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Cranial Osteology and Function in the Tree Sloths, *Bradypus* and *Choloepus*

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ABSTRACT

Fossil and Recent sloths show great diversity in the structure of the skulls and dentition. Many of the characters seen in adult sloths are growth related, or depend on the mechanical relationships of skull elements. The teeth in sloths are of persistent growth and erupt as evenly spaced simple cones. These teeth acquire "cuspid" occlusal surfaces with both growth and wear. In *Choloepus* the anterior teeth are caniniform; in adults they are separated from the cheek teeth by a diastema which develops in juveniles with rapid growth of the most anterior part of the maxilla. The pattern of the tooth "cusps" differs between *Choloepus* and *Bradypus*. In *Choloepus* the teeth alternate; in *Bradypus* they are more directly apposed. In both sloths the biting and chewing functions are separated, the mandible is positioned more anteriorly in the glenoid fossa for biting with the caniniform teeth (*Choloepus*) or anterior chisel-shaped teeth (*Bradypus*), and moves posteriorly into position for chewing. This is analogous to the

shift in mandibular position in rodents. *Choloepus* and some megalonychid ground sloths resemble carnivorans in that the cranio-mandibular joint (CMJ) is close to the occlusal plane of the cheek teeth. In *Bradypus* a raised CMJ results in an improvement in the mechanical advantage of the masseter and medial pterygoid muscles and changes the path of mandibular movement, emphasizing forward motion. This is also true of herbivores, where it is beneficial to optimize the mechanical advantage of the masseter and medial pterygoid muscles. Analysis of both the pattern of wear facets and the muscles shows that jaw movement in the power-stroke is anteromedially directed. In sloths, the retention or loss of elongate anterior teeth and the ramifications that follow from these changes can be regarded as the most important factors in explaining the differences seen in cranial structure between *Choloepus* and some megalonychids and *Bradypus* and some megatheriids.

INTRODUCTION

A heterogeneous assemblage of New and Old World mammals was included by many early workers (see Romer, 1966) in the Eden-

tata. Many of these animals feed on ants or termites. As the dentition is reduced in number and attenuated in form or completely lost

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in many of these groups, dental characters were significant in the original definition of the order, and classically [e.g., Tims and Henry (1923)], attributed to the adoption of the anteating habit. More recently, these dental changes have been considered as possibly indicative of convergence rather than phylogenetic unity (e.g., Simpson, 1945). A reassessment of the order Edentata (Wetzel, in press) argues that the Cingulata (armored edentates, i.e., the extinct glyptodonts and the armadillos) and the Pilosa (hairy edentates, i.e., the anteaters, three extant genera); the tree sloths (two extant genera, and the extinct ground sloths) are members of a single order, preferably called the Xenarthra.

Glyptodonts, armadillos, and ground sloths have an extensive fossil record, while that of the anteaters is sparse, and fossils of the tree sloths are unknown. Most authors (Simpson, 1945; Patterson and Pascual, 1972; Romer, 1966; Kraglevitch, 1923, 1928; McKenna, 1975; personal commun.) recognize three major ground sloth lineages; mylodonts, megalonychids, and megatheres. The relationship of these animals to the tree sloths has not been established although several possible phylogenies have been proposed (fig. 1). The most commonly accepted classification (Simpson, 1945) groups the two genera of tree sloths on the basis of their arboreal habitus, reduced number of digits on both fore and hind feet coupled with a peculiar suspensory mode of locomotion and, as compared with other xenarthrans, unusual cranial characters. However, many of the characters used to group the genera *Choloepus* and *Bradypus* as the Bradypodidae (Simpson, 1945) are also found in other sloth lineages. *Bradypus* has three digits on both fore and hind feet, while *Choloepus* has two digits on the fore feet and three on the hind. This reduction in digit number resembles that seen in the most recent members of some of the ground sloth lineages. Whether the unique locomotor pattern shared by the tree sloths reflects a common ancestry or arose through convergence given a separate origin for the two genera is not clear. In the absence of a fossil record for the tree sloths, it is not possible to assess the structural changes which might reflect an in-

creased capacity to exploit the arboreal environment. Further, the phylogenetic relationships of earlier tree sloths to the ground sloths in terms of locomotor apparatus cannot be examined.

A number of cranial and dental characters were used to group the tree sloths as the Bradypodidae. Sicher (1944) augmented a series of earlier anatomical descriptions of the jaw musculature, jaw joint, and the dentition of *Choloepus* and *Bradypus* (Schulman, 1906; Lubosch, 1908; Windle and Parsons, 1899; Leche, 1876–1900; Toldt, 1908; Edgeworth, 1935). Based on his dissection of the jaw muscles and an examination of the form of the teeth when worn, Sicher concluded that despite great similarity in the organization of the temporalis, masseter and pterygoids, the direction of the power-stroke in chewing was opposite in the two groups. He suggested that *Bradypus* has an anteriorly directed power-stroke whereas in *Choloepus* this movement was upward and backward. Based on an examination of wear facets in *Adapis*, Gingerich (1972) postulated that these early primates had a similar upward and backward power-stroke, a movement he termed "orthal retraction." However, a wide range of mammals has now been studied experimentally (see Hiiemae, 1978). In all cases the power-stroke is variably medial and anterior as well as upward in direction.

Therefore, given the uncertainties of the exact relationships between *Choloepus* and *Bradypus* as well as of both the three sloths to the other xenarthrans, it seems appropriate to reassess the cranial and dental characters of these mammals. This study compares the skeletal, dental and soft tissue anatomy of several species of both genera. A model for the mechanisms of chewing in each group is proposed.

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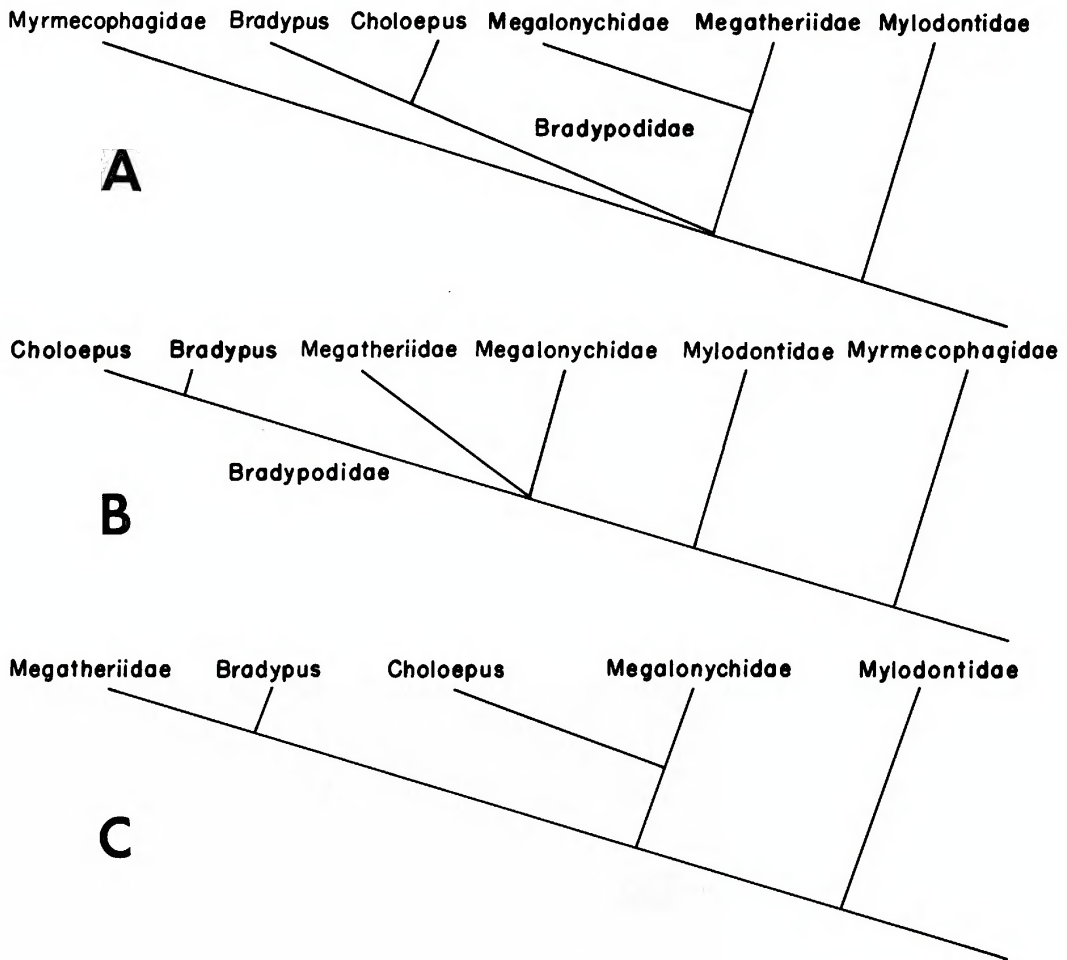


FIG. 1. Alternative phylogenetic relationships of the sloths, proposed by Simpson, 1945 (A), Romer, 1966 (B) and by Patterson and Pascual, 1972 and McKenna, 1975 (C).

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MATERIALS AND METHODS

A series of skulls and mandibles of *Choloepus* and *Bradypus* (figs. 2, 3, 4) from the

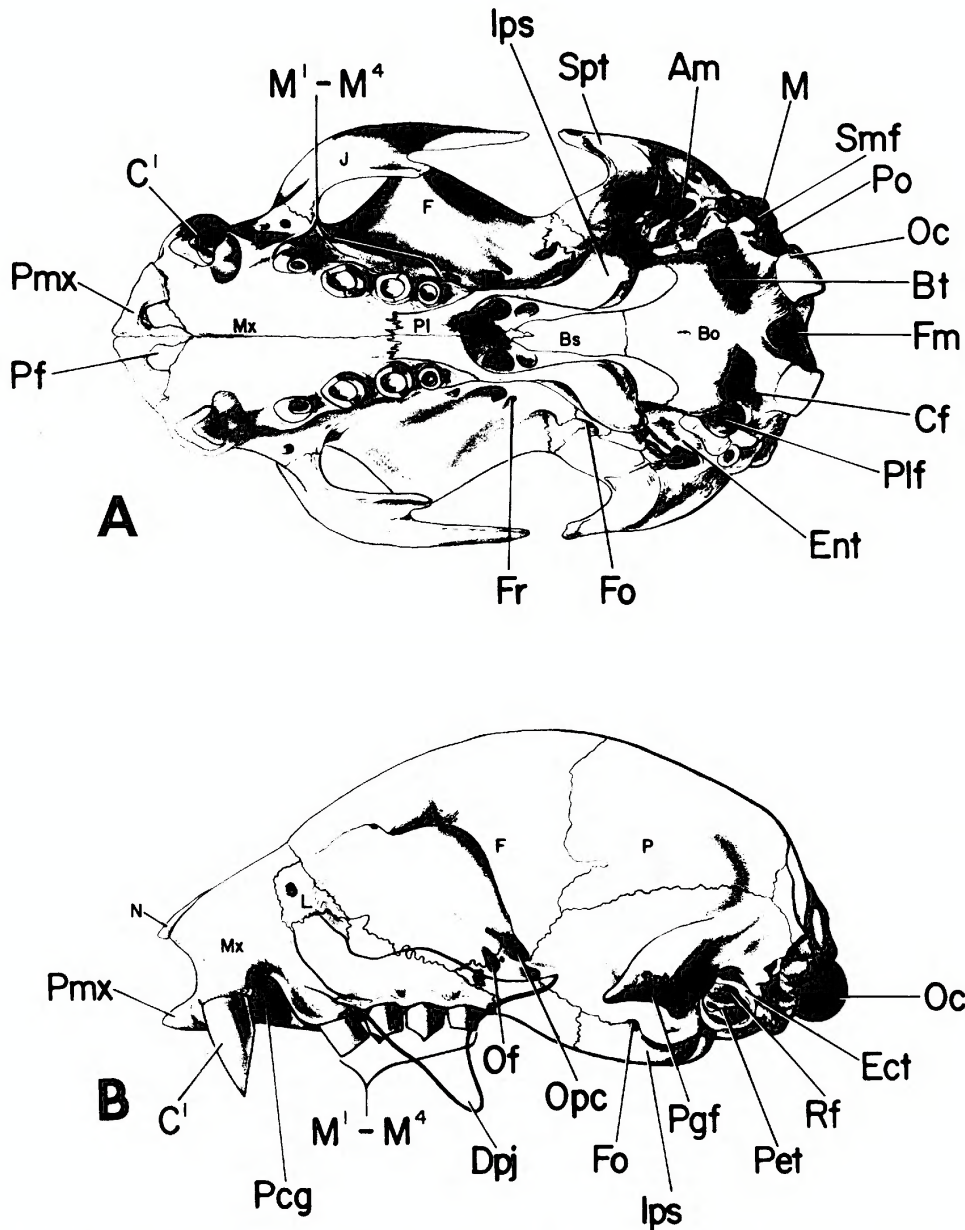


FIG. 2. Ventral (A) and lateral (B) views of the skull of *Choloepus*. Abbreviations: auditory meatus (Am), basilar tubercles (Bt), basioccipital (Bo), basisphenoid (Bs), caniniform tooth (C), condyloid foramen (Cf), descending process of jugal (Dpj), ectotympanic ring (Ect), entotympanic bone (Ent), external carotid foramen (Ecf), foramen magnum (Fm), foramen ovale (Fo), foramen rotundum (Fr), frontal bone (F), inflated sinus of pterygoid (Ips), jugal bone (J), lacrimal bone (L), mastoid process (M), molariform teeth 1-4 (M¹-M⁴), maxilla (Mx), nasal bone (N), occipital condyle (Oc), optic fissure (Of), parietal bone (P), petrosal bone (Pet), postcaniniform groove (Pcg), palatine foramen (Pf), profile of glenoid fossa (Pgf), palatine bone (Pl), posterior lacerate foramen (Plf), premaxilla (Pmx), paroccipital process (Po), fenestra rotundum (Rf), stylomastoid foramen (Smf), squamosal process of temporal bone (Spt), and vomer (V).

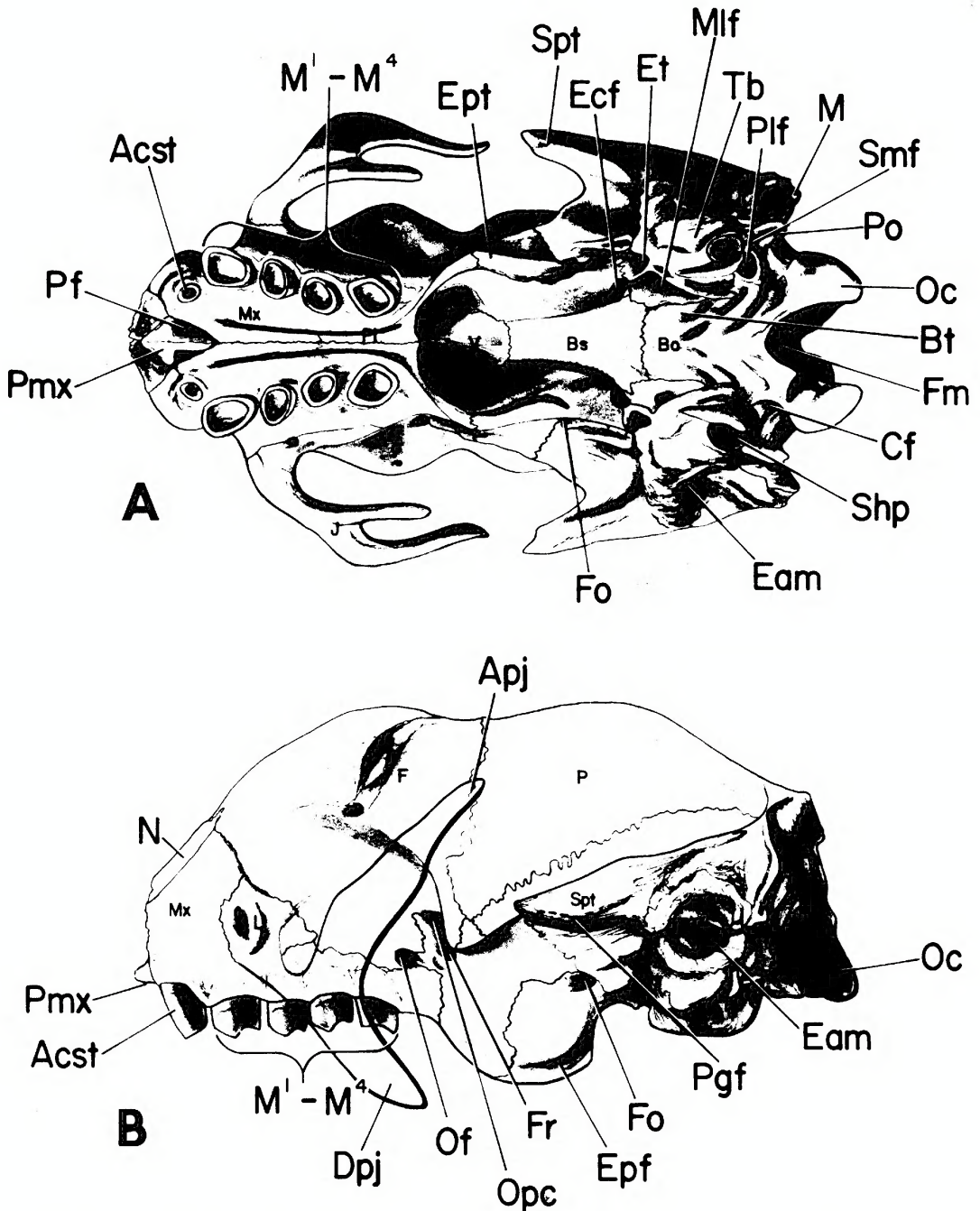


FIG. 3. Ventral (A), and lateral (B), views of skull of *Bradypus*. Abbreviations for structures in common with *Choloepus* are as in figure 2. Abbreviations for structures present only in *Bradypus* are: anterior chisel-shaped tooth (Acst), ascending process of jugal (Apj), external auditory meatus (Eam), expanded pterygoid flange (Ept), eustachian tube (Et), median lacerate foramen (Mlf), stylohyal pit (Shp) and tympanic bulla.

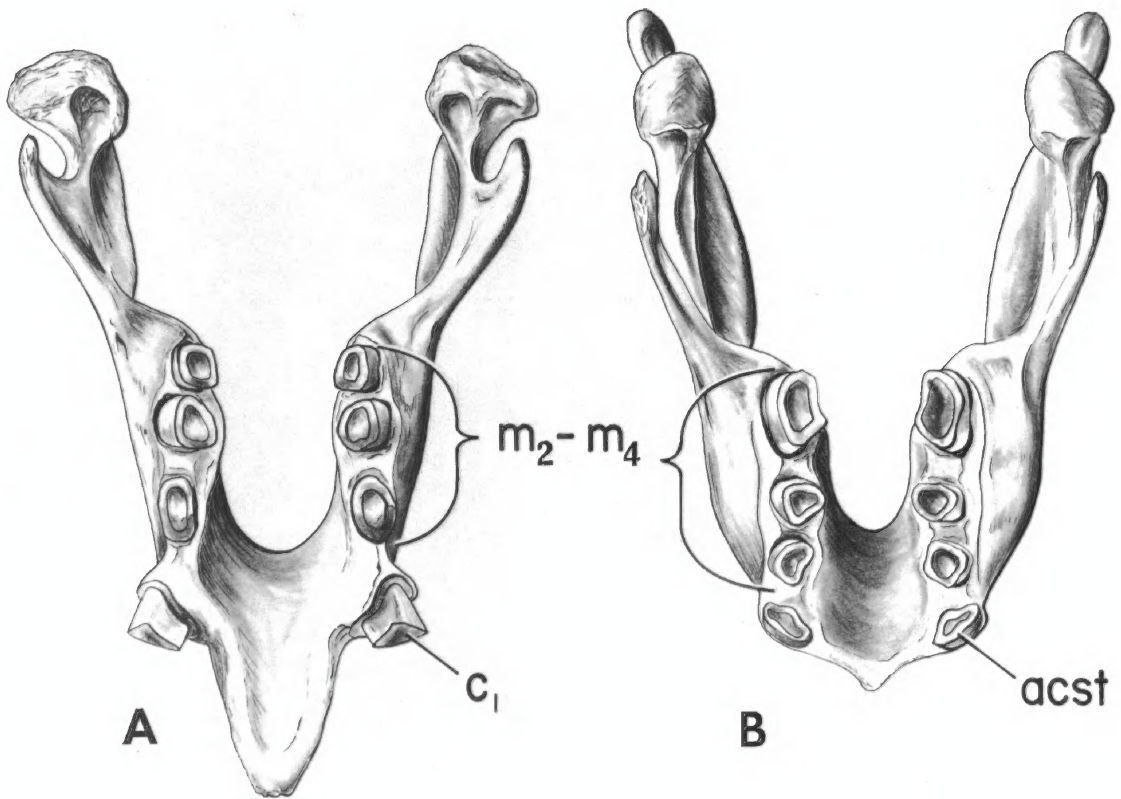


FIG. 4. Dorsal view of mandibles of *Choloepus* (A) and *Bradypus* (B). The teeth are identified as: molariform teeth in both sloths (M_2-M_4), caniniform tooth (C_1) in *Choloepus* and anterior chisel-shaped tooth (*acst*) in *Bradypus*.

collections of the American Museum of Natural History (AMNH), the National Museum of Natural History Smithsonian Institution (USNM), Field Museum of Natural History (FMNH), and the Museum of Zoology, University of Massachusetts (UMA) was examined. The fluid collection of the University of Massachusetts provided specimens that were used for complete craniofacial dissection. Appendix 1 lists all specimens examined; those dissected are labeled with an asterisk.

There were no specimens of accurately known age available; therefore specimens were grouped in an age series based on several criteria. (1) *Size coupled with the amount of compact bone.* Sloth skulls grow greatly from birth to full adulthood (Parker, 1885). (2)

Sutural closure. As in other mammals such as humans (Todd and Cooke, 1934), monkeys (Zuckerman, 1926; Chopra, 1957; Dolan, 1971) and hyenas (Schweiker, 1930) the degree of sutural closure increases with age. (3) *Tooth size.* Sloths lack deciduous teeth (Tims and Henry, 1923), and as the cheek tooth surfaces wear with age, the crown diameter approaches the size of the root, causing the teeth to appear larger in older animals. As the persistently growing teeth wear in the adult the conical tips are eroded away and the wider tooth shaft is pushed upward. These criteria provide a clear grouping of specimens into juveniles, young adults, and aged adults. Juvenile specimens were not only significantly smaller than adults, but had relatively smaller, conical-shaped teeth, many

unfused cranial sutures, and more delicate cranial bones than the adults. Specimens were judged to be adult if (a) their teeth appeared to be larger (and no longer conical in shape); (b) they showed a greater degree of cranial suture fusion; and (c) they approached maximum size for the specimens available of each species, based upon skull length (condylobasal length), and width (greatest width of zygomatic arch and braincase). Old adults showed relatively the largest teeth, almost complete fusion and obliteration of the ectocranial sutures, as well as the largest size and on examination, the greatest density of compact bone.

Differences in proportion between the crania of *Choloepus* and *Bradypus* were examined using the method of coordinates (Thompson, 1959); this method requires that the outline of one of the skulls (here *Choloepus*) be inscribed (fig. 5A) into a net of regular coordinates. The "O" line of the vertical axis was located at the anterior edge of the orbit, and the "O" line of the horizontal axis was at the level of the cheek tooth row (Colbert, 1935). Skulls and mandibles in the figures were illustrated either from camera lucida drawings (figs. 2–6, 10, 18–19, 21) or from photographs of associated skulls and mandibles opened to a specific gape. Gape was measured using the technique of Herring and Herring (1974) and Herring and Scapino (1973) where the degree of mandibular opening was measured on the skulls where the occlusal planes of the upper and lower tooth rows intercepted, whether or not this occurred at the actual level of the mandibular condyle (fig. 10).

In *Choloepus* (figs. 2, 4), and many of the megalonychid ground sloths the anterior maxillary teeth are canine-like, and occlude on the posterior face with a canine-like mandibular tooth. This arrangement is the reverse of that seen in other mammals, and since the ontogeny and homology of these teeth is unknown, they are referred to here as caniniform, C_1 for the maxillary and C^1 for the mandibular teeth. In other sloths such as *Bradypus* (figs. 3, 4) and some megalonychids and mylodonts the anterior maxillary and mandibular teeth are chisel shaped. In

this study these teeth are referred to as anterior chisel-shaped teeth (ACST₁ or ACST¹ for the maxillary and mandibular teeth, respectively). It is not possible to distinguish premolars from molars in sloths. Therefore, in this study, cheek teeth are called molari-form, and numbered consecutively from the anterior of the cheek tooth row, M_{1-4} for maxillary and M^{2-4} for mandibular cheek teeth (figs. 2, 3, 4).

The method of Herring and Herring (1974) was used to quantify the effect of the orientation of the muscles of mastication on gape. This method predicts the distance to which a muscle segment must stretch to enable the animal to achieve a given angle of mandibular rotation. The equation used is:

$$(L/l)^2 = \frac{a^2 + b^2 - 2ab \cos(\theta + \phi)}{a^2 + b^2 - 2ab \cos \phi}$$

The stretch factor for each muscle (the ratio L/l) is the positive square root of the equation. The authors assigned the variables in the equation such that a and b are the lengths from the origin and insertion, respectively, of the muscles from the craniomandibular joint, with ϕ the angle between them, and L and l are the lengths of the muscle in the closed position and when the mandible is opened to an angle θ .

RESULTS

Xenarthran crania differ from those of other mammals by having an anteroposteriorly elongated maxilla and reduced premaxilla. The dentition is reduced in both number and tooth type: the teeth also lack enamel (Romer, 1966; Scott, 1937). Among xenarthrans the sloths show several additional distinctive cranial characters; many have rostra reduced in length, incomplete zygomatic arches, pterygoid bones modified into elongate flanges or inflated sinuses, and strongly fused mandibular symphyses. There are two genera of tree sloths, and these mammals differ from one another in the robustness of the skull and mandible, the number and extent of cranial sinuses, the extent of rostral reduction, the development of a pre-

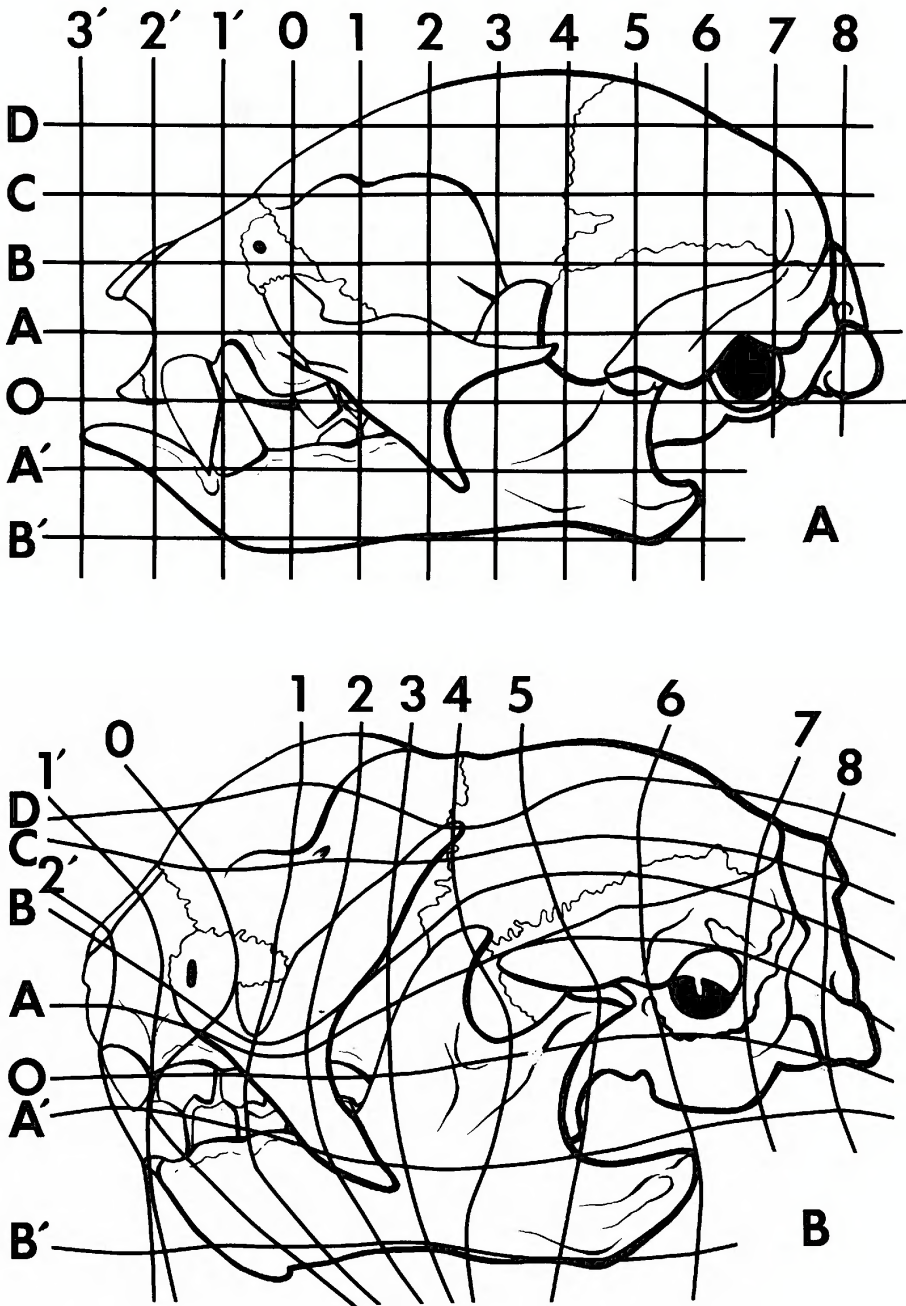


FIG. 5. Lateral views of *Choloepus* skull and mandible (A), and *Bradypus* skull and mandible (B). Equidistant vertical and horizontal lines using the anterior border of the orbit, and the level of the tooth row respectively, as "O" points, have been superimposed upon *Choloepus*, forming a grid. In *Bradypus*, the vertical and horizontal lines have been drawn through the same points as in *Choloepus* with the differences in skull proportions resulting in a distortion of the grid.

dental spout and the structure of the dentition.

Sloths of very different sizes are represented in the fossil record. Some ground sloths were only slightly larger than the extant genera of tree sloths *Bradypus* and *Choloepus*, which have an average adult condylobasal length of 67 mm. (N = 83) and 108 mm. (N = 76), respectively. The largest known sloths are the extinct megatheriid ground sloth genera *Eremotherium* and *Megatherium* which had condylobasal lengths of 650 mm. (N = 5) and 860 mm. (N = 3), respectively. Other lineages do not reach the size of the Pleistocene megatheriids, but all those known from both North and South America tended to become larger over time (Oligocene to Pleistocene). On the other hand, the megalonychid sloths of the Caribbean Islands remained small to moderate in size. There are no fossil tree sloths, so changes in body size in this lineage over time are unknown.

Sloths show great diversity in the combination of their cranial characters, both within and between the three fossil families and the family of Recent tree sloths. The fossil family Megalonychidae has the largest number of recognized genera, some with long tubular skulls, and lost or reduced caniniform teeth (e.g., *Nothrotheriops*, *Nothrotherium*, *Schismotherium*, and *Hapalops*). Others have shorter rostra and have retained caniniform teeth (e.g., *Megalocnus*, *Mesocnus*, *Parocnus*, *Acratocnus*, and *Eucholoeps*). The family Megatheriidae includes few genera, all with moderate length rostra, no caniniform teeth and square molariform cheek teeth (Romer, 1966), but based upon an initial examination of the crania of *Eremotherium* (N = 5) and *Megatherium* (N = 4) it appears that the genera with larger body sizes have massive skulls and mandibles when compared with other sloths. Several genera which have extreme development of long tubular skulls (e.g., *Scelidodon* and *Scelidothorium*), several with moderate length skulls (e.g., *Mylodon*, *Paramylydon* and *Glossotherium*), and some with very broad and short maxillary regions

(e.g., *Lestodon* and *Pseudolestodon*) are grouped in the third fossil family, the Mylodontidae (Winge, 1941; Romer, 1966). Caniniform teeth are present in most megalonychid genera but the shape of the shearing surfaces and the way in which they occlude differ widely. The tree sloth family, Bradypodidae, is represented by two genera both with shortened rostra, one with caniniform teeth (*Choloepus*) and one without (*Bradypus*). The distribution among sloth families of other cranial characters mentioned earlier, such as the form of the pterygoid bone and the zygomatic arch, is even more complex and is not discussed in detail here.

An understanding of sloth cranial morphology is further complicated by the apparent variability of characters within a single species. The crania of both fossil and Recent sloths vary greatly in robustness of the elements, length and breadth of processes, thickness of individual bony elements, amount of compact bone present, and degree of sutural fusion. An examination of a large series of crania of the tree sloths *Bradypus* and *Choloepus* (Appendix 1) indicates that these changes correlate with increased age of individuals, such that the crania of young animals may look very different from aged adults of the same species collected from the same geographic region, rather than resulting from specific differences.

COMPARATIVE CRANIAL OSTEOLOGY OF THE TREE SLOTHS

Many of the characters distributed through the families of fossil sloths are found in the two living genera (figs. 2, 3). Some of the more important cranial differences between the two sloth genera are seen in the zygomatic arch. Although it is incomplete in both genera (as in many of the small- and moderate-sized ground sloths), the orientation and shape of the jugal processes differ. In both sloths the jugal bone has two processes. In *Choloepus* the upper one extends posteriorly, almost contacting the anteriorly oriented squamosal

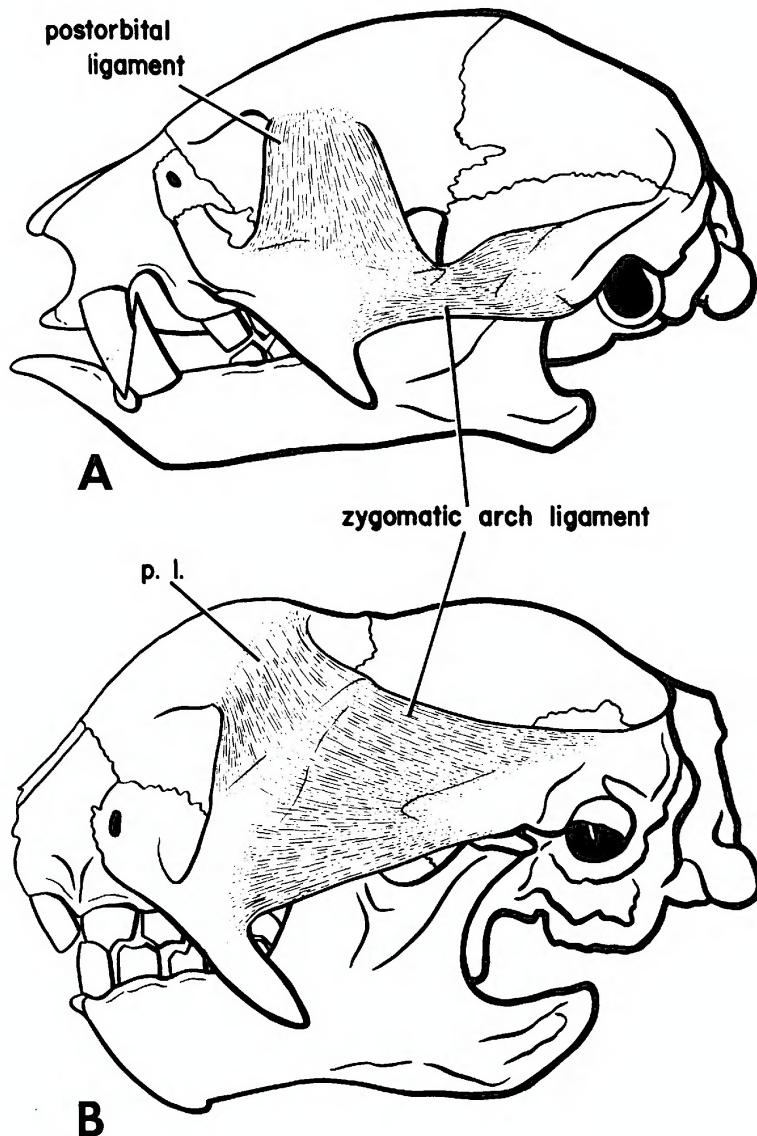


FIG. 6. Lateral views of *Choloepus* (A), and *Bradypus* (B), to show the ligaments connecting the anterior and posterior processes of the zygomatic arch.

process of the temporal bone (fig. 2). The lower, descending process is also oriented posteriorly, but there is no anteriorly projecting lower part of the squamosal process to join it. The zygomatic arch in *Bradypus* also shows two processes; however, the upper process is absolutely and relatively longer than that of *Choloepus* and is oriented in a

more dorsal direction (fig. 3). Although the squamosal process of the temporal bone in *Bradypus* is relatively longer than that of *Choloepus*, there is a greater space between it and the ascending process of the anterior portion of the zygomatic arch. The shape of the descending jugal process in *Bradypus* is similar to that of *Choloepus*, although it is

generally somewhat longer (fig. 3). In both *Choloepus* and *Bradypus* the anterior (both processes) and posterior parts of the zygomatic arch are connected by tough ligaments which also form the posterolateral wall of the orbit. The connecting ligament system in *Bradypus* is larger than that of *Choloepus* because of its more dorsal origin from the ascending jugal process in the former genus (fig. 6).

The tree sloths have the two pterygoid bone morphologies found among the sloths. In *Choloepus* the pterygoid region is inflated, forming large sinuses in the posterior aspect of the bone (fig. 2). In contrast, *Bradypus* has an elongated flange projecting ventrally from the pterygoid (fig. 3). *Bradypus torquatus*, the maned sloth, has a flange which is also slightly inflated. Since this reflects a combination of traits found in both *Choloepus* and *Bradypus*, *Bradypus torquatus* is of uncertain systematic position.

The only significant difference between the basicranial regions of the two sloth genera is in the structure of the ear region. There is no tympanic bulla in *Choloepus*, (nor in most of the ground sloths); the tympanic membrane is supported by an open tympanic ring. The ectotympanic, if present, forms a flat plate lying posterior to the auditory meatus of the petrotic bone. The ear region in *Bradypus* is covered by a tympanic bulla composed of both the ectotympanic and entotympanic bones (van de Klaauw, 1931).

Both tree sloths have large frontal sinuses (fig. 7). These are also found in most ground sloths. In *Bradypus* the sinus is quite deep, and without internal compartmentalization other than a single thin and incomplete midsagittal septum. The sinus occupies the entire length of the frontal bone, but does not extend anteriorly into the nasal bone, nor posteriorly into the parietal. In the specimens of *Bradypus* examined the frontal sinus never extends posteriorly beyond the anterior wall of the intracranial cavity. When compared with *Choloepus* the inflated frontal bone bulges dorsally in *Bradypus*, increasing the slope of the forehead, as well as the height of the supraorbital ridge and the width of the postorbital process. Even more prominently,

inflation of the sinus in this fashion is also seen, in some of the ground sloths; particularly in megalonychids such as *Acratocnus* (Anthony, 1918). In these forms a large sagittal crest continues behind the sinus and maintains the high skull profile. In *Choloepus* a frontal sinus is also present, but it differs from *Bradypus* in three respects: (1) anteriorly, the sinus extends into the nasal bones; (2) there are several midsagittal supporting bone pillars, or mediolaterally oriented septae which partially divide the sinus into several chambers (anteroposteriorly in the frontal region), and (3) although the sinus does not extend behind the frontoparietal suture, it does surmount the anterior quarter of the intracranial cavity. In diverse ground sloths, such as the mylodont *Glossotherium* and the megalonychid *Nothrotheriops* (Stock, 1925) the frontal sinus extends dorsal to the braincase to a variable degree. In all specimens examined (some X-rayed, others where the full extent of the skull sinuses could be seen directly), the profile in lateral view of sloth skulls with sinuses present was either a smooth or slightly bulging arch (fig. 7). In the case of some of the larger ground sloth genera with elongate skulls (*Nothrotheriops*, *Glossotherium*, and *Schismotherium*) the convexity of the dorsal profile of the arch was slight, but in these animals the sinuses extended posteriorly dorsal to the entire length of the braincase, and at the occiput of the skull to form a crest for the attachment of the nuchal muscles.

The skull and jaw of *Choloepus* and *Bradypus* have quite different proportions. In figure 5 the crania have been drawn to the same size and compared, using Thompson's coordinate method (Thompson, 1959). Since *Choloepus* typifies these character states, it was used as the base with which the cranium of *Bradypus* was to be compared. Cranial characters such as a low craniomandibular joint position, large anterior (frequently caniniform) teeth separated from the molari-form tooth row by a diastema and a long premental spout are all present not only in members of the Megalonychidae but also their sister group the Mylodontidae, and are therefore considered primitive here. If the

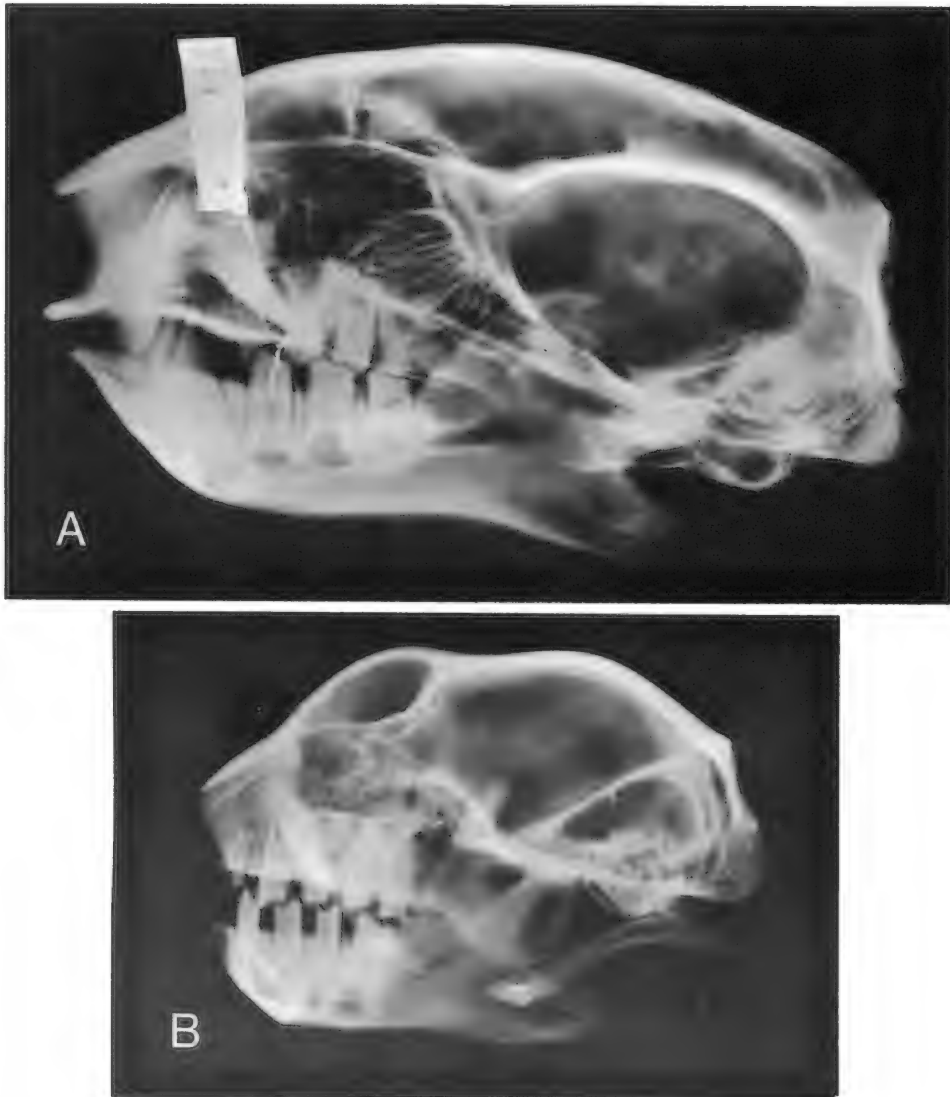


FIG. 7. Radiographs of *Choloepus* (A) and *Bradypus* (B) at natural size, to show the large frontal sinuses and extensive open roots of the dentition.

polarities of characters used here are assumed to be correct, then the distortion of the grid shows that the anterior portion of the skull of *Bradypus* has been modified more than the posterior region, whereas the mandible has been repropotioned throughout. Both *Choloepus* and *Bradypus* have reduced premaxillae, which do not contact the nasal bone (figs. 2, 3). This condition also obtains in all ground sloth groups, where the bone is small,

shaped like a spearhead, perforated by large palatine foramina and poorly fused to the maxillae. (All of these factors contribute to the frequent loss of this element during preparation of Recent study materials or during fossilization of extinct sloths making accurate cranial reconstructions, especially of the fossils, more difficult.) The maxillae are also short in *Bradypus* even when compared with the same region in *Choloepus*. Correspond-

ingly, the nasal bones in *Bradypus* are particularly short, and the nasofrontal suture is located farther forward than in *Choloepus*. Further evidence for the shortening of the rostral area of the skull in *Bradypus* when compared with *Choloepus* derives from the anteroposterior shortening of the frontal bones and the location of the frontoparietal suture. This suture is located about 55 percent of the distance posteriorly along the dorsal surface of the skull (*Bradypus variegatus*, N = 10). These features could reflect a general trend toward shortening of the face in the tree sloths, since a comparison of *Choloepus* with other xenarthrans (armadillos and anteaters) in particular, but to other mammals in general (e.g., opossum, dog, and shrew) shows that in this sloth both the nasofrontal and frontoparietal sutures are located more anteriorly than is usual. When compared with other mammals, the maxilla in *Choloepus* is also unusually short.

STRUCTURE OF THE CRANIOMANDIBULAR JOINT

The shape and orientation of the mammalian craniomandibular joint (CMJ) varies widely in conjunction with the diversity in mammalian jaw structure. As a rule, carnivorous mammals tend to have a jaw joint that is capable of little movement beyond that required for the primarily hingelike action of their jaws (Scapino, 1972). In some of these animals the articular condyle is so closely surrounded by pre- and post-glenoid processes that the mandible is not easily dislocated from the skull (some felids, ursids, and canids) or cannot be dislocated at all from a dried cranium (*Gulo*, *Crocuta*, and *Hyaena*). On the other hand, many herbivores (most artiodactyls and perissodactyls) have relatively shallow glenoid fossae which allow the mandibular condyle great freedom of movement in both the labiolingual and anteroposterior directions. An unrestricted glenoid fossa correlates well with the ability of herbivorous mammals to make anteroposterior and translatory movements of the mandible (Hiimae, 1978; Greaves, 1980).

Although located in relatively the same

position with respect to the braincase, the glenoid fossa differs strikingly in shape between the two genera of tree sloths. There are no pre- or post-glenoid flanges to restrict anterior or posterior sliding of the condylar head of the mandible in either sloth. An articular disk is lacking in both sloths. In *Choloepus* the glenoid depression (fig. 8A) is crescent shaped, shallow, and has a smooth cartilage covered articular surface which extends laterally onto the undersurface of the squamosal process of the temporal bone. The glenoid articular surface is inclined, with the anterior aspect being more dorsal. In *Bradypus*, in contrast (fig. 8B), the glenoid cavity is troughlike, and the articular surface of the condylar head does not extend onto the ventral surface of the squamosal process. The troughlike shape of the glenoid fossa in this sloth appears to result from an anterior extension of the articular surface (in comparison to the mylodonts), and is better shaped to guide the head of the mandible mostly in anteroposterior movements during mastication.

As the glenoid fossae in the two sloths have different shapes, in both cases, the articular condyles of the mandibles are equally different. In *Choloepus* (fig. 9, left) the condylar head is broad mediolaterally, with the two articular surfaces distinctly separated in adults by an anteroposteriorly oriented groove or depression. In juvenile *Choloepus* the separation between articular surfaces is frequently unclear, but in all adult *Choloepus* specimens examined (Appendix 1) this separation is fully developed. The degree to which the two articular surfaces of the condylar head are distinct increases with age in individuals. The medial articular surface of each condyle is large, strongly convex mediolaterally, and inclined, with the posterior surface more ventral than the anterior. The lateral articular surface is smaller, flatter, and only in some cases is the posterior aspect slanted ventrally. In *Bradypus*, in contrast, the articular condyle is single, oval in shape, and has the long axis oriented anteroposteriorly. The single articular surface is convex mediolaterally and appears to correspond to the medial articular surface in *Choloepus*.

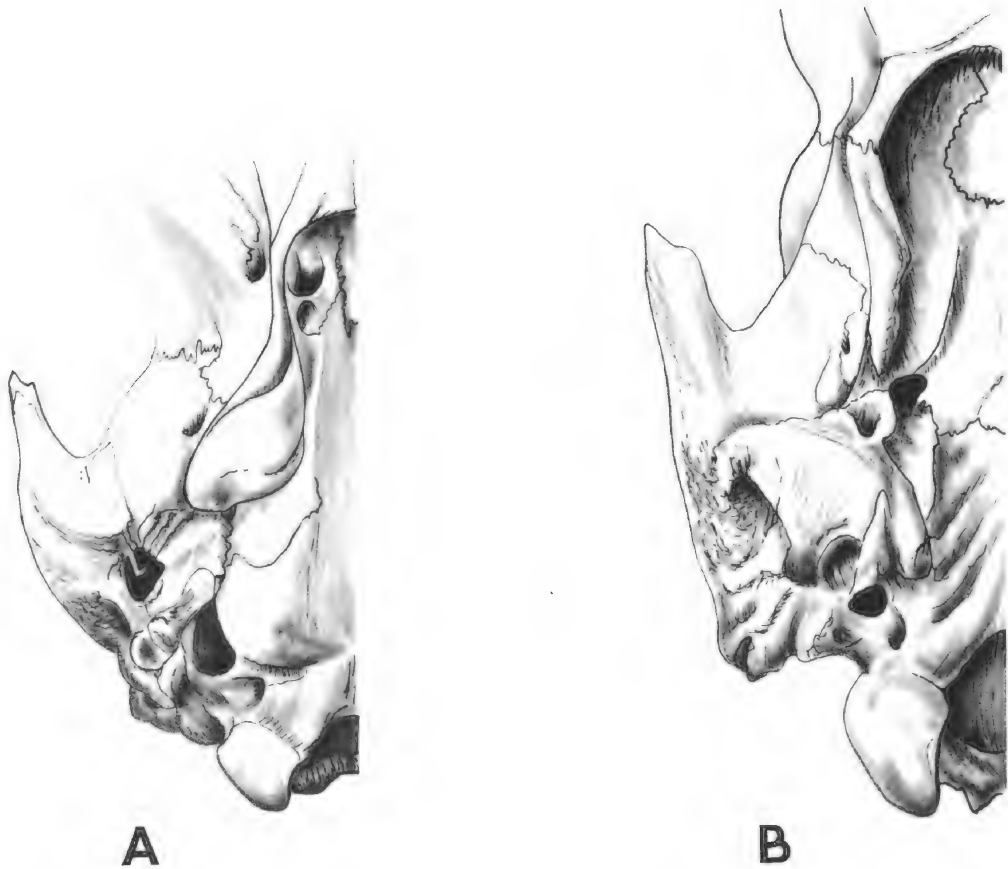


FIG. 8. The shape of the glenoid fossa in *Choloepus* (A), and *Bradypus* (B). Note the lateral expansion of the glenoid cavity in *Choloepus*, which acts as a bony stop, preventing the mandibular condyle from sliding anteriorly.

The posterior aspect of the condylar head is slanted ventrally, and as in *Choloepus* there are neither anterior nor posterior projections to restrict sliding movements of the mandibular condyle.

The height of the articular condyle in *Choloepus* shows consistent change which correlates with change in age from juvenile to adult. Nevertheless, when the occlusal plane of the cheek tooth row is extended back to the position of the condyle, the two are at approximately the same level (fig. 10). The condyle in *Bradypus* differs from that of

Choloepus by being located dorsal to the level of the cheek tooth row (figs. 10, 11), but in both animals the upper and lower tooth rows are still an equal distance from the CMJ, thus maintaining simultaneous occlusion along the cheek tooth row (Greaves, 1974). The slopes of growth curves comparing the increase in mandibular condylar height with condylobasal length were significantly different ($P > .0001$ with 22 degrees of freedom). The height of the mandibular condyle in *Choloepus* also has an inverse relationship that is significantly correlated ($P > .001$) to

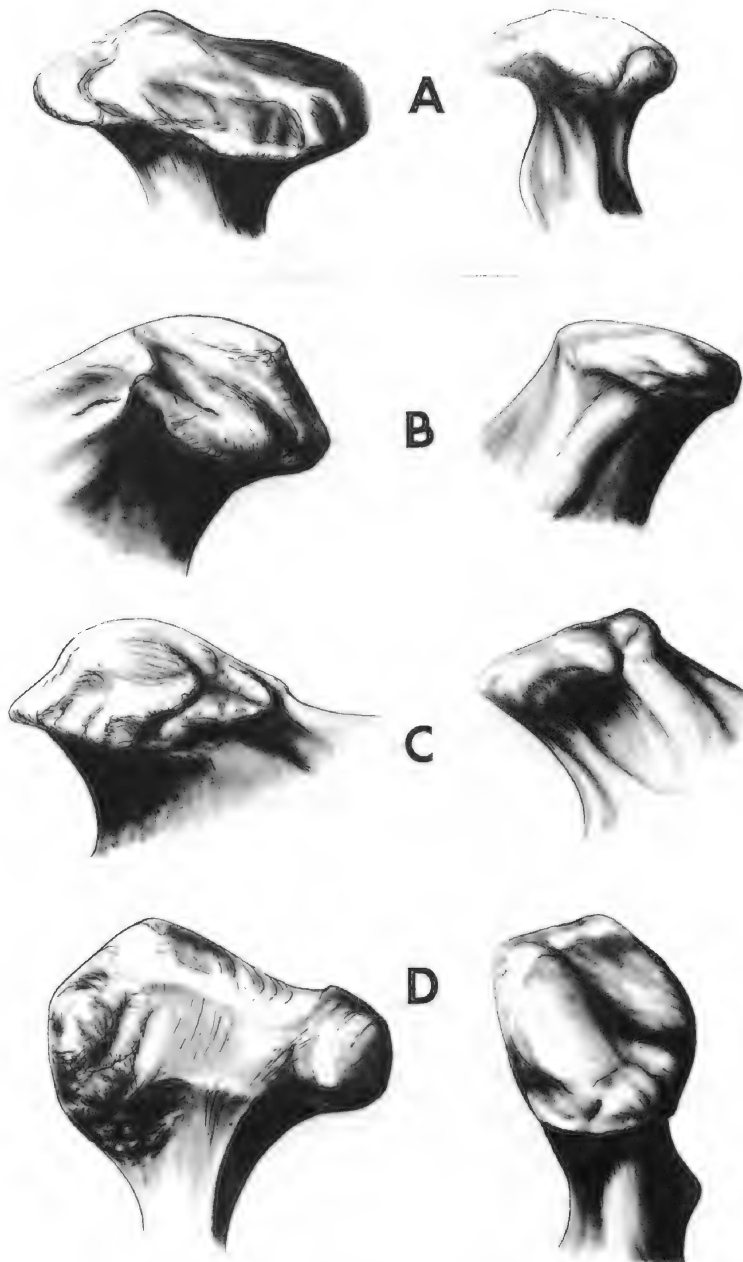


FIG. 9. Views of the mandibular condyle in *Choloepus* (left), and *Bradypus* (right). Posterior (A), lateral (B), medial (C) and dorsal (D) aspects.

the height of the condyle above the cheek tooth row (fig. 12). The longer the caniniform teeth in an individual are, the closer does the level of the CMJ approach the level of the

occlusal plane. In contrast, the anterior teeth in *Bradypus* do not project farther from the maxillae or mandibles than do the teeth in the cheek tooth row (fig. 3), so no significance

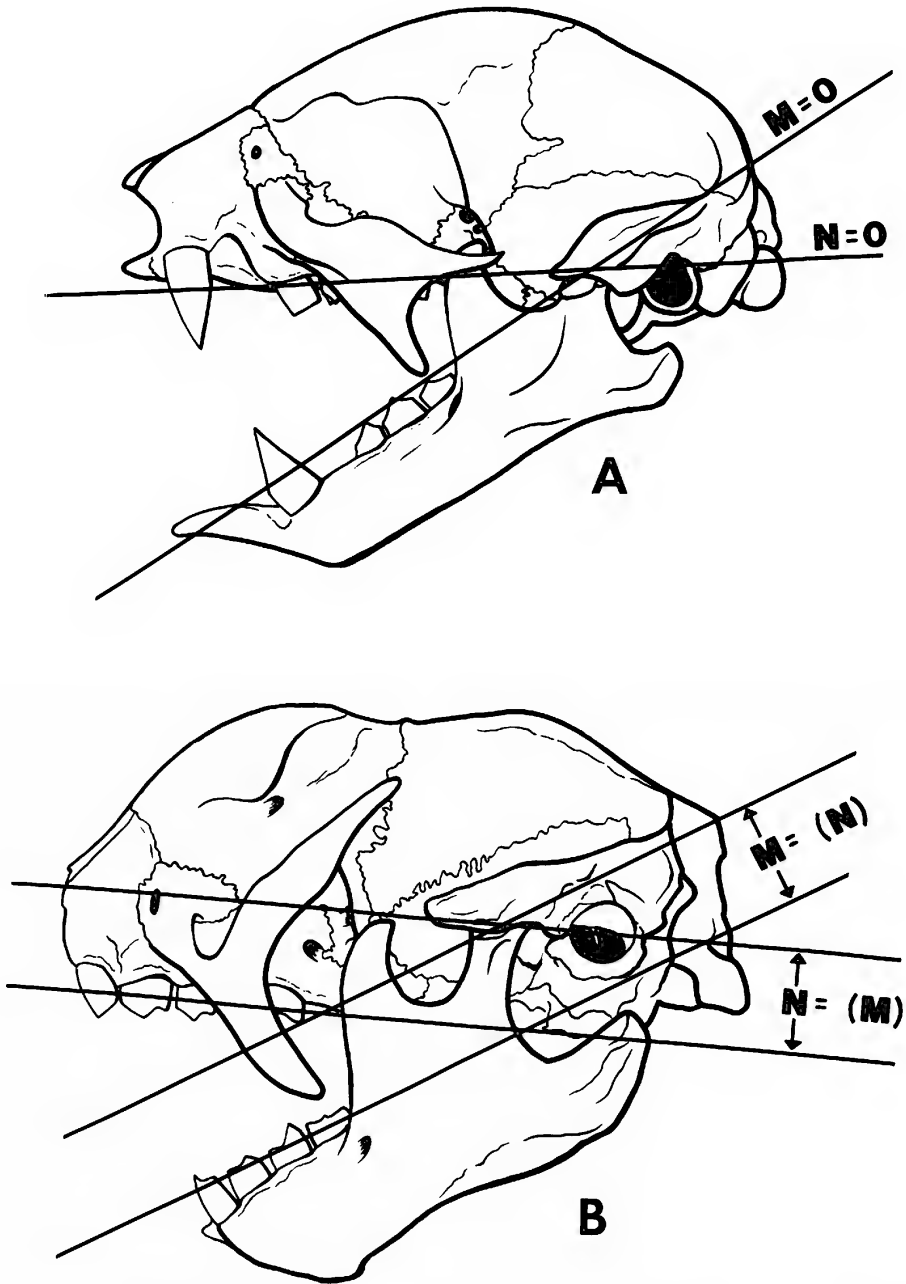


FIG. 10. Lateral views indicating the distance from the craniomandibular joint to the level of the upper and lower tooth rows in *Choloepus* (A) and *Bradypus* (B). M is the distance from the CMJ to the level of the lower tooth row, and N is the distance from the CMJ to the level of the upper tooth row.

can be established between the elevated condylar height and the height of any specific tooth above the cheek tooth row. The in-

creased distance of the condyle above the cheek tooth row in *Bradypus* as compared with *Choloepus* can be explained by elonga-

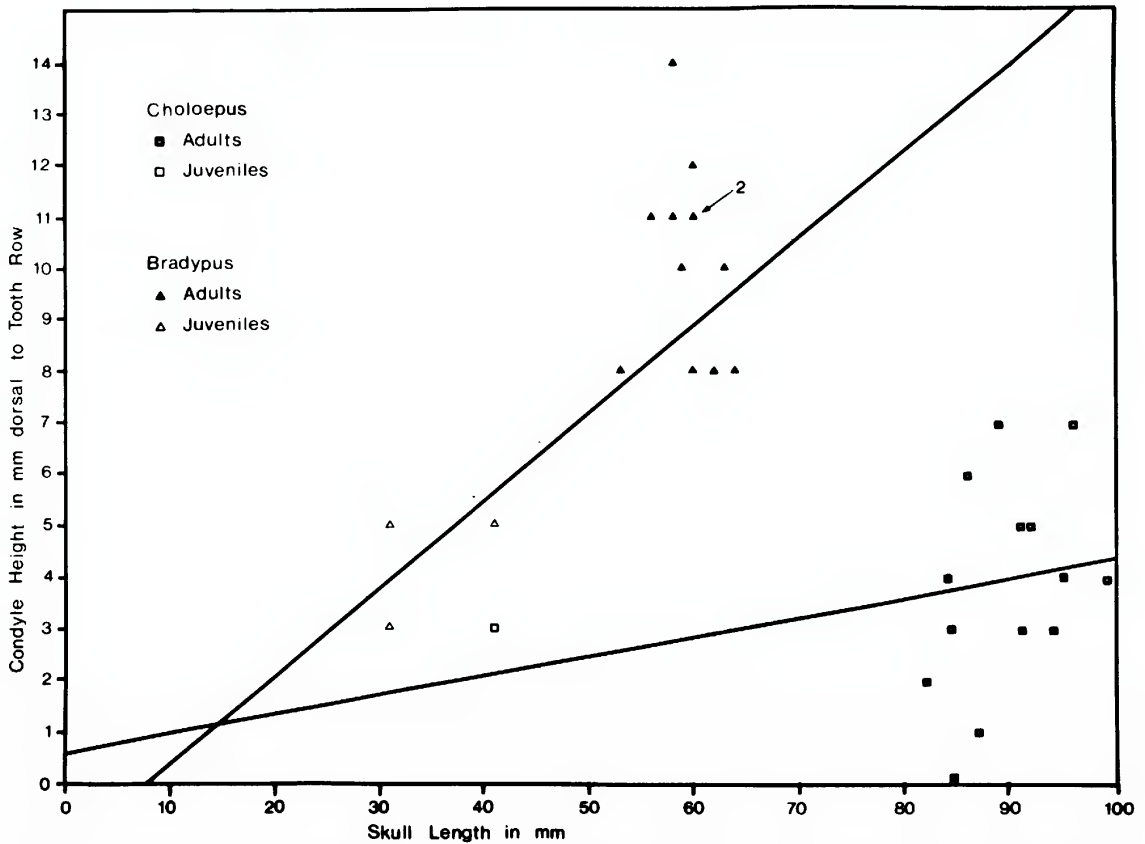


FIG. 11. Growth curves for *Choloepus* (squares) and *Bradypus* (triangles), relating the distance the mandibular condyles are located dorsal to the occlusal plane of the tooth row, and the condylobasal length of the skulls. There were 15 specimens used per genus.

tion of the condylar neck of the mandible in *Bradypus*, given outgroup comparisons with early mylodont sloths.

Another important difference can be found between *Choloepus* and *Bradypus* in the structure of the mandible. Both sloths have a well ossified and extensive mandibular symphysis, but in *Choloepus* this area is elongated anteriorly into a premental spout (fig. 4). The spout is spoon-shaped, rounded anteriorly, and covered by a thick lip. Tree sloths frequently use this spout extensively to position pieces of food for biting both in the wild and in captivity (personal observ.). Most fossil sloths have premental spouts. In genera with particularly elongate skulls (e.g., *Schismotherium* and *Scelidodon*) the spout

is deep and narrow, whereas animals with broader skulls have spouts that are wider anteriorly (e.g., *Glossotherium*). Extreme development of a wide spout occurs in *Lestodon*, another late mylodont genus.

DENTAL MORPHOLOGY

The ontogeny, and therefore, the homology of sloth teeth is unknown. Sloth teeth are of persistent growth. They are not preceded by a milk dentition (Parker, 1885), and lack enamel (Romer, 1966). The outer "shell" of each tooth is formed instead, of a hard layer of dentin which surrounds a softer dentinal core. The difference in hardness of the two types of dentin results in differential rates of

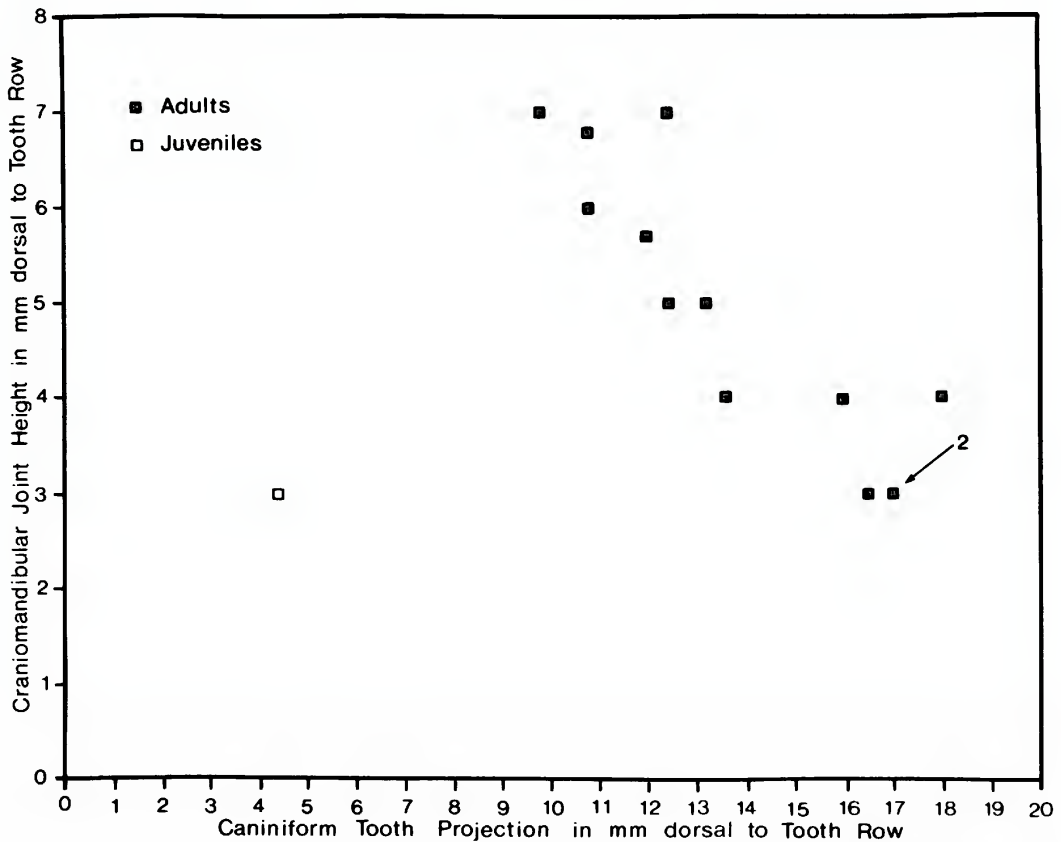


FIG. 12. The inverse relationship of the height of the CMJ and the distance the caniniform teeth project dorsal to the occlusal plane of the cheek tooth row.

wear of the tooth surfaces; the outer dentinal layer behaving much like the enamel of other mammals. As in other mammals, the face in sloths changes with age to adulthood (Parker, 1885). Infant sloths of both genera have short faces, small premaxillae, and short maxillae in comparison to the adults. All the teeth in sloths erupt as simple cones, evenly spaced apart, and are covered initially by the hard layer of outer dentin. In juvenile sloths truncated occlusal surfaces are present, sometimes showing basins with a small amount of the softer inner dentin exposed in the center of the occlusal surface (fig. 13). As the teeth grow through the life of an individual sloth, the small conical tips are worn away and the entire exposed part of the tooth then reflects the size of the largest part, i.e., the root, allowing teeth in adult sloths to be ab-

solutely larger than those of juveniles. Since sloth teeth acquire their individual characteristics through wear, it is very difficult to distinguish the young of one genus from those of the other based upon shape or location of the dentition. As wear of the teeth progresses the basins become deeper and larger and the cutting edges of the hard outer dentin become sharper. In the oldest adult animals (Appendix 1, aged adults) the tooth basins are the largest and deepest, and the hard dentin "cusps" the most sharp edged.

In comparison with other herbivorous mammals, sloths have few teeth. The premaxilla is reduced in size, frequently poorly fused to the maxilla, and does not bear incisors. There are only two types of teeth in the dentition; one upper and lower anterior tooth on each side, which differ between the

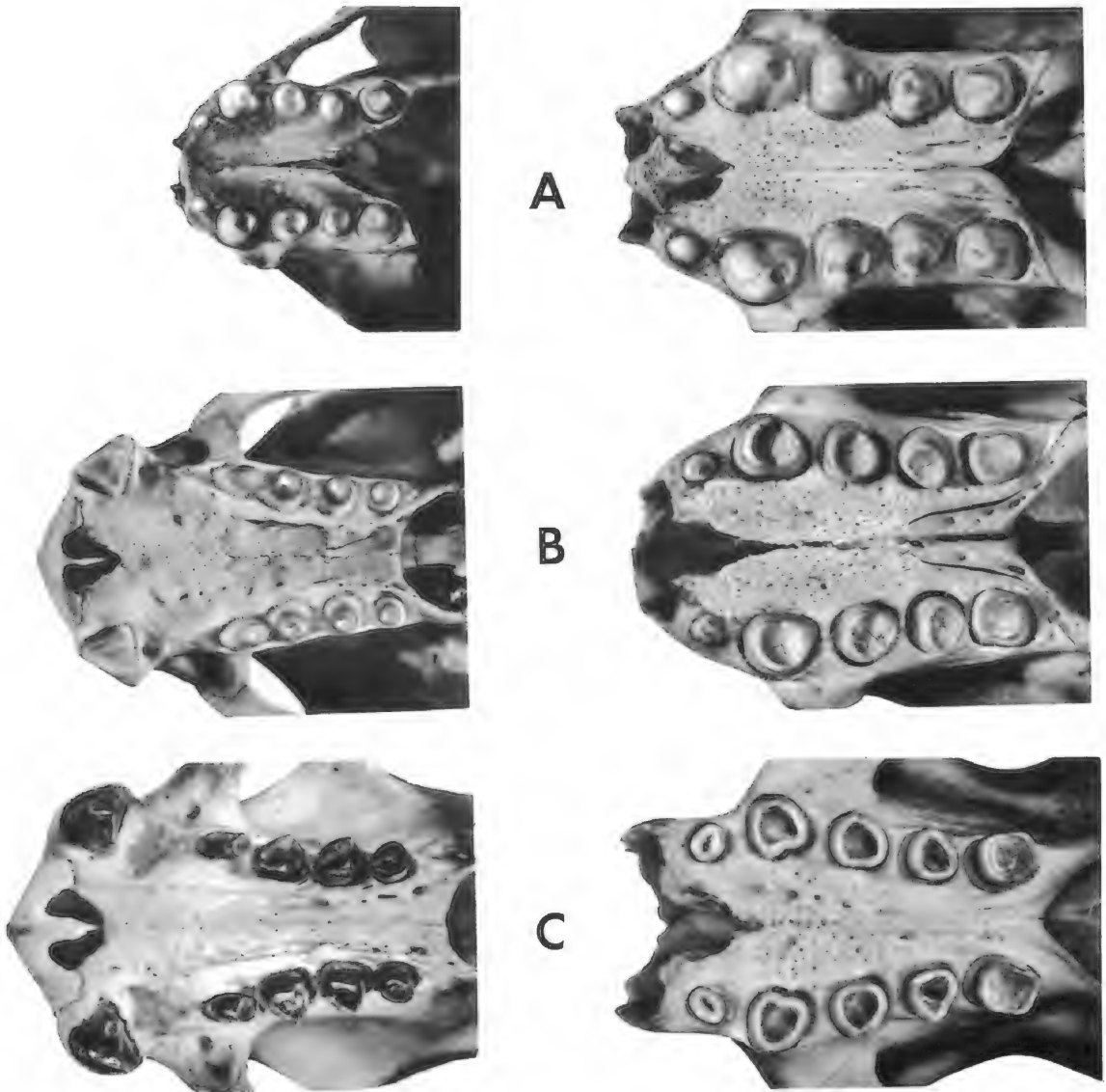


FIG. 13. Palatal views of newborn (A), juvenile (B), and young adult (C) sloths. *Choloepus* is on the left, and *Bradypus* is on the right. The length of the cheek tooth row has been held constant to show the rapid growth of the anterior part of the maxilla, which forms the postcaniniform recess and diastema in *Choloepus*.

two tree sloths, and four upper and three lower simple peglike cheek teeth in each side, which differ little between the genera.

Unworn anterior teeth of *Choloepus* of both sexes are quite small and rounded (fig. 13). With growth, they become elongate tri-

angles with rounded apices in cross section, with the longest axis of the tooth located anteroposteriorly in the mandible. During mastication, the hard outer dentin layer is worn from the occlusal faces of these teeth and a wear facet forms. As the teeth continue

to grow, the rounded juvenile tips are worn away, the tooth becomes more sharply triangular, and is caniniform in shape later in the adults. In the youngest specimens examined (fig. 13 and Appendix 1, labeled juveniles), there was either no wear facet present, or only a slight indication of the formation of one. In somewhat older individuals (fig. 14 and Appendix 1, adults), a posterior wear facet on the upper caniniform tooth occluded with an anterior wear facet on the lower. In many cases these facets did not occupy an entire face of the tooth, and sometimes had rather rounded edges or tips, although usually the teeth of the older individuals had the sharpest edges and apices (Appendix 1, aged adults). The sharp points on the apices and cutting edges of the caniniform teeth are maintained by tooth-tooth contact through special tooth sharpening movements made during some mandibular closing cycles (personal observ.). Although the surfaces of the wear facets formed in the caniniform teeth are flat, they are oriented slightly obliquely (lingual edge more anterior), and the edges of the facets are curved, being slightly concave lingually and convex laterally. As the teeth continue to erupt, the maxilla grows longer and wider, and a diastema posterior to the caniniform teeth begins to appear in juveniles of *Choloepus* (Parker, 1885 and fig. 13). In *Choloepus* adults the diastema is well developed, resulting from the additional increment of growth of the anterior maxilla. A fossa to receive the tip of the lower caniniform tooth also develops in the maxilla behind the upper caniniform tooth, so allowing the mouth to close fully. The posterior face of the upper tooth in *Choloepus* occludes with the anterior face of the lower, opposite to the relationship of the canine teeth in other mammals, and since the ontogeny of these teeth is unknown, it is therefore not possible to tell whether either the upper or lower caniniforms actually are canine teeth.

The anterior teeth in *Bradypus* are peg or chisel shaped, less differentiated from the cheek teeth than in *Choloepus*, and not separated from them by a diastema. The upper anterior teeth in *Bradypus* show more vari-

ability than do those of *Choloepus*. The majority are simple cylinders, slightly compressed labiolingually, with the long axes oriented anteroposteriorly in the jaw, or are rounded triangles with the long axes oriented obliquely. However, the form of these teeth appears to vary with species. The upper anterior teeth of juvenile *Bradypus* are simple pegs and wear much as do the more posterior cheek teeth in this genus. A single posteriorly facing facet appears in the upper anterior tooth with wear, as can be seen in adult *Bradypus* (figs. 3, 4 and Appendix 1). The anterior lower chisel-shaped teeth in *Bradypus* are broad labiolingually and differ from the cheek teeth only by being more compressed anteroposteriorly. With age, these teeth often show an anterior wear facet similar in orientation to the one seen in the lower caniniform teeth in *Choloepus*, although much smaller. However, these teeth develop the most prominent wear facet on the posterior tooth face. This facet is present in juvenile *Bradypus* (fig. 13 and Appendix 1) but appears with wear, and becomes larger and sharper edged with age (figs. 3, 4, 13). The peglike cheek teeth in both *Choloepus* and *Bradypus* are ovoid or subrectangular. Given the absence of clear homologies it is not possible to determine whether the postcanines are premolars or molars. Both genera of tree sloths have four maxillary and three mandibular cheek teeth set into tooth rows which converge posteriorly (figs. 2, 3, 13). As is true of the anterior teeth in sloths, "cusps" form on the cheek teeth from wear. The tooth wear pattern characteristic of each genus develops rapidly in juveniles and is maintained by the pattern of mandibular movements used in chewing specific to each sloth. In both sloths the angle at which the teeth erupt helps to determine which parts of each occludes with those of the opposing tooth row; these factors combined with the pattern of mandibular movement produce the characteristic wear facets.

The maxillary cheek teeth in *Choloepus* (fig. 13, left, 14B) are wider and longer in the middle of the tooth row (M^2 and M^3) than either the anterior M^1 or the posterior M^4 . The angle at which these teeth are set into

the jaw changes from slightly lingual (M^1) to slightly labial (M^2 – M^4). In all specimens of *Choloepus* examined, M^1 tends to be rounded, M^2 and M^3 are wide oval shapes, and M^4 is rounded. In contrast, the cheek teeth in the maxillary tooth row of *Bradypus* (figs. 13, right, 14D) change size in a different manner than do those of *Choloepus*. In *Bradypus* M^1 is much larger than all the other maxillary teeth, with a teardrop shape (the wide end facing anteriorly, and the narrower tail located posterolingually). M^2 is smaller, and sometimes a more rounded version of M^1 , with its long axis oriented labiolingually in the maxilla. M^3 is the smallest of the upper cheek teeth, and also teardrop-shaped, but oriented obliquely in the maxilla so that its widest edge is posterolingually located. M^4 is the most rectangular of the maxillary cheek teeth, and is oriented squarely in the jaw. As in *Choloepus*, M^1 is tilted slightly toward the lingual, but in *Bradypus* this is also true of M^2 . However, M^3 and M^4 show a distinct labial slant.

In *Choloepus* (fig. 14A) the first mandibular tooth (M_2) is slightly labially inclined, but M_3 and M_4 are strongly slanted lingually. Since M_2 – M_4 in *Choloepus* are approximately the same size, the differences in their appearance after wear are mostly due to the different angles at which they occlude with the maxillary teeth. In *Bradypus* in contrast, the mandibular teeth differ in size with M_2 and M_3 being teardrop-shaped, and about equal in size, with their larger ends posteriolingually oriented, whereas M_4 is larger, and kidney-shaped, with the concave edge on the lingual side. The differences in the appearance of the worn mandibular cheek teeth in *Bradypus* can be attributed both to initial tooth shape and wear.

OCCLUSION

In *Choloepus* the cheek teeth alternate, as is the case with most mammals, with the mandibular teeth preceding the maxillary ones by half a tooth length (figs. 13, 14) so that during occlusion the first maxillary cheek tooth only contacts the anterior facing wear

facet of the first mandibular cheek tooth. In *Choloepus* the ridged sidewalls of this tooth permit it to maintain a flat, dorsally oriented occlusal surface but a sloping lateral profile. However, in *Bradypus*, where the teeth are more directly above one another, M^1 is much broader than the other cheek teeth, and this permits the resistant anterior edge of the narrower M_1 to occlude entirely within the softer center of M^1 , forming a deep basin. A ridge on the posterior edge of M^1 wears into the central basin of M_1 . The absence of a diastema between the anterior teeth in *Bradypus* and the cheek teeth produces an anteriorly facing wear facet on M^1 as a result of contact (during grinding with the cheek teeth only) with the posteriorly oriented occlusal surface of the anterior chisel-shaped mandibular tooth (fig. 14).

In *Choloepus* the anteriorly facing wear facet of M^2 occludes with the posteriorly oriented wear facet of M_1 . The larger posteriorly facing occlusal surface of M^2 occludes with the equally large anteriorly facing wear surface in M_2 . The situation in *Bradypus* is more complex, although the anterior wear facet of M^2 is similarly related to the posterior wear surface on M_1 as in *Choloepus*. However, the large basin in M^2 of *Bradypus* is formed by the narrower anterior ridge of M_2 . The hard dentin forming the posterior ridge of M^1 occludes into the basin of M_2 .

In *Choloepus* the anterior facing wear surface of M^3 occludes with the posterior facing wear facet of M_2 . In *Bradypus* the anterior ridge of M^3 occludes against the posterior part of M_2 . The obliquely oriented basin in M^3 is formed by contact with the anterior ridge of M_3 , which is also oriented obliquely. There is very little wear on the posterior aspect of M^3 .

In *Choloepus* the fourth and last maxillary cheek tooth is smaller than those anterior to it, and is more rounded than oval. It has one slightly anterolabially oriented occlusal surface which contacts the elongate posterior wear facet of M_3 . In *Bradypus* M^4 is subrectangular in shape. As in *Choloepus* it occludes entirely with the posterior part of M_3 . The anterior ridge of M^4 occludes in the basin of M_3 , and its own basin is formed by the side

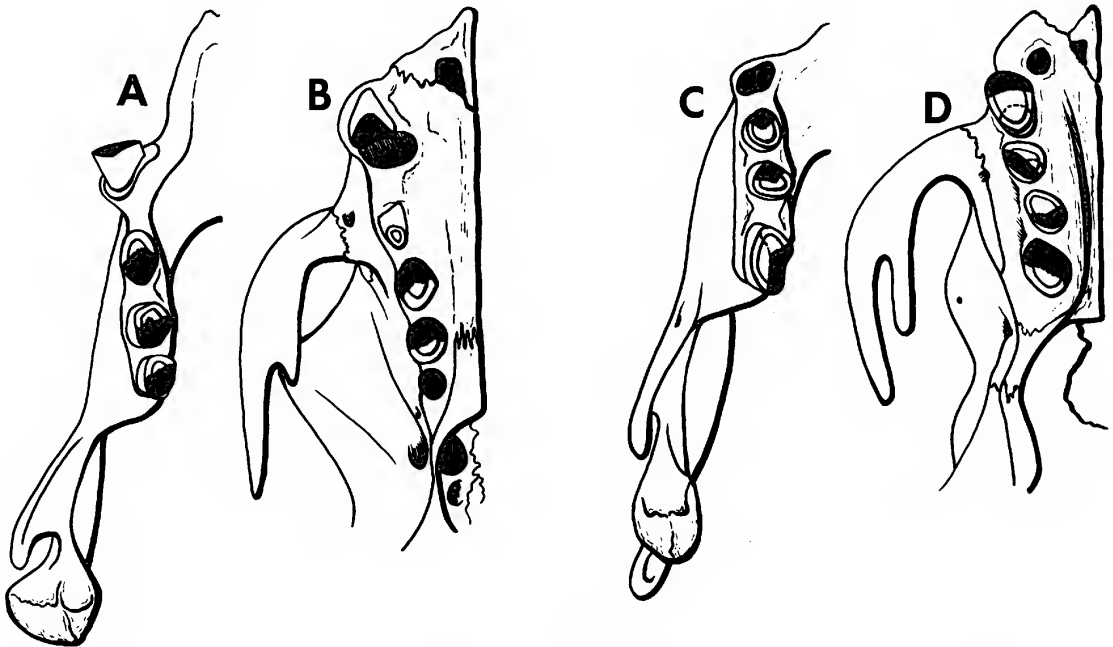


FIG. 14. The pattern of wear facets formed by masticatory movements on the mandibular (A) and maxillary (B) tooth rows of *Choloepus*, and the mandibular (C) and maxillary (D) tooth rows of *Bradypus*. In both sloths the shaded and unshaded areas of the mandibular tooth rows occlude against the shaded and unshaded areas of the maxillary tooth row, respectively.

and posterior hard walls of M_3 . The posterior hard dentin ridges of the last teeth show little wear.

Not only do sloths have different types of teeth for biting and chewing, but they also position the mandibles differently for the two actions as do many other mammals, such as rodents (figs. 15, 16). Most rodents show a distinct separation of function between the anterior gnawing incisors and the grinding cheek teeth, and must locate the mandible anteriorly in the glenoid fossa to bring the incisors into occlusion, and posteriorly to bring the cheek teeth into occlusion (Hiimae and Ardran, 1968). This is true for both sloths which are also unable to have both the anterior biting teeth and the posterior grinding teeth in complete occlusion simultaneously. Rodents may vary in the degree to which the jaw positions differ, from the large shift needed to bring both incisors and cheek teeth into occlusion in *Castor* (fig. 15) to the very small mandibular position shift needed

to bring either type of tooth into occlusion in *Aplodontia*. *Choloepus* resembles rodents such as *Castor* in that the mandibular positions for biting and chewing are so different that two types of teeth cannot be in occlusion simultaneously. The less distinct separation of mandibular positions in *Bradypus* resembles that of such rodents as *Aplodontia*. *Bradypus* lacks the diastema present in *Choloepus*, and so the location of the anterior teeth close to the cheek tooth row as well as their more opposite arrangement, makes it possible for the posterior occlusal surface of the anterior mandibular tooth to occlude easily against the anterior face of M^1 .

For the present study, the occlusal surfaces of the teeth in both sloths were reexamined. Sicher stated that these teeth showed "glossy narrow facets that originate by sharp contact of the teeth during the masticatory power stroke," but that this sort of attrition facet was present only on "the anterior (mesial) edges of the lower and the posterior (distal)

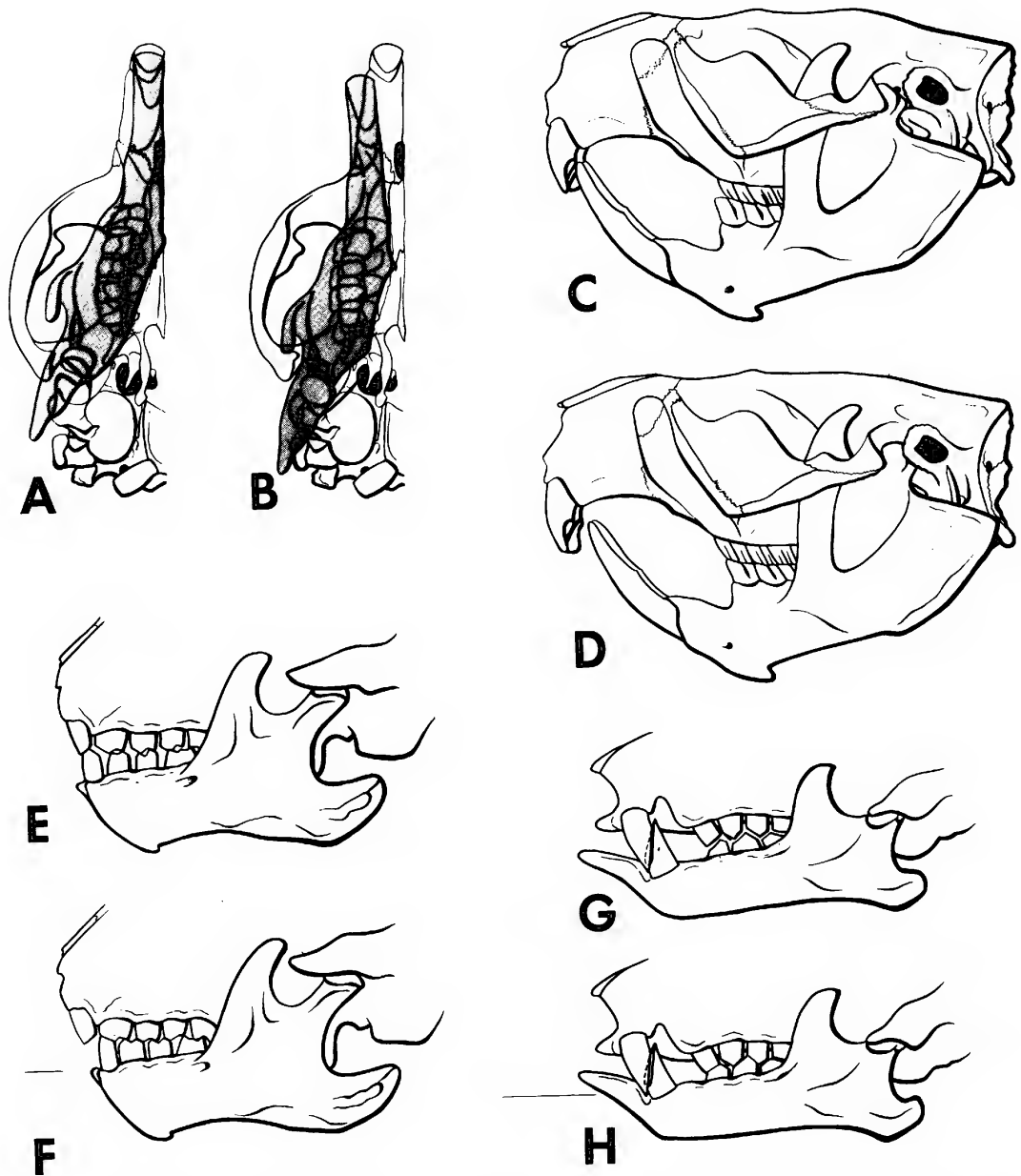


FIG. 15. Ventral (A, B) and lateral (C, D) views of the pattern of mandibular occlusion in *Castor* as compared to *Bradypus* (E, F) and *Choloepus* (G, H). The anterior biting teeth are in occlusion in all three genera (A, C, E, G) and the more posterior position of the mandible allowing cheek tooth occlusion is shown in (B, D, F, H).

edges of the upper teeth" in *Choloepus*, whereas in *Bradypus* "the glossy narrow attrition facets on the 'molars'" show a reversed arrangement compared with that of

Choloepus. Sicher considered all the other wear facets to be "dull, irregular facets, giving the tooth irregular pointed 'cusps,'" implying that these wear facets differed from the glossy

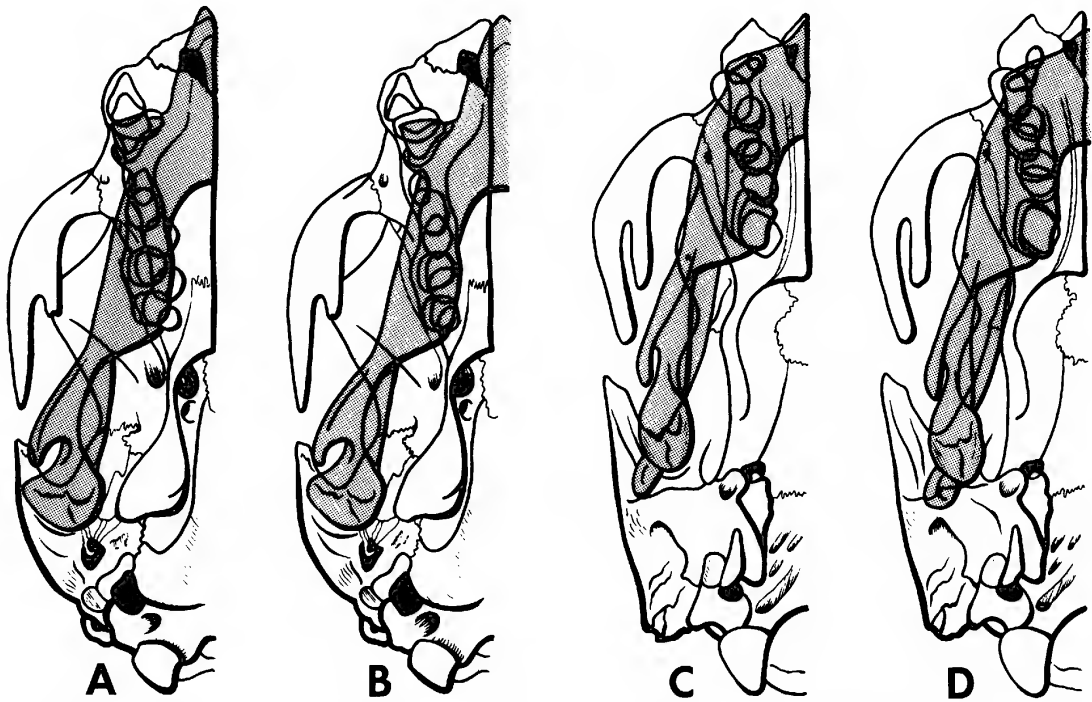


FIG. 16. The two positions for tooth occlusion in *Choloepus* (A, B) and *Bradypus* (C, D). The caniniform teeth (*Choloepus*) and anterior chisel-shaped teeth (*Bradypus*) are in occlusion (A, C) and the cheek teeth in occlusion in (B, D).

ones because they were not formed by direct tooth-tooth contact. Glossy attrition facets are found on the cheek teeth of both sloth genera. In contrast to Sicher's observations, however, the edges of wear facets formed in the hard outer layer of dentin in both sloths appeared to be identical (under microscopic examination) in sharpness whether they were located anteriorly (mesial) or posteriorly (distal) on the occlusal surfaces of the teeth. The sharp edged character of both the anterior and posterior facets results from tooth-tooth contact, (Greaves, 1973) but manipulation of the skulls and jaws of specimens of *Choloepus* and *Bradypus* shows, in contrast to Sicher's conclusion that when some of these glossy attrition facets are in occlusion it is physically impossible for the others to be out of occlusion. Since the anterior and posterior wear facets on the cheek teeth are acquired similarly through wear in both sloths, Sicher's

failure to include all of them to deduce the direction of the masticatory power-stroke was invalid, and an alternative method to determine the power-stroke direction must be sought. Sicher also stated, on the basis of his wear facet study, that sloths chewed strictly in an anterior-posterior direction. This idea must now also be reevaluated. The teeth in both sloths were examined under the light microscope to determine whether wear striations resulting from either tooth-tooth or tooth-food-tooth contact were present in the hard outer layer of dentin. Striations were seen on the teeth of both sloths, and trended in an anteromedial direction in *Choloepus*, and slightly more anteroposteriorly in *Bradypus*. This refutes the existence of a strictly anterior-posterior power-stroke. However, since wear striations can only indicate the line along which tooth movement takes place, the actual direction of the power-stroke

was investigated using the model presented independently by Rensberger (1973) and Greaves (1973). These authors show that the direction of the masticatory power-stroke can be determined by looking at the way in which the surface wears in a tooth that has harder and softer tissues on its occlusal face. The model predicts that the softer dentin center of the tooth on the side where the power-stroke begins is protected by the harder outer dentin layer, functioning as does the enamel in other mammals, and therefore is abraded away along a more gradual slope. However, food that is carried before the moving tooth gouges the softer central surface more deeply than it does the hard leading edge. As the teeth continue to move past one another during the power-stroke the food in the central basin is compressed close to the trailing side of the softer center. The large amount of food trapped against this edge gouges the soft surface more deeply than the area behind the leading edge. Frequently, there is a step formed between the deeply gouged central basin on the trailing side and the more resistant outer layer surrounding the edge of the tooth encountered last during the power-stroke (fig. 17). As this pattern of tooth wear is not symmetrical, the side of the tooth on which the power-stroke originated and ended while crossing a given tooth can be determined. Greaves (1973) demonstrated that this pattern exists in artiodactyls where the gently sloping leading edges are located posterolabially on the mandibular cheek teeth and anterolingually on the maxillary cheek teeth. This evidence, as well as data gathered from cineradiographic studies on artiodactyls (de Vree and Gans, 1973; Herring and Scapino, 1973) confirm that these animals have an anteromedially directed power-stroke during chewing. The pattern of a more gradual slope to the leading edge of the softer dentin center being posterior and slightly labially located in the mandible, and anterior and slightly lingually located in the upper cheek teeth in *Bradypus* (fig. 17) is in agreement with what is described for other animals and suggests that the power-stroke in *Bradypus* is also anterior and slightly medially directed.

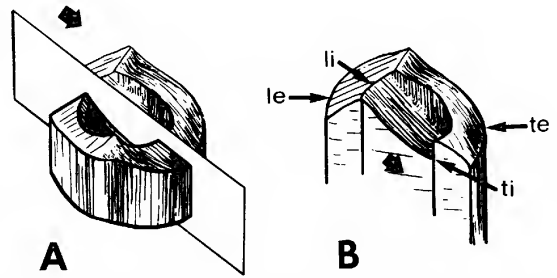


FIG. 17. Cross section of a mandibular tooth to show the step formed between the deeply gouged central basin in the softer core dentin on the trailing side of the tooth during occlusion, and the more resistant outer layer of hard dentin surrounding the outer edge of the tooth. The arrow indicates the direction of travel of the occluding tooth. *Abbreviations:* le, leading edge; li, leading interface; te, trailing edge and ti, trailing interface.

DENTAL EFFECTS ON GAPE

The anterior caniniform teeth in *Choloepus* are elongate, and project farther from the maxillae and mandibles than do the cheek teeth (in contrast to *Bradypus* in which the anterior peg- or chisel-shaped teeth project no farther from the maxillae and mandibles than do the teeth in the cheek tooth row). These long teeth make it necessary for *Choloepus* to be able to open the mouth far enough not only to clear these teeth, but also to enable the sloth to bite into food items such as tree buds or fruiting masses that are large in relation to its mouth. The length of the opposing caniniform teeth decreases the space between their tips by approximately 20 degrees in *Choloepus* in comparison to *Bradypus* when both sloths have the mouth open to the same degree of mandibular rotation (fig. 18). The maximum observed gape for *Choloepus* is approximately 60 degrees, whereas that for *Bradypus* is only 40 degrees. It does not seem coincidental that this difference corresponds to the amount of additional mandibular depression needed to separate the caniniform teeth to the same distance as the anterior peg- or chisel-shaped teeth in *Bradypus*. The presence of caniniform teeth places other constraints on the structure of the mandible in *Choloepus* as

well. Scapino (1972 and personal commun.) investigated the characteristics defining the relationship of the upper and lower canine teeth to one another in carnivores, especially mustelids. Scapino noted that in order for the canine teeth of carnivores to be efficient in capturing, killing, and dismembering large prey they must be able to resist forces applied in all directions, and to maintain the concentration of force on points or sharp edges of the teeth during all phases of mandibular closing and opening. The necessity of maintaining so precise a relationship between the points or cutting edges of canine teeth must also place restrictions upon the shape, length and orientation of the mandible, the structure and location of the CMJ, and the location of the muscles of mastication. One of the corollaries of the structure of the mandible and the arrangement of the muscles of mastication in a typical carnivore is that large forces are generated at the CMJ (Davis, 1955). Although *Choloepus* is herbivorous, the presence of long caniniform teeth in this sloth would suggest that mandibular form, if those teeth absorb significant loads, is subject to the restrictions imposed upon carnivores. In contrast, the form of the mandible in *Bradypus* (figs. 3, 19), which lacks elongate anterior teeth would not be limited by the same constraints. In this sloth the neck of the mandibular condyle is long (fig. 19), and the position of the tooth row is located as though the level of the CMJ is higher than that of *Choloepus*, although the glenoid fossae are similarly located relative to the braincase in the two sloths (figs. 2, 3, 10, 11). This arrangement is advantageous for a herbivore, since it gives the masseter complex and the medial pterygoid musculature a greater mechanical advantage (Smith and Savage, 1959). This muscular arrangement also generates significantly less pressure at the CMJ for a given force at the tooth row (Scapino, 1972), and therefore might be expected to be advantageous. However, lengthening the condylar neck in *Choloepus* would necessarily alter the way in which the caniniform teeth meet. There is also a difference in the angle of the occlusal surfaces of the cheek teeth

between the two sloths, of approximately 18 degrees (55 degrees from vertical for *Choloepus* and 37 degrees for *Bradypus*), which again correlates with the differences in the effective heights of the CMJ (fig. 20). The lower angle formed by the occlusal surfaces in *Choloepus* puts less stress on the peripheral cusps of the cheek teeth formed by thin walls of hard dentin, as well as spreading the chewing surface over a greater length of the relatively larger mandible in *Choloepus* as compared with *Bradypus*. The short mandible in *Bradypus* contributes to the anteroposterior compression of the cheek teeth in this sloth when compared with those of *Choloepus* (fig. 7). This correlates with a steeper angle of the cusps of the cheek teeth in *Bradypus* when compared with *Choloepus*. The relationship of the upper to the lower cheek teeth in *Bradypus* results in the more complicated pattern of the occlusal surfaces which is also necessary to achieve an occlusal surface area similar to that of *Choloepus* in this sloth. The greater risk of breakage to thin sharp edged cusps may explain why the peripheral areas of harder dentin are relatively and absolutely thicker in *Bradypus* than in *Choloepus* cheek teeth.

Caniniform tooth function in *Choloepus* is enhanced by several specializations. There is a recess open to the labial surface of the maxillary bone behind the upper caniniform tooth that can receive the tip of the lower tooth during full occlusion. The recess also extends lingual to the upper caniniform tooth. Correlated with the fossa in the maxillary bone is a recess in the soft tissues of the mouth which prevents them from being cut by the sharp edges of the caniniform occlusal surfaces during mandibular closing. The pre-dental spout on the mandible is narrow enough to allow the lower caniniform teeth the ability to pass lingual to the occlusal faces of the upper caniniform teeth.

TRANSMISSION OF STRESSES IN SLOTH SKULLS

The structural framework of the craniofacial skeleton is made up of a series of bony

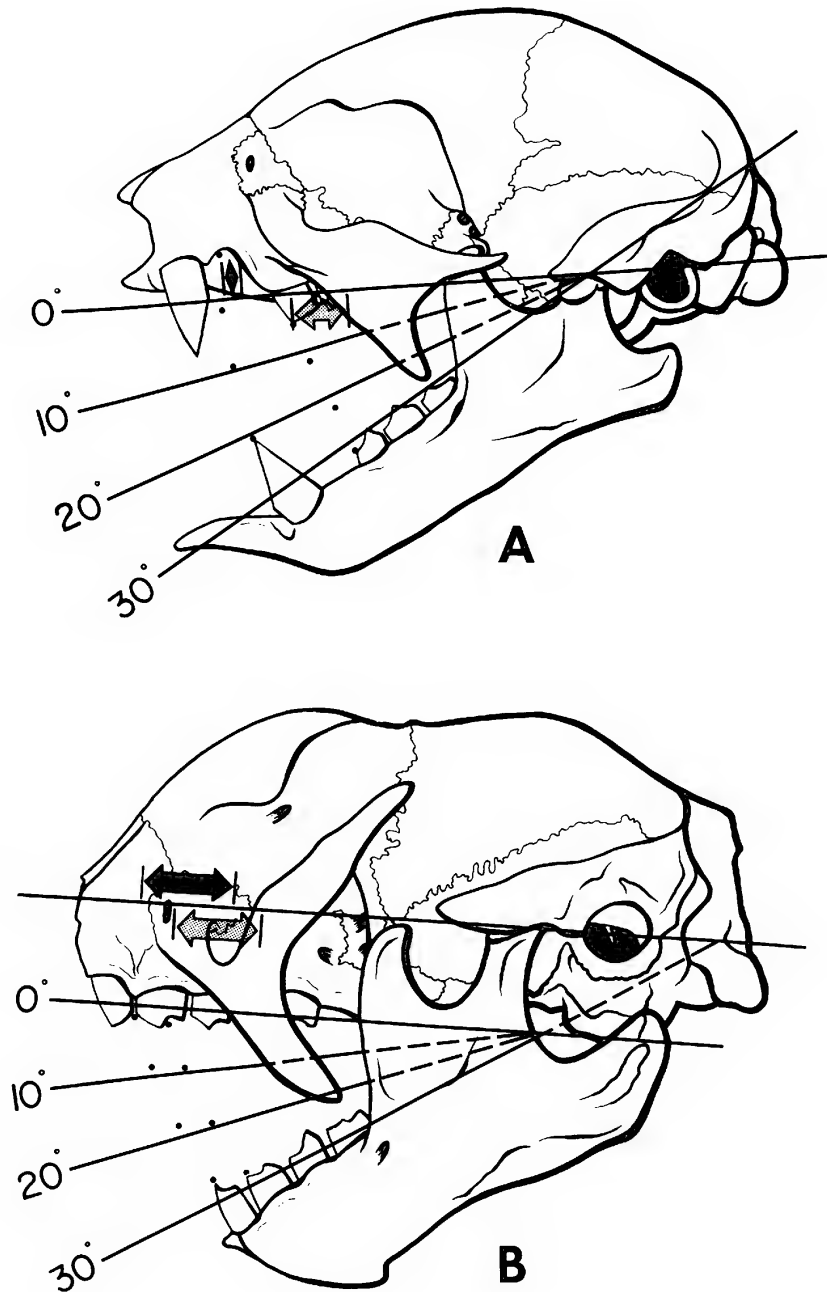


FIG. 18. Lateral views of the skull of *Choloepus* (A) and *Bradypus* (B), with the mandibles depressed to a gape of 30 degrees. The solid arrow (\leftrightarrow) shows the anteroposterior distance through which the caniniform or anterior chisel-shaped teeth must travel, and the gray arrow (\leftrightarrow) shows the same for the cheek teeth as the mandibles are brought into occlusion. Vertical movement is emphasized as the mandible comes into occlusion in *Choloepus*, while horizontal movement is emphasized in *Bradypus*.

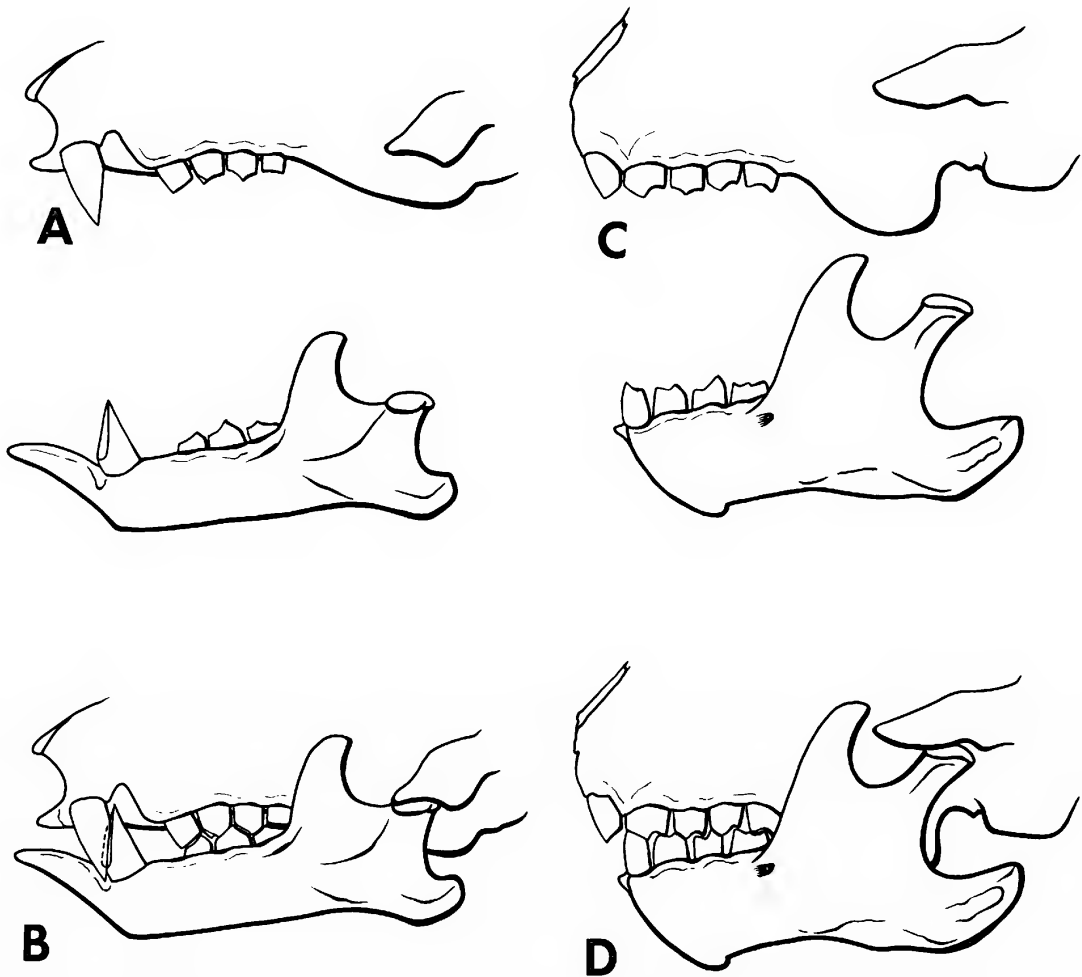


FIG. 19. Lateral views of the maxillary and mandibular tooth rows in *Choloepus* (A), and *Bradypus* (C). The mandibles are positioned for proper occlusion of the cheek teeth in *Choloepus* (B) and *Bradypus* (D).

stress-bearing bridges (Badoux, 1964, 1966; Roberts, 1979), and it is this framework that must absorb the occlusal forces at the dentition generated by the muscles of mastication (Roberts and Tattersall, 1974). Both tree sloths have frontal cranial sinuses (fig. 7) giving the skulls arched dorsal profiles, which help in the dispersal of bite forces (Buckland-Wright, 1978) but the structure of the sinuses differs between *Choloepus* and *Bradypus* (figs. 2, 3, 7). *Choloepus* has a longer maxillary region than does *Bradypus* (fig. 5), and therefore the lines of action of the temporalis

and masseter muscles are more horizontal than are those of *Bradypus* (fig. 21). It is the presence of large caniniform teeth, the most striking difference between the skulls of the two sloths, which requires longer rostral length to operate effectively in *Choloepus* that restricts the possible orientation of the masticatory musculature. The caniniform teeth in *Choloepus* are important both for threat display and biting (personal observ.) and therefore have been retained in this sloth, although such teeth have often been either lost or modified in other sloth lineages. Cor-

1974) and the average line of action is more vertical in the masseter and temporalis (fig. 21) in *Bradypus* than in *Choloepus*. In addition, a shorter cheek tooth row allows the force of the masticatory muscles to be distributed more equally anteroposteriorly (Roberts and Tattersall, 1974) in *Bradypus* in comparison with *Choloepus*, with the force vector of the average line of the temporalis more parallel to that of the compressive bite force. This allows the area of the origin of the muscles, particularly the temporalis, to change such that the vertical components, more efficient for mandibular closing, are emphasized in *Bradypus*. The bony maxillary buttresses in *Bradypus* are evenly distributed in comparison with those of *Choloepus*, and oriented so that the bite force stresses are transmitted to the same point more directly. In *Bradypus* this point is the bulge of the frontal sinus, and corresponds to a similar point of the anterior portion of the frontal bone in humans (Roberts and Tattersall, 1974). The ring of bone at the anterior of the rostrum is not so well developed as is that of *Choloepus*, probably because more of the stress forces are directed dorsally than in *Choloepus*.

The pattern of stresses generated by biting in the cat (Buckland-Wright, 1978) indicated that the presence of a movable zygomaticotemporal suture and moderately extensible postorbital ligament facilitated the vertical bending moment of the facial bones relative to the neurocranium during biting. It was shown (Buckland-Wright, 1972) that the maxillo-facial sutures moved when cats bit against resistance, and that forces acting at the zygomaticotemporal suture were primarily tensile. Further, this author noted that there was greater displacement of the bones where the tensile forces crossed sutures, and that flexible connections at this point would allow greater flexibility in the skull, permitting cats to exert larger forces during biting without danger of overstressing the facial bones. In sloths the possibilities for movement between the anterior and posterior parts of the zygomatic arch are great, since these regions as well as the postorbital process are

connected to one another only by ligaments (figs. 2, 3, 6).

COMPARATIVE MYOLOGY OF THE MUSCLES OF MASTICATION

The muscles of mastication in sloths have been described by several authors (Windle and Parsons, 1899; Edgeworth, 1935; Sicher, 1944; Toldt, 1908; Schulman, 1906; Leche, 1874-1900) but only Sicher (1944) presents a functional hypothesis concerning the action of the components of this musculature in mastication. However, Sicher's hypothesis attempts only to explain how the presence of an elongated descending process of the zygomatic arch in sloths reflects the increased number of horizontal fibers present in the superficial masseter muscle. None of the early authors have discussed the implications of the orientation of the muscles of mastication in relation to joint location which could affect the efficiency of chewing or extent of the gape in sloths, or how the distance to which it is possible to stretch a muscle can influence the ability of the animal to perform these functions. It therefore seems appropriate to re-evaluate the structure and arrangement of the muscles of mastication and to reassess the effect of each of these components upon the different requirements of the masticatory cycle. The method of Herring and Herring (1974) was used to provide an estimate of the distance to which a masticatory muscular component could be expected to stretch at a given gape. The four main muscles of mastication, the masseter, temporalis, lateral pterygoid, and medial pterygoid were analyzed in both sloths. In agreement with the earlier workers mentioned previously, the muscles were divided into components based upon gross muscular division. The origins and insertions of each of these components were discrete, and their orientations differed both from one another, and with respect to the CMJ, reflecting the differences in the mechanical advantage of components of muscles with large areas of origin and insertion. The masseter was divided into five components from anterior to posterior, and the

temporalis into three parts. Each of the two heads of the lateral pterygoid was considered separately, and the medial pterygoid was analyzed as a unit. Measurements were taken on crania of all available species of *Choloepus* and *Bradypus*, the sample size totaling 27 individuals per genus (table 1). The amount of stretch was analyzed at the maximum observed gape for each sloth genus, 60 degrees for *Choloepus* and 40 degrees for *Bradypus*. For comparison between the genera, muscle stretch was also analyzed at 40 degrees for *Choloepus* and at 60 degrees for *Bradypus*, although this last measurement is at a gape greater than any that has been seen for this genus. The maximum observed gapes chosen for this analysis are probably close to the actual limits upon gape in the two sloths, since manipulation of freshly killed dissection specimens to all possible gapes in all head and neck positions showed that the angular processes of the mandibles in both sloths interfered with neck tissues at a gape of approximately 60 degrees in *Choloepus* and approximately 40 degrees in *Bradypus*. The smaller apparent gape possibly in *Bradypus* results from the presence of a larger angular process of the mandible in this sloth as compared with that of *Choloepus*, as well as the exaggeration of the anterior-posterior components of mandibular movement in *Bradypus*, which are related to the elongated neck of the mandibular condyle in this genus, as can be seen when mandibles of both sloths are opened to 30 degrees of gape (fig. 18).

Experiments that tested the ability of the superficial masseter muscle to stretch during mastication in pigs were performed by Herring, Grimm and Grimm (1979). Results of these studies indicated that muscles were able to stretch in vivo to almost twice their resting length without incurring irreparable structural damage. These authors also report that in contrast to previous assumptions (Alexander, 1968) multipinnate muscles are able to stretch to greater distances without loss of force generating capacity than are parallel fibered muscles of the same size. At 60 degrees of gape the model of Herring and Herring (1974) predicts that the anterior segment of

the superficial masseter muscle of *Choloepus* is stretched to 2.23 times its resting length. This is somewhat longer than has been demonstrated for the superficial masseter muscle of the pig, but since the superficial masseter in sloths is very highly pinnate, it might be capable of the predicted amount of stretch, although this is probably near the maximum limit (S. W. Herring, personal commun.) The amount of stretch of the anterior segment of the superficial masseter appears to be the muscular factor limiting gape among the muscles of mastication in sloths, since the degree to which all the other muscle components are stretched is much smaller (table 1).

There are slight differences in the length, orientation, and shape of the descending jugal process in *Choloepus* and *Bradypus* (figs. 2, 3), which correspond to slight changes in orientation of the components of the superficial masseter muscle in the two sloths. To test whether these changes in orientation might correlate with the different extent to which the two sloths are able to open their mouths, Student's T-test was used to compare the amount of stretch necessary for each sloth to open the mouth to 40 degrees and 60 degrees. The most anterior portion of the superficial masseter was selected for this test, since the muscle stretch analysis (table 1) suggested that this was the only segment of all the major muscles of mastication that was stretched to its predicted limit when sloths opened their mouths to the maximum observed gape for each genus. It is shown (table 2) as might be expected (see above) that significantly greater muscle stretch ($P > .01$) is required for either sloth to open its mouth to 60 degrees than to 40 degrees. Table 2 also shows that the anterior segment of the superficial masseter in *Bradypus* is stretched to a significantly greater amount ($P > .001$) at both 40 degrees and 60 degrees than is the same muscle segment in *Choloepus*. Finally, a comparison between the extent of muscle stretch of the anterior superficial masseter component at the maximum observed gape in the two sloths was not significant. It appears, therefore, that this segment of the su-

TABLE 1
Means (X) and Standard Deviations (S.D.) of the Measurements of Stretch of the Main Masticatory Muscles in *Choloepus* and *Bradypus*^a

Muscle	<i>Choloepus</i>				<i>Bradypus</i>			
	40		60		40		60	
	X	S.D.	X	S.D.	X	S.D.	X	S.D.
SUPERFICIAL MASSETER								
Part 1	1.877	.1174	2.23	.1518	2.033	.0927	2.47	.1335
Part 2	1.2978	.0866	1.40	.1277	1.35	.0513	1.46	.0774
Part 3	1.1822	.0393	1.23	.0576	1.22	.0473	1.29	.0676
Part 4	1.1667	.0296	1.21	.0457	1.20	.0474	1.26	.0586
Part 5	1.1978	.0412	1.26	.0538	1.24	.0483	1.32	.0681
TEMPORALIS								
Part 1	1.4456	.0662	1.59	.2234	1.44	.0482	1.61	.0689
Part 2	1.3352	.0371	1.46	.0601	1.32	.0762	1.46	.794
Part 3	1.1381	.0449	1.16	.0726	1.13	.0528	1.17	.1288
LATERAL PTERYGOID								
Part 1	1.10	.0152	1.18	.0173	1.13	.0814	1.23	.1286
Part 2	1.12	.0152	1.22	.0231	1.18	.0757	1.32	.1021
MEDIAL PTERYGOID								
Part 1	1.52	.1152	1.72	.1682	1.73	.0400	2.03	.0550

^a Calculated according to the method of Herring and Herring (1974) for 40 and 60 degrees of gape. For details see discussion in text.

perforial masseter muscle in *Bradypus* is stretched at 40 degrees to an extent approaching as close to its physiological limit as is the corresponding segment of the superficial masseter of *Choloepus* when stretched to a gape of 60 degrees. Since these muscles in both sloths are stretched to their predicted limits at 60 degrees for *Choloepus* and 40 degrees for *Bradypus*, it seems likely that these maxima approximate the actual maximum extent of gape in the two sloths, as was also predicted from observations of the gapes at which the mandibular angles caused interference with neck tissues.

DISCUSSION

The diversity of sloth cranial characters may correlate with various biomechanical factors as well as reflecting the structural constraints placed on Recent sloths, given their phylogeny (Winge, 1941; Romer, 1966; Scott, 1937; Patterson and Pascual, 1972; Hirschfeld and Webb, 1968). Many of the

diverse osteological characters seen among fossil sloths are present in the two Recent tree sloths, *Choloepus* and *Bradypus*. The purpose of this study has been to examine sloth crania, correlating structure as far as is possible with function, by comparing the living animals with one another, and referring to the known fossils. Tree sloths are a good model for investigations into cranial structure in both fossil and Recent forms, since only in extant animals can the importance of soft tissues in relation to cranial structure and function be examined. Three main suites of osteologic characters are described. They are interrelated, but not solely dependent upon one another: (1) cranial sinuses and the buttresses in the skull for force transmission; (2) the morphology of the dentition and its effects on the shape of the maxilla and mandible, leading to a hypothesis of masticatory movement patterns; and (3) orientation of the zygomatic arch and construction of the craniomandibular joint as they relate to a theoretical model for interpreting the bio-

mechanical sequence of events that governed the structural changes in the evolution of sloth skulls, and which produced the different dentitions and skull characteristics in *Choloepus* and *Bradypus*.

TRANSMISSION OF STRESSES IN SLOTH SKULLS

Although the bony buttresses of the maxilla and the extensive frontal sinuses of the tree sloths differ in mechanical detail, these structures provide a mechanism for the dispersal of the large forces which can be generated at the teeth in biting (personal observ.) in both animals. The more extensive buttressing in *Choloepus* is correlated with the presence of a longer rostrum in this sloth as compared with *Bradypus*. The sloths, like herbivores such as the horse, must accommodate two different sets of masticatory requirements, i.e., cropping with the anterior teeth and grazing with the posterior teeth. In *Choloepus* the anterior biting teeth are caniniform, separated in space by a diastema and in function from the chewing cheek teeth; as is the case in rodents (Hiemae and Ardran, 1968). However, in *Bradypus* tooth functions are less discrete; the bony buttresses support the short maxilla more evenly as reflected by their anatomy (fig. 7), and allow the forces generated at the teeth to be absorbed in a more uniform fashion than is possible in *Choloepus*. Stresses can also be absorbed by structures which flex or stretch under tension. Buckland-Wright (1978) noted that forces acting at the zygomaticotemporal suture during mastication in cats were primarily tensile. The flexibility in this area enabled cats to exert greater forces during biting without overstressing the facial bones than would have been possible had the area been totally rigid. The bony architecture of the skull and arrangement of the muscles of mastication differ between *Choloepus* and *Bradypus*. The presence of caniniform teeth in *Choloepus* presents this sloth with different biomechanical problems for stress transmission than those faced by *Bradypus*. Although both sloths have interrupted zygomatic arches, the pattern of bony facial buttressing and the size and shape of the frontal sinuses differ, and

TABLE 2
Comparison of the Stretch of the Anterior Segment of the Superficial Masseter Between *Choloepus* and *Bradypus*^a

Genus Significance	Degrees of gape	Comparisons		
		T	D. o. f.	
<i>Choloepus</i>	40 to 60	3.057	26	†.01
<i>Bradypus</i>	40 to 60	3.440	26	†.01
<i>Choloepus</i> @ 60 – <i>Bradypus</i> @ 40		0.3398	52	N. S.
<i>Choloepus</i> @ 40 – <i>Bradypus</i> @ 40		5.4185		
<i>Choloepus</i> @ 60 – <i>Bradypus</i> @ 60		6.1739	52	†.001
			52	†.001

^a The anterior part of the muscle was selected, since it is the most stretched in both sloths at the maximum gapes observed for both genera. "T" is for the values resulting from Student's T-test, and d. o. f. is the number of degrees of freedom for each test. See text for details.

therefore the patterns of transmission of stresses through the front ends of sloth skulls differ. Ligaments also transmit stresses particularly well, while permitting greater flexibility than do bony connections. The ligaments connecting the processes of the sloth zygomatic arch might provide a mechanism for resisting tensile forces at this site, while providing the flexibility needed to prevent damage to the facial bones during hard biting. This may also explain why the anterior and posterior parts of the zygomatic arch in some medium-sized ground sloths, such as *Glossotherium*, *Nothrotheriops*, *Mylodon*, and *Megalonyx* are closely approximated, but never fused. However, in the largest ground sloths, *Eremotherium* and *Megatherium* the anterior and posterior parts of the zygomatic arches are solidly fused although these animals have large ascending and descending jugal processes bound only by ligaments to the rest of the zygomatic arch, suggesting that some flexibility is important in this area, even for the largest animals.

DENTAL MORPHOLOGY

Although they are not homologous to the cusps found on the teeth of other mammals,

functional "cusps" are formed by the differential wear of the hard outer and soft inner dentin layers on all sloth teeth. The outer dentin layer forms sharp cusps and ridges with use, while the softer dentin center wears away more easily, forming the prominent central basins of worn sloth teeth. Although the "cusps" are formed in the same way, the morphology of the adult dentitions of *Choloepus* and *Bradypus* differs in several respects (figs. 2, 3, 4, 14, 20). The anterior teeth in *Choloepus* acquire a caniniform shape with growth and wear, and due to an additional increment of maxillary and mandibular growth, become separated from the cheek tooth row by a diastema. There is no diastema in *Bradypus*, and so the anterior mandibular chisel-shaped teeth also occlude with an anterior facet on the first upper molariform teeth. The difference in the occlusal pattern in the two sloths also results from the alternating arrangement of the maxillary and mandibular teeth in *Choloepus*. This contrasts with the more directly opposed alignment of the upper and lower teeth in *Bradypus* (figs. 7, 19).

Differences in the shape of the anterior teeth in the tree sloths are reflected in their use in the two animals. In *Choloepus* the caniniform teeth are used not only for biting and piercing food, but also for slicing foods by forcing the pieces against the sharp edges of the labial and lingual wear surfaces. *Choloepus* manipulates and maintains foods in the proper position for biting by the caniniform teeth using the tongue and premental spout (personal observ.). *Choloepus* can only bite with one set of caniniform teeth at any time. Sometimes correct positioning of the food requires considerable mediolateral mandibular movement. Although *Bradypus* lacks a premental spout, this sloth also uses the tongue and lips as well as one or both forelimbs to position foods for biting. This is an important difference from the food ingestion behavior of rodents such as *Rattus*, in which the incisors and forefeet are used to manipulate a piece of food but the tongue or lips are not so used (Hiimae and Ardran, 1968). This behavior is similar to that re-

corded in larger herbivores (Hiimae and Kay, personal commun.).

It has been suggested, in the only previous study of sloth chewing mechanisms, that it is possible to deduce the pattern of sloth mandibular movements from the wear on the teeth (Sicher, 1944). Sicher developed his hypothesis on the function of sloth teeth based on only some of the wear facets, and used the muscles of mastication to substantiate his view. In particular, he argued that the masseter was a strong mandibular protractor in both sloths, and the temporalis and pterygoid muscles were weak. Intrinsic to his argument was the view that the sternomandibular muscle (=sternohyoid plus anterior digastric of other mammals) is a mandibular retractor (? depressor) in *Choloepus*. He said that this muscle is missing in *Bradypus*. From this Sicher concluded that the muscles of mastication showed no significant differences in organization between the two sloth genera, and any differences seen in masticatory function in the two sloths were related to dental structure. Features that Sicher thought to be important in developing his explanation of the mechanisms of mastication in sloths were: (1) the caniniform and molariform teeth in *Choloepus* were not in simultaneous contact; (2) the caniniform teeth were not in contact when the jaws were "at rest"; (3) in *Choloepus* there were two types of wear facets on the molariform teeth, i.e., a suite of "glossy narrow facets" made by sharp tooth-tooth contact during the masticatory power-stroke, and other dull, irregular facets that "gave" the teeth their cusps; (4) "glossy wear facets" in *Choloepus* were located anteriorly and mesially on the uppers and posteriorly and distally on the lowers; (5) the "glossy" attrition facets on the molariform teeth in *Bradypus* were located anteromesially on the uppers and posterodistally on the lowers, which is the reverse of the arrangement seen in *Choloepus*; and (6) in *Bradypus* the larger attrition facet was on the distal surface of the first lower tooth, rather than being mesial as in *Choloepus*. Resulting from his analysis of masticatory muscles, tooth form and wear facets, Sicher concluded (1) that sloth man-

dibles moved only in an anterior-posterior direction; (2) that the pattern of mandibular movement was the same for both sloths but the power-stroke occurred in the opposite direction. Sicher argued that the power-stroke was anteriorly directed in *Bradypus*, but was posteriorly directed in *Choloepus*. The "location of the power-stroke in different parts of the chewing cycle" dictated (3) that the mandibles were positioned in an opposite fashion at the beginning of the grinding stroke in each sloth. Given the essential similarity of the two sloths, it is difficult to accept that they can have, biomechanically, power-strokes that are oriented exactly in opposite directions. A reexamination of the teeth in both sloths has shown: (1) that occlusal facets on all the teeth are formed similarly from tooth-tooth contact; (2) that tooth wear striations trend along an anterolingual (anteromedial)-posterolabial (posterolateral) axis; and (3) that the softer dentin in the centers of sloth teeth wears in an asymmetrical pattern, with more gently sloping leading edges located posterolabially on the mandibular cheek teeth and anterolingually on the maxillary cheek teeth as described by Greaves (1973) and Rensberger (1973) in the teeth of artiodactyls and other grazers. The evidence presented in this paper argues against Sicher's hypothesis, in that the location of the more gradually sloping leading edges of the central basin in the teeth of both sloths is similar and on the posterolabial aspect of the mandibular teeth and the anterolingual aspects of the maxillary teeth. This is more clearly seen in *Choloepus* than *Bradypus*, perhaps because the former has a more pronounced medial movement to the chewing power-stroke as shown by the orientation of the wear striations on all *Choloepus* teeth. Several additional pieces of evidence support the view that the power-stroke is anteromedially directed in the two sloths. These are: (1) when the mandible is seen in lateral view the wear facets are not seen in direct profile; (2) the pointed "cusps" are somewhat offset when the teeth are seen in occlusal view (figs. 2, 3, 13, 14), the labial ones more posterior in both the mandible and maxilla and; (3) the surface

of the hard outer dentin is more worn and has a slightly more rounded leading edge posterolabially on the mandibular teeth and anterolingually on the maxillary teeth. An anteromedially directed power-stroke is the only explanation which will account for all of the observed tooth structure in both sloths.

ZYGOMATIC ARCH- CRANIOMANDIBULAR JOINT RELATIONSHIPS; AND THEORETICAL CONSIDERATIONS

Outgroup comparisons with early myodont sloths indicate that the retention of long anterior teeth in *Choloepus* is pleisomorphic. The loss or modification of these teeth is a derived character. Other sloths have reorganized the masticatory apparatus to resemble that of artiodactyls and perissodactyls by eliminating the long anterior teeth (*Scelidotherium*, *Glossotherium*) or incorporating them at least partially into the cheek tooth row (*Bradypus*, *Megalonyx*). If the long caniniform teeth of *Choloepus* and ground sloths, such as the megalonychids are to occlude they must be precisely aligned throughout the chewing cycle. Further, the maintenance of so precise an occlusal relationship correlates with the presence of a low CMJ, which optimizes the vertical component of motion along the path in which the mandible travels, keeping the points of the anterior teeth oriented toward one another at all times. In contrast, in *Bradypus*, which has a short face, the masticatory muscles have been rearranged to optimize their mechanical advantages, and reduce the pressures that act at the CMJ (Scapino, 1972). Smith and Savage (1959) suggest that the mechanical advantage of the masseter can be improved by raising the level of the jaw joint, thus increasing the masticatory efficiency in the herbivores in which this occurs. These authors further state that this change does not result in a loss of force acting at the tooth row, and as long as both the upper and lower tooth rows remain an equal distance from the CMJ (Greaves, 1973) the teeth can still occlude simultaneously along the entire length of the

cheek tooth row (fig. 10). When compared with early sloths, the CMJ in *Bradypus* and some of the megatheriids has been raised by elongation of the condylar neck of the mandible, and these changes and their biomechanical consequences appear to correlate with the loss of the elongate form of the anterior teeth. In addition to having an improved mechanical advantage for the masseter and medial pterygoid, in *Bradypus* this is also true for the anterior part of the temporalis since this part of the muscle has been reoriented to arise from the ventral surface of the ascending process of the zygomatic arch. The anterior movement of this muscle segment moves the average moment arm of the entire muscle anteriorly, while allowing this sloth to retain a raised CMJ. The presence of this new muscle segment is unique to sloths, and is a derived condition. The elongation of the mandibular condyle affects the location of the tooth row in these sloths in two ways: (1) the upper tooth row and palate as well as the mandibular tooth row are depressed ventral to the level of the basicranium, and are inclined ventrally posteriorly, forming a basicranial angle greater than zero; (2) this correlates with the more steeply inclined occlusal surfaces of the short cheek tooth row in *Bradypus*. The elongation of the mandibular condyle carries the insertions of the masseter and medial pterygoid muscles ventrally. In *Bradypus* and some of the megatheriids the descending jugal process of the zygomatic arch is relatively longer than that of *Choloepus*, and the pterygoid hamulus in all ground sloths so far examined which have a raised CMJ (e.g., *Megatherium*, *Eremotherium*), the pterygoid plate has elongated greatly into a flange projecting posteroventrally. The origin of the medial pterygoid muscle has maintained its attachment to the lateroventral edge of this bony projection. These changes allow both of the muscles to maintain an optimum orientation in effecting both anterior and medial mandibular movements. The size of the masseter muscle in these sloths has also been enlarged in comparison to *Choloepus*, and inserts on an expanded angular process, which projects ventrally and posteriorly in *Bradypus*. Despite

these changes, the distance over which the masseter contracts is much the same in *Choloepus* and *Bradypus* as demonstrated by the muscle stretch analysis performed earlier in this study. This reorientation of the masseter and medial pterygoid muscle also has the advantage of aligning the direction in which the muscles exert force more closely to the direction in which the lowered and posteroventrally depressed tooth rows move in the power stroke. The restructuring of the mandible in *Bradypus* allows the absolute and relative enlargement of the masseter musculature, in this genus as compared with *Choloepus*. In contrast, farther enlargement of the masseter in *Choloepus* is not possible since either a dorsoventrally or anteroposteriorly deepened angular process in this sloth would interfere with neck tissues at lower degrees of mandibular opening than in the present condition. The long caniniform teeth in *Choloepus* require the mouth to be opened approximately 20 degrees farther for biting than chewing: *Choloepus* and the megalonychids which retain long caniniform teeth are prevented from improving their efficiency as herbivores by reorienting the origin, insertion, or size of the masticatory muscles or increasing the height of the CMJ as other herbivores have done.

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APPENDIX 1: LIST OF SPECIMENS

SPECIES	AMNH No.	SEX	AGE	SPECIES	AMNH No.	SEX	AGE
<i>Bradypus boliviensis</i>	211663	F	J	<i>Bradypus infuscatus infuscatus</i>	73757	F	J
<i>Bradypus boliviensis</i>	61791	F	J	<i>Bradypus infuscatus infuscatus</i>	76496	F	YA
<i>Bradypus boliviensis</i>	133435	?	YA	<i>Bradypus infuscatus infuscatus</i>	76408	F	AA
<i>Bradypus boliviensis</i>	209940	?	AA	<i>Bradypus infuscatus infuscatus</i>	73575	F	J
<i>Bradypus cuculliger</i>	42871	F	J	<i>Bradypus infuscatus infuscatus</i>	73758	F	AA
<i>Bradypus cuculliger</i>	48104	F	AA	<i>Bradypus infuscatus infuscatus</i>	73759	F	AA
<i>Bradypus cuculliger</i>	74131	F	YA	<i>Bradypus infuscatus infuscatus</i>	74429	F	AA
<i>Bradypus cuculliger</i>	42454	F	YA	<i>Bradypus infuscatus infuscatus</i>	73572	F	AA
<i>Bradypus cuculliger</i>	48180	F	AA	<i>Bradypus infuscatus infuscatus</i>	118196	?	YA
<i>Bradypus cuculliger</i>	42888	M	J	<i>Bradypus infuscatus infuscatus</i>	76423	F	J
<i>Bradypus cuculliger</i>	142992	?	J	<i>Bradypus tridactylus</i>	95105	M	YA
<i>Bradypus cuculliger</i>	130106	F	AA	<i>Bradypus tridactylus</i>	95329	M	YA
<i>Bradypus griseus</i>	42838	F	AA	<i>Bradypus tridactylus</i>	95841	F	YA
<i>Bradypus griseus castaniceps</i>	28477	F	J	<i>Bradypus sp.</i>	95103	F	YA
<i>Bradypus griseus castaniceps</i>	28478	F	YA	<i>Bradypus sp.</i>	95102	M	YA
<i>Bradypus griseus castaniceps</i>	139313	F	YA	<i>Bradypus sp.</i>	95101	M	AA
<i>Bradypus griseus castaniceps</i>	2824	?	AA	<i>Bradypus sp.</i>	95104	M	AA
<i>Bradypus griseus castaniceps</i>	38616	?	AA	<i>Bradypus sp.</i>	95328	M	YA
<i>Bradypus griseus castaniceps</i>	31427	F	AA	<i>Bradypus sp.</i>	95325	M	AA
<i>Bradypus griseus castaniceps</i>	139833	F	YA	<i>Bradypus sp.</i>	95326	M	YA
<i>Bradypus griseus castaniceps</i>	29441	F	YA	<i>Bradypus sp.</i>	95327	M	YA
<i>Bradypus ignavus</i>	38191	F	J	<i>Bradypus sp.</i>	95106	M	YA
<i>Bradypus ignavus</i>	37621	F	YA	<i>Bradypus sp.</i>	95105	M	YA
<i>Bradypus ignavus</i>	37620	F	YA	<i>Bradypus sp.</i>	95329	M	YA
<i>Bradypus ignavus</i>	76495	F	AA	<i>Bradypus sp.</i>	95841	F	YA
<i>Bradypus ignavus</i>	38102	F	J	<i>Choloepus andinus</i>	33039	F	J
<i>Bradypus infuscatus</i>	98820	?	YA	<i>Choloepus andinus</i>	33051	M	AA
<i>Bradypus infuscatus</i>	73574	F	AA	<i>Choloepus andinus</i>	34125	F	AA
<i>Bradypus infuscatus</i>	98530	M	AA	<i>Choloepus andinus</i>	34126	F	J
<i>Bradypus infuscatus ephippiger</i>	32699	F	AA	<i>Choloepus andinus</i>	33179	M	J
<i>Bradypus infuscatus ephippiger</i>	34153	F	AA	<i>Choloepus didactylus</i>	133444	?	AA
<i>Bradypus infuscatus ephippiger</i>	34270	F	AA	<i>Choloepus didactylus</i>	133447	M	AA
<i>Bradypus infuscatus ephippiger</i>	62876	F	YA	<i>Choloepus didactylus</i>	133439	?	AA
<i>Bradypus infuscatus ephippiger</i>	62877	F	YA	<i>Choloepus didactylus</i>	133452	?	AA
<i>Bradypus infuscatus flaccidus</i>	78515	F	AA	<i>Choloepus didactylus</i>	133453	?	AA
<i>Bradypus infuscatus flaccidus</i>	144824	?	J	<i>Choloepus didactylus</i>	133446	?	AA
<i>Bradypus infuscatus flaccidus</i>	30201	F	J	<i>Choloepus didactylus</i>	133417	M	YA
<i>Bradypus infuscatus flaccidus</i>	16134	F	J	<i>Choloepus didactylus</i>	133414	?	YA
<i>Bradypus infuscatus flaccidus</i>	17560	F	AA	<i>Choloepus didactylus</i>	133407	F	J
<i>Bradypus infuscatus flaccidus</i>	76904	F	AA	<i>Choloepus didactylus</i>	133427	F	AA
<i>Bradypus infuscatus flaccidus</i>	135474	?	AA	<i>Choloepus didactylus</i>	78591	M	AA
<i>Bradypus infuscatus flaccidus</i>	16934	F	J	<i>Choloepus didactylus</i>	41944	?	YA
<i>Bradypus infuscatus flaccidus</i>	16933	?	AA	<i>Choloepus didactylus</i>	21307	F	AA
<i>Bradypus infuscatus flaccidus</i>	16135	?	AA	<i>Choloepus didactylus</i>	71821	M	AA
<i>Bradypus infuscatus flaccidus</i>	16932	F	AA	<i>Choloepus didactylus</i>	60648	?	AA
<i>Bradypus infuscatus flaccidus</i>	98545	M	J	<i>Choloepus didactylus</i>	71823	F	AA
<i>Bradypus infuscatus infuscatus</i>	76497	F	AA	<i>Choloepus didactylus</i>	71824	F	YA
<i>Bradypus infuscatus infuscatus</i>	73573	M	YA	<i>Choloepus didactylus</i>	71820	F	AA
<i>Bradypus infuscatus infuscatus</i>	76403	F	YA	<i>Choloepus didactylus</i>	62875	F	J
				<i>Choloepus didactylus</i>	182946	?	AA

APPENDIX 1—(Continued)

SPECIES	USNM		
	No.	SEX	AGE
<i>Bradypus tridactylus</i>	256676	F	AA
<i>Bradypus tridactylus</i>	362241	F	AA
SPECIES	UMA		
	No.	SEX	AGE
<i>Bradypus infuscatus</i> *	3	M	YA
<i>Bradypus infuscatus</i> *	4	M	YA
<i>Bradypus infuscatus</i> *	5	M	YA
<i>Choloepus hoffmanni</i> *	1	?	YA
<i>Choloepus hoffmanni</i> *	2	?	YA

^a Abbreviations are: American Museum of Natural History (AMNH), Field Museum of Natural History (FMNH) National Museum of Natural History, Smithsonian Institution (USNM) and Museum of Zoology, University of Massachusetts (UMA). Specimens labeled with an asterisk (*) were used for craniofacial dissections.

