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## *Xenothrix* and Ceboid Phylogeny

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The known morphology of the subfossil Jamaican primate, *Xenothrix mcgregori*, is described and systematically analyzed. A provisional phylogeny of living ceboid genera, based upon cladistic interpretation of available data, is presented. *Xenothrix* shares derived character states with a monophyletic group of cebids which excludes the genera *Cebus* and *Saimiri*. Loss of  $M_3$  in *Xenothrix* occurred convergently to two-molared callithricids. In view of the great adaptive diversity of the living Ceboidea, and the probable phyletic affinities of the subfossil to an internally diverse, monophyletic group currently classified within Cebidae, separate familial status for *Xenothrix* is unwarranted. Until a secure, falsifiable phylogeny of ceboids is worked out the designation of new higher taxa is undesirable.

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### 1. Introduction

*Xenothrix mcgregori* Williams & Koopman, 1952 is known from a single partial mandible containing two left molar teeth. The specimen was recovered in 1920 by H. E. Anthony from beneath a kitchen midden on the island of Jamaica which yielded other vertebrates thought to be of Pleistocene or Recent age. Several of the numerous postcranials coming from the same site are possibly primate but Williams & Koopman judiciously refrained from designating these as paratype. There are, of course, no living non-human primates native to Jamaica or the entire West Indian subregion (Hershkovitz, 1972). A single distal tibia, designated *Cercopithecus?* sp.? (*sic*) by Miller (1929), is known, however, from a Dominican Republic deposit associated with an indigenous, partially extinct fauna (Williams & Koopman, 1952).

In their initial study of the genus, Williams & Koopman (1952) allocated *Xenothrix* to Cebidae. Simpson (1956) and Hill (1962) accepted this assignment but Romer (1971) did so only with a query. Simpson later (1969) sunk all living and fossil ceboids into a single family, Cebidae. Recently, Hershkovitz (1970) proposed that a new family, Xenothricidae, be erected to receive this single specimen. The new ranking was adopted in the classifications of Simons (1972) and Hoffstetter (1974).

This paper is an attempt to clarify the phyletic affinities of *Xenothrix mcgregori*. This can be done only within a phylogenetic framework that treats at least all extant ceboid genera. I therefore present a provisional phylogeny of living Ceboidea. Although my major concern here is not classification, it is important to recognize that most classifications, regardless of how they are formulated, are based upon hypotheses of evolutionary relationships. To my knowledge no clear evidence bearing on the affinities of *Xenothrix* has yet been presented, rendering the evolutionary meaning of the classifications of other authors somewhat ambiguous. I hope to demonstrate that there is in fact no current need to recognize a novel family-rank taxon in order to describe the biological significance of *Xenothrix*; phyletically and adaptively it can nest comfortably within a bifamilial (perhaps unifamilial) Ceboidea.

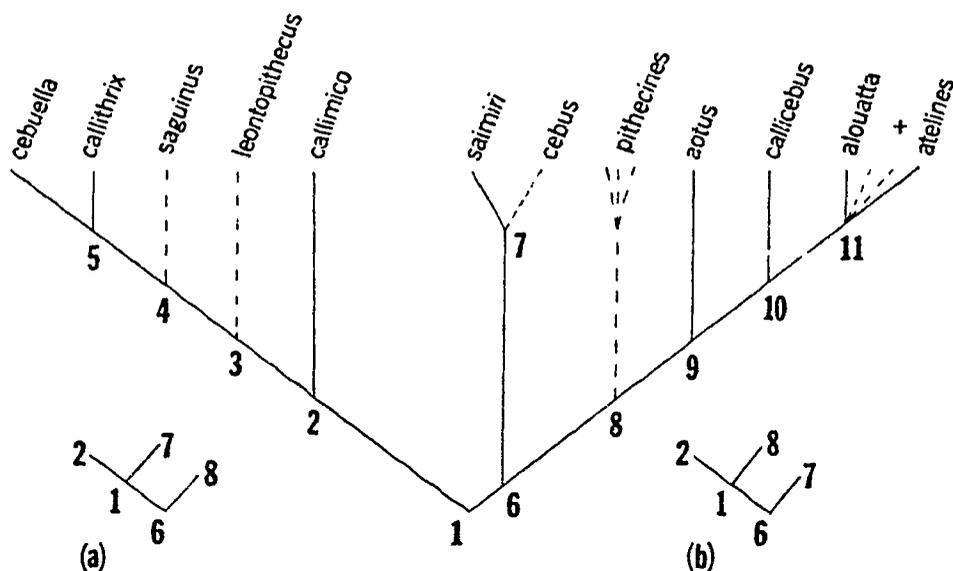
In developing the phylogeny presented below, careful attention has been paid to delimiting presumed, strictly monophyletic sets of taxa defined by their mutual possession

of derived characters or character states not shared with other taxa. Branching sequences of these monophyletic groups were then determined by comparing the character states of their hypothetical ancestors, or morphotypes. (See Schaeffer, Hecht & Eldredge (1972) for discussion of the method and its theoretical foundations.) For convenience, I have adopted familiar, informal designations for several of these assemblages or their plesiomorphic sister-groups, i.e. taxa not possessing the derived condition of an increasingly exclusive character state. I emphasize that the proposed phylogeny, like all phylogenies, is a theory of relationships. It, or part of it, is subject only to disproof, not to proof. Its validity should be assessed by its testability and plausibility, by the hypotheses it generates and the explanations it offers. It will certainly require revision as more becomes known.

## 2. Phylogeny of Living Ceboids

The dendrogram of Figure 1 is a representation of my proposed phylogeny of living ceboids, mostly taken to the level of genus. For simplicity, the dichotomies are referenced by number in the diagram and text. Each node represents the morphotype of a monophyletic group which includes all taxa distal to that particular junction. The derived character states of each morphotype are briefly discussed below as evidence of each group's strictly monophyletic origin. Alternative arrangements [Figures 1(a) and (b)] are compatible with my interpretation of data and until additional information is advanced each must be entertained as a viable hypothesis. Although the differences between these alternatives are profound, in retrospect they do not largely affect the arguments concerning *Xenothrix*.

Figure 1. A provisional phylogeny of living ceboids: (a) and (b) are alternative basal cladistics. Dotted lines indicate uncertainties. Each node represents a reconstruction of the last common ancestor of all taxa distal to that node. Derived characteristics manifest at each node segregate all distal taxa into strictly monophyletic groups and are explained in the text.



### Node 1

Many of the features used by modern authors (e.g. Gregory, 1920, 1922; LeGros Clark, 1959; Simons, 1972) to describe or diagnose Ceboidea, for example, the "broad nosed" condition, short face, three premolared dental formula, increased size and complexity of brain, are probably manifestations of ancestral conditions retained since the differentiation of either haplorhines or anthropoids. Assuming that platyrrhines and catarrhines shared a common ancestor prior to the differentiation of the living ceboid lineages, none of these would be acceptable as evidence for a monophyletic origin of the former.

Characteristics of the cranium, however, may provide us with some. The extensive study by Ashley-Montagu (1933) documented a unique sutural pattern of the pterion region found only in the platyrrhines: zygomatic contacts parietal, precluding a frontal-alisphenoid suture. The basic pattern among non-platyrrhines, of which there are but minor variations, is a frontal-alisphenoid union, separating the zygomatic and parietal bones. The later condition is found also among Insectivora and is probably the ancestral condition in mammals. Ashley-Montagu (1933) found the zygomatic-parietal contact invariable among Callithricidae ( $N = 231$ ). Among nine cebid genera studied ( $N = 1490$ ) the maximum observed variability was only 2.2%, in *Pithecia* ( $N = 138$ ), whereas departures from the predominant platyrrhine condition occurred in 40.6% of *Ateles* ( $N = 182$ ) and 60% of *Alouatta* ( $N = 262$ ). Despite these variations, it seems clear that a zygomatic-parietal union, termed a specialization of platyrrhines by LeGros Clark (1959: 155), was present as a derived character state in the last common ancestor of all living ceboids. It may also be indicative of historically independent phases of post-orbital closure in platyrrhines and catarrhines. The presence of substantial variability in *Ateles* and *Alouatta* may reflect variability in their last shared ancestral population (see below) or some other factor(s), possibly related to the larger body size of this group.

A second, perhaps related, characteristic of the platyrrhine pterion region is the presence of one or more foramina at or near the zygomaticoparietal suture, the zygomaticoparietal foramen (see Anthony, 1946: "lateral orbital fissure" of Hershkovitz, 1974). This foramen is not present in *Tarsius* or strepsirrhines and may thus also be a uniquely derived character indicative of the ceboid's monophyletic origin.

### Node 2

For the moment this junction will be considered along with Node 6. The separatedness of these nodes reflects the widely accepted taxonomic division of Callithricidae and Cebidae respectively. These taxa are distinguishable by the distribution of claws and nails: long, recurved claws are present on all terminal phalanges but the hallux of callithricids: shorter, biconcave nails are found on all digits of cebids as well as on the callithricid hallux. Numerous workers have argued whether or not clawed or nailed digits were present in the ancestral platyrrhines. LeGros Clark (1936) and, more recently, Thorndike (1968) demonstrated that platyrrhine nails and claws are composed of the same histologic elements. Weber (1928) and LeGros Clark (1936) referred to these appendages collectively as tegulae, differentiating them from tupaiid claws (falculae) by their reduced terminal matrix and deep stratum, and from catarrhine nails (ungulae) which have entirely lost these constituents (LeGros Clark, 1936). After initially maintaining that callithricid-like tegulae were ancestral in ceboids, LeGros Clark (1936), retreated from this position (1959: 205–206). Cartmill (1974) has recently suggested that the presence of "vestigial" histology in the flattened hallucial tegula of *Cebus*, and in the grooming "claws" of *Tarsius*, indicates that ceboid tegulae evolved from falculae. The shortened tegulae of cebids is then explicable as a locomotor adaptation relating to an evolutionary increase in body size (Hershkovitz, 1972; Cartmill, 1974), coupled with a habitat shift to higher forest strata (Cartmill, 1974). In contradistinction, Pocock (1917) held that callithricid tegulae are derived, and are functionally related to their reduced hallux and narrow hands and feet. Gregory (1922) proposed that the weakness of the digital flexors, great length of the metapodials, presence of an hallucial nail, lack of manual

opposability, and other aspects of the locomotor skeleton were evidence that callithricid tegulae are derived.

Following the remarks of LeGros Clark (1959), the histological evidence alone seems insufficient to determine whether cebid- or callithricid-like tegulae were the ancestral condition in platyrrhines. The fact that these structures have a common histology in ceboids and *Tarsius*, no matter what their form, suggests that this underlying pattern was present in the last common ancestor of haplorrhines. If the ancestral ceboid condition is the callithricid-like character state, ceboids may be evidenced as monophyletic on the basis of their shared possession (Node 6) of the derived, nail-like condition. If, however, cebid-like tegulae are considered ancestral, all living callithricids may be regarded monophyletic for their last common ancestor (Node 2) evolved claws on all digits but the hallux. Parenthetically, acceptance of the first polarity hypothesis and either of the two alternative cladograms of Figure 1 would require convergent evolution of nail-like morphology in at least two cebid lineages.

I contend that a stronger argument can be advanced to support the hypothesis that callithricids are more derived:

(1) According to LeGros Clark, in considering the functional significance of falcular histology, "The deep stratum is the mechanically important part . . . on it depends the maintenance of a sharp and strong point . . ." (1959: 173). If the last common ceboid or haplorrhine ancestor depended on sharp, recurved falculae for efficient postural and locomotor functions, it would then be difficult to explain why selection favored the reduction of (a) the mechanically advantageous deep stratum and (b) important anatomical features of the primitive but well developed flexor and extensor mechanism (LeGros Clark, 1936).

(2) Evolution of relatively flattened nails is possibly related to the elaboration and increased tactile efficiency of apical pads (LeGros Clark, 1936; Preuschoft, 1970). Significantly, apical pads are well developed in *Callithrix*, *Saguinus*, *Leontopithecus* (LeGros Clark, 1936; Thorndike, 1968) and probably other callitrichids. They lie ventral to the body of the terminal phalanx rather than beneath the distal interphalangeal joint as in tupaiids. The association of long, recurved tegulae and well developed terminal pads is somewhat difficult to reconcile, for the pad's position distal to the interphalangeal falcrum suggests it does not play an important sensory role during claw-clinging. In fact, in *Saguinus* it often does not contact the substrate while the tegulae are embedded (Sonek, 1969). Moreover, assuming claw-like tegulae to have been present before the origination of living callithricids creates additional difficulties in explaining selection for elaborate pads since they are decidedly inferior to claws in the arboreal locomotion of small primates (Cartmill, 1974).

(3) Apart from the anatomical aspects and evidence discussed above and by other workers, the fact that callithricids alone among all living primates but *Daubentonia* lack a flatly "nailed" pollex, suggests its pollical tegulae to be a derived condition.

In view of the above, it seems reasonable to assume that ancestral ceboids manifested cebid-like tegulae on all manual and four pedal digits, and that the last common ancestor of living callithricids had evolved long, recurved tegulae on the four lateral digits of hands and feet plus the pollex. Selection may have favored these anatomical modifications as integral parts of an adaptive complex which enabled ancestral callithricids to efficiently exploit a small-body-size niche, utilizing a large variety of substrate sizes in both the forest canopy and understory (see Cartmill, 1971, 1974; Moynihan,

1975; Kinzey, Rosenberger & Ramirez, 1975; Coimbra-Filho & Mittermeir, in press). The overlapping distribution of body weights in *Saimiri* and the larger callitrichids (Napier & Napier, 1967) points to broad adaptive difference rather than a simple locomotor Rubicon for the clawed and the clawless.

#### *Nodes 3 and 4*

The precise interrelationships of *Saguinus* and *Leontopithecus*, the tamarins, is unclear. Character states present in the morphotype of each genus include absence of  $M_3$ , certainly a derived feature, and the absence of a hypocone on  $M^2$ . Kinzey (1973) reviewed the distribution of  $M^2$  hypocones in most living platyrrhines and found it to be invariably present in cebids but absent in all of 80 examined specimens of callitrichids, including two species of *Saguinus* and one of *Callithrix*. An  $M^2$  hypocone is also absent in *Leontopithecus* and *Cebuella*, and variably present, but not well developed, in *Callimico*. Hypocones are rare on  $M^1$  of two-molared callitrichids but are generally present in *Callimico*. Thus, on distribution grounds, it appears that lack of an  $M^2$  hypocone in two-molared callitrichids is also derived (see below).

#### *Node 5*

Derived characteristics of the anterior dentition and mandibular morphology suggest that marmosets, *Cebuella* and *Callithrix*, are descendants of a common ancestor not shared with other living ceboids. The ceboid mandibular dental arcade mophocline, described and discussed by Hershkovitz (1970) and Kinzey (1974), depicts an array having three poles: posteriorly divergent and narrowed anteriorly (V-shaped), divergent but rounded anteriorly (U-shaped), and parallel sided (U-shaped). By analogy with living strepsirrhines and Tertiary primates, these authors assert that the V-shaped jaw is the ancestral ceboid condition. Distribution of arcade shape within platyrrhines and examination of functionally interrelated aspects of the anterior teeth and mandible strongly indicate the contrary, that the V-shaped jaw is derived. This condition, seen only in *Cebuella* and *Callithrix*, is presumably related to the *en echelon* spacing of the incisor and canine teeth (see Hershkovitz, 1970); the medial incisors are set anterior to the lateral and the lateral anterior to the canine. The incisors themselves, however, differ radically from those of all other anthropoids, and the probable ancestral anthropoid condition, in lacking spatulate, blade-like crowns and in being greatly enlarged buccolingually. In part, this may explain the transversely narrow symphyseal region. The buccolingual diameter of the canine is also markedly greater than the mesiodistal (Table 1) and differs from the typically ovoid-roundish cross-section seen in other anthropoids. Further, *Cebuella* and *Callithrix* have long been characterized as the "short tusked" callitrichids, as the difference in cervical-apical heights of canines *versus* incisors is not marked. Contrary to the implications of this colloquialism, the "short tusked" condition will probably prove to be a function of a novel relative increase in incisor crown height, not a decrease in canine size.

I suggest that these characters of the anterior teeth and jaws of marmosets, and probably others in the masticatory apparatus still to be elaborated, are critical parts of a derived adaptive complex which is related to gouging and scraping holes in bark in pursuit of exudates. The small body size of *Cebuella*, and the vertical positional behaviors seen in both marmoset genera (Moynihan, 1975; Kinzey, Rosenberger & Ramirez,

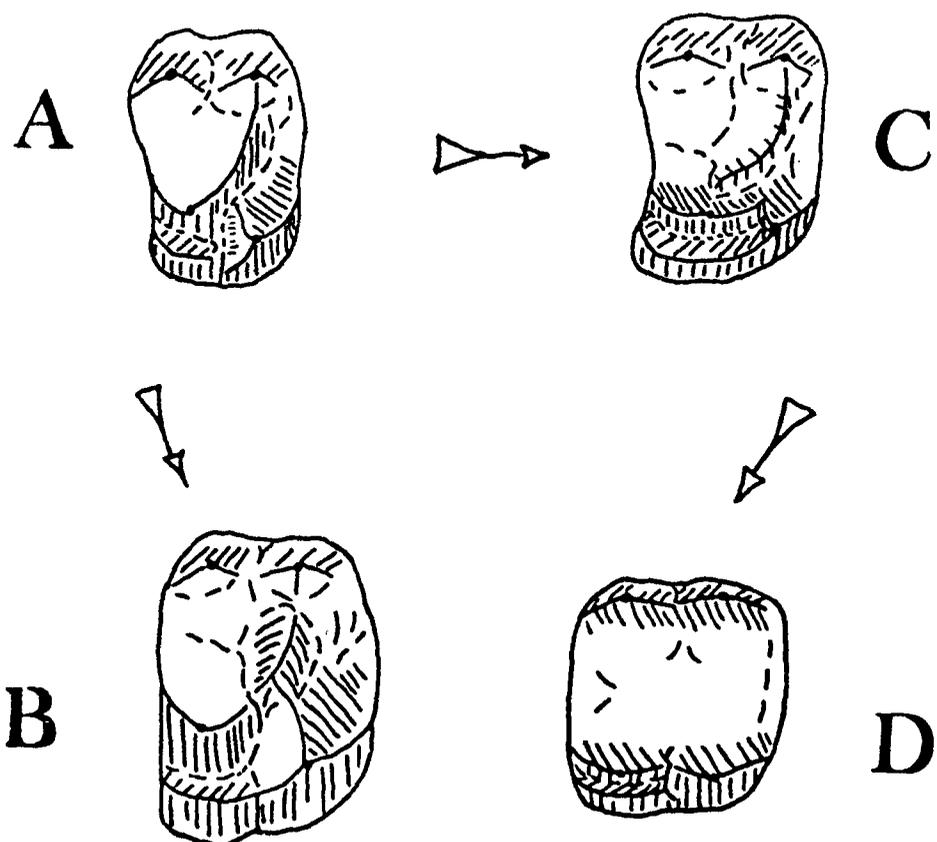
1975; Coimbra-Filho & Mittermeir, in press) are related adaptations and strongly indicate that relatively *tiny* body size is not the ancestral condition among callithricids or ceboids.

### Node 6

In my brief search of the literature I was unable to confidently note derived characters shared by cebids to the exclusion of callithricids. This lack of positive evidence makes the alternative phylogenies [Figures 1(a) and (b)] feasible. However, character states present in a cebid morphotype (if we tentatively assume monophyly) can be inferred through a study of morphoclines. Since aspects of molar morphology figure importantly in deducing relationships among genera distal to Node 6, I have attempted to reconstruct features of the ancestral cebid molar pattern.

As I have suggested above, the tricuspid molar pattern found in some callithricids is probably a derived state. But what is the ancestral ceboid condition? In his discussion of the enigmatic *Callimico*, Thomas (1913) noted that the maxillary molars of the ceboids can be arranged in a graded series based upon the size of the hypocone and its connections to the trigon. He cautioned, however, that the morphocline from tricuspid to quadricuspid includes no abrupt transitions, with *Callimico* and *Saimiri* together occupying the critical middle zone between the extremes. Hypocones are totally lacking in *Callithrix* and *Cebuella*, are extremely rare in *Saguinus* and *Leontopithecus*, and small when present in *Callimico*. A well developed hypocone is found on all cebid first and second molars but varies in size and morphology. Study of the taxonomic distribution of the morphocline and the occlusal function of its major character states suggests that a small, low hypocone, possibly lacking a direct connection to the complete postprotocrista running between protocone and metacone, was present in the common ancestor of all ceboids (Figure 2A). Because of its size and elevation, the entoflexus between the hypocone and protocone was relatively deep and appeared acute in the occlusal view. It is as yet unclear whether the ancestral condition was more similar to *Callimico* or to *Saimiri*.

Figure 2. Generalized left maxillary first molars to illustrate polarity (arrows) sequence discussed in text. Based upon: A, *Saimiri*; B, *Cebus*; C, *Aotus*; D, *Cacajao*. Top is buccal, left is mesial. Not to same scale.



Several derived conditions evolved. In marmosets (not figured), the hypocone was reduced to a tiny cingulum or lost altogether. Evidence supporting this polarity hypothesis is the possible reduction in importance of lingual phase processing during the chewing cycle of *Callithrix* (Rosenberger & Kinzey, 1976). In a second group, the hypocone increased in size and height, the entoflexus began to close, and the postprotocrista remained either complete or broken into discrete elements (Figure 2C). In at least one secondary derivation from condition "C", the hypocone evolved into a size and height comparable with the protocone, and the entoflexus and postprotocrista became much reduced (Figure 2D). Further configurations evolved but are unimportant in regard to *Xenothrix*. On other grounds, each of the sister groups exhibiting the patterns depicted in Figure 2 is believed to be monophyletic. Retracing the polarity sequence then correlates with the proposed phylogeny: the possibly ancestral condition "A" is found in *Saimiri*, derived state "B" is seen only in *Cebus* and is most easily derivable from "A", derived state "C" is most similar to the molars of *Callicebus* and *Aotus*, derived state "D" is found in pithecines, *Pithecia*, *Cacajao* and *Chiropotes* (but see below). Thus, although clearly derived character states shared by Cebidae as a whole may not yet be recognizable, morphocline polarity of at least one character complex provides important initial clues to their phylogeny.

Gregory (1920, 1922) also attempted reconstruction of the ancestral ceboid molar pattern. His list of "stem characters", essentially equivalent to a morphotype, includes "... upper molars tritubercular, with small hypocone . . ." (1922: 226). Gregory claims that *Callicebus* (though occasionally *Alouatta*, (1922: 217) reflects this ancestral condition most closely and that *Saimiri* is highly derived. Although Gregory's numerous allusions to this molar pattern are less precise than one would wish, in concept it evidently agrees with my hypothesis outlined above. However, I believe a *Saimiri*- or *Callimico*-like pattern best represents this prototype. The basic assumption underlying Gregory's choice of a *Callicebus* analogue is his assertion that the distolingual cusp of this genus is a homologue of the *Notharctus* "pseudohypocone", a point for which there is no real evidence (see Butler, 1956; Kinzey, 1973). Reference to the molar morphology of the earliest known cebid *Branisella boliviana*, early Oligocene (Deseadan) of Bolivia, has led Orlosky & Swindler (1975) to also postulate a *Saimiri*-like ancestral ceboid condition.

#### Node 7

A particularly close phylogenetic relation between *Saimiri* and *Cebus* has been argued for and against by numerous workers (see Hill, 1960, 1962). Characters which may unite them as sister taxa include specialization of the visual cortex (LeGros Clark, 1959), relative narrowness of interorbital distance and relative enlargement of premolar size. In addition, the unique maxillary molar morphology of *Cebus* (Figure 2B) is probably derived from a *Saimiri*-like molar. Modifications such as enlargement of the entoflexus, transverse alignment of the crista obliqua, and frequent contact between the crista obliqua and the prehypocrista, all seen only in the upper molars of genus *Cebus*, are far different from the derived character states described above and this pattern is likely not to have been ancestral to or descendant from any of them.

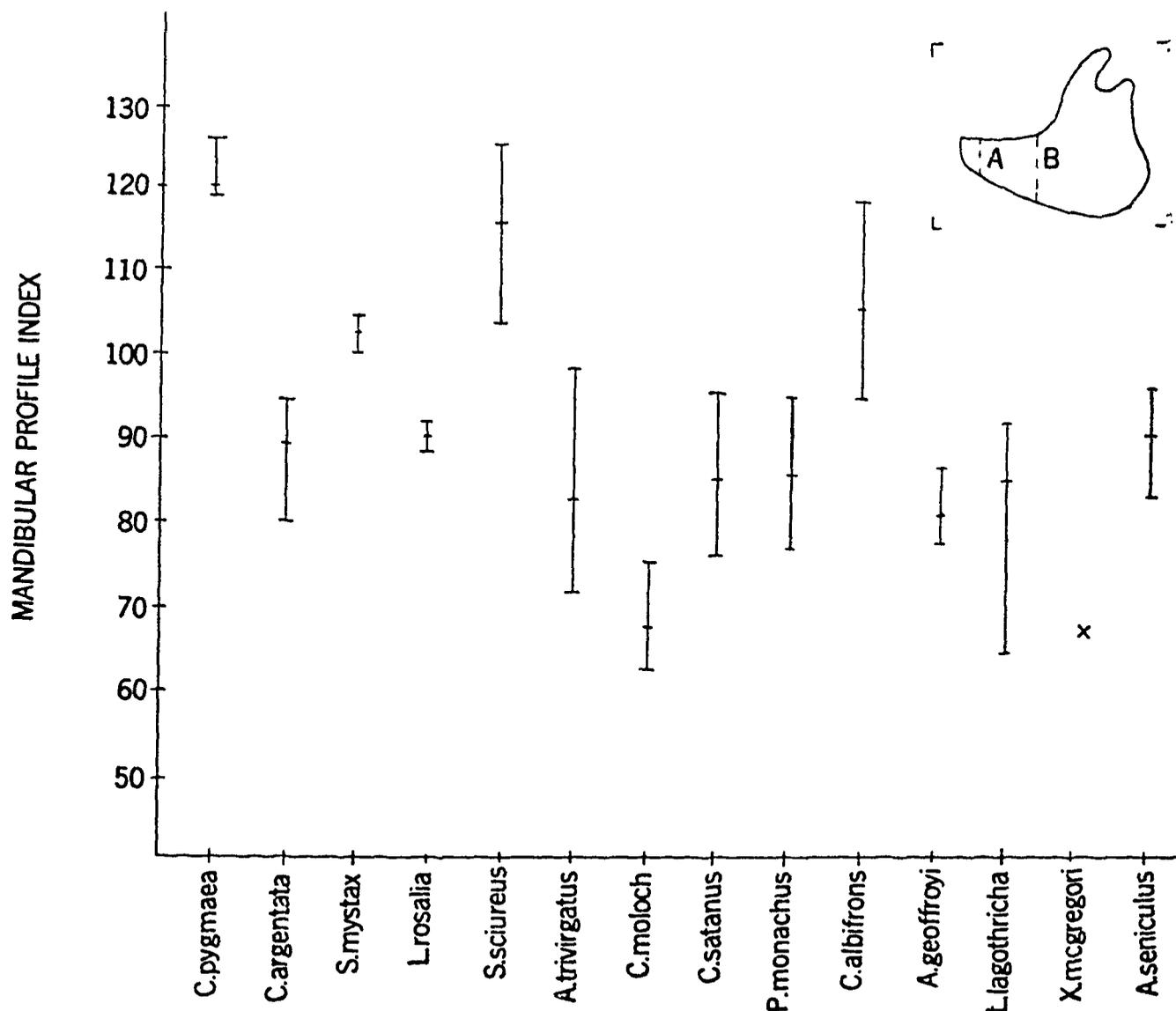
#### Node 8

As a generic assemblage, *Pithecia*, *Chiropotes* and *Cacajao*, the pithecines, are united by clearly derived characteristics of the dentition: upper and lower incisors narrow, elongate

and procumbent; large canines with a roughly cylindrical cross-section; drastically reduced relief of cheek teeth; enlarged hypocones and reduced entoflexus (Figure 2D). Preliminary study suggests *Chiropotes* and *Cacajao* to be more closely related to one another. Since many of these shared characters are secondarily derived, evolving after the initial differentiation of the pitheciine lineage, few intermediate conditions remain to facilitate a tracing of their history. Upper molars (Figure 2D), for example, are presumed to be modifications of a molar form closest to *Aotus* or *Callicebus* (Figure 2C). Hence, the latter condition was probably present at Node 8 as an ancestral condition for pithecines but a derived one relative to Node 6. The cautionary dotted line at Node 8 alludes to alternative interpretations of pitheciine affinities currently under study.

The placement of pithecines at this junction is based upon mandibular shape, and the fact that pithecines are not known to share additional derived states with taxa distal to Node 9. Among ceboids, the profile of the mandibular corpus exhibits two fundamental character states. In one condition the inferior border of the corpus slopes ventrally from the anterior premolar to the gonial region. This configuration is seen in pithecines,

Figure 3. Means and ranges of mandibular profile index;  $A/B \times 100$  (see insert). "A" is depth of shallowest point posterior to symphysis, or between  $P_2$  and  $P_3$ , "B" is depth behind  $M_2$ . Sample sizes: 5 males + 5 females for all cebids; 3 males + 3 females for all callithricids but *L. rosalia*, where  $N = 1$  male + 4 unknown sex. Arrangement of taxa in ascending size of mean  $M_1$  length, from left to right, based upon the individuals measured, indicating that the ratio is unaffected by size. Note the position of *Xenothrix*, X. The inferior-most border of the mandible is broken away at B, making its value (68) a minimal estimate.



*Callicebus* (Plate 3A), *Aotus*, *Alouatta* and the atelines, *Ateles*, *Brachyteles* and *Lagothrix*. In all other ceboids the inferior border anterior to the angular region is essentially horizontal and approximately parallel to the alveolar plane, save for an occasional middle bulge (Plate 3B). A conservative metrical description of the mandibular profile is given in Figure 3. Variations of the "even-depth" condition are found in *Saimiri* and *Cebus* where anterior depth increases, perhaps a mechanical result of a relatively large canine and anterior premolar, and in some callithricids, where hypertrophied anterior teeth (*Callithrix*) or a curve of Spee (*Leontopithecus*) account for their values falling below 100. The widespread distribution of the even-depth character state, and its persistence as the *bauplan* underlying several variations, suggests that it is a retention and that the mandibular profile of ancestral platyrrhines did not deepen posteriorly. Thus, a posteriorly deepening mandibular corpus, the condition at Node 8, is derived. This hypothesis receives support from Delson & Andrews (1975), whose catarrhine morphotype includes a mandibular corpus of relatively even profile.

#### Node 9

*Aotus*, like *Callicebus* and *Brachyteles*, and unlike all other ceboids, has relatively small maxillary and mandibular canines. Sexual dimorphism in canine size is not marked and is not present in all dimensions of the maxillary tooth (Kinzey, 1972; Orlosky, 1973). Zingesser (1973), among other workers, maintains that a small, sexually non-dimorphic canine is a "primitive" condition, but does not clarify whether he believes it to be primitive for ceboids or cebids. Relatively high-crowned, non-dimorphic canines are found in callithricids and the dentally plesimorphic hylobatids (Frisch, 1963). Both high- and relatively low-crowned canines, with and without statistically significant dimorphism, are found among congeneric cebid species (Orlosky, 1973). This suggests that ancestral ceboids had relatively high-crowned canines, possibly in both sexes. Therefore, the presence of reduced, non-dimorphic canines in *Aotus*, *Callicebus*, and *Brachyteles* is presumed to be a shared derived character state present in their last common ancestor, Node 9, while the variably dimorphic canines of *Alouatta*, *Ateles* and *Lagothrix* are secondarily enlarged.

#### Node 10

In conjunction with its reduced maxillary canine, features of the *Callicebus* lower anterior premolar related to canine honing, such as crown height and preprotocrista length, are also reduced (Plate 3A). A similar morphological pattern is seen in the small-canined *Brachyteles* and even the relatively larger canined *Ateles*, *Lagothrix*, and *Alouatta*, corroborating the hypothesis that their last common ancestor had a relatively small maxillary canine. *Aotus*, however, like most other ceboids (e.g. Plate 3B), has better developed honing features on P<sub>2</sub>. Its anterior premolar is relatively long (Table 1), especially when compared to other small-canined forms. The association of both large and small canines with and without well developed premolar honing features, suggests that the Node 9 morphotype exhibited an *Aotus*-like configuration, that is, a reduced canine but an unreduced honing mechanism. Elimination of the P<sub>2</sub> flange evolved as a derived state at Node 10. Thus the last common ancestor of *Callicebus*, *Alouatta*, and the atelines probably had reduced canines and a reduced canine honing mechanism.

*Node 11*

*Alouatta* is discussed with atelines, *contra* the implication of most current classifications, to emphasize the monophyletic nature of these four genera combined and the fact that little is known of their interrelationships. Earlier classifications recognized the unity of this group, dubbed "gymnuri" by Spix (1823) on account of their partially hairless tail. Conclusive evidence of their monophyletic origin is the unique prehensile tail with its glabrous, distal underside (Biegert, 1963) and generous innervation through an enlarged sacral canal aperture (Ankel, 1972). Proportions of the limbs and vertebral column (Erikson, 1963) are also likely to be derived. The semi-prehensile tail of *Cebus* evolved independently and can be shown not to be homologously derived by virtue of its completely haired skin, presence of six rather than eight vertebrae in the first caudal region and their lack of lumbar-like articular facets (Ankel, 1972). The evolution of different anatomical bases and different modes of prehensility in widely separate ceboid taxa is not surprising since all infant ceboids possess highly manipulable tails (Thorington, pers. comm.).

**3. Description of *Xenothrix***

The partial mandible is robustly built and contains two left molar teeth which are in excellent condition (Plate 1). The alveoli of the left  $P_2$  thru  $P_4$  are undamaged, but those of the four incisors, two canines, and right  $P_2$  and  $P_3$  are less well preserved. Dental formula was well established as  $\overline{2.1.3.2}$  by Williams & Koopman (1952), whose published radiograph reveals no developing or emergent tooth behind the fully erupted  $M_2$ . The symphysis is solidly fused and the symphyseal shelf slopes gently posteriorly to form a well developed superior torus, but the inferior border of the mandible is missing in the midline region.

In lateral view (Plate 2A), the mandibular corpus deepens evenly posteriorly from approximately beneath  $P_3$  to  $M_2$ , where the more complete left side is broken away. The alveolar plane is more or less horizontal, with only  $M_2$  offset in a tilt reminiscent of the curve of Spee. The remaining portion of the largely incomplete ascending ramus suggests that the temporomandibular joint was situated well above the occusal plane. The anterior margin of the ramus is rather vertical and partially conceals  $M_2$  from view. The position of the mylohyoid foramen relatively close behind  $M_2$  is unique according to Williams & Koopman (1952). Anteriorly, a single, relatively large mental foramen lies beneath  $P_3$ . In the gonial region, there are no obvious rugosities or fossae for the superficial masseter laterally or medial pterygoid medially. Numerous irregular pittings on the surface bone of both medial and lateral facies, however, indicate a high degree of vascularization.

Although Williams & Koopman (1952) suggest that "The incisors may have been somewhat procumbent, as in marmosets . . ." (1952: 10) their orientation is not really discernible from the broken alveoli. The incisors of pithecines are also obliquely oriented but, as Williams & Koopman imply, those of *Xenothrix* are not so reduced in caliber or closely packed as in pithecines. The canine alveolus, which conforms reasonably well with canine crown diameter, is relatively small (Williams & Koopman, 1952), even when compared with the size of female canines (Table 1). (The  $C_1/M_1$  area values in the table are presented to indicate general orders of magnitude. Intertaxa comparisons of this ratio

Table 1 Comparative dental dimensions (mm)\*

	C <sub>1</sub>		P <sub>2</sub>		P <sub>3</sub>		P <sub>4</sub>		M <sub>1</sub>		M <sub>2</sub>		Shape: (MD/BL) × 100		Area: (MD × BL) × 100	
	MD	BL	C <sub>1</sub>	P <sub>2</sub>	(MD/BL) × 100	C <sub>1</sub> /M <sub>1</sub>										
<i>Xenothrix mcgregori</i> †	2.4	3.2	2.3	3.2	2.7	3.9	2.9	4.4	6.1	5.1	6.0	4.5	75	72	25	
<i>Cebuella pygmaea</i> ‡	0.8	1.6	1.5	1.1	1.4	1.2	1.4	1.3	1.9	1.5	1.8	1.3	50	136	45	
<i>Callithrix argentata</i> ‡	1.5	2.5	2.2	2.0	2.0	1.9	1.9	1.9	2.3	1.9	2.0	1.6	60	110	86	
<i>Leontopithecus rosalia</i> §	3.1	3.2	3.1	2.5	2.6	2.8	2.5	3.0	3.2	2.8	2.8	2.3	97	124	111	
<i>Saimiri sciureus</i>	2.6	2.7	2.3	2.4	2.2	2.5	2.2	2.6	2.9	2.7	2.6	2.6	96	96	90	
<i>Aotus trivirgatus</i>	2.6	2.4	2.2	2.2	2.1	2.3	2.4	2.6	3.3	3.0	3.2	2.9	108	100	63	
<i>Callicebus moloch</i>	2.4	2.6	2.0	2.4	2.0	2.5	2.2	2.8	3.4	3.2	3.6	3.2	92	83	57	
<i>Pithecia monachus</i>	4.6	4.7	3.7	3.5	3.1	3.5	2.9	3.6	4.0	3.8	4.1	4.0	98	106	142	
<i>Cebus apella</i>	5.7	5.6	4.5	4.4	4.0	4.7	3.9	5.0	5.2	4.9	4.7	4.7	102	102	125	
<i>Ateles geoffroyi</i>	4.7	4.9	3.9	4.3	3.6	4.3	3.8	4.3	5.4	5.1	5.3	5.3	96	91	84	
<i>Lagothrix lagothricha</i>	5.1	5.8	4.5	5.2	4.1	4.9	4.1	4.9	5.5	5.3	5.7	5.4	88	87	101	
<i>Alouatta seniculus</i>	5.0	5.1	4.9	5.1	4.9	5.0	5.2	5.0	7.1	5.5	7.6	6.1	98	96	65	
<i>Brachyteles arachnoides</i>	4.5	5.8	4.4	5.3	4.6	5.0	4.9	5.0	7.2	5.6	7.1	5.7	78	83	65	

\* *Brachyteles* data from Zingesser (1973),  $N=3$  female + 2 male. Other cebid data from Orlosky (1973), females only, minimum  $N=4$ , mean  $N=12.3$ . Buccolingual breadths are maxima.

† Antemolar values estimated from alveoli. All metrics are the average of five consecutive measurements.

‡  $N=3$  female + 3 male.

§  $N=1$  male + 5 sex unknown.

including pithecines and marmosets are not especially meaningful since they do not distinguish between drastically different and highly derived morphologies. Comparisons among other taxa, however, are more instructive.) A rough estimate of crown shape can be inferred from the shape of the premolar alveoli. In *Xenothrix* these teeth appear to have been relatively broader buccolingually than in the other ceboids for which data is available (Table 1). Their estimated areas increase progressively posteriorly.

Judging from the rather small alveoli for the mandibular canine and anterior premolar, and the short mesiodistal length of the latter, it is likely that the maxillary canines were similarly reduced. Small canines may of course be a function of sexual dimorphism, but the tiny size and shape of the  $P_2$  alveolus suggests that a canine honing mechanism was indeed poorly developed. I would therefore expect even males of *Xenothrix* to display relatively small maxillary canines.

After careful comparison, Williams & Koopman concluded: "In dental pattern the Jamaican form resembles the advanced genus, *Cebus* . . ." (1952: 12). To Hershkovitz, "The weak relief of the quasi rectangular molar crowns recalls nothing nearer to the Malagasy prosimian *Daubentonia* . . ." (1970: 3). I do not concur with either of these opinions but agree with Hershkovitz that one is hard pressed to find a living morphologic analogy to the molars of *Xenothrix* (Plate 1). The gross morphology of each molar tooth is distinctly different from all living ceboids. Moreover, the morphology of  $M_1$  differs considerably from  $M_2$ . The degree of heteromorphy surpasses that seen among other ceboids

A striking feature of the molar teeth is their large size, compared to the overall size of the jaw itself (Williams & Koopman, 1952) or to the length of the postcanine toothrow (see below). The bunodonty of the fossil's crowns, implied by Williams & Koopman (1952: 6) to be strongly reminiscent of *Cebus*, is probably a factor of their large absolute size, and details of crown morphology differ between the two. For example, in *Cebus* (Plate 2B) the protoconid and hypoconid are convex buccally but concave on their lingual faces. Similarly, the metaconid and entoconid are flared lingually and concave buccally. Thus, the crown margin appears inflated but the area of its occlusal foveae are maximized and contoured (Rosenberger & Kinzey, 1976). In *Xenothrix*, on the other hand, the protoconid and hypoconid are greatly convex buccally and lingually. The metaconid and entoconid also flare buccally, thereby constricting the basins and reducing their relief. As a result, the talonoid fovea of *Xenothrix* is more like a shallow platform than a dished basin, as it is in *Cebus*.

Another unusual feature of the molars is the pattern of enamel deposition. The enamel on the mesial border of  $M_2$  is beaded and there is a series of vertical frills buccal to the protoconid (Plate 1). Evidence of enamel papillation can be seen deep to the planed surface of the protoconid wear facet and elsewhere. Various manifestations of enamel crenulation are frequently seen in specimens of *Callicebus* and *Aotus* and are especially well developed in pithecines. Peripherally, the enamel seems to overflow into the alveoli without exposing the cemento-enamel junction. Also, a curious pattern of developmental grooves, not really comparable with any living ceboid, marks the occlusal surface.

In both molars of the *Xenothrix*, the trigonid is taller than the talonid but they are of approximately equal buccolingual breadth. On  $M_1$  the protoconid and metaconid are large and separated by a longitudinal groove. A continuous cristid connecting these cusps is frequently seen in other ceboids. The large lingual wear facets on both protoconids indicate that the two upper molars had correspondingly large hypocones. The

Plate 1. *Xenothrix mcgregori* (AMNH 148198). Occlusal view, left  $M_1$  and  $M_2$ . Scale approximately 9 X. Note shape heteromorphy of teeth, large wear facets on protoconids, enamel irregularities on  $M_2$  paracristid, buccal enamel frills on  $M_2$  protoconid, polycuspate  $M_2$  talonid.





Plate 2. (A) *X. mcgregori*, lateral view. Scale approximately  $3\times$ . (B) *X. mcgregori* and *Cebus* sp.  $M_1$  (AMNH 95023). Scale approximately  $3\times$ . Note in *Xenothrix*: the relatively much larger molar size; marked size graduation of premolars; relatively small  $P_2$  alveolus; partial alveolar outline (left side) and more complete alveolus (right side) of the smallish canine; irregular pittings on symphyseal torus. Note in *Cebus*: relatively open trigonid and talonid basins; integration of concave entoconid within talonid; lack of distalward expansion of talonid.



Plate 3. (A) lateral view of *Callicebus moloch* mandible, female (AMNH 94982). Note deepening profile of mandibular corpus; small size of  $C_1$ ,  $P_2$  and lack of honing flange on  $P_2$ . Female/male  $C_1$  dimorphism is 94% (Orlosky, 1973). (B) lateral view of *Saimiri sciureus* mandible, male (AMNH 76007). Note relatively parallel profile of mandibular corpus anterior to angular region; large size of  $C_1$ ,  $P_2$  and well developed honing flange on  $P_2$ . Female/male dimorphism is 74% (Orlosky, 1973). Not to same scale.

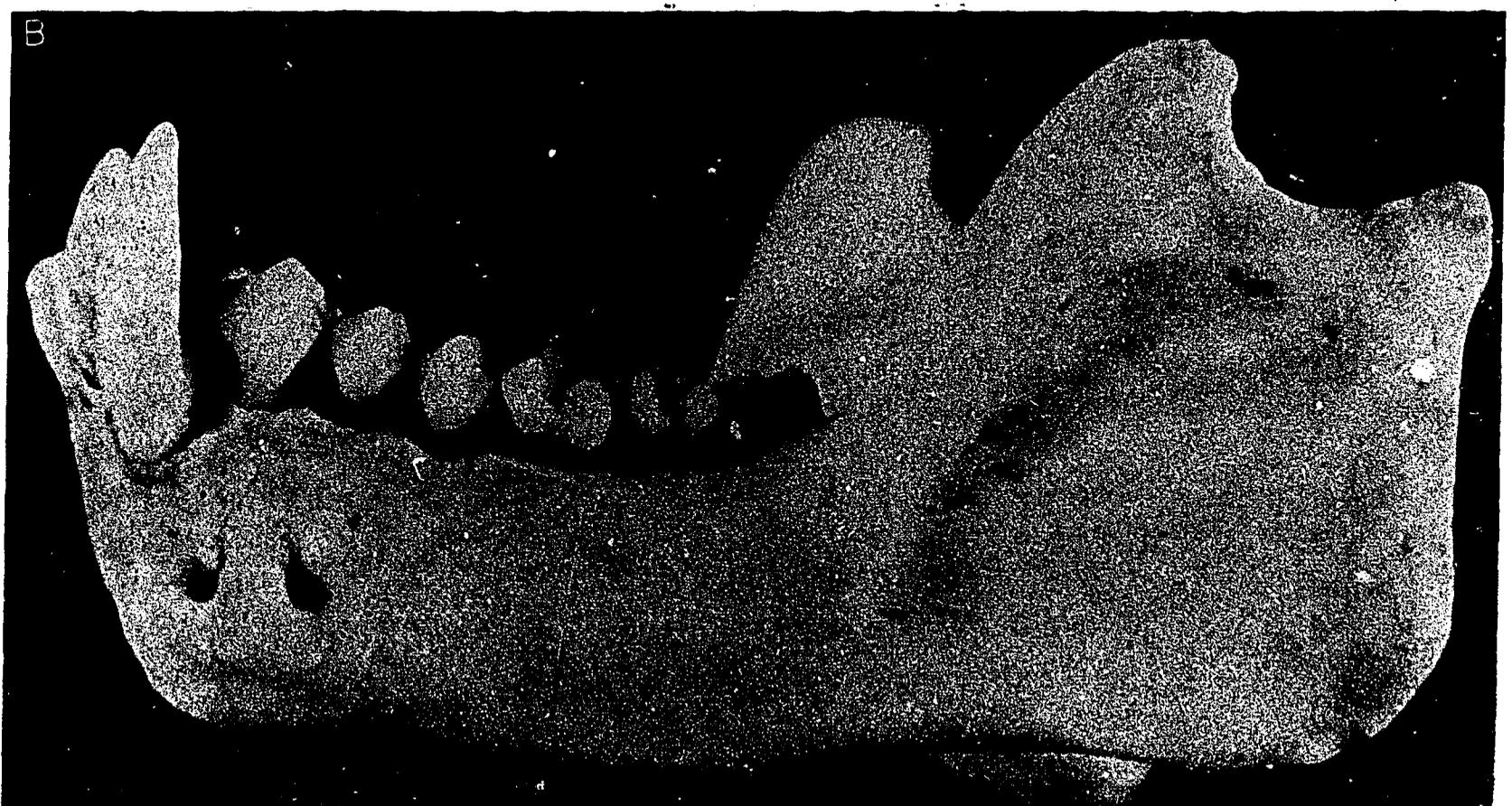
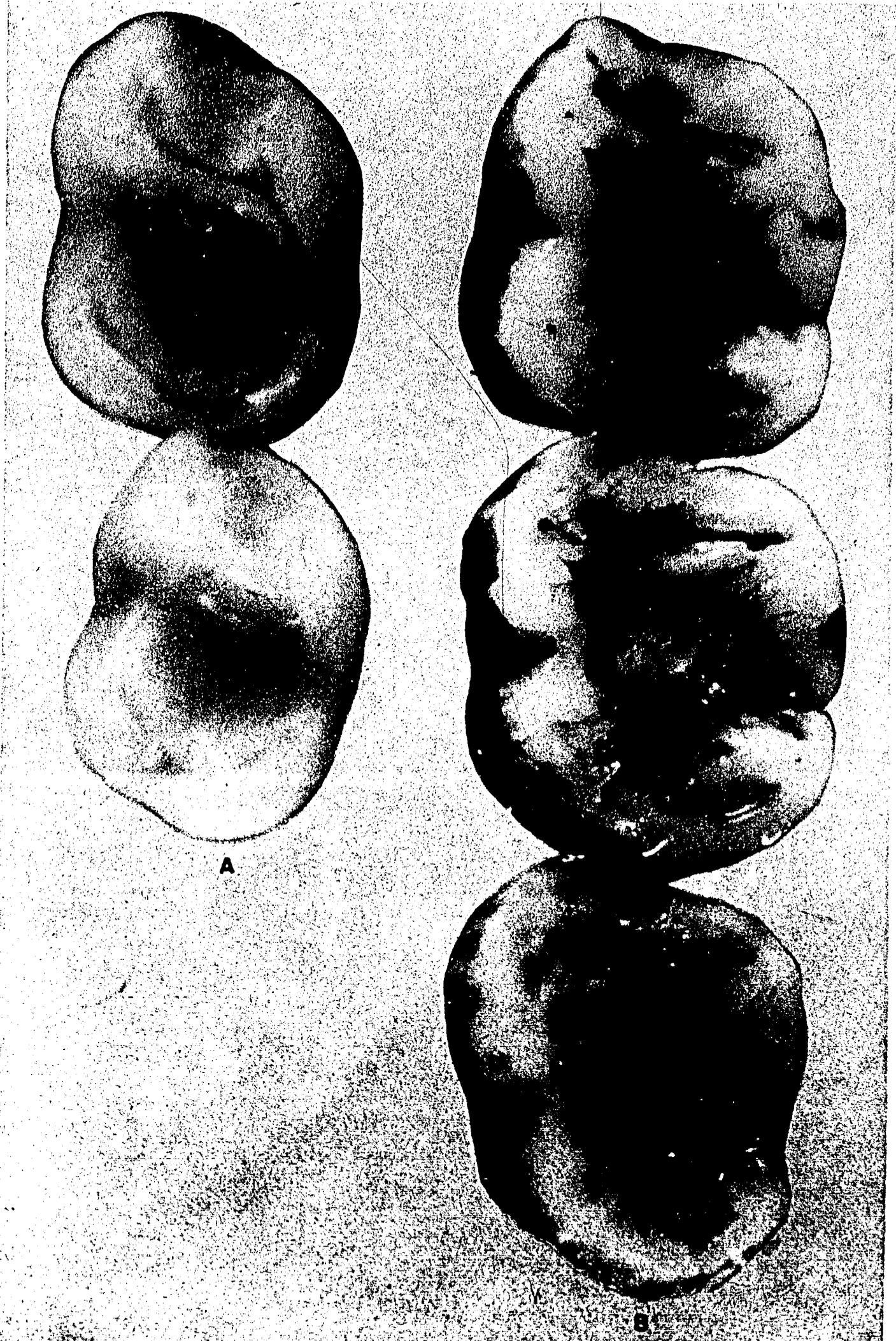


Plate 4. (A) Occlusal view of left  $M_1$ - $M_2$  of *Callithrix argentata*, sex unknown (AMNH 94940). Scale approximately  $25\times$ . Note molar homomorphy; position, concavity and integration of entoconid within talonid; lack of distalward talonid expansion. (B) Occlusal view of left  $M_1$ - $M_3$  of *Pithecia pithecia*, female (AMNH 94131). Scale approximately  $15\times$ . Note convexity of entoconid; separation of entoconid from other talonid elements; distalward expansion of talonid.



ectoflexid is large, but this is more a function of buccally bulging cusps than the orientation of the cristid obliqua, which is predominantly mesiodistal. There is no buccal cingulum. The entoconid is convex, set off by grooves, and bears distinct mesial and distal wear facets, indicating that the entoflexus of the upper molar was notch-like (see Rosenberger & Kinzey, 1976). A shelf-like hypoconulid (perhaps only an expanded post cristid) lies slightly buccal to mid-distal. Orlosky (1973) found that presence or absence of hypoconulids varies significantly both intraspecifically and interspecifically among species of *Alouatta* and *Ateles*. I have also observed hypoconulids on specimens of *Cebus*, *Aotus* and *Callicebus*.

Metrically, mesiodistal length of the talonid is appreciably greater than the trigonid. Upon closer inspection of the morphology, however, it appears that "trigonid" elements contribute largely to "talonid" surface area. That is, the protoconid and metaconid are unfolded so that the distal wall of the taller trigonid lies in a relatively horizontal plane and, because it is located distal to where the protocristid would be, this element may be considered topographically to be talonid. The general pattern among ceboids differs from this because the protocristid does make a distinct division between mesial and distal moieties and the trigonid wall is generally more vertical.

The second molar bears supernumerary cusps on the talonid, one buccally and another lingually, with grooves demarcating the boundaries of each. Both appear to be derivations of cristae. Greatest talonid width is somewhat less than trigonid width, and the distal aspect tapers to a rounded end.

#### 4. Affinities of *Xenothrix*

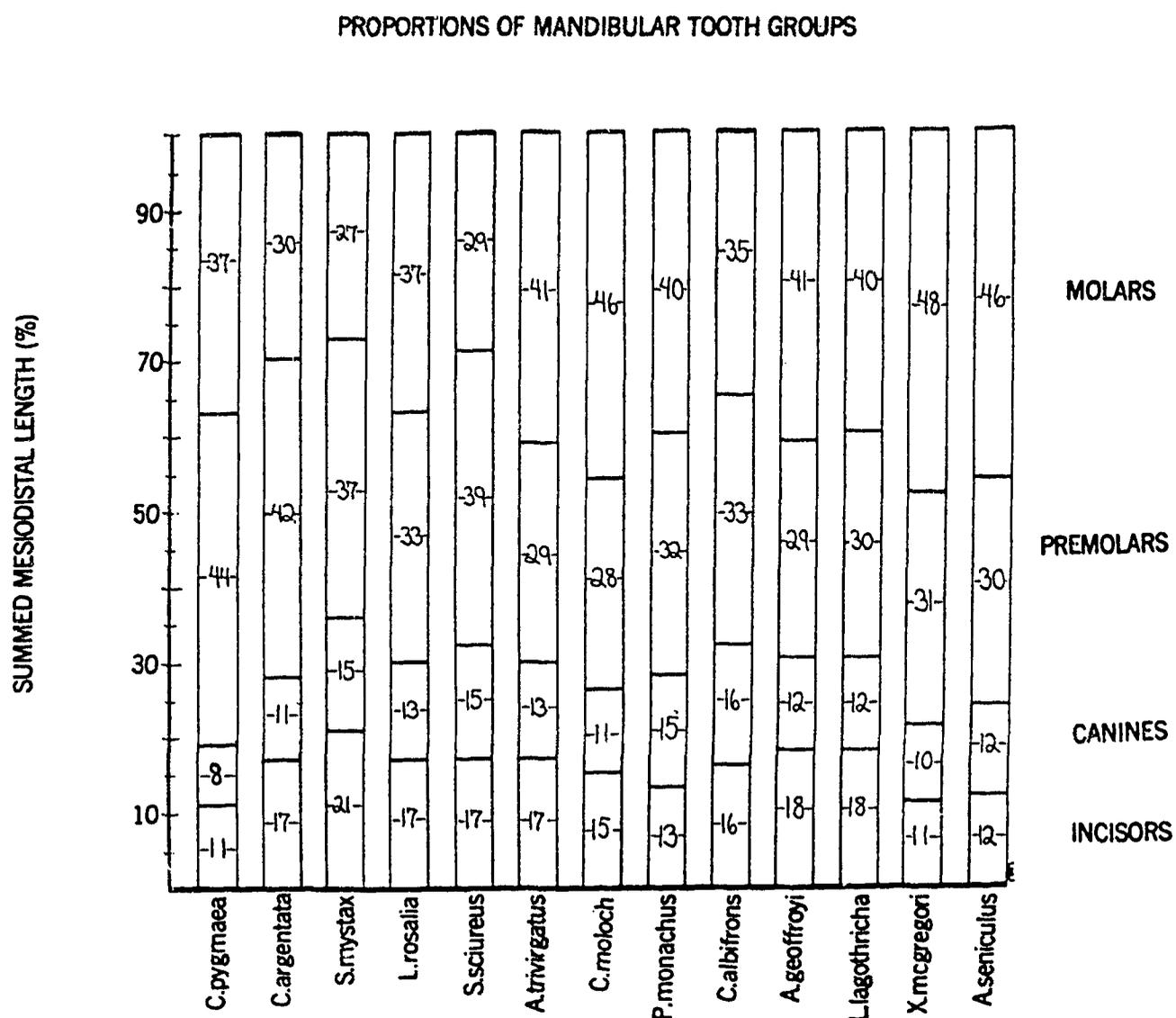
##### *Negative evidence*

The most obvious feature of potential systematic value is dental formula. Having two molars rather than three is clearly a derived condition in Ceboidea and among living forms is seen only in marmosets and tamarins. There are, however, several reasons why one must question whether like absence of  $M_3$  in *Xenothrix* and these living taxa is due to their descent from a common ancestor or to convergence (=non-homology). (1) A third molar is present in *Callimico*, the pleisomorphic sister taxon of the monophyletic *Callitrichidae*. (2) The third molar is small (reducing?) in several ceboids and is occasionally absent in some specimens. (3) A decision that equivalence of this character state is a function of an homologous loss is discordant with the polarity sequence of other states discussed below.

Decision as to homology is always difficult, especially when one is dealing with "loss" characters, for such determinations inevitably are based upon similarity. According to Bock, "generally accepted criteria used to recognize homologous features include morphological similarity, position in the body, relationship to other features, similar ontogenetic development. . ." (1969: 416). Criteria for suspecting character states to be non-homologous would be manifest when enough conditions are not satisfied. I believe there is sufficient evidence which, considered as a whole, provides a strong argument that loss of  $M_3$  in *Xenothrix* and two-molared callithricids was achieved convergently. I recognize a degree of circularity in the full argument but feel that it can be retrospectively substantiated by my phylogenetic conclusions. Moreover, the most powerful test of homology is a phylogeny itself. The basis for the argument is that the *evolved* character state assemblages of the molar regions of *Xenothrix* and marmosets and tamarins are actually

quite different from one another. Thus, a primary criterion of homology, similarity, is not fulfilled. First, the total morphological pattern of molar complexes are different. In the callitrichids,  $M_1$  and  $M_2$  are virtually identical in shape and differ only slightly in size,  $M_1$  generally being larger than  $M_2$  (Table 1, Plate 4A). In *Xenothrix* there are profound differences in the morphology of the two molar teeth (Plate 1).

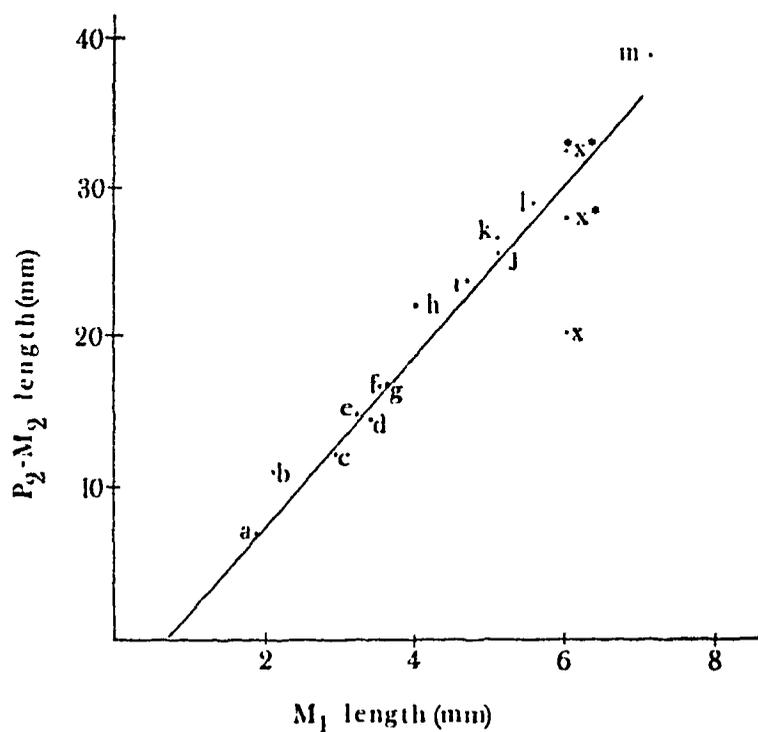
Figure 4. Bar graph illustrating the relative proportions of the summed mesiodistal length of each mandibular tooth group. Antemolar values for *Xenothrix* estimated from alveoli. Individual group means noted in appropriate segments. Cebid data based only on females to reduce effects of sex dimorphism. Cebid data from Orlosky (1973): minimum  $N = 4$ ; mean  $N = 12.3$  individuals per species; callitrichid sample and arrangement of taxa as in Figure 3. Note error: for *C. albifrons* read *C. apella*.



Second, the proportionate lengths of the molar regions are markedly different (Figure 4). In most callitrichids, the relative contribution of the molar battery to the summed mesiodistal length of the tooth row is less than the contributed length of the premolars. Among cebids, *Saimiri* shows this pattern. In all other cebids relative molar length exceeds relative premolar length. Although *Xenothrix* has lost a molar tooth, the proportionate length of its two molars is comparable to the summed three-molar length of *Alouatta seniculus*, whose  $M_1$  length (range of females + males 6.6–8.6 mm; Orlosky, 1973) is 108% to 141% larger. In other words, as the number of molars lessened in callitrichids, their total relative length was probably reduced proportionately, while in *Xenothrix* the total relative length of the molars appears to have remained stable or to have increased, the absolute number of components notwithstanding.

Comparisons of this sort may be subject to misinterpretation due to the considerable size and morphological heterogeneity of incisors and canines seen among ceboids. These teeth are also missing in *Xenothrix*. Thus a correlation and regression analysis was performed on the cheek teeth alone to test whether or not linear proportions in *Xenothrix* conform to general ceboid patterns of scaling. The two variables chosen were  $M_1$  and  $P_2-M_2$  length. The third molar was not included in order to increase comparability between two- and three-molared ceboids. Correlation coefficients and regression equations were computed for cebid and callithricid samples individually, then pooled as a ceboid sample, with *Xenothrix* excluded from each data set. It was found, not unexpectedly, that a simple relationship exists between these two variables with  $r = 0.995$  in each case (Figure 5). Based upon the callithricid regression equation, the estimated cheek tooth length for *Xenothrix* is 27.60 (mm). The cebid and ceboid formulas each yield estimates of approximately 32. The actual measure of the summed  $P_2-M_2$  length of *Xenothrix* is 20.00. The estimates are thus far too large, indicating relatively large  $M_1$  compared to  $P_2-M_2$  length.

Figure 5. Scatter diagram of mean values for  $M_1$  and summed  $P_2-M_2$  length with least squares ceboid regression line (see text) drawn in. Samples as in Figure 4. Key: A, *C. pygmaea*; B, *C. argentata*; C, *S. mystax*; D, *L. rosalia*; E, *S. sciureus*; F, *A. trivirgatus*; G, *C. moloch*; H, *P. monachus*; I, *C. calvus*; J, *C. apella*; K, *A. geoffroyi*; L, *L. lagotricha*; M, *A. seniculus*. X\*, estimated  $P_2-M_2$  length for *X. mcgregori* based upon callithricid equation ( $r = 0.995$ ;  $\bar{Y} = -0.4801 + 4.603 \bar{X}$ ); \*X\* estimated value based upon cebid ( $r = 0.995$ ;  $\bar{Y} = 1.957 + 5.5758 \bar{X}$ ) and ceboid equations ( $r = 0.995$ ;  $\bar{Y} = -2.927 + 5.5758 \bar{X}$ ); X, observed value for *Xenothrix*.



Apparently, the metrical linear organization of the cheek teeth in *Xenothrix* differs substantially from each of three theoretically appropriate models. The relative size of its molars, an important feature noted by several workers, is exceedingly large and certainly does not follow the allometric tendency of two-molared callithricids. Nor does it follow the pattern of similar sized or even larger ceboids. Whether elimination of a third molar in *Xenothrix* and callithricids is allometrically related to decrease in body size or to a shift in dietary habits (see Pilbeam & Gould, 1975; Kay 1975), loss in *Xenothrix* must have occurred independently for the absolute size of its jaw suggests a skull size similar to *Aotus* and *Callicebus*, both middle-sized ceboids. In total, there is sufficient reason to proceed with the hypothesis that the absence of  $M_3$  in *Xenothrix* and two-molared callithricids is an artifact of convergence.

*Shared derived characters*

There is, on the other hand, solid evidence aligning *Xenothrix* with other taxa based upon common possession of derived character states.

*Mandibular corpus profile.* As discussed above, posterior deepening of the inferior border of the mandibular corpus is a derived condition found in *Aotus*, *Callicebus*, pitheciines, "naked-tails" (*Alouatta* + atelines) and *Xenothrix* (Figure 3, Plates 2A, 3A). This character state was present in the last common ancestor of all these forms (Node 8) and is evidence of their strictly monophyletic origin. In pattern, the *Xenothrix* mandibular profile possibly resembles *Callicebus* more than it does other taxa. The functional and adaptive significance of the different expressions of this feature is unknown and merits careful study.

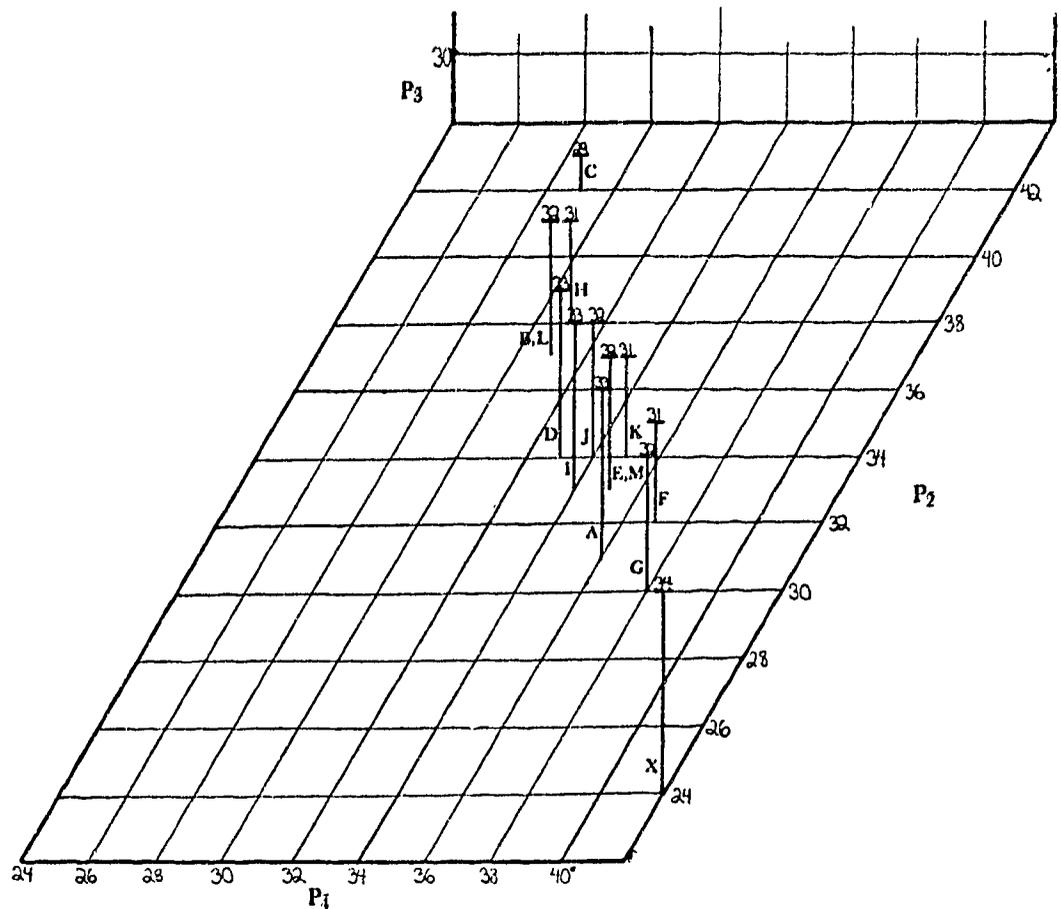
*Morphology of the entoconid.* Another character uniting *Xenothrix* with this same monophyletic group is the morphology of its entoconid. The distribution of two alternative character states corresponds to aspects of the previously discussed maxillary molar morphocline and is specifically related to the configuration of the entoflexus, the entoconid's occlusal reciprocal. In all callitrichids the entoconid forms the distolingual corner of the talonid (Plate 4A). Its distal cristid is actually the disto-lingual aspect of the talonid basin and lingual arm of the postcristid. The buccal face of the entoconid is generally plano-concave and is smoothly integrated into the shallowing contours of the talonid basin. *Saimiri* and *Cebus* closely conform to this pattern, which, on grounds of distribution, is considered ancestral in ceboids. In most other platyrrhines, for example, *Aotus*, *Callicebus*, *Alouatta* and *Pithecia*, the buccal face of the entoconid is frequently offset from the remainder of the talonid by proximal and distal grooves, and does not form the corner of the talonid. The lingual arm of the postcristid is not confluent with the bulge of the entoconid but joins this cusp at its apex. The general appearance of this character state, the derived condition, suggests that the entoconid may have evolved a developmental pattern which differs from the presumed ancestral condition. *Xenothrix*, too, displays the derived morphology. The entoconid is convex, separated from the middle and buccal portions of the talonid basin by a surrounding groove which also sets it apart from the postcristid. The morphology of *Xenothrix* compares very well with specimens of *Callicebus* and *Pithecia*. Distinct proximal and distal wear facets on the fossil's entoconid indicate that the maxillary entoflexus would have been notch-like and tight-fitting, with the postprotocrista and the hypocrista at approximately equal elevations. The polarity of the entoconid-entoflexus complex is concordant with the polarity of the mandibular morphocline and is strong evidence linking *Xenothrix* to a monophyletic group comprising all taxa distal to Node 8.

*Canine-premolar size.* Small canine size may be an additional character which could allow an even more definitive conclusion regarding the affinities of *Xenothrix*, although more specimens and additional work is required before polarity decisions can be made with real confidence. As previously noted, comparison with other species indicates that the relative area of the lower canine was quite small, and the upper canine is also inferred to be small (Table 1). Relatively small canines are present as a derived character state at Node 9.

The anterior premolar of this morphotype, despite a relatively reduced  $C^1$ , retains relatively well developed honing features. Since  $P_2$  is lacking in *Xenothrix* we have no direct knowledge of its shape. Inspection of the specimen itself, however, suggests a relatively small but broad tooth, possibly indicative of a reduced honing mechanism (see also Table 1). Estimation of premolar areas from their alveoli allows indirect metrical

comparison of *Xenothrix* with other ceboids. The relative area of each premolar, expressed as a percentage of summed premolar area, is depicted in Figure 6 for females and

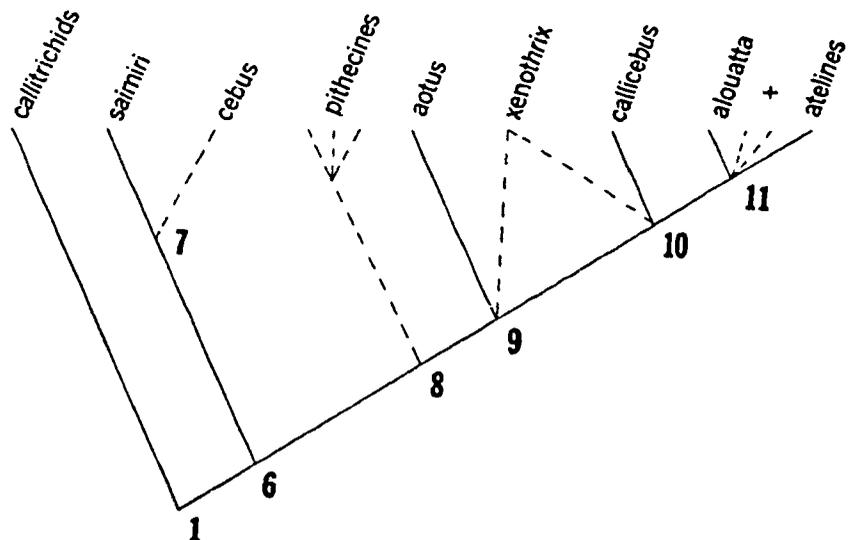
Figure 6. Trivariate plot (%) of individual premolar area relative to summed premolar area. Actual values for  $P_3$ , vertical axis, are noted. Conventions as in Figure 5, sample size as in Figure 4. *Brachyteles* is not figured but clusters with E,M. Distribution of taxa does not sort according to body size. Note the proximity of *A. trivirgatus* (F) and *C. moloch* (G) to *X. mcgregori* (X).



sexpooled samples of non-dimorphic species of ceboids. The areal proportion of  $P_3$  appears rather stable. The  $P_2$  and  $P_4$  morphoclines, on the other hand, obtain a much greater spread and *Xenothrix*, *Callicebus*, and *Aotus* tend to gravitate toward the same pole. In each of these genera,  $P_2$  is relatively small and  $P_4$  relatively large. The isolated position of the fossil probably results from underestimation of  $P_2$  area and the residual "field" effect of molar enlargement upon  $P_4$  size. Nevertheless, the pattern of metrical similarities shared by *Xenothrix* and, especially, *Callicebus* is coincident with visually assessed likeness of cheek teeth size and shape.

Thus, postulated small canine size suggests that the *Xenothrix* lineage is part of a monophyletic group including *Aotus*, *Callicebus*, and the prehensile-tailed monkeys. Should additional specimens demonstrate a reduced anterior premolar, we may further refine this determination by designating *Aotus* a symplesiomorphic sister-taxon. These two alternatives are depicted in Figure 7.

Figure 7. Possible relationships of *Xenothrix* among living Ceboidea. Each of the alternatives is compatible with the evidence presented in the text.



### 5. Summary and Conclusions

I have attempted to demonstrate that *Xenothrix mcgregori* is a different but not grossly aberrant form. It shares several features with living ceboids which are phyletically interpretable. More distinctive attributes of the genus are in need of functional and adaptive explanations. Loss and hypertrophy of molar teeth in this lineage may be analgous to loss and hypertrophy of the anterior teeth in several Tertiary primate lineages. It is neither homologous nor *strictly* analgous to loss and reduction found among living marmosets and tamarins.

In aligning *Xenothrix* with Cebidae, Williams & Koopman (1952) apparently reached the same conclusion, although their reasoning is not made explicit. Relegation of *Xenothrix* as the lone "xenothricid" without a detailed phylogenetic or character analysis, as Hershkovitz (1970) has done, sidesteps this issue. Apart from the phyletic evidence, morphological support for the former view comes from the shape heteromorphy of the fossil's molars, their relatively large size and pattern of scaling. In particular, marmosets and tamarins (excluding *Callimico*) exhibit loss of  $M_3$  together with a virtual absence of hypocones on  $M^1$  and  $M^2$ . These features may have been functionally correlated during the evolutionary reorganization of the two-molared dentition. *Xenothrix*, too, lacks a third molar, but in conjunction with exceptionally well developed  $M^1$  and  $M^2$  hypocones. This implies that radically different sets of selective forces were responsible for the common loss, and/or that each stems from markedly different morphological prototypes.

Derived characters indicating that the affinities of *Xenothrix* are with a monophyletic assemblage of cebids which does not include *Saimiri* and *Cebus* (Figure 7) are posterior deepening of the mandibular corpus and separation of the entoconid from nearby talonid elements. Probable reduction of the canine, which is not preserved in the fossil, further suggests that *Xenothrix* may have shared a most recent ancestry with the cebids united at Node 9. Should new specimens of *Xenothrix* reveal an anterior premolar lacking a honing flange, or dental and mandibular similarities to *Callicebus* prove to be derived, the *Aotus* lineage can be reassigned as a symplesiomorphic sister-taxon to *Xenothrix* and possibly, *Callicebus*.

These conclusions are based on a cladistic interpretation of morphological evidence, primarily of skulls and teeth. Recent attempts to reconstruct ceboid phylogeny with nonmorphological data are in some ways consistent, in others contrary, to the arrangement I have proposed. For example, based on immunodiffusion evidence, Baba, Goodman, Dene & Moore (1975) have tenuously supported a close relationship between *Saimiri* and *Cebus*, and their early differentiation, possibilities which I have also advanced. Their dendrogram, in opposition to my interpretation, depicts *Cacajao* and *Chiropotes* as more distant from one another than either is from a third non-pithecline taxon. Serum albumin and transferrin data (Cronin & Sarich, 1975), on the other hand, supports the close association of *Pithecia* and *Cacajao*. A host of cardinal morphological characters unite all three pithecline genera. Cronin & Sarich (1975) have also suggested that *Callimico* shares a more recent common ancestry with *Callithrix* and *Cebuella* than with either *Leontopithecus* or *Saguinus* or any cebid. This assumption would require at least two non-homologous losses of  $M_3^3$  in a radiation comprising only five living genera or, alternatively, re-evolution of  $M_3^3$  in *Callimico*. A third possibility, that *Callimico* is phyletically a cebid rather than a callithricid, is inconsistent with their own interpretation of their data.

Both Cronin & Sarich (1975) and Baba *et al.* (1975) argued for a close relationship

between *Alouatta* and *Ateles* and *Lagothrix*. The morphological evidence presented above strongly supports this hypothesis and, with the addition of *Brachyteles*, these taxa comprise what appears to be an unequivocal monophyletic group. This point is obscured by currently accepted classifications but is implicit in several of the earliest taxonomic arrangements of ceboids (e.g. Spix, 1823; Gray, 1835; Slack, 1862). The interrelationships among these four naked-tailed genera is still unclear. Baba *et al.* (1975) and Cronin & Sarich (1975) suggest a closer relationship between *Ateles* and *Lagothrix* than between either of the two and *Alouatta*. This hypothesis was also advanced by Zingesser (1973) in his recent analysis of the jaws and teeth of this group, although an important basis for his argument is “. . .the clearly primitive nature of many shared dental characteristics is *Brachyteles* and *Alouatta*.” (1973: 384). Morphometric study of the ceboid femur (Ciochon & Corruccini, 1975) unexpectedly reveals greatest similarity between *Alouatta* and *Lagothrix*, with *Brachyteles* apparently most distinct. Myological evidence, in contrast, distinguishes *Alouatta* from the other three genera (Schön, 1968). The absence of an external thumb only in *Ateles* and *Brachyteles* suggests a shared ancestry postdating the divergence of the *Lagothrix* lineage, although I suspect this feature is variable in *Brachyteles*.

Discrepancies such as these, as well as obvious gaps in our understanding of phylogeny, like those discussed above, should be carefully considered during the classifying procedure as the systematist seeks some sort of taxonomic balance. Still, the grouping or formation of higher taxa depends largely on one's desire to express cladistic, patristic or cladistic plus patristic information in a classification (Mayr, 1969). Patristic differences among living ceboids are substantial and can be conceptualized by a glance at their present adaptive diversity. Platyrrhines exhibit all major patterns of aboreal locomotion seen among Old World haplorhines and strepsirhines combined (Erikson, 1963), while prehensile-tailed primates evolved only in the Neotropics. The masticatory systems of ceboids include tricuspid and quadricuspid molar complexes, two- and three-molared dentitions, cylindrical and spatulate anterior teeth, several patterns of jaw shape, short and long faces, etc. The spectrum of dietary adaptations include insectivory, frugivory, folivory, omnivory (Rosenberger & Kinzey, 1976) and exudativory. *Xenothrix* almost certainly lived within and evolved adaptations related to one or more of these generalized niches. What is known of its mandibular and dental morphology is really no more divergent from any of several hypothetical ancestral conditions than, say, *Pithecia*, *Alouatta* or *Cebuella*.

Viewed in this light, the decision to adopt a monotypic family for the inception of *Xenothrix* or to sink this genus into one which already exists is really not philosophically different from the longstanding debate over the number of “good” ceboid families (see Hill, 1960; Miranda-Ribeiro, 1940). Advocates of a unifamilial classification emphasize the morphocline-like distribution of characters separating the recognized genera, while proponents of the multifamilial arrangement see several morphological segregations and appear to have adopted a typological approach to define the segregates. To date, none have classified Ceboidea on the basis of a well-thought-out phylogeny describing cladistic interrelationships among genera. One of the conclusions which has emerged from this preliminary study is that much more hard data is necessary before a secure phylogeny can be reconstructed. However, I submit that since *Xenothrix* does display derived characters that link this genus to an adaptively diverse group of living cebids, there is insufficient reason to classify *Xenothrix* in an ambiguous, self-limiting higher category. Such a move, without an accompanying detailed character analysis or clear-cut statement of historical

affiliations, raises a critical question: Is *Xenothrix* more closely related to extant two-molared or three-molared ceboids? I suggest that we advocate a bifamilial classification, Cebidae and Callithricidae, to delimit what is obviously a "natural", documentable dichotomy, and refrain from further emmendations until interpretable data is researched and systematically analysed within a falsifiable framework. Until then, I believe the classification of *Xenothrix* ought to remain: Family Cebidae, subfamily *incertae sedis*.

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