongate anterior teeth, has an elevated CMJ. The occlusal plane of the upper and lower tooth rows are equidistant from the CMJ in *Glossotherium* and other sloths (Naples, 1982, 1985a, 1987), insuring simultaneous occlusion and equal intercuspsation along the length of the tooth row.

Pterygoid Region

*Glossotherium* pterygoid morphology is unusual in comparison to other mammals (Stock, 1925; Turnbull, 1970). The bones are plate-like flanges, elongated ventrally, with a rounded inferior border and buttressed medial to the articulation with the medial condylar facet. The external surface is roughened, and shows scars for the origin of the medial pterygoid muscle. Other sloths (*Bradytypus*, *Nothotheriops*) have a similar pterygoid morphology, although the entire character complex associated with pterygoid development is unique to *Glossotherium* and other mylodont sloths.

Palate

The palate in *Glossotherium* is widest anteriorly adjacent to the small caniniform teeth. It is thickened dorsoventrally by two ridges that continue anteriorly to the premaxillary suture. The palate tapers posteriorly, becoming narrowest between M*³* and M*⁴*, widening again slightly at the rear of M*⁴*. The entire palate is roughened with many pits; some are undoubtably for foramina. It is strongly convex between M*²* and M*³* and flat or slightly concave anteriorly. A sharp midline ridge begins at the anterior concavity and ends anterior to M*⁴*, where the palate exhibits a smooth V-shaped depression bounded laterally by sharp ridges. At the postero-
lateral edges of this V-shaped depression, the greater palatine foramina are large and accompanied by a row of smaller foramina along the edges of the maxillae that end anterior to the caniniform teeth. The choanae open in a V-shaped notch and are wider than the smooth part of the palate.

CRANIAL LIGAMENTS

The three major cranial ligaments in sloths include (1) the postorbital ligament (POL), (2) an anterior-posterior ligamentous connection between the jugal and squamosal processes of the zygomatic arch (zygomatic arch ligament, ZAL), and (3) ligaments of the CMJ (Fig. 1A). In contrast to most other mammals, anterior and posterior processes of the zygomatic arch in the sloth skull are loosely opposed and were probably connected by a ligament.

Postorbital Ligament

Based upon comparison with the tree sloths, a ligament covered the upper zygomatic arch of Glossotherium. It arose from the broad postorbital process and attached to a rounded process formed where the anterior surface of the ascending jugal process turns posteriorly, then continued superficially to the outer surface of the temporal musculature. The postorbital ligament was thick and completed a round orbit, separating the eye region superficially from the temporal fossa. In addition to the ligament covering the upper jugal process, attachment scars located posteriorly and medially on the lower half of the jugal notch and on the dorsal, lateral, and anteroventral surfaces of the broad, flat squamosal process indicate the presence of a large zygomatic arch ligament. This is reminiscent of the condition found in Choloepus, which has a more posteriorly directed upper jugal process than Glossotherium and an even clearer division of the two ligaments. In contrast, with a strongly vertical ascending jugal process, the POL and ZAL in Bradyus appear to be almost continuous.

In Glossotherium, as in tree sloths, the ZAL continues ventral to the apposed jugal and squamosal processes. In tree sloths, particularly Bradyus, this ligament is large. The zygomatic arch orientation in Glossotherium precludes a large ligament; however, an attachment scar is located on the ventral surface of the jugal notch, opposite an oval depression posterior to the broad, flat ventral area of the squamosal. These scars suggest that the zygomatic arch attachment was strengthened ventrally by a thickened, and perhaps separate, ligamentous band between jugal and squamosal.

Ligaments of the CMJ

A medial ridge marks the limit of the glenoid fossa in Glossotherium. In general, the ridge is small and thin but becomes thicker and more prominent near the medial vertical facet. Muscle scars on the mandibular condyle are more pronounced, particularly medially and posterolaterally. Approximately 50% of the condylar head is medial to the coronoid process. The area for insertion of the two lateral heads of the pterygoid muscle is sharply defined and surrounded medially and ventrally by a prominent roughened ridge. This suggests that the lateral pterygoid attachments pierce the joint capsule as in other mammals. Tree sloths lack an articular disc. The extensive flat area of glenoid fossa–condyle articulation in Glossotherium suggests a similar absence. The glenoid surface in Glossotherium is much larger than the condyle area, suggesting that the CMJ capsule was loose and thin (except medially) and permitted extensive condylar movement. Although the glenoid fossa and condyle differ in shape, the capsule in both Recent genera of tree sloths is both thin and lax (Naples, 1985a).

DENTAL MORPHOLOGY

Sloths have an ever-growing adult dentition, a reduction in the tooth number, and lack a deciduous dentition (Parker, 1883). This makes tooth homologies difficult to discern. Sloth teeth also lack enamel (Romer, 1966) and the cuspation pattern shown in other mammals. Typical tooth forms are oval, subrectangular, or elongate irregular ovoids. Anterior teeth are called caniniform (or chisel-shaped), and cheek teeth are termed molariform (Fig. 2A, B).

Upon eruption, the teeth are cone-shaped and only acquire their characteristic facet and “cusp” pattern with wear during the life of the animal (Naples, 1981, 1982). Each tooth has a perimeter of harder dentine and a softer dentine center, which explains the formation of central basins. In Glossotherium, the perimeter hard dentine layer is of approximately equal thickness on all aspects of the teeth, as in Choloepus. In contrast, the perimeter dentine layer on anterior and posterior faces is thicker than on lingual and labial faces in the megatheriids Bradyus and Nothrotheriops (Naples, 1982, 1987). Parker (1885) suggested that tree sloths also have a layer of cementum surrounding the teeth, but in many specimens this is indistinct. However, in Glossotherium, the cementum is obvious and surrounds all cheek teeth. Traces of cementum have also been found on the anterior caniniform teeth in some specimens.

The dental formula (2) in Glossotherium is the same as in tree sloths; however, the teeth are more elongate, more complicated in shape, and relatively larger than in Bradyus and Choloepus and occupy more space along the tooth row. Some Glossotherium specimens lack development of the caniniform teeth, giving them a reduced dental formula (2) as compared to the tree sloths, but loss of these teeth does not change the occlusal relationship of the molariform teeth. A description of tooth structure in Glossotherium has been presented by Stock (1925), although the pattern of wear facet formation and occlusal relationships were not discussed.
Sloths reverse the typical mammalian tooth occlusion order with the mandibular caniniform or chisel-shaped tooth anterior to the corresponding maxillary tooth. The maxillary cheek teeth also precede the mandibular cheek teeth by half a tooth length, a derived character shared with other sloths (Owen, 1842; Anthony, 1918; Stock, 1925; Hirschfeld and Webb, 1968; Naples, 1981, 1982, 1987).
Glossotherium shows the typical intercuspidation arrangement seen in other sloths, with four maxillary molariform teeth occluding against three mandibular molariform teeth (Fig. 2C, D). The M1 and M4 have only one opposite occlusal surface in Choloepus, whereas the M2 and M3 each occlude with two mandibular cheek teeth. In megatheriids, in contrast, the M1 may occlude with a posterior face of the anterior lower caniniform or chisel-shaped tooth (if present) and with the anterior face of the M1. However, in megatheriids, the M4 also occludes only with the M1. In Glossotherium (a mylodontid), the M1 occludes with C1 and M1, and the M4 with the posterior aspect of the M1. The M1 has a more elongated anteroposterior axis than in other sloths studied here. Occlusion of the M1 with more than one mandibular tooth requires the mandibular teeth to occlude in more than one position (Fig. 2C, D), which is true in tree sloths (Naples, 1982: fig. 15E–H). In tree sloths, the occlusal position for biting with the anterior teeth differs from the mandibular position required to appose the cheek teeth for chewing. However, the difference between the biting and chewing occlusal positions in Glossotherium is small, because the diastema separating the anterior caniniforms from the cheek tooth row is less pronounced.

The first maxillary tooth (C1) in Glossotherium (when present) is oval in cross-section. It has a single posterior-facing occlusal surface that only wears against the anterior facet of C1 (Fig. 2A). Stock (1925) described the outer hard dentine layer of C1 as thicker than in the cheek teeth and that the occlusal face contained a slight depression.

The second maxillary tooth, M1, is elliptical, with the long axis of the oval oriented approximately anteroposteriorly. The posterior aspect is directed more lingually. In contrast to Stock's (1925) observations, the anteroposterior tooth axis is shorter than that of M1 (Fig. 2A). A basin, which is deeper posterolingually, occupies the tooth center; the entire occlusal surface is concave along the anteroposterior axis and occludes with the M1. The hard outer dentine layer shows a slight anterior depression and a posterior ridge labially but is uniformly concave lingually. A distinct anterolabial wear facet occludes with the posterior facet of the C1, wearing almost through the outer hard dentine layer but leaving a pointed “cusp” anteriorly. This may have provided a sharp-edged cutting surface.

The M1 is triangular with two rounded lingual angles and one rounded labial angle. As noted by Stock (1925), the anterolingual lobe occludes with the posterolingual M1 lobe; the labial and posterolingual M1 lobes occlude with the M2.
vex lingual and concave labial edges. The long axis is oriented obliquely to the tooth row and the tooth is more lingual posteriorly. In contrast to Stock (1925), this tooth has the longest axis of any molariform tooth along the cheek tooth row. All M<sup>2</sup>'s studied have a concave central basin that occludes with the anterior portion of the elongate M<sub>1</sub>. The anterior basin portion in one M<sup>2</sup> contained two anomalous “islands” of hard dentine projecting above the surface.

The M<sup>2</sup> is kidney-shaped, with the long axis oriented anteroposteriorly. The anterior lobe is larger than the posterior, with a central basin continuous between the two. This tooth occludes with the posterior M<sub>1</sub>.

The first mandibular tooth, C<sub>1</sub>, was described (Stock, 1925); in addition, he discussed the presence or absence of C<sub>1</sub>. As with C<sub>1</sub>, the hard outer dentine layer in C<sub>1</sub> is thicker than in cheek teeth. The softer dentine basin is more deeply scoured labially on the anterior wear facet, and both hard and soft dentine areas bear wear striations along an anterolingual-posterolabial axis. This indicates that Glossotherium used an anteromedially directed mastiatory power stroke similar to that observed in most other mammals (Hiemae, 1978).

The M<sub>1</sub> is roughly triangular, with two rounded angles antero- and posterolingually and with one broader angle labially. Within the anterolingual lobe of the M<sub>1</sub>, the transition from outer hard dentine to inner soft dentine is smooth and flush. The labial basin is deeper, and a step exists between hard and soft dentine, suggesting that the masticatory stroke in Glossotherium was anteromedially directed (Greaves, 1973; Rensberger, 1973; Costa and Greaves, 1981; Gordon, 1982; Naples, 1982; Fig. 2B). The anterolingual and labial occlusal surfaces and the posterolingual lobe are concave; however, the posterolingual lobe is separated by a rounded convex ridge located on the occlusal surfaces corresponding to wear facets created by the M<sup>1</sup> and M<sup>2</sup>.

The M<sub>2</sub> has two lobes on the main anterolabial-posterolabial axis and a third, smaller posterolabial lobe. The concave surface and central soft dentine basin show a smooth transition from the hard perimeter dentine on the anterolingual aspect of the tooth and a deeper depression and step-like transition between soft and hard dentine on the posterolabial aspect of the tooth. Wear striations are discernible along an anterolingual-posterolabial axis.

The M<sub>1</sub> is the largest tooth in Glossotherium, with an anteroposterior long axis approximately twice the individual lengths of the other teeth. The elongated oval tooth shape is made irregular by two lingual lobes. The first lingual lobe is near the long axis midpoint, and the second is located at the tooth rear. As in other teeth, a central soft dentine basin is present; however, in M<sub>1</sub>, it is nearly pinched off posterior to the anterior lingual lobe. The flush transition between hard and soft dentine is obvious in two places: along the anterolingual face and (lingually) posterior to the anterior lingual lobe. A step-like transition is present along much of the labial surface and posteriorly. The M<sub>1</sub> occludes with the M<sup>2</sup> and M<sub>2</sub> and the gap between occlusal surfaces results in retention of a sharp labial ridge opposite the anterior lingual lobe.

**CRANIAL MUSCULATURE**

Bradypus and Choloepus show the typical trigeminal (mandibular branch, V<sub>3</sub>) masticatory muscle innervation seen in other mammals. The innervation of the tongue, throat, and hyoid regions in the tree sloths also reflects the typical mammalian pattern. Nerve branch patterns could not be traced in Glossotherium; however, the foramen ovale and hypoglossal canal are in positions similar to those in the tree sloths.

**MASTICATORY MUSCLES**

**M. masseter superficialis, Part 1 (M.m.s.—1; Fig. 3A, C, D, I).** In Glossotherium, part 1 arises from an oval depression on the lateral jugal surface anterior to the jugal notch. This segment is similarly positioned in Choloepus but not Bradypus; in the latter, the strongly vertical ascending jugal process orientation has permitted expansion and reorientation of the M.m.s.—1 origin. The fibers of M.m.s.—1 in Glossotherium pass posteroventrally to insert posterolaterally on the mandibular condylar process.

**M. masseter superficialis, Part 2 (M.m.s.—2; Fig. 3A, C, E, I).** In Glossotherium, part 2 arises from a U-shaped depression ventral to the origin of M.m.s.—1. The fibers pass posteroventrally to attach on slightly more than the upper 50% of the mandibular angle. This arrangement is similar in tree sloths, where the more ventral segments of the M.m.s. partially cover the more dorsal ones, especially near the insertions.

**M. masseter superficialis, Part 3 (M.m.s.—3; Fig. 3A, C, F, I).** In Glossotherium, part 3 arises from a large crescentic depression ventral to the origin of M.m.s.—2. This is the largest M.m.s. segment in Glossotherium, with an origin approximately twice the size of that of the M.m.s.—1 and M.m.s.—2.
Roughening of the surfaces of origin and insertion suggest that this segment may have been fleshy and divided by several tendons. The fibers pass posterovertrally to a dorsal, ridged insertion on the mandibular angular process. In *Choloepus*, *M.m.s.*—3 is relatively smaller and inserts dorsal to the tip of the angular process. In *Bradyus*, the *M.m.s.*—3 is relatively larger than in *Choloepus* and encompasses the tip of the angular process. In *Glossotherium*, *M.m.s.*—3 is relatively larger than in tree sloths and inserts more ventrally on the ventral 40% of the angular process, entirely ventral to the tip. In *Glossotherium*, fibers trend posterovertrally in contrast to tree sloths, wherein *M.m.s.*—3 is approximately horizontal and parallel to the plane of the cheek tooth row.

*M. masseter superficialis*, Part 4 (*M.m.s.*—4; Fig. 3A, C, G, I). In *Glossotherium*, part 4 originates from an elongate V-shaped depression trending posterovertrally on the descending jugal process, where a posterior notch occurs for muscle fiber and tendon passage. Part 4 inserts into a round mandibular depression bounded anteriorly and posteriorly by rough ridges but unmarked dorsally. In
tree sloths, the muscle arises by a single tendon, is multipinnaeate, and is divided into many fascicles. This was the probable arrangement in Glossotherium, considering the large size and position of the M.m.s. — 4 muscle scars.

**M. masseter superficialis, Part 5 (M.m.s. – 5; Fig. 3A, C, H, I).** In Glossotherium, part 5 originates from the most ventral depression on the descending jugal process, separated dorsally from the origin of M.m.s. — 4 by a ridge. In contrast to M.m.s. — 5 in tree sloths, this muscle in Glossotherium does not originate either from the anterior edge or extend onto the ventral surface of the descending jugal process. A rough knob at the tip of the descending jugal process (which probably is not an origin for fibers of M.m.s.) is at the posterior end of the ridge separating the origins of M.m.s. — 4 and M.m.s. — 5. M.m.s. — 5 is more doroventrally oriented than M.m.s. — 4. The bony knob reflects divergence in fiber direction between these segments as they pass dorsal and ventral to the knob. Fibers of M.m.s. — 5 pass posterovertrally, about 60 degrees from horizontal, to insert into a ridge-bounded depression laterally and ventrally on the mandible. The depression is ventral to the posterior edge of M.l. The M.m.s. — 5 forms the anterior and ventral cheek bulges in Glossotherium. In tree sloths, part 5 is complex, with many tendons and fascial planes. Pinnation of this segment would also have been important in Glossotherium to enhance the ability of the muscle to stretch (Herring, 1975). This anterior segment has the shortest distance from origin to insertion and, therefore, would limit the degree to which the sloth could gape.

The subdivisions, fiber arrangement, relative size, and overall line of actions of the M.m.s. in Glossotherium are similar to those of the tree sloths (Naples, 1985a). However, there is a greater range of orientation of segments in Glossotherium to affect the masticatory pattern.

**M. masseter profundus (M.m.p.; Fig. 3B, C, I).** In Glossotherium, this muscle originates from a smooth depression on the medial surface of the descending jugal process. Fibers pass posterovertrally to insert into a smooth, ridge-bounded depression on the lateral surface of the mandibular ramus, which is anterodorsal to the superficial masseter. This muscle is probably thin and sheet-like as in tree sloths, with many fibers but few tendons extending from origin to insertion. Also, the space between the descending jugal process and the mandibular ramus in Glossotherium is narrow, although the origin and insertion of M.m.p. is relatively larger than in tree sloths. The M.m.p. has a more vertical origin site than in Choloepus and an anterodorsal line of action. These derived characters are also exhibited in Bradypus but for different structural reasons (Naples, 1985a).

**Temporalis musculature (M.t.; Fig. 4).** In Glossotherium, the M.t. is large and thick, relative to that of tree sloths, and probably undivided. As is true of some other sloths, Glossotherium lacks a sagittal crest, but the dorsal origin of the M.t. is marked by a prominent roughened ridge—the parasagittal crest. The origin covers most of the dorsal and lateral aspects of the frontal and parietal bones (Fig. 4A, B) and the posterior one-third of the dorsal surface of the temporal squamosal process. The M.t. fills the depression between the parietal and squamosal process and passes ventrally anterior to these bones. Anteriorly, the origin continues from the postorbital process posterovertrally to a point immediately dorsal to the vertical ridge lateral to the optic canal. It then proceeds posteriorly to the anterior edge of the squamosal process to join the

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**Figure 4.** The origin (4A, dorsal view; 4B, lateral view), insertion (4C, medial view; 4D, lateral view), and reconstruction of the M. temporalis (4E) in Glossotherium. In 4B and 4E, portions of the zygomatic arch have been removed (sections through the cut edges are designated by hatching).
parietal bone. The muscle is a thick mass forming the posterior wall of the orbit. Fibers pass ventrally to attach to the roughened lateral, anterior, and medial surfaces of the coronoid process. The insertion area is small compared to the area of origin, indicating a fleshy origin for M.t. in Glossotherium and a tendinous insertion, as exhibited in other mammals (Turnbull, 1970; Naples, 1983a). The line of action of M.t. in Glossotherium is approximately 45 degrees to the plane of the tooth row and permits both mandibular elevation and retraction. The origin of the M.t. in Glossotherium is relatively more elongate than in either Bradypus or Choloepus, reflecting the relatively greater length of the skull (a primitive condition).

*M. zygodicomicandibularis* (=M. temporalis superficialis pars zygodicomicandibularis; M.z.; Fig. 3B, C, K). In Glossotherium, this muscle arises from a smooth depression on the medial surface of the broad posterior and ascending jugal processes. In contrast to the tree sloths, especially Bradypus, the ZAL in Glossotherium provides no additional surface area for the muscle origin, even though it probably is relatively as large as in Bradypus and relatively much larger than in Choloepus. Fibers of M.z. in Glossotherium pass posteroventrally to insert into a ridge-bounded, smooth, oval depression at the base of the coronoid process, anterodorsal to the M.m.p. insertion. The M.z. has a relatively large origin and insertion, and the distance between the medial zygomatic arch surface and the mandibular ramus is short; therefore, as in tree sloths, this muscle is sheet-like and lacks tendinous divisions. The orientation of the M.z. in Glossotherium is posteroventral, similar to that in Choloepus and most other mammals, and is probably a primitive character.

Pterygoideus Musculature (Fig. 5)

In general, these muscles in sloths are large relative to the pterygoid mass in other mammals (Toldt, 1906, 1907, 1908; Edgeworth, 1935; Turnbull, 1970; Naples, 1985a). However, the division of *M. pterygoideus* in sloths resembles that seen in other mammals.

*M. pterygoideus lateralis*, upper portion (M.p.l.u.; Fig. 5). In Glossotherium, this muscle arises from a shallow, round depression high on the lateral aspect of the elongate pterygoid flange. The muscle passes posteroventrally to insert in a roughened depression on the anterior edge of the mandibular condyle, medial to the condylar notch. The origin and insertion are similar in tree sloths but less distinct in Glossotherium. The posteroventral line of action in Choloepus is typical of most mammals and also is seen in Glossotherium (Turnbull, 1970; Naples, 1983a). In contrast, this muscle is oriented posterodorsally in Bradypus, a derived character (Naples, 1985a), and is associated with ventral elongation of the pterygoid flanges. In tree sloths, the muscle is thick and fleshy and divided by few internal fascial planes, as is probable in Glossotherium.

*M. pterygoideus lateralis*, lower portion (M.p.l.l.; Fig. 5). In Glossotherium, this muscle arises ventral to the M.p.l.u. from a larger and more oval depression. The line of action is slightly posterodorsal, differing from the M.p.l.u. The M.p.l.l. inserts into a roughened oval depression ventral to the M.p.l.u., anterolaterally on the condyle, and medial to the condylar notch. The M.p.l.u. line of action is reminiscent of Bradypus but not of Choloepus. In contrast to the tree sloths, with two similarly oriented M.p.l. segments, the lines of action of the two parts differ in Glossotherium. This is also exhibited in another ground sloth, Nothotheriops (Naples, 1987). The upper and lower portions of the M.p.l. in Glossotherium are separate and relatively larger than those of Choloepus but similar to the relatively large muscles in Bradypus.

The M.p.l. in Choloepus pulls anteromedially, with a small vertical force component, whereas in Bradypus the M.p.l. pulls posterodorsally with a medial force component greater than the vertical force directed ventrally (Naples, 1985a, 1987). However, the M.p.l. functions similarly in both tree sloths. The downward force component (which would dislocate the mandibular condyle if large movements were involved) is canceled by the bony stop present only on the medial gelenoid surface in Bradypus, presuming that the masseter and medial pterygoid muscles involved in this movement are active on both sides of the head simultaneously (Gysi, 1921; Herring et al., 1979). In most mammals, the mandibular condyle slides downward upon opening (Carlsson, 1942). Therefore, although different structurally from the typical mammalian arrangement, this mechanism prevents mandibular dislocation in tree sloths (Naples, 1985a, 1987). The medial gelenoid surface in Glossotherium is a better bony stop than that in Bradypus, and therefore limits downward condylar movement more effectively (Fig. 5B). In Glossotherium, the dorsal and ventral force components of similarly sized, but differently oriented, M.p.l.u. and M.p.l.l. would cancel one another, resulting in a primarily anterior pull on the medial aspect of the condyle.

*M. pterygoideus medius* (M.p.m.; Fig. 5). In Glossotherium, this muscle arises from a roughened oval depression, located posteroventral to the M.p.l.l. origin, on the lateral side of the elongated pterygoid flange (Fig. 5). The fibers pass posteroventrally, to insert into a large teardrop-shaped fossa posterior to the M. alveolus; the fossa is outlined by sharp ridges medially on the mandibular ramus and angle (Fig. 5). The M.p.m. in Glossotherium is relatively larger than in Choloepus and has a more anteroposterior line of action. This muscle has a mechanical advantage similar to that of Bradypus and a similar relative size (Fig. 5; Naples, 1985a).

In tree sloths, the M.p.m. largely lacks internal fascial planes and has few ridges for tendon attachment, in contrast to the strongly roughened origin
Figure 5. The origin (SA), insertion (SB), dorsal view (SC), lateral view, and a reconstruction (SD) of the upper and lower heads of *M. pterygoideus lateralis* (M.p.l.u. and M.p.l.l., respectively) and the *M. pterygoideus medius* (M.p.m.). The zygomatic arch and the coronoid process of the mandible have been removed (sections through the cut edges are designated by hatching) and at the site of insertion the mandible is shown as if it is transparent. A key to the muscle shading patterns for Figures 3–5 is shown at the right.
Figure 6. Lateral view of the skull and mandible of Glossotherium in occlusal relationship shows the lines of action of the muscles of mastication. Muscle abbreviations are as in the previous figures.

and insertion of this muscle in Glossotherium. This suggests that the M.p.m. was more tendinous in Glossotherium than in tree sloths.

DISCUSSION

Diverse characters of cranial osteology, dental structure, occlusal pattern, and reconstruction of masticatory musculature permit analysis of cranial function in Glossotherium. Interpretation of the significance of the structural-functional relationship makes it possible to distinguish primitive and derived characters by showing the relationship of different individual character states and character complexes to one another. Biomechanical principles shape the selection pressures upon these characters and, therefore, must be considered in an evolutionary analysis. Analysis of these characters and character complexes thus clarifies the evolutionary history and relationships of Glossotherium among the mylodonts and other sloth lineages. Characters examined in Glossotherium include those of previously determined functional significance that have been studied in other sloths (Naples, 1982, 1985a, 1986, 1987).

Premaxilla and Predental Spout

All sloths possess a reduced premaxilla when compared to other mammals. It is non-tooth bearing, unfused, or sometimes only partially fused to the maxilla. It has lost bony contact with the nasals, and sometimes the left and right premaxillae do not contact one another (Owen, 1842; Parker, 1885; Winge, 1941; Romer, 1966; Naples, 1982). Premaxillae may be small and arrowhead-shaped (Bradypus); larger, broader, and triangular (Choloepus); or may form a pair of slender, poorly fused elongate rods (Notothrichiops). The triangular premaxilla in Glossotherium is more elongate than in Choloepus, with left and right elements fused midventrally as well as to the maxilla, and lacks the large single foramen emarginating the anterior maxillary border. In addition to being longer, the premaxilla in Glossotherium is wider than in Choloepus.

The predental spout in Glossotherium is broad, slightly flared, and fused in a thick and deep mental symphysis (Fig. 1). The predental spout and premaxilla lengthen the anterior facial region in Glossotherium. Although a bony nasal septum is lacking, the large, rough-edged, trapezoid-shaped nasal opening provides attachment for extensive nasal cartilages and other soft tissues, allowing the presence of a thick flexible upper lip to aid food manipulation, as in Choloepus (Naples, 1982). The predental spout occurs in all sloth lineages and therefore is considered primitive in Glossotherium, although distal spout breadth is a derived character appearing in later mylodont sloths. Because earlier cranial reconstructions omitted a large amount of nasal tissue anteriorly, the face in Glossotherium has previously been reconstructed as too short and blunt (Owen, 1842; Stock, 1925; Fig. 6).

Relationship Between the Zygomatic Arch, Postorbital Process, and Cranial Ligaments

The typical sloth zygomatic arch consists of a jugal bone with upper and lower processes and an elongate temporal squamosal process. In small ground sloths and tree sloths, the anterior and posterior
zygomatic arch portions are unfused (Ameghino, 1889; Anthony, 1918; Stock, 1925; Romer, 1966; Webb, 1985). In the moderate-sized *Nothotheriops*, the two portions meet but do not fuse, and in large sloths the arch is fused anteroposteriorly. Primitive ground sloths were small and had unfused zygomatic arches (Stock, 1925; Winge, 1941). This condition was probably retained from more insectivorous antecedents which had a reduced and divided zygomatic arch (Naples, 1985a) similar to Recent anteaters (Flower, 1882; Romer, 1966; Wetzcl, 1983). Therefore, the fused jugal and squamosal process in *Glossothterium* (and a few other sloths) is a derived character and is probably necessary, in a biomechanical sense, to withstand large bending forces at the maxillo-jugal suture (Alexander, 1968; Currey, 1984).

Although all sloth jugals have at least two processes for attachment of the ligaments that complete the zygomatic arch, their orientations differ; horizontal (*Choloepus* and *Scelidotherium*) or vertical and above the posterior zygomatic arch attachment (*Eremotherium*). Other genera have upper processes ranging from nearly vertical (*Bradyapus*) to only slightly above the squamosal process attachment (*Glossothterium*). The postorbital and upper jugal processes determine size, thickness, and orientation of the postorbital ligament. In *Choloepus*, the postorbital process is pointed with a small protuberance for postorbital ligament attachment. In other sloths the postorbital process is an elongate ridge (*Bradyapus*). The jugal attachment in *Choloepus* is broad, resulting in an approximately triangular ligament, whereas that in *Bradyapus* and *Nothotheriops* is more rectangular. The posteriorly oriented upper jugal process in *Choloepus* and *Scelidotherium* minimizes the size of the jugal-temporal portion of the zygomatic arch ligament, whereas the more vertically oriented upper jugal process in *Bradyapus* and *Nothotheriops* maximizes ligament size and simultaneously covers more of the temporal fossa. In *Glossothterium*, the postorbital process is a long, rounded ridge, inflated by the frontal sinus. The expanded frontal bone maximizes the attachment area for the postorbital ligament posteriorly, shortening the distance to the attachment on the upper jugal process. The large sinus underlying the frontal bone is buttressed by bony ridges that divide the sinus into a series of rounded openings, somewhat like a honeycomb. These reinforcing ridges function as a series of I-beams, allowing the bone to withstand the greater multidirectional tensile stresses transmitted by the large, broad postorbital ligament (Alexander, 1968; Currey, 1984).

**Implications of CMJ Structure**

The shape, orientation, and distance of the CMJ above the tooth row varies greatly among mammals and is directly correlative with diet. Typically, herbivores have shallow glenoid fossae that permit greater anteroposterior and labiolingual freedom of mandibular movement (Greaves, 1980). The glenoid fossa of *Glossothterium* and other fossil and Recent sloths exhibits this typical herbivore structure (Naples, 1982, 1987), even though other osteological structures may restrict condylar movement in one or more planes.

Several mechanisms for controlling the amount of freedom of mandibular movement have been described: (1) In *Choloepus*, a bony shelf forms an expansion of the lateral glenoid fossa that contacts the lateral projection of the mandibular condyle. When these surfaces meet during mastication, further anteromedial movement is prevented (Naples, 1982, 1985a). (2) *Bradyapus* lacks a bony stop mechanism; condyle position control is maintained by the posterodorsally oriented lateral pterygoid muscles (Naples, 1985a). (3) In *Nothotheriops*, lateral movement is restricted by a ridge on the ventral temporal squamosal process; medial movement is limited by a curved temporal surface, buttressed by thickening of the temporal-pterygoid suture (Naples, 1987).

Mandibular movement in *Glossothterium* is restricted medially by a bony stop that consists of a sharply defined depression on the lateral surface of the pterygoid bone that apposes the medial condylar occlusal facet. Although the bony stop in *Glossothterium* is medial rather than lateral (as in *Choloepus*), anterior and medial mandibular movements are similarly confined. Restriction of anterior and medial mandibular movement is important, because these genera possess caniniform teeth that require precise dorsoventral alignment during occlusion. This condition precludes the elevation of the CMJ which occurs in *Bradyapus* and *Nothotheriops*, genera that do not possess caniniform teeth.

These occlusal requirements correlate with the location of the CMJ, in approximately the same plane as the cheek tooth row in *Glossothterium*, a relationship that minimizes anteroposterior movement as the teeth occlude. A precise occlusal relationship between upper and lower caniniform teeth is of particular importance to *Choloepus*, a sloth with long caniniform teeth. It is also significant to *Glossothterium* because proper alignment of dental wear surfaces on the short caniniform teeth is required for biting. However, because the caniniform teeth are relatively short it is unnecessary for *Glossothterium* to gape as widely as *Choloepus*. At 45 degrees of gape the mandibular condyle in *Glossothterium* dislocates. This gape angle is 15 degrees less than the maximum gape predicted for *Choloepus*. The short anterior teeth in *Glossothereium* require an equivalent distance to clear as do those of *Bradyapus* (another sloth with short anterior teeth), in addition to a greatly elevated CMJ and much anteroposterior mandibular movement during occlusion.

**Occiput and Occipital Condyles**

Thickened parasagittal and lambdoidal crests surmount a large buttressed parietal-occipital sinus in
Glossotherium. The sinus is incompletely divided from the more anterior frontal-parietal sinus. Together, these partitioned sinuses elevate and reinforce the skull table anterodorsal to the braincase (Stock, 1925), increasing surface area for attachment of the postorbital ligament and temporal musculature laterally, and the M. splenius capitus, M. trapezius, and other deep neck and back muscles posteriorly.

The occipital condyles are sharply convex and postero inferio rly oriented, indicating that the head of Glossotherium was carried slightly higher than has been described or illustrated previously (Owen, 1942; Stock, 1925). The occipital condyles are broad and widely spaced. This arrangement would restrict horizontal cranial movements if the head were short; however, the long relatively narrow skull in Glossotherium compensates for restricted mobility of the head on the neck at the occiput, while requiring a strong bony support platform and neck muscles with a large mechanical advantage upon which to pivot the skull. Extension of cranial sinuses into the occipital area is not seen in tree sloths or in other fossil sloths (Owen, 1842; Allen, 1913; Stock, 1925; Naples, 1982, 1985a, 1987). Expansion of the cranial sinuses into the parietal area increases the surface area for the attachment of neck muscles including the M. trapezius, M. splenius capitus, M. semispinalis capitus, and M. longissimus capitus. These muscles, in conjunction with muscles of the occipital triangle and other intrinsic back muscles, move and maintain posture of the head and neck in mammals.

The head of Glossotherium is relatively larger and more robust than that of Nothrotheriops and the tree sloths and, therefore, requires relatively larger muscles (and other structural modifications in the occipital region) to control head movement and posture. Movement of the head from side to side, a motion useful in browsing or grazing, is enhanced in Glossotherium by a triangular gap between the transverse processes of the atlas and axis (cervical vertebrae 1 and 2). This gap is created by the posterolateral orientation of the transverse process of the axis. The triangular-shaped gap receives the transverse process of the atlas, permitting Glossotherium a wider range of head movement than would be possible otherwise. This osteological and muscular arrangement is different from other sloths studied here, and therefore can be considered a derived condition (Alexander, 1968).

Pterygoid Region

In Glossotherium, the elongate pterygoid bones are similar in profile to Nothrotheriops, with the greatest elongation anteriorly; however, Glossotherium lacks the inflated pterygoid sinuses seen in Nothrotheriops and Choloepus. As in Bradypus, the elongated pterygoid flanges are thin-walled in Glossotherium and buttressed laterally by ridges marking the origins of the medial and lateral pterygoid muscles.

Dental Wear Striations

Wear striations on the teeth of Glossotherium trend along the anterolingual–posterolabial axis. The transitions from hard to soft dentine are smooth and flush lingually, and stepped labially (Greaves, 1973; Rensberger, 1973; Costa and Greaves, 1981). These striations indicate that this genus has an anteromedially directed power stroke common to other mammals (Hiemae, 1978). The amount of anteroposterior movement in Glossotherium is somewhat less than that observed in Bradypus or Nothrotheriops.

Masticatory Musculature

The muscles of mastication in Glossotherium conform to the general plan observed in other sloths with respect to muscle division, probable fiber architecture and bony attachments. The most anterior segment of the superficial masseter (M.m.s.— 5) restricts the gap in Glossotherium to 22 degrees, a derived condition (Table 3). Manipulation of skulls and mandibles indicates that gap would not be restricted by joint structure until at least 45 degrees. Superficial masseter length in Glossotherium is shorter than in other sloths because the insertion on the mandibular angle projects less far posteriorly. However, the overall insertion area is probably comparable because the angular process is deeper dorsoventrally than in other sloths. Resolution of the forces generated by superficial masseter segments results in a line of action oriented approximately halfway between the lines of action of the same muscle segments in the tree sloths, and illustrates a retention of the primitive muscle orientations in the tree sloths and Glossotherium (Table 4). The short deep insertion of the superficial masseter makes the range of muscle segment orientation greater in Glossotherium than in other sloths and may enhance mandibular movement patterns in this genus, particularly in the vertical plane (Fig. 7).

The deep masseter (M.m.p.) in Glossotherium is relatively larger than in the tree sloth Choloepus, but similar in relative size to its homologues in Bradypus and Nothrotheriops. Of these four sloths, only Choloepus retains the primitive small relative mass, the distance from origin to insertion, and the line of action for the deep masseter. In megaethersids and Glossotherium, the deep masseter is relatively larger than in Choloepus. This muscle is anterodorsally oriented in Bradypus and Glossotherium, although the origin is mostly from the relatively wider descending jugal process in Glossotherium, emphasizing the anterior component of the line of action (Table 4).

The temporalis (M.t.) in Glossotherium has a more elongate origin than in other sloths and a resolved
line of action between the lines of action of this muscle in the tree sloths. The temporalis in Glossotherium is relatively larger than in tree sloths and Notbrotheriops and could have produced greater forces in mandibular elevation, while retaining primitive muscle orientation.

The zygoarticomandibulairis (M.z.) in Glossotherium is relatively as large as those in Bradypus and Notbrotheriops and relatively larger than that of Choloepus. Choloepus lacks an ascending jugal process, and therefore has retained the primitive condition of a relatively small, horizontal origin for the M.z. In Glossotherium, the M.z. originates from an expanded, posterodorsally oriented ascending process and emphasizes the anterior component of the line of action more than in other sloths. This is a derived condition (Table 4).

Although relatively larger, the superior lateral pterygoid head in Glossotherium is typical of that in other mammals and Choloepus with regard to origin and insertion. The anterodorsal orientation of the lateral pterygoid in Glossotherium and Choloepus reflect the primitive condition in contrast to the posterodorsally oriented lateral pterygoids in megatheriids. The inferior lateral pterygoid head in Glossotherium converges slightly toward the superior lateral pterygoid head at its insertion, which is in contrast to the condition found in Choloepus. For both sloths, the anteroposterior alignment of the anterior teeth is critical; in addition, the mandibular condyles are wider mediolaterally and not freely movable anteroposteriorly as they are in Bradypus and Notbrotheriops. The two lateral pterygoid heads converge strongly in Bradypus and Notbrotheriops, perhaps to permit them to act in concert across a smaller area, giving the mandibular condyle greater anteroposterior freedom of movement. Minor convergence of the lateral pterygoid heads in Glossotherium decreases mechanical advantage slightly; however, the broad condyle in Glossotherium may compensate for this. Close apposition of the insertion of the lateral pterygoid heads in Glossotherium may refine the mediolateral mandibular movements important for chewing with the molariform teeth and biting with the anterior teeth.

The medial pterygoid in Glossotherium is more vertical and anterodorsal than in Choloepus and Bradypus, reflecting a derived orientation (Table 4). This muscle is relatively larger than in tree sloths or Notbrotheriops and may be important in controlling the position of the mandibular angle during elevation in order to occlude the short caniniform teeth properly. Such muscular control may act as an occlusal guide mechanism to allow proper wear surface apposition, rather than the size and shape of the caniniform teeth (Scapino, 1972).

ESTIMATION OF GAPE

The degree to which sloths can gape is one factor that may limit the manner in which they feed. The ability to open the mandible to a given degree is determined by several factors, which include (1) mandibular length and shape; (2) position, orientation, and structure of the CMJ; and (3) shape, length, and orientation of the masticatory muscle segments. From skull and jaw manipulations, it is
Table 4. The angle in degrees of the orientation of the masticatory muscles in four sloth genera compared in this study. The angles were measured as the number of degrees of divergence from the occlusal plane in each specimen (N = 5 of each genus). Zero degrees is toward the anterior of the cranium at the plane of the cheek tooth row. The numbers in italics denote derived muscle orientations.

<table>
<thead>
<tr>
<th>Masticatory muscle</th>
<th>Sloth lineages</th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mylodontid</td>
<td>Megatheriid</td>
<td>Megalonychid</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Glossotherium</td>
<td>Nothrotheriops</td>
<td>Bradypus</td>
<td>Choloepus</td>
<td></td>
</tr>
<tr>
<td>M. masseter superficialis</td>
<td>325°</td>
<td>349°</td>
<td>318°</td>
<td>323°</td>
<td></td>
</tr>
<tr>
<td>M. masseter profundus</td>
<td>20°</td>
<td>111°</td>
<td>48°</td>
<td>123°</td>
<td></td>
</tr>
<tr>
<td>M. temporalis</td>
<td>125°</td>
<td>112°</td>
<td>118°</td>
<td>141°</td>
<td></td>
</tr>
<tr>
<td>M. zygomatico mandibularis</td>
<td>57°</td>
<td>83°</td>
<td>90°</td>
<td>79°</td>
<td></td>
</tr>
<tr>
<td>M. pterygoideus lateralis</td>
<td>12°</td>
<td>130°</td>
<td>125°</td>
<td>20°</td>
<td></td>
</tr>
<tr>
<td>M. pterygoideus medius</td>
<td>300°</td>
<td>330°</td>
<td>330°</td>
<td>318°</td>
<td></td>
</tr>
</tbody>
</table>

clear that osteologic restrictions on gape are not limiting up to 45 degrees. At greater gape than 45 degrees, the mandibular condyle dislocates and the mandibular angle impinges upon the paroccipital process. In addition, gape is limited by the degree to which masticatory muscles can be stretched without damage, about twice the resting length (Carlsöö, 1942).

The distance to which masticatory muscle segments in Glossotherium would be stretched at gaps of 20, 25, 30, 35, 40, and 45 degrees suggests that M.m.s.—5 could stretch no more than 22 degrees without damage (Table 3). No other superfluous masster set segments restrict mandibular opening to less than 45 degrees, although three other muscles (the M. temporalis, M. zygomatico mandibularis, and M. pterygoideus medius) would have been overstretched. The Recent tree sloth Choloepus can gape to approximately 60 degrees; the larger distance is important in an animal with elongate caniniform teeth. In the other Recent tree sloth, Bradypus, the maximum gape is approximately 40 degrees (Naples, 1984a). Similarly, this method predicts a 25-degree gape in Nothrotheriops, a sloth with a more elongate skull and mandible and no anterior teeth (Naples, 1987).

In Glossotherium, the anteroventral segment of the superficial masster limits maximum gape to less than 23 degrees, although no other muscle or segment is limiting until almost 35 degrees. In all sloths studied to date, gape is limited by M.m.s.—5, whether other muscles or segments constrain mandibular opening more than do bones and joints. The variable presence of short caniniform teeth in this sloth indicates that caniniform tooth length, rather than presence or absence, is the most important factor in setting maximum gape requirements. Even though the maximum degree of mandibular rotation in Glossotherium was small, the buccal opening was large, because of the large skull, long maxillae, premaxillae supporting a thick upper lip, long mandible, and broad predental spout. The large buccal opening in Glossotherium was important for ingestion of the bulky leafy vegetation preferred by these sloths (Stock, 1925).

DETERMINATION OF DERIVED CHARACTERS AND IDENTIFICATION OF CHARACTER COMPLEXES IN GLOSSOTHERIUM

Cranial characters in Glossotherium were compared to the distribution and state of those characters among other sloth lineages. Refinement of our understanding of xenarthran relationships relies upon the ability to test hypotheses concerning “the distribution of characters that can be assumed to be uniquely derived within the group (Engelmann, 1985).” Therefore, identification of derived characters and their interrelationships, by studying biomechanical constraints upon them, can provide important information regarding sloth relationships and evolutionary history.

Previous studies identifying sloth cranial characters generally agree (Patterson and Pascual, 1972; Engelmann, 1985; Webb, 1985; Naples, 1982, 1985a, 1987), based upon comparison with the earliest mylodont sloths and other mammals, that the following eight cranial characters are primitive for sloths: (1) a large diastema, (2) a CM at the level of the cheek tooth row, (3) elongate caniniform anterior teeth, (4) a large gape, (5) a basicranial angle approaching zero degrees, (6) an incomplete zygomatic arch, (7) a long facial region, and (8) bilobate teeth. The present study has identified 24 additional cranial characters, both primitive and derived, based upon their relationships with the eight characters listed above (Table 5).

In all animals, morphology is determined, in part, by biomechanical constraints delimiting the function of critical aspects of character associations. Identification of interrelated characters is important because treating a character complex as a unit reduces the likelihood that biases will be introduced.
Table 5. The distribution and state of cranial characters in four genera of sloths, representing all three sloth lineages. Characters in italics are derived.

<table>
<thead>
<tr>
<th>Cranial character</th>
<th>Glossotherium</th>
<th>Nothrotrochiops</th>
<th>Bradypus</th>
<th>Choloepus</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dental formula</td>
<td>⅓ or ⅔</td>
<td>¼ or ⅜</td>
<td>⅓ or ⅔</td>
<td>Elongate</td>
</tr>
<tr>
<td>Anterior tooth length</td>
<td>Short</td>
<td>None</td>
<td>Short</td>
<td></td>
</tr>
<tr>
<td>Anterior tooth shape</td>
<td>Caniniform</td>
<td>Chisel-shaped</td>
<td>Caniniform</td>
<td></td>
</tr>
<tr>
<td>Upper cheek teeth</td>
<td>Lobate; anterior-posterior &gt; labio-lingual axes; M1-M4 = size</td>
<td>Subrectangular; labio-lingual &gt; anterior-posterior axes; M1, M2 &lt; M3, M4</td>
<td>Ovoid; labio-lingual = anterior-posterior axes; M1, M2 &lt; M3, M4 = size</td>
<td>Ovoid; anterior-posterior &gt; labio-lingual axes; M1, M2 &lt; M3, M4</td>
</tr>
<tr>
<td>Lower cheek teeth</td>
<td>Lobate; anterior-posterior &gt; labio-lingual axes; M1 = M2, M唾 &lt; M3</td>
<td>Ovoid; labio-lingual &gt; anterior-posterior axes; M1 &lt; M2, M3</td>
<td>Ovoid; subrectangular; anterior-posterior = labio-lingual axes; M1 = M2 &lt; M3</td>
<td>Ovoid; anterior-posterior &gt; labio-lingual axes; M1 = M2 &lt; M3, M4</td>
</tr>
<tr>
<td>Premaxilla</td>
<td>Large, arrowhead</td>
<td>Elongated, slender, unfused</td>
<td>Arrowhead</td>
<td>Arrowhead</td>
</tr>
<tr>
<td>Nasal</td>
<td>Elongate</td>
<td>Elongate</td>
<td>Extremely short</td>
<td>Short</td>
</tr>
<tr>
<td>Maxilla</td>
<td>Flares widely</td>
<td>Narrow</td>
<td>Flares widely</td>
<td>Flares slightly</td>
</tr>
<tr>
<td>Tooth row shape</td>
<td>Wider anteriorly</td>
<td>Parallel</td>
<td>Wider anteriorly</td>
<td>Wider anteriorly</td>
</tr>
<tr>
<td>Postorbital process</td>
<td>Small, rounded</td>
<td>Small, rounded</td>
<td>Large, rounded</td>
<td>Large, pointed</td>
</tr>
<tr>
<td>Location of coronal suture</td>
<td>⅓ toward rear</td>
<td>⅔ toward rear</td>
<td>⅔ toward rear</td>
<td>⅔ toward rear</td>
</tr>
<tr>
<td>Zygomatic arch</td>
<td>Complete</td>
<td>Complete</td>
<td>Open</td>
<td>Open</td>
</tr>
<tr>
<td>Ascending process</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
<td>No</td>
</tr>
<tr>
<td>Angle from cheek tooth row</td>
<td>30°</td>
<td>60°</td>
<td>55°</td>
<td>—</td>
</tr>
<tr>
<td>Descending process</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
</tr>
<tr>
<td>Angle from cheek tooth row</td>
<td>70°</td>
<td>40°</td>
<td>45°</td>
<td>60°</td>
</tr>
<tr>
<td>Height of CMJ</td>
<td>Equals tooth row level</td>
<td>Above tooth row</td>
<td>Above tooth row</td>
<td>Equals tooth row level</td>
</tr>
<tr>
<td>Condyle shape</td>
<td>Labio-lingual axis wider</td>
<td>Anterior-posterior axis longer</td>
<td>Anterior-posterior axis longer</td>
<td>Labio-lingual axis wider</td>
</tr>
<tr>
<td>Bony stop present</td>
<td>Yes; medial</td>
<td>None</td>
<td>None</td>
<td>Yes; lateral</td>
</tr>
<tr>
<td>Degrees gape</td>
<td>22°</td>
<td>25°</td>
<td>40°</td>
<td>60°</td>
</tr>
</tbody>
</table>

into a phylogenetic analysis from inadvertent over-representation of a single complex. Some of these interrelationships, and the most important aspect of the character or character states involved, have been revealed in Glossotherium by the present study (Table 6). Twelve derived characters from Table 5 have been grouped into complexes according to interdependence of function (Table 6). For each of the four complexes identified, the state of one character determines the morphology of those associated with it, and whenever one of these derived characters is present, the others must be also to enable the complex to function.

In Complex I, the shortness of the caniniform teeth is critical because short caniniforms reduce the need for a wide gape or a long diastema between molariform and caniniform teeth. Because a wide gape is not necessary to clear the anterior teeth for
Table 6. Derived cranial characters forming functional complexes in *Glossotherium*. For each complex the character listed first is acted upon most strongly by biomechanical constraints, which determine the state of others in the complex.

Complex I
1. Short caniniform teeth
2. Lack of a diastema between caniniform and molariform teeth
3. Reduced distance for gape

Complex II
1. Caniniform teeth (sometimes) present
2. Differentiated facets on mandibular condyle (wider labiolingually); forms a bony stop mechanism
3. Concave glenoid fossa with a facet for the bony stop

Complex III
1. Increased mechanical advantage of superficial masseter and medial pterygoid muscles
2. Angular process of mandible deepened posterovertrally
3. Pterygoid flange elongated posterovertrally

Complex IV
1. Increased mechanical advantage of the *M. zygomaticomandibularis*; line of action more vertical and anteriorly oriented
2. Posteriorly oriented ascending jugal process
3. Increased area for origin of the *M. zygomaticomandibularis* by reduction of the size of the condylar notch

biting, *Glossotherium* can retain the primitive state of the CMJ (in the same plane as the cheek tooth row). Likewise, a long diastema which would increase the distance between the anterior teeth and the joint to maximize the clearance distance of the caniniform teeth at a given degree of mandibular rotation is unnecessary. The resulting (relatively short) mandible in *Glossotherium* also permits the muscles of mastication to have a greater mechanical advantage.

In Complex II, the presence of caniniform teeth (even if only in some specimens), which require precise alignment for proper function, is critical. A CMJ at the same level as the cheek tooth row minimizes the anteroposterior tooth movement during occlusion. Although retention of a low CMJ is primitive, the bony stop developed on the mandibular condyle (preventing excess mediolateral mandibular movement) is derived.

The limiting character in Complex III is the maximization of mechanical advantage of the *M. pterygoideus medius* and the *M. masseter superficialis*, which is achieved in *Glossotherium* by retaining the primitive muscle orientation seen in animals with elongate anterior biting teeth (Turnbull, 1970; Herring and Herring, 1974; Weijs, 1980; Lucas, 1981; Greaves, 1983). Optimization of the mechanical advantage of these jaw closing muscles is important because they generate much of the force that produces the pattern of mandibular movement during the masticatory power stroke. In animals with elongate anterior teeth, maximum force is needed at the time of intercuspatation of the tooth tips to grip and pierce any objects bitten (Herring and Herring, 1974; Weijs, 1980; Lucas, 1981; Greaves, 1983). In contrast, the caniniform teeth in *Glossotherium* are blunt and were probably used for crushing thick plant stems and gripping bulky clumps of leaves. Whereas the maximum force needed in animals with pointed anterior teeth is after intercuspatation, when the jaw is almost closed (10 to 0 degrees; Weijs, 1980), in *Glossotherium* maximum force would be needed from prior to intercuspatation to the beginning of intercuspatation (when the jaw is open from 22 to 5 degrees). In contrast to the condition in the other animals, the origins of the *M.p.m.* and the *M.m.s.* in *Glossotherium* are from an elongated pterygoid flange and a descending jugal process, and the insertions are on the lingual and labial sides of a posterovertrally elongated angular process. Ventral displacement of these muscles shifts the arc of maximum muscle effectiveness to the larger gapes (22 to 10 degrees) in *Glossotherium* without sacrificing either the distance to which the sloth could gape or the amount of force the muscles could generate.

In Complex IV, maximization of mechanical advantage in the *M. zygomaticomandibularis* is critical and results in the posterior orientation of the ascending jugal process and decreased size of the mandibular notch. The *M.z.* in *Glossotherium* is largely responsible for horizontal translation of the mandible (an important action in the latter portion of the masticatory stroke) as well as some elevation. Optimization of the mechanical advantage and mass of this muscle is important because ventral displacement of the *M.p.m.* and *M.m.s.* (described in Complex III) reorients the lines of action of those muscles to be less effective in mandibular translation.

CRANIAL MORPHOLOGY AND DIET

IN GLOSSTHERIUM

Stock (1925, 1930) suggested that *Glossotherium* was primarily a grazer, based upon tooth structure he determined to be of a "grinding" type. *Glossotherium* is the most common of the three sloth genera preserved in the Rancho La Brea asphalt deposits; *Notrotheriops* is less common and *Megalonyx* Jefferson, 1799, is quite rare. The diet of *Notrotheriops* is well documented through the analysis of dung contents in Rampart Cave, New Mexico (Hansen, 1978). Analyses of cranial structure and dental occlusion patterns (Naples, 1987) agree well with Hansen's (1978) results, suggesting that morphological analyses predict food habits accurately for sloths. Details of the diet of *Glossotherium* are unknown; no dung deposits are available.
for analysis, therefore dietary preferences must be deduced from sloth morphology.

In comparison to the teeth of *Nothrotheriops* and the tree sloths, which are all considered browsers, the cheek teeth in *Glossotherium* are relatively larger, have more complicated shapes, and retain a layer of cementum surrounding all sides. Analyses of wear striation orientation and flush or stepped transitions between hard and soft dentine (Greaves, 1973; Rensberger, 1973) has demonstrated that *Glossotherium* had an anteromedially directed masticatory power stroke. The path of mandibular movement is arcuate, with more medial translation than anterior movement (Fig. 2B). Emphasis on the medial component of motion ensures maximum shearing efficiency because this movement pattern brings the obliquely oriented cheek tooth cutting edges into contact perpendicular to their widest axes. The widest axes of the cheek teeth become less oblique posteriorly along the tooth row. This correlates with a change in the path of mandibular movement from anterior to posterior, with the greatest component of motion present at C₃, and the least at M₄.

Other evidence suggesting that the environment near Rancho La Brea was partially open scrub and grassland is the relative abundance of herbivores that both browse and graze. For example, camels, horses, antilocaprids, and bison were among the most common animals preserved. Conversely, the more strictly browsing forms, such as deer, are rare, as is the browsing sloth, *Nothrotheriops*. A mixed-forest, scrub, and grassland setting is also supported by the presence of both mastodons and mammoths. The former were browsers whereas the latter were grazers (Stock, 1930; Shaw and Quinn, 1986; Akersten et al., 1988).

Although more suited to grazing than the other sloths in the La Brea region, on the basis of dental evidence, *Glossotherium* was probably less efficient at ingesting grasses than some of the other local grazers (Janis, 1976). In comparison to horses, camels, antilocaprids, and bison, which have high-crowned, ever-growing teeth, and mammoths, which have continually replaced teeth, the sloth dental apparatus, with intermittent shearing surfaces acting alone, would have been too inefficient at reducing plant materials to small particle size to permit the sloths to obtain sufficient nutritive value from the food (Hansen, 1978). However, with a low projected metabolic rate, leading to a reduced energy requirement per unit body weight (Almeida and Fialho, 1924; Britton, 1941; McNab, 1978) a large body size, and an unusually capacious gut with a probable foregut fermentation site, *Glossotherium* could probably survive better on foods of lower nutritional value than could other sloths and browsing herbivores in the area. Observations on Recent tree sloths show that they have an unusually slow rate of passage of ingesta through the gut (Jeuniaux, 1962; Denis et al., 1967; Moir, 1968; Goffart, 1971; Bauchop, 1978; Parra, 1978). It is reasonable to assume that *Glossotherium* also had a slow rate of passage of food through the digestive tract. This might have enabled these sloths to obtain sufficient nutrition from high fiber foods to compete effectively for resources with the other La Brea herbivores. Although it is likely that grasses were more important in the diet of *Glossotherium* than in *Nothrotheriops*, the former probably ate a variety of foliage plants as well, and would probably be better considered a browser-grazer than a "pure" grazing form.

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