The fossil record of callitrichine primates

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Six out of the 16 recognized species of fossil New World monkeys have been discussed as possible relatives of the modern callitrichines. The dental evidence for these views is examined, with emphasis on the homologies and polarities of the relevant characteristics. We conclude that there is no support for the idea that either *Xenothrix* or "*Saimiri*" *bernensis* are related to callitrichines, thus leaving unconfirmed the interpretation that some subfossil postcrania from the Caribbean pertain to the group. The middle Miocene La Venta forms *Micodon* and *Mohanamico* (shown not to be synonymous with *Aotus dindensis*) appear to be callitrichines: the first, largely on account of its very small size; and the second, by the morphology of the lower canine and canine/premolar complex. Potentially derived features shared by callitrichines and *Soriacebus*, an older form from Patagonia, are convergent, however. *Soriacebus* is referred to a new higher taxon of the Tribe Pitheciini (Subfamily Pitheciinae), Subtribe Soriacebina, distinguished from its sister-group, the monophyletic Subtribe Pitheciina, by exhibiting a more primitive morphology than the characteristic saki-uakari dentition. The La Venta *Neosaimiri*, an alleged intermediate between callitrichines and other platyrrhines, is autapomorphically linked with squirrel monkeys, as is another cebine from the early Miocene, *Dolichocebus*, once classified as a callitrichine. The fossil record thus indicates that callitrichines were in existence by the middle Miocene, but their rarity as fossils reveals little of their broader phylogenetic ties or adaptive history.

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Introduction

The discovery of fossils pertaining to the evolution of the callitrichine New World monkeys is a recognized objective of current field work and has been a focus of platyrrhine paleontology for decades. Indeed, a rather large number of fossils have been associated with callitrichines during the past 40 years or so. Some have been formally classified as callitrichines, while others have been advanced as having special relevance to their history, as "intermediates" indicative of the broader affinities or origins of the group.

The evolution of the callitrichines is an elusive piece of the platyrrhine puzzle. Many of the basic hypotheses regarding their history came from neontological studies. In a way, this places us in the interesting position of being able to test hypotheses developed from horizontal comparisons against what is now a rapidly improving fossil record and geochronology. Hence the purpose of this paper is to review critically what we know now of the fossil evidence for callitrichine evolution. We confine ourselves to the craniodental evidence and will not review the Caribbean postcranial remains that have been proposed as callitrichine (see Ford, 1990); these cannot as yet be allocated to taxa diagnosed by dental remains.

The modern callitrichines include the genera *Callithrix*, *Cebuella*, *Leontopithecus*, *Saguinus* and *Callimico*. There are several views on their cladistic relationships and classification. The reader is referred elsewhere for more complete discussions (e.g., Hershkovitz, 1977; Rosenberger, 1981, 1984; Rosenberger & Coimbra-Filho, 1984; Ford, 1986*b*; Sussman &

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Kinzey, 1984). Our preference is to classify the entire monophyletic group as a subfamily and to divide its members into tribes and subtribes in so far as these categories usefully delimit genealogical and adaptive units (Table 1). Thus, in general terms, the tribes Callimiconini (informally callimiconins) and Callitrichini (callitrichins) separate the three-molared *Callimico* from the others, which have two molars and give birth to twins rather than singletons; and the subtribes Leontocebina (leontocebinans) and Callitrichina (callitrichinans) distinguish *Saguinus*, with non-triangular upper molars, anteriorly wide jaws and low-crowned lower incisors, from *Callithrix*, *Cebuella* and *Leontopithecus*, which may have more V-shaped lower jaws, triangular upper molars and moderate- to high-crowned incisors, among other features. [Leontocebina Miranda Ribero, 1940, is based upon *Leontocebus* Wagner, 1840, a junior synonym of *Saguinus* Hoffmannsegg, 1807. Leontocebina retains its status as an available family-group name even though its nominal basis has been rejected as a junior synonym (Art. 40, Int. Code Zool. Nomen.)].

Methods

For simplicity, our discussion is organized taxonomically and proceeds in reverse chronological order, from youngest to the oldest fossils. Our primary focus is to assess the homologies and polarities of dental characters thought to link fossils with modern callitrichines, using the comparative method. The product of such "tests" are probability or confidence statements reflecting the degree to which we believe it is likely that a given similarity (or transformation sequence) shared by two or more taxa was inherited from their last common ancestor (or represents primitive-to-derived transformations of state). In our view the level of confidence one has in a postulated homology relates to the heuristic value of that hypothesis, from its robustness as an evolutionary explanation of a specific shared similarity to its more general value in elucidating problems of phylogeny and adaptation.

Assessing homology involves the evaluation of similarities and differences in a series of hierarchical comparisons within the form-function continuum, and includes related inferences on the biological roles and higher-level adaptations of features (see Szalay, 1981, and references therein). The first level in such an analysis is strictly empirical (but not lacking assumptions) and involves observations on the phenetics of anatomy and development, for example. The other stages inherently involve more assumptions and generalizations. For example, it may be inferred that pairs or sets of similar features shared by two taxa are linked into anatomical patterns. Such features or patterns may then be assessed at a more general level, by ascribing specific biological roles and adaptive explanations. Ultimately, the greater the degree of similarity that obtains within and across each of these levels, the more likely it is that the features or patterns under test are homologous.

These assessments or tests of hypothetical homologies result in both positive and negative findings, but negative results—finding that two non-identical similarities are descriptively alike (suggesting homology) but differ in their detailed functional interactions within patterns, or in their biological roles—are often the most valuable. Thus the clear recognition of analogy is what often invalidates a homology hypothesis. That is, when in equivalent structural systems (i.e., a molar tooth) dissimilarities predominate at all the secondary levels (pattern, function, role, adaptation) in spite of a similar aspect in a

Table 1 **A classification of New World monkeys to genus level**

- Infraorder Platyrrhini E. Geoffroy, 1812
  - Superfamily Ateloidea Gray, 1825 [new rank][1]
    - Family Atelidae Gray, 1825 [Szalay & Delson, 1979]
      - Subfamily Atelinae Gray, 1825 [Pocock, 1925]
        - Tribe Atelini Gray, 1825 [Szalay & Delson, 1979]
          - Subtribe Atelina Gray, 1825 [new rank]
            - *Ateles* E. Geoffroy, 1806
            - *Brachyteles* Spix, 1831
          - Subtribe Lagotrichina Gray, 1870 [new rank]
            - *Lagothrix* E. Geoffroy, 1812
        - Tribe Alouattini Trouessart, 1897 [Szalay & Delson, 1979][1]
          - *Alouatta* Lacépède, 1799
          - †*Stirtonia* Hershkovitz, 1970
      - Subfamily Pitheciinae Gray, 1849 [Mivart, 1865]
        - Tribe Pitheciini Gray, 1849
          - Subtribe Pitheciina Gray, 1849 [Szalay & Delson, 1979]
            - *Pithecia* Desmarest, 1820
            - *Chiropotes* Lesson, 1840
            - *Cacajao* Lesson, 1840
            - †*Cebupithecia* Stirton & Savage, 1951
          - Subtribe Soriacebina [new rank]
            - †*Soriacebus* Fleagle *et al.*, 1987
        - Tribe Homunculini Ameghino, 1894 [new rank]
          - Subtribe Homunculina Ameghino, 1894 [new rank]
            - †*Homunculus* Ameghino, 1891
          - Subtribe Aotina Poche, 1908 [new rank][1]
            - *Aotus* Illiger, 1811
            - †*Tremacebus* Hershkovitz, 1974
          - Subtribe Callicebina Pocock, 1925 [Rosenberger, 1981]
            - *Callicebus* Thomas, 1903
            - †*Xenothrix* Williams & Koopman, 1952
        - Tribe indet.[2]
          - †*Carlocebus* Fleagle, 1990
    - Family Cebidae Bonaparte, 1831 [Swainson, 1835]
      - Subfamily Cebinae Bonaparte, 1831 [Mivart, 1865]
        - Tribe Cebini Bonaparte, 1831 [Gray, 1870]
          - *Cebus* Erxleben, 1777
        - Tribe Saimiriini Miller, 1912 [Rosenberger, 1981]
          - *Saimiri* Voigt, 1831
          - †*Neosaimiri* Stirton, 1951
          - †*Dolichocebus* Kraglievich, 1951
        - Tribe indet.
          - †"*S.*" *bernensis* (Rimoli, 1977)
      - Subfamily Callitrichinae Thomas, 1903 [Napier & Napier, 1967][1,3]
        - Tribe Callitrichini Thomas, 1903 [Szalay & Delson, 1979]
          - Subtribe Callitrichina Thomas, 1903 [new rank]
            - *Callithrix* Erxleben, 1777
            - *Cebuella* Gray, 1886
            - *Leontopithecus* Lesson, 1840
          - Subtribe Leontocebina Miranda Ribero, 1940 [new rank]
            - *Saguinus* Hoffmannsegg, 1807
        - Tribe Callimiconini Thomas, 1913 [Szalay & Delson, 1979]
          - *Callimico* Thomas, 1913
          - †*Mohanamico* Luchterhand *et al.*, 1987

Table 1 —*continued*

Tribe indet.
†*Micodon* Setoguchi & Rosenberger, 1985
Subfamily Branisellinae Hershkovitz, 1977 [Szalay & Delson, 1979]
†*Branisella* Hoffstetter, 1969
†Unnamed genus (Rosenberger *et al.*, in preparation)

Square brackets specify the first use of higher taxa at the rank presently employed. Fossils are marked by daggers (†).

[1] As Eric Delson pointed out to us, the correct superfamily *nomen* for platyrrhines appears to be Ateloidea, based upon Atelina Gray, 1825, a suprageneric taxon including *Ateles*, *Brachyteles* and *Lagothrix*. Ateloidea Gray, 1825, has priority over all family-group names derived from Cebina Bonaparte, 1831, based upon *Cebus*. Mycetina Gray, 1825 (including *Alouatta*), Nyctipithecinae Gray, 1870 (including *Aotus*) and Hapalina Gray, 1870 (including *Callithrix*) are available names rejected here because their replacement names (junior synonyms) have won general acceptance.

[2] Fleagle (1990) has shown that his new genus *Carlocebus* resembles pitheciines, especially *Callicebus*, *Aotus* and *Homunculus*.

[3] Pocock (1920) did not employ the term Callitrichinae, because he believed that Hapalidae had priority as the family-group name. However, he (p. 113) was the first to specify the necessity of employing Callimiconinae (for *Callimico*) as a subfamily within the "Hapalidae" to contrast with the other marmosets and tamarins, which he would have undoubtedly placed in its own subfamily had his 1920 paper been a taxonomic work.

morphological feature (i.e., presence of a hypocone), the hypothesis of homology is rejected.

As an example, consider the hypothesis that monomorphy of the canines of *Callicebus* and *Callimico* is a homologous quality. Apart from this lack of sexual dimorphism, the unit character under test, other indicators point to convergence of this similarity: (1) Anatomy—their teeth differ in many particulars contributing to overall shape. *Callicebus* canines are small and nonprojecting; *Callimico* canines are large and tusk-like. (2) Functional relationships—their canine/premolar complexes differ. *Callicebus* P_2 bears little or no canine honing correlates; *Callimico* has a tall, peaked P_2, with a well developed preprotocristid. (3) Biological roles—one is used primarily in feeding, the other as a display organ. The smaller lower canines are apparently not used in communication in *Callicebus*, but are important in feeding. In callitrichines, the role of the canines in feeding is probably less important than in the open-mouth threat display, which bares the large lower canines. (4) Adaptation and phylogeny—distinctive, derived cases of canalization are probably represented by these canine complexes. *Callicebus*, here regarded as a pitheciine on the basis of *other* characters, is part of a phylogenetic group where the anterior dentition as a whole, including the lower canine, tends to become modified as a harvesting tool. *Callimico*, a callitrichine, is part of a group with an unusual social organization (e.g., Sussman & Kinzey, 1984), where derived features of the canines (e.g., large size relative to body size; large canines in both sexes; large upper *and* lower canines) may have special significance as display organs and/or in aggressive encounters. Therefore, the hierarchy of biological details relating to the adaptive history of the canines tends to nullify the proposition that monomorphism is homologous in this comparison. Furthermore, since dimorphism and monomorphism is also known to be somewhat labile intragenerically (e.g., Kay *et al.*, 1988), it may be fundamentally prone to convergence. Thus we can be fairly confident that monomorphism in *Callimico* and *Callicebus* is analogous.

Our approach to polarity inference is transformational (Szalay, 1981). Once the probable homologies of a morphocline are identified, a hypothetical transformation sequence is proposed to explain the most likely pathway of anatomical and functional change, given hypothetical functional constraints and the implications for the evolutionary biology of the structures and species under study. We argue below, for example, that the unique character of the pitheciin (*Pithecia*, *Chiropotes*, *Cacajao*, *Cebupithecia*) anterior dentition, with large diastemata, procumbent incisors and widely spaced canines, could have evolved from a form with tall, compressed incisors and V-shaped jaws (such as *Soriacebus*), as the canines enlarged and everted to serve a new functional role. This is not the only logical explanation of the taxonomic distribution of the relevant characters and taxa (see Kay, 1990). However, in our view it is consistent with other dental features, with temporal data and with more general hypotheses regarding morphocline polarities among other platyrrhines.

Analysis of fossil taxa

Xenothrix mcgregori

The Jamaican subfossil *Xenothrix* (Figure 1) is known from a single, well preserved jaw with two molar teeth, extensively discussed by Williams & Koopman (1952), Hershkovitz (1970) and Rosenberger (1977). Williams & Koopman (1952) evaluated the possibility that the specimen is a callitrichine. Recently, Ford (1986) reopened the question of its affinities after examining a long neglected subfossil tibia from Haiti, which she interpreted as a callitrichine closely related to *Saguinus*. She remarked (p. 86): "In light of the apparent gigantism that has occurred in at least one callitrichid taxon in the Antilles, Ceboid M [the tibia], it is possible that *Xenothrix* also represents an enlarged callitrichine". Although new postcranial and dental material has persuaded her to reconsider the basis of these points (Ford, 1990), the issue of *Xenothrix* affinities continues to be a difficult one.

Features that suggested to Williams & Koopman (1952) the possibility of a relationship with the callitrichins, included the two-molar dental formula and the condition of the incisor alveoli which, they suggested, could have supported somewhat procumbent incisors. Williams and Koopman also discussed a variety of phenetic similarities shared with members of other platyrrhine groups, such as cebines, pitheciines and atelines, and emphasized specific resemblances shared with the genera *Cebus* and *Callicebus*. They rejected the tacit implications of a two-molar dental formula because the crown patterns of *Xenothrix* and callitrichins are vastly different. Rosenberger (1977) essentially extended this argument.

The low-relief, crenulate molars of *Xenothrix* appear to be large relative to jaw size, unlike the two-molared callitrichins. They are subequal in size, M_2 measuring 86·8% the area of M_1 (see Rosenberger, 1977). This is unlike the proportions of modern callitrichins. For example, M_2/M_1 percentage ratios in samples of *Cebuella pygmaea*, *Callithrix argentata* and *Leontopithecus rosalia*, which range in body size from the smallest to nearly the largest species of the group, are 82%, 73% and 72%, respectively. This reflects a basically inverse allometric relationship between these parameters among callitrichins (Kanazawa & Rosenberger, 1988). Thus the "unreduced" M_2 of *Xenothrix*, whose body size must have been considerably larger than the largest living callitrichine, shows precisely the opposite proportions that one would expect using a callitrichin model, even though dental formulae are the same. This implies that the factor(s) controlling molar allometry in *Xenothrix* is not

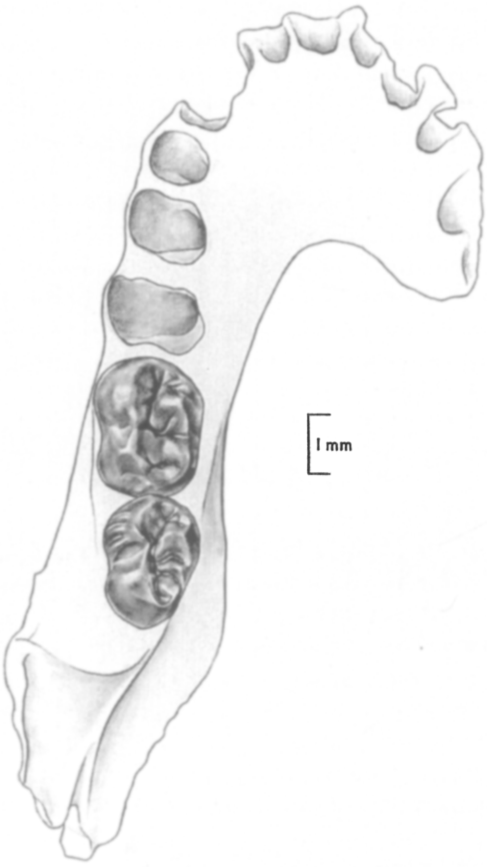

Figure 1. Occlusal view of *Xenothrix mcgregori*. Note relatively large molars; enamel crenulations in unworn portions of trigonids and sulcal remnants of crenulations in more worn areas of talonid; sharply delimited entoconid; post-talonid extension distal to entoconid-hypoconid plane; short cristid obliqua connected to postprotocristid, reducing ectoflexid. The skewed trigonid, with protoconid situated more mesially than metaconid, is not adequately represented in this orientation.

homologous with that of callitrichins, which in turn suggests that their lack of an M_3 is a convergent feature. The morphology of M_2 is consistent with this point, for in *Xenothrix*, unlike callitrichins (Figure 4), the talonid is clearly secondarily elongate.

The occlusal morphology of *Xenothrix* also presents differences from that of callitrichins. Among the most notable contrasts are: (1) The large protoconid, which indicates by its size, shape and well developed wear facets the presence of a large hypocone/talon on the upper molars. Callitrichines do not have enlarged protoconids and, primitively, hypocones were lost on callitrichin M^{1-2} and at least on the M^2 of ancestral callitrichines (e.g., Rosenberger, 1977). In contrast, the hypocone is secondarily enlarged in some pitheciines (see Table 1 for taxonomy), especially. (2) The strongly cuspate talonid with a post-talonid extension behind the entoconid and hypoconid. This is unlike all known callitrichines, which tend not to exhibit much talonid cusp differentiation or accessory occlusal basins. Thus, assuming that crown pattern and molar proportions are functionally linked, it appears that the morphology and proportions of the molars of *Xenothrix* resemble neither callitrichins nor callitrichines in any specific way.

Rosenberger (1977) suggested that the offset entoconid and the post-talonid extension of *Xenothrix*, both of which are associated with a hypocone or large talon region of the uppers, were similar to *Callicebus* and *Pithecia* in particular. In *Cebupithecia* there is also a clearly distinct entoconid, with a sulcus behind it, and a post-talonid extension. In the Miocene genus, however, the rounded, puffy occlusal details of *Xenothrix* are lacking, and the crowns resemble the nearly featureless molars of *Pithecia*, for example. Other possible resemblances to *Callicebus* and pitheciins generally include the low cusp relief, perhaps the tendency towards enamel crenulation, a very short cristid obliqua and a differentiated postprotocristid. Also, the occlusal morphology of the ectoflexid suggests that *Xenothrix* had a relatively well developed paracone and metacone, like *Callicebus*, and unlike the highly reduced ectolophs of pitheciins.

With the discovery of new fossils, comparisons of molar morphology must now be extended. *Soriacebus ameghinorum* (Fleagle *et al.*, 1987) from the ?early-middle Miocene of Argentina, also has a small, distinctly separate entoconid combined with a post-talonid extension. Its trigonid, as with *Xenothrix* (not captured adequately by the illustration in Figure 1), is also skewed lingually. Although the affinities of *Soriacebus* are debatable (compare Fleagle *et al.*, 1987; Fleagle, 1990; Kay, 1990; and below), we consider this genus to represent an early pitheciin stock. Thus some of the features that *Soriacebus* shares with *Callicebus* and *Xenothrix* may represent ancestral pitheciine character states, reinforcing our assessment that *Xenothrix* is part of that group.

Other features that are relevant to the affinities of *Xenothrix* include the small canine socket (small even for a female: Rosenberger, 1977), premolars (from alveoli) that broaden posteriorly, parabolic dental arcade and a jaw that deepens strongly toward the rear. None of these are features seen among callitrichins, nor are they expected in a callitrichine morphotype. Just this combination, however, is shared specifically with *Callicebus* (and possibly with some of the new Pinturas forms; see Fleagle, 1990). Canine reduction and the parabolic jaw shape is uniquely derived in *Callicebus* as a functional/spatial pattern relating to narrow incisors, small canines and small anterior premolars (see Rosenberger, 1977), in the context of a relatively great bimolar breadth that is controlled by a broad braincase, or large body size (Kanazawa & Rosenberger, 1989). Jaw deepening is an atelid synapomorphy, but the extreme version of the condition in *Xenothrix* closely resembles *Callicebus* metrically (Rosenberger, 1977). Both genera lack the ancestral, wave-like curve of the inferior border of the mandibular corpus retained in more primitive pitheciines, such as *Aotus* and *Homunculus* as well as some *Pithecia*, to a lesser extent.

Thus the bulk of the evidence indicates that *Xenothrix* is phyletically a pitheciine, rather than a callitrichine, possibly most closely related to *Callicebus*. However, with the discovery of more fossil species from the Miocene Pinturas area of Argentina, including taxa with very deep jaws and relatively small canines (see Fleagle, 1990), the picture of pitheciine evolution is rapidly changing (see below), and *Xenothrix* may prove to be less closely related to the extant *Callicebus* than to other members of this still poorly known radiation.

Still another alternative that merits consideration is that *Xenothrix* is most closely related to a living cebine, notably *Cebus*. The morphological argument here might emphasize their sharing of thick enamel (although this is not well demonstrated for the fossil) and bunodont crowns, which are derived among platyrrhines. Furthermore, the highly reduced M_3 of cebines, an antecedent to the callitrichine pattern (Rosenberger, 1977, 1979*b*, 1981), may be interpreted as a preadaptation to the loss of M_3 in *Xenothrix*. Ancillary support for this hypothesis might be the presence of "*Saimiri*" *bernensis*, a cebine (see Rosenberger, 1978*b*; MacPhee & Woods, 1982; Ford, 1990), on Hispaniola. The intrinsic evidence, however, is not compelling. The cusp morphology and tooth proportions of *Xenothrix* contrast with that of *Cebus* and "*S.*" *bernensis* in much the same way as has been described above for callitrichins (see MacPhee & Woods, 1982). These features, therefore, do not carry as much weight as the combination of derived traits that *Xenothrix* shares with the pitheciins and *Callicebus*.

Neosaimiri fieldsi

R. A. Stirton (1951: 328), upon first describing the type specimen of *Neosaimiri* from the La Venta badlands of Colombia, 12–15 Ma (million years ago) (dates employed here are reviewed in MacFadden, 1990), observed: "Possibly we have tended to obscure the true relationships of the marmosets by recognizing them as a family distinct from the Cebidae. Of course the evidence available does not prove that the Miocene *Neosaimiri* is directly ancestral to either *Saimiri* or *Callimico* or *Callithrix*, but the retention of certain *Neosaimiri* features in these Recent forms would support the contention for a position at least close to that common ancestry". None have, to our knowledge, gone so far as to claim a closer relationship between *Neosaimiri* and callitrichines. Nevertheless, Stirton's view of the fossil as a phylogenetic link between callitrichines and *Saimiri*, or as an indicator of a genealogical link between callitrichines and a specific group of non-callitrichine platyrrhines, stood in contrast to the prevailing notion of callitrichines as being genealogically isolated. Rosenberger also argued later (e.g., 1977, 1979*a*,*b*, 1981), from neontology, that the callitrichines are the nearest cladistic relatives of the living cebines, *Cebus* and *Saimiri*.

To whom is *Neosaimiri* most closely related? The most detailed recent commentaries are by Hershkovitz (1970), Szalay & Delson (1979) and Delson & Rosenberger (1984). Hershkovitz considered a phyletic tie between *Neosaimiri* and *Saimiri* as a possibility (p. 22) and referred to the fossil as squirrel-monkey-like (p. 2), but he also noted features that "point away from the squirrel monkey" (p. 4), such as a "V-shaped mandible and small, crowded, laterally constricted and forwardly oriented . . . well spaced expanded and nearly erect incisors". It is well to point out that the mandibular corpora of the type and only known dental specimen of *Neosaimiri* are completely broken apart, and this might have contributed to Hershkovitz's impression of a V-shaped arcade. Delson and Rosenberger, while mentioning differences between *Saimiri* and *Neosaimiri* in the acuity of cusps, construction of the occlusal basins and cingulid development, considered these forms so similar that (by analogy with the operational standards of catarrhine systematics) they should be lumped in the same genus, perhaps separated at the subgenus level only.

The molars of *Saimiri* and *Neosaimiri* are jointly distinguished from other platyrrhines by a suite of integrated molar characters (Figure 2), including: sharply cusped cheek teeth, well developed entoconids and hypoconids, broad trigonids, well developed buccal cingulids, strong buccal flare of the molars and deep ectoflexids. These all contribute to a strong shearing/puncture-crushing design and there is little doubt that *Neosaimiri* occupied a *Saimiri*-like, insectivorous feeding niche. The canine, premolars and mandibular structure of the fossil are also very similar to *Saimiri*, as many authorities appear to agree. Therefore, given the age of *Neosaimiri* and the apparent absence of any known autapomorphic features of the genus, there is no reason to reject the hypothesis that *Neosaimiri* represents the *Saimiri* clade and is potentially a direct ancestor of living species.

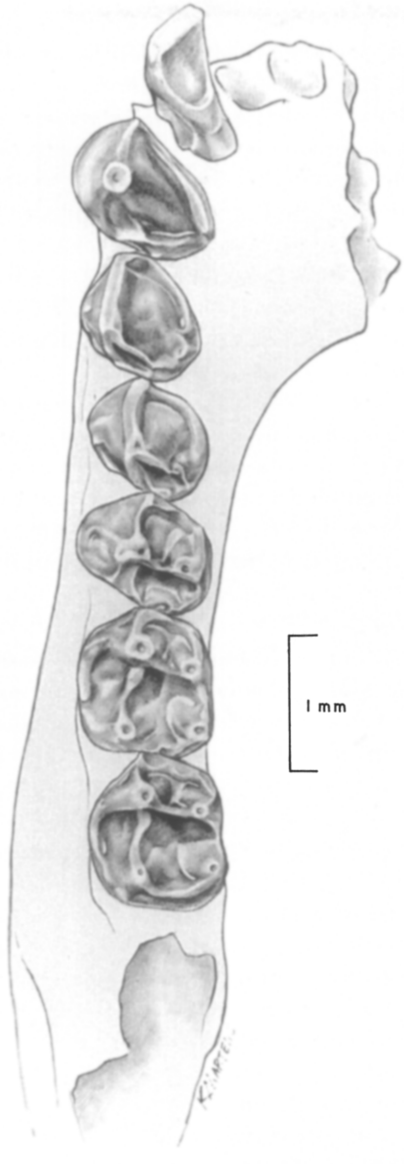

Figure 2. Left side of toothrow of *Neosaimiri fieldsi*. Note large size of P_2, with elongate preprotocristid for C^1 occlusion; transversely broad P_4; large ectoflexid and strong buccal cingulid on molars.

Stirton's (1951) claim for morphological intermediacy, on the other hand, was stated in vague terms and cannot be supported. His discussion (p. 328) makes it clear that allusions to a relationship between callitrichines and *Neosaimiri* were based upon a morphocline (see Figure 6) in upper molar morphology (i.e., *Callimico*, *Saimiri*, *Callicebus*; see Rosenberger, 1977), still unknown for the fossil.

Mohanamico hershkovitzi

Mohanamico also comes from the La Venta area of southwestern Colombia. Luchterhand *et al.* (1986) outlined a series of resemblances to pitheciins and callitrichines, especially *Callimico* and *Saguinus*. They concluded that *Mohanamico* is a primitive pitheciin (for them Pitheciinae: *Pithecia*, *Chiropotes*, *Cacajao* and *Cebupithecia*) and stated that certain resemblances of pitheciins and callitrichines may be evidence that these monophyletic groups are sister-taxa. The more recent contention of Kay (1988, 1990), that *Mohanamico* and *Aotus dindensis*, known by a mandible and facial fragment from a nearby locality (Setoguchi & Rosenberger, 1987), are synonymous will also be considered here as a way of evaluating the systematic position of *Mohanamico*. In doing so, we will argue that *Mohanamico* shares with callitrichines, and with *Callimico* in particular, several traits that suggest this form is a primitive callitrichine.

In response to Kay's (1988, 1990) interpretation that *Mohanamico* and *A. dindensis* are synonymous we provide a listing of features that, in our view, most clearly demarcate them (see Figure 3). It is well to keep in mind that the identification of *A. dindensis* as *Aotus* is based upon dental and mandibular similarities, and the evidence of orbital enlargement is a facial fragment of the same individual that is represented by the mandible (Setoguchi & Rosenberger, 1987). Beginning with the most discriminating contrasts, these taxa differ as follows:

Incisors. Mohanamico: I_2 lanceolate, narrow mesiodistally; crown axis straight to vertically recurved, with flexed apical margin, long I^2 occlusal ridge and convex lingual fossa. *Aotus:* I_1 broader, asymmetrically flaring crown with horizontally straight apical margin and short I^2 occlusal ridge; crown axis more procumbent that in *Mohanamico*, with enlarged scoop-like lingual fossa.

Canines. Mohanamico: C_1 with enlarged concave mesiolingual fossa, no lingual entocristid but a distinct vertical torus; long precristid; horizontally disposed lingual cingulum with no basal bulge of enamel or distobasal notch; small distal surface for C^1 occlusion. *Aotus:* C_1 mesiolingual fossa convex with incipient (as in modern *Aotus*) entocristid (see also Figure 7 for an example of a more derived entocristid in *Pithecia*) bounded by steeply angled lingual cingulum (that probably shortens downward length of precristid) and distobasal enamel bulge and notch; large distal occlusal surface for C^1.

Lower premolars. Mohanamico: P_2 extremely tall and pyramidal in profile; convex lingual surface with no basal prominence or well defined mesiolingual fossa below lingual torus and a thin, non-notched, horizontal cingulum. P_3 virtually unicuspid, smaller than P_4, with small mesial fovea; $P_{3,4}$ with elevated transverse protocristids. *Aotus:* P_2 moderately tall and acute, with well developed entocristid and mesiolingual fossa, basal bulge and notched cingulum. $P_{3,4}$ subequal in size, with better developed lingual cingula and mesial foveae; P_3 transverse protocristid moderately developed.

Mandible. Mohanamico: Symphyseal region and anterior section of mandibular corpus massive; bilateral, prominent subalveolar fossae situated laterally below premolars; inferior border of corpus does not decrease posteriorly; curve of Spee shallow. *Aotus:* Less massive symphysis, anterior mandible and planum alveolare; no lateral subalveolar fossae; sinusoidal ventral mandibular border that deepens posteriorly; more marked curve of

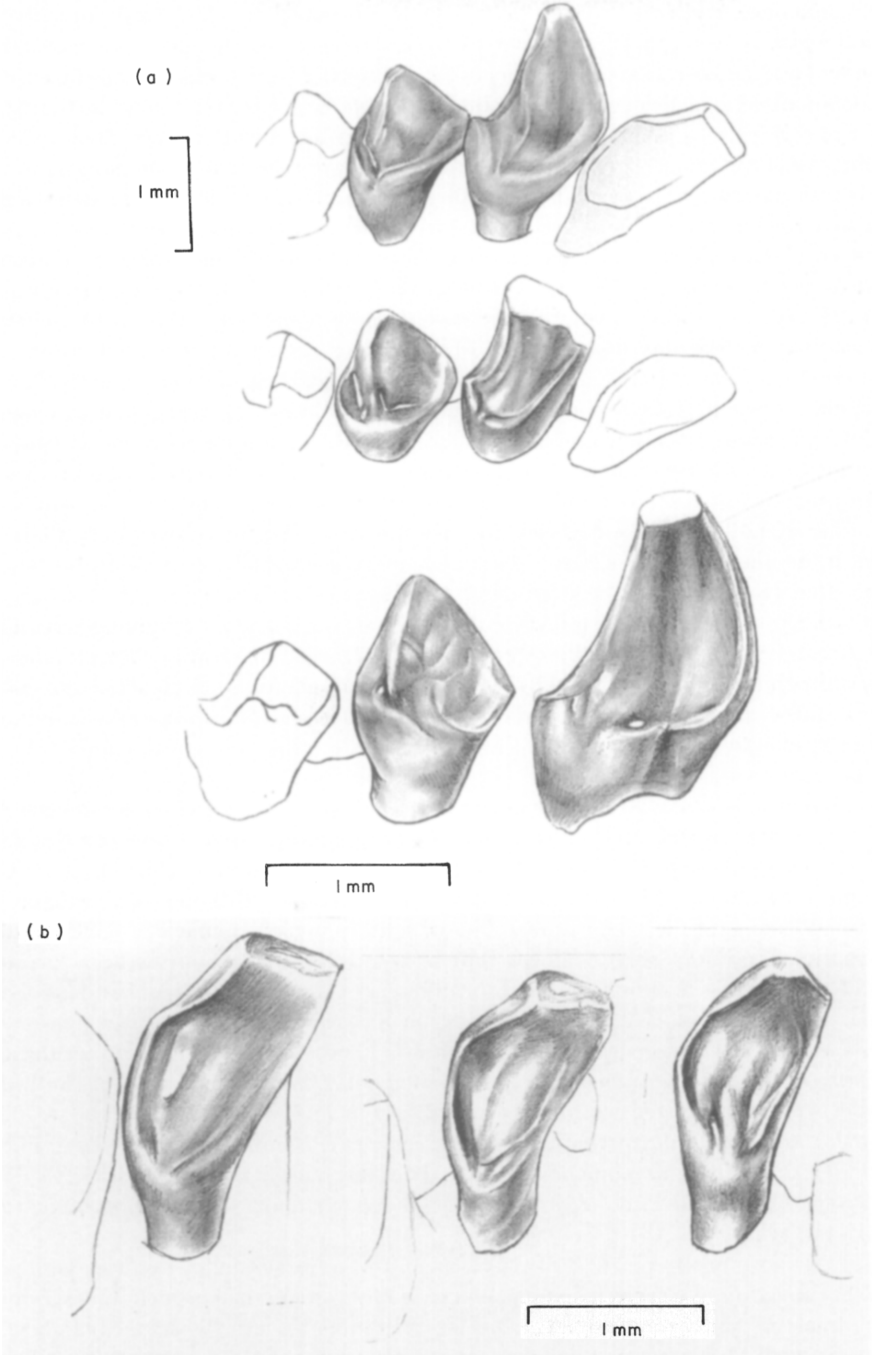

Figure 3. (a) Three-quarter lingual views of the left lower canine and P_2 of *Aotus trivirgatus* (top), *A. dindensis* (middle) and *Mohanamico hershkovitzi* (bottom), the latter with P_2 reversed from right side. (b) Lingual views of I_2 of same individuals as in sequence (a).

Spee. (See Luchterhand *et al.*, 1986, Setoguchi & Rosenberger, 1987, and Kay, 1990, for lateral views).

To generalize, the lower lateral incisors of *M. hershkovitzi* were evenly tall and narrow, with short, pointed incisal edges, whereas those of *A. dindensis* were relatively broad in the mid-crown, contributing a long I_2 incisal edge to a scoop-like incisal battery. In our view, combining the lanceolate (tapering to a point) morphology of the I_2 of *Mohanamico* with the flaring I_1 of *A. dindensis*, as required by their alleged synonymy, would result in an unlikely pattern of shape heteromorphy not seen elsewhere among platyrrhines, and certainly not among known pitheciines (including even *Callicebus* and *Aotus*), where there is a strong tendency to use all lower incisors together as a closely integrated functional (harvesting) unit. The resulting $I_{1,2}$ homomorphy would involve a misalignment of their apical incisal edges as well as the orientations of the axis of the crowns, which are flexed forward in *A. dindensis* ($I_{1,2}$) and seem to arise more vertically in *M. hershkovitzi* (I_2).

The canine crown of *M. hershkovitzi* has a lingual reinforcement (torus) against breakage, like callitrichines and especially *Leontopithecus* (see Figure 4) and some other taxa with tall C_1 crowns. We believe this is not homologous with the entocristid of *A. dindensis*, a pitheciin trait (see Figure 7) that is a consequence of their characteristic, triangular canine cross-section. The mandibular morphologies are also distinctive (in our view, more than is depicted in the line drawings of Kay, 1990), although the reliability of some features are being debated (Kay, 1990). The even-depth condition of the lower jaw of *Mohanamico* contrasts with the deepening/posteriorly enlarging state of *A. dindensis*. Although there is expansion cracking and distortion posteriorly in *M. hershkovitzi* (Kay, 1990), whatever posterior deepening might have actually occurred in a population of *M. hershkovitzi* would have resembled the typical, inconspicuous patterns evident in other even-jawed platyrrhines, namely cebids, and would have been quite unlike the conspicuously deep profiles of all known atelids.

The similarities shared by *A. dindensis* and living *Aotus* have been discussed in some depth (Setoguchi & Rosenberger, 1987). It was emphasized that only minor details of premolar and molar form distinguish them, in contrast to the incisor morphology, which discriminates them well. The essential differences reflect the fact that the fossil presents a less modified version of the modern *Aotus* incisor battery, which is characterized by tall, highly spatulate incisors that conform into a scoop-like instrument with a broad, continuous incisal edge. As implied above, the differences between *A. dindensis* and modern *Aotus* bears on the question of synonymy between *A. dindensis* and *M. hershkovitzi*, for it provides a reference of intrageneric variation. Thus in Figure 3 we present a detailed visual comparison of the incisor, canine and P_2 morphology of *A. dindensis*, *A. trivirgatus* and *M. hershkovitzi*. Among the *Aotus*, we find the variability in incisal form comparable to the variation documented for the three species of *Leontopithecus* (Rosenberger & Coimbra-Filho, 1984), which is surely a monophyletic genus. However, adding *M. hershkovitzi* to this anatomical continuum does not accord well with the pattern nor with our morphological concept of the genus.

Turning to the phyletic position of *Mohanamico*, in our preliminary analysis we find features that suggest it is related to callitrichines. In *Mohanamico*, the lower canine is a very strongly projecting, fairly robust tooth. It is 1·68 times taller than the adjacent P_2 and 2·29 × the height of P_4. The sex of the specimen is indeterminate, although it is difficult to imagine the type as a female of a sexually dimorphic species: the male canine would be absolutely enormous. Despite the size of this tooth, P_2 is not especially modified as a canine honing platform. It has a simple pyramidal shape, and bears a simple precristid for occlusion with the upper canine. The latter must also have been a tall tooth in *Mohanamico*, following the usual anthropoid pattern.

Among platyrrhines, C^1/P_2 occlusal relationships vary broadly (Figure 4; see also Figures 2 & 7). High-crowned lower canines are associated with uniquely modified P_2 morphologies in cebines, pitheciins and atelines. In cebines, which are sexually dimorphic, males and females have large, blocky P_2s that are low-crowned in both sexes but carry an elongate precristid for canine honing (Figure 4). In pitheciins, frequently with no dimorphism, P_2 tends to resemble that of *Soriacebus*, as discussed below. They are unique in being canted medially or posteromedially (Figure 7) to expose a broad buccal occlusal surface, which is typically reinforced by an enamel swelling near the cervix. In atelines, the mesiobuccal face of the P_2 is rounded to engage the C^1 occlusal surface, especially in males.

Two related points are of significance here. (1) Only among callitrichines is there no clear-cut differentiation of a P_2 occlusal surface for C^1 occlusion in either sex, apart from an increase in the apical height of the crown which geometrically increases the length of the honing surface. (2) Only among callitrichines is this lack of a modified P_2 honing associated with tall, projecting *upper and lower* canines in both sexes (e.g., Hershkovitz, 1977). In other platyrrhines where P_2 is relatively undifferentiated for honing functions, the lower canines are either reduced in crown height (*Callicebus*) or are only moderately tall and somewhat slanted laterally (*Aotus*), unlike *Mohanamico*. When the lower canine is tall in both sexes, in pitheciins, P_2 is modified to engage their unusual morphology. Thus *Mohanamico* shares with callitrichines a derived pattern of lower, and evidently upper, canine enlargement without an attendant development of a "specialized" honing P_2. Additionally, if P_2 is especially elevated in crown height, as we think it is, this may be a specific resemblance to *Callimico* (Figure 4), where $P_{2,3}$ are uniquely tall. This character was also listed by Luchterhand *et al.* (1986: 1758) as potential evidence of an affinity with callitrichines.

A feature of the anterior dentition that may also be uniquely shared by *Callimico* and *Mohanamico* is the combination of a gracile, moderately tall second lower incisor with a canine having an enlarged mesiolingual fossa (Figure 4; see Hershkovitz, 1977: Figures XII. 14–17). The latter is conditioned by the development of a strong lower canine precristid which flares from the body of the crown. A similar pattern can be seen in *Callimico* and, in a different fashion, in some *Leontopithecus*. It is worth noting here, as above, that there are descriptive differences relating to lower canine morphology that widen the gap between the interpretation of *Mohanamico* presented here and that of Luchterhand *et al.* (1986). We do not regard the strong lingual crest of *Mohanamico* as an entocristid, which is a pitheciin synapomorphy. Platyrrhines with tall lower canines often have a convex lingual torus running vertically to reinforce the lower canine, but the way in which this feature is developed in pitheciins is distinctly different. It is a strongly beveled crest, rather than a rounded torus, best differentiated near the base of the crown to create the triangular cross section (see Figure 7). The least modified states of the entocristid pattern are found in *Aotus dindensis* and *A. trivirgatus* (Figure 3).

Finally, Luchterhand *et al.* (1986) claim that *Mohanamico* shares with both pitheciins and callitrichines the reduction and/or loss of a hypoconulid and hypoconulid/entoconid sulcus, which they note might either be due to parallelism or to their monophyletic ancestry. We believe it is more likely, as previously argued (e.g., Rosenberger, 1977), that the distinct entoconid with distal fovea is a derived pitheciin trait, occurring also in

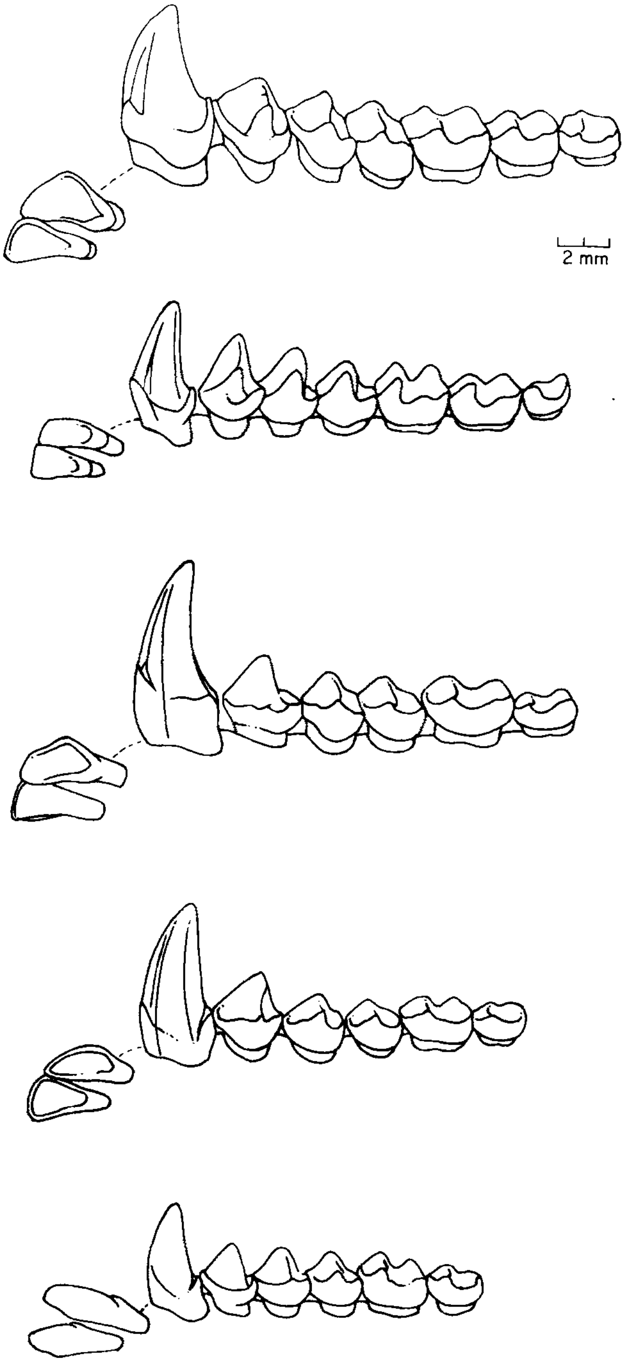

Figure 4. Simplified lingual views of lower right toothrows of (top to bottom) *Saimiri sciureus*, *Callimico goeldii*, *Leontopithecus rosalia*, *Saguinus oedipus* and *Callithrix jacchus* (after Hershkovitz, 1977; Figure V.26). With rare exceptions, callitrichines are essentially monomorphic in canine size. The *Saimiri* appears to be a male. Contrast its blocky P_2 with relatively horizontal preprotocristid, to the relatively taller P_2s of callitrichines, and the extremely elevated P_2 crown of *Callimico*. Compare with *Mohanamico*.

Soriacebus, *Cebupithecia*, *Xenothrix* and living saki-uakaris. There is no vestigial evidence in the occlusal anatomy of callitrichines to suggest that they ever had such a well defined entoconid. Also, catarrhine-like hypoconulids of the first and second molars were probably not present in the platyrrhine morphotype (see Rosenberger, 1986; *contra* Fleagle & Kay, 1987). The sporadic occurrence of a third talonid cusp within some living platyrrhine species makes the assertion that these are homologous with catarrhines highly questionable (e.g., Rosenberger, 1986). Thus their absence in callitrichines and pitheciins is probably not due to homology.

Micodon kiotensis

Micodon is a very small primate from La Venta that is based upon a single isolated upper molar, with an upper incisor and a lower premolar tentatively referred to the genus as well (Setoguchi & Rosenberger, 1985). It was referred to Callitrichinae largely because of its small size. In absolute dimensions, *Micodon* is comparable to medium-sized *Callithrix* or small *Saguinus* species. It is smaller than, and appears to be a poor occlusal match for, *Neosaimiri*, *Mohanamico* or *A. dindensis*.

The molar morphology of *Micodon* is still poorly known, although the crown evidently lacked well developed styles or conules (Figure 5). Its most distinctive trait is the moderately developed hypocone. As is well known, there is a range of hypocone size among the callitrichines (Figure 6). It is moderately well developed on first molars of *Callimico*, where it is very small or missing on M^2, variably small to absent on *Saguinus* M^1, absent on M^2; absent and replaced by variably developed postcingula on $M^{1,2}$ of *Leontopithecus*, *Callithrix* and *Cebuella* (e.g., Kinzey, 1973; Rosenberger, 1977, 1979*b*). This array has been interpreted as a morphocline, with the primitive pole represented by *Callimico* and the derived pole by the callitrichinans (e.g., Rosenberger, 1977; but see Hershkovitz, 1977). In contrast, enlarged, elevated hypocones are found in most atelids, probably synapomorphically.

The morphology of *Callimico* may support the hypothesis that ancestral callitrichines retained the hypocone. However, the anatomical details of hypocone structure in the callitrichine morphotype are more ambiguous and probably cannot be reconstructed accurately without fossils. The condition in *Callimico* (Figure 6) is not to be taken literally as the ancestral state, for its morphology is quite different from the patterns evident among cebines, *Saguinus* and all of the relevant fossils, such as *Branisella* (Figure 8). The condition in *Micodon*, which is also quite distinctive, may therefore represent still another form of hypocone development in callitrichines. A point of functional interest is that *Micodon* may exemplify a small platyrrhine with a fairly well developed hypocone cusp. This is not in accord with allometric models that postulate a linkage between the absence of a hypocone and small body size in living callitrichines (see Hershkovitz, 1977).

The precise affinities of *Micodon* are clearly difficult to discern. Small body size is one of the cardinal derived features of the known callitrichines, although there has perhaps been some overemphasis of its significance. Not only is there significant overlap between their size and that of cebines, such as *Saimiri* (e.g., Rosenberger, 1983), but Ford (e.g., 1986*b*, 1990) and Rosenberger (in press) both propose independently that some callitrichine lineages have experienced body size increases. Further study of the premolar, which resembles *Leontopithecus*, for example, and is far smaller than those of other La Ventan primates, and the upper incisor, which is an I^2 rather than an I^1 as reported, is necessary.

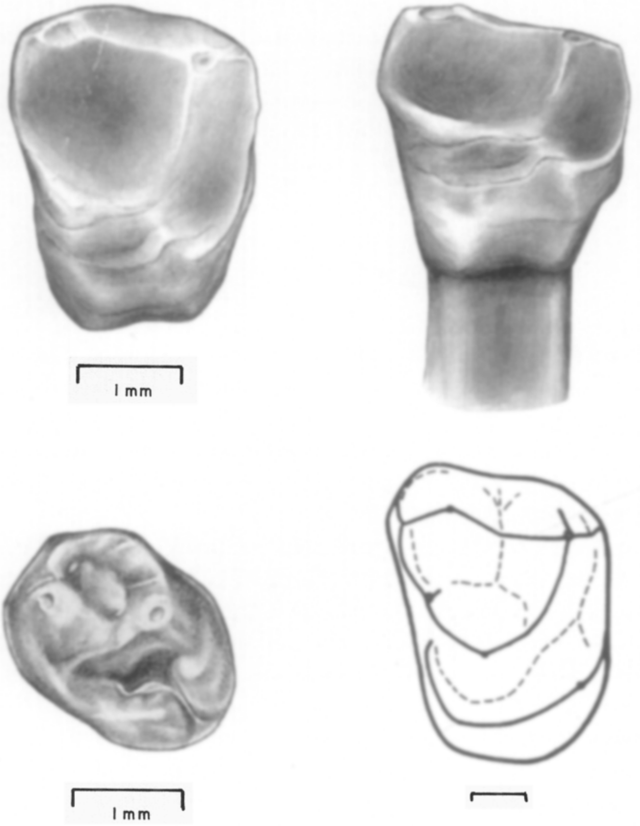

Figure 5. Upper left molar of *Micodon kiotensis* (top) in occlusal and lingual views; lower left premolar of same (bottom left) and upper left molar of *Dolichocebus gaimanensis* (bottom right), redrawn stereoptically from stereophotograph [Figure 6] in Fleagle & Bown (1983).

Nevertheless, the very small size of *Micodon* may be an indicator that it is a callitrichine. An alternative might be that it is a small cebine, but the evidence here is not compelling either.

Dolichocebus gaimanensis

Kraglievich (1951) presented the first comprehensive discussion of the skull of *Dolichocebus*, a relatively complete but somewhat distorted, edentulous specimen from the late Oligocene Colhuehuapian deposit at Gaiman, Argentina. New specimens from the same locality (Fleagle & Bown, 1983), including numerous isolated teeth and an astragalus, have recently been recovered. Bordas (1942) described the skull as an alouattine, whereas Kraglievich (1951) allocated it to the Callitrichidae.

Kraglievich's (1951) assessment was based upon general cranial features and the dental formula, which he interpreted as having only two upper molars. Hershkovitz (1970) noted that the correct count was three molars; a small third molar was broken away from the skull, along with the pterygoid region and posterior maxilla. The new dental material (Fleagle & Bown, 1983) includes an M^3 that fits well with the type skull. Hershkovitz (1970) suggested that *Dolichocebus* had affinities with *Homunculus* and placed the genus in Homunculidae (1977). He later (1982) criticized Rosenberger's (1979*a*) interpretation of

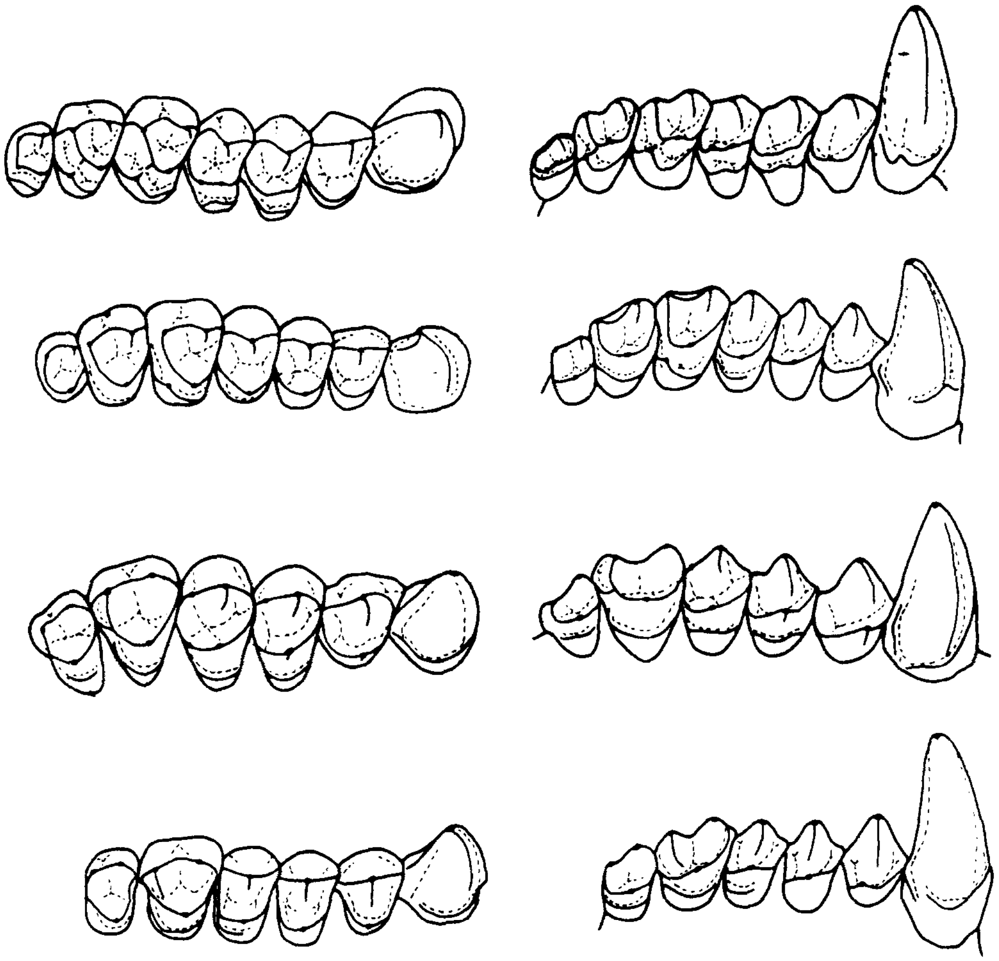

Figure 6. A morphocline of selected cebid molar morphologies. Occlusal (left column) and three-quarter lingual (right column) views of upper right canines and postcanines of (top to bottom rows) *Saimiri sciureus*, *Callimico goeldii*, *Leontopithecus chrysomelas* and *Saguinus* sp., all drawn to approximately same length.

Dolichocebus but gave no indication of a revised taxonomic placement, other than to say that the genus is "isolated" among the known platyrrhines. Ford (1986*b*) allocated *Dolichocebus* to a "plesion", a rankless category outside of any of the named monophyletic groups.

Rosenberger (1979*a*) and Fleagle & Rosenberger (1983), on the basis of the cranial evidence, argued that *Dolichocebus* was a cebine, most closely related to *Saimiri* and thus to *Neosaimiri* as well. Derived features linking the fossil with cebines include a dolichocephalic braincase, narrow interorbital pillar, relatively short and narrow nasal bones, a possibly inclined ectotympanic (preserved in the right ear region) and a convex glabella. Derived characters potentially aligning the genus with *Saimiri* include: a probably vaulted frontal, elongate descending interorbital process of the frontal, a fenestrated interorbital septum (but see Hershkovitz, 1982), a relatively large frontal lobe and a sharply delimited Sylvian sulcus. The new molar specimens attributed to *Dolichocebus* species (Fleagle & Bown, 1983) display the basally wide crowns typical of *Saimiri* and a roughly similar—but probably more primitive—crown pattern, with a moderately large, low hypocone (Figure 5). Fleagle (1985) noted that the talus lacked the derived features of callitrichines, pitheciines or atelines and resembled *Saimiri*, *Aotus* or *Callicebus*. Gebo & Simons (1987) identified resemblances shared with *Cebus*.

At present, therefore, it is most likely that *Dolichocebus* is not a callitrichine but a cebine. Its face is relatively larger than in *Saimiri* or *Cebus* and the apparent convergence of the anterior dental arcade, emphasized by Hershkovitz (1982), also contrasts with them. These features together may indicate that *Dolichocebus* preserves some ancestral gnathic characters of the subfamily. If so, they imply that the squared anterior jaw of *Cebus* and *Saimiri*, possibly a correlate of their shared derived, large, highly dimorphic maxillary canines and broad anterior premolars (see Rosenberger, 1979*b*), is evidence of a closer relationship between *Saimiri* and *Cebus* than between *Saimiri* and *Dolichocebus*, contrary to what is argued above. An alternative is that some facial abbreviation occurred in parallel in *Cebus* and *Saimiri*, or that the facial structure of *Dolichocebus* is somewhat autapomorphic.

Soriacebus ameghinorum

Soriacebus ameghinorum is an exciting new find from the Santacrucian middle Miocene of Argentina (15–18 Ma; MacFadden, 1990). In initially describing the species, Fleagle *et al.* (1987; see Fleagle, 1990, on a second species) did not allocate it to a suprageneric taxon, arguing that its unusual morphology did not correspond closely with any of the available taxa. They emphasized a variety of dental features, especially the tall procumbent lower incisors, deep V-shaped mandible and small, "marmoset-like" cheek teeth, holding that *Soriacebus* shared them unevenly with two separate groups of platyrrhines, the callitrichines and pitheciins. Kay (1990) also discussed the relationships of *Soriacebus*, concluding that incisal resemblances to callitrichines are convergent and that the genus is phyletically the most primitive of the entire platyrrhine radiation. Another logical solution was rejected that would be in accordance with the notion of Luchterhand *et al.* (1986), that *Soriacebus*, callitrichines and pitheciines are a monophyletic group, based upon sharing of reduced $M_{1,2}$ hypoconulids and a hypoconulid/entoconid sulcus, in addition to the phenetic resemblances in anterior dentition and arcade shape noted by Fleagle *et al.* (1987), such as the tall incisors and V-shaped jaws.

In our view, *Soriacebus* shares a pattern of resemblances with pitheciins which does not occur among other platyrrhines. More importantly, these features are functionally integrated elements of a hard-fruit husking, and probably seed predation, feeding complex (see Ayres, 1989). In contrast, the idea that *Soriacebus* resembles callitrichines (Fleagle *et al.*, 1987) or represents a suite of primitive platyrrhine characters approximating the platyrrhine dental morphotype (Kay, 1990), tends to be based either upon traits isolated in different parts of the dentition, or upon superficial resemblances to the dentally derived callitrichinans and to Fayum primates, respectively. Not only is this an unlikely duality, but under any circumstances such isolated traits would be of lower phyletic weight than definable structural patterns. Nevertheless, the potentially significant callitrichine-like features of *Soriacebus* need to be evaluated here (see also Kay, 1990).

Among the most important features are jaw shape and incisor morphology (Figure 7). In callitrichines, a V-shaped symphyseal region combined with high-crowned, staggered incisors occurs only in *Callithrix* and *Cebuella*. Although there has been debate about the polarity of these traits (e.g., Rosenberger, 1977; Hershkovitz, 1970, 1977), the evidence strongly favors the idea that this dental pattern is a highly derived, bark-peeling adaptation (e.g., Rosenberger, 1978*a*). Thus the height of the incisor crowns is functionally related to the pointed (flexed) apical margin, strongly recurved crown profile, staggered emplacement, transversely compressed symphysis, reduced lingual enamel, hypertrophic buccal enamel, caniniform lateral incisors, etc. It is also of interest that: (1) this pattern occurs only among the smallest platyrrhines; (2) the canines are not relatively more enlarged than is typical for callitrichines; and (3) the jaws are not especially deep anteriorly and tend to get shallower from front to back before expanding in the angular region.

In *Soriacebus*, on the other hand, the jaw is relatively deep at the symphysis and its depth increases posteriorly. The shafts of the lower incisors (at least half their crown appears to be preserved; see also Fleagle, 1990) are straight rather than recurved. The I_2 root shows no indications of a heteromorphic, canine-like anatomy but is identical to I_1. $I_{1,2}$ roots appear to be greatly enlarged, showing a smooth cementum-enamel transition near the cervix rather than a basal enlargement or cingulum. The lower canine is massive at the base, with a large, oval (as opposed to a laterally compressed) cross-sectional area, and does not resemble the adjacent I_2. None of these details can be matched among callitrichines. All are unequivocally derived characteristics of pitheciinans (living pitheciins plus *Cebupithecia*). Thus, the anterior teeth of *Cebuella* and *Callithrix* may resemble *Soriacebus* in superficial ways, as Kay (1990) also argued, but the fossil conforms to a functional pattern of resemblances that is restricted in distribution, and one of the most unique patterns seen among modern primates.

The massive *Soriacebus* canine is followed by a tall, posteromedially canted P_2 which carries a strong bulge of buccal enamel at the base of the crown (Figure 7). This pattern serves to align and strengthen the P_2 for honing a large C^1. As mentioned above, it is one of a number of derived C^1/P_2 honing arrangements among platyrrhines. The condition of *Soriacebus* is uniquely shared with pitheciinans, although C_1 retains a more primitive shape and orientation.

An important distinguishing feature of the mandible of *Soriacebus* is the compressed symphysis and staggered incisors. The fact that the fossil's incisors may be more staggered than in *Pithecia*, *Chiropotes* or *Cacajao*, and the jaw much narrower anteriorly than in *Cebupithecia* and the others, should not negate the weight of the derived characters just discussed. Rather than simply explaining these differences as autapomorphies of the genus, we propose that this unexpected morphology is consistent with models of the evolution of the platyrrhine dentition (e.g., Rosenberger, 1977, 1979*b*) and tends to reinforce the suggestion that anteriorly convergent jaws, as in *Homunculus*, are ancestral in pitheciines (and platyrrhines generally).

The squared-off, U-shaped arcade of pitheciinans, which is derived and related to a biomechanically advantageous positioning of the cheek teeth (Rosenberger, 1979*b*), is also a correlate to a radical canine morphology, i.e., their enlargement, triangular cross-section, laterally splayed emplacement and large incisor/canine diastemata. We suggest that the broadening of the anterior jaw of modern pitheciinans may have involved a retraction and transverse realignment of the incisor alveoli from a condition not unlike the one in *Soriacebus*, as bicanine width increased to accommodate changes in the lower incisor and especially the occlusion of the modified, splayed upper and lower canines. Therefore, the condition in *Soriacebus* possibly represents the ancestral pattern, preadaptive in presenting the basic design of a pitheciinan P_2 and in the configuration of tall, compressed lower

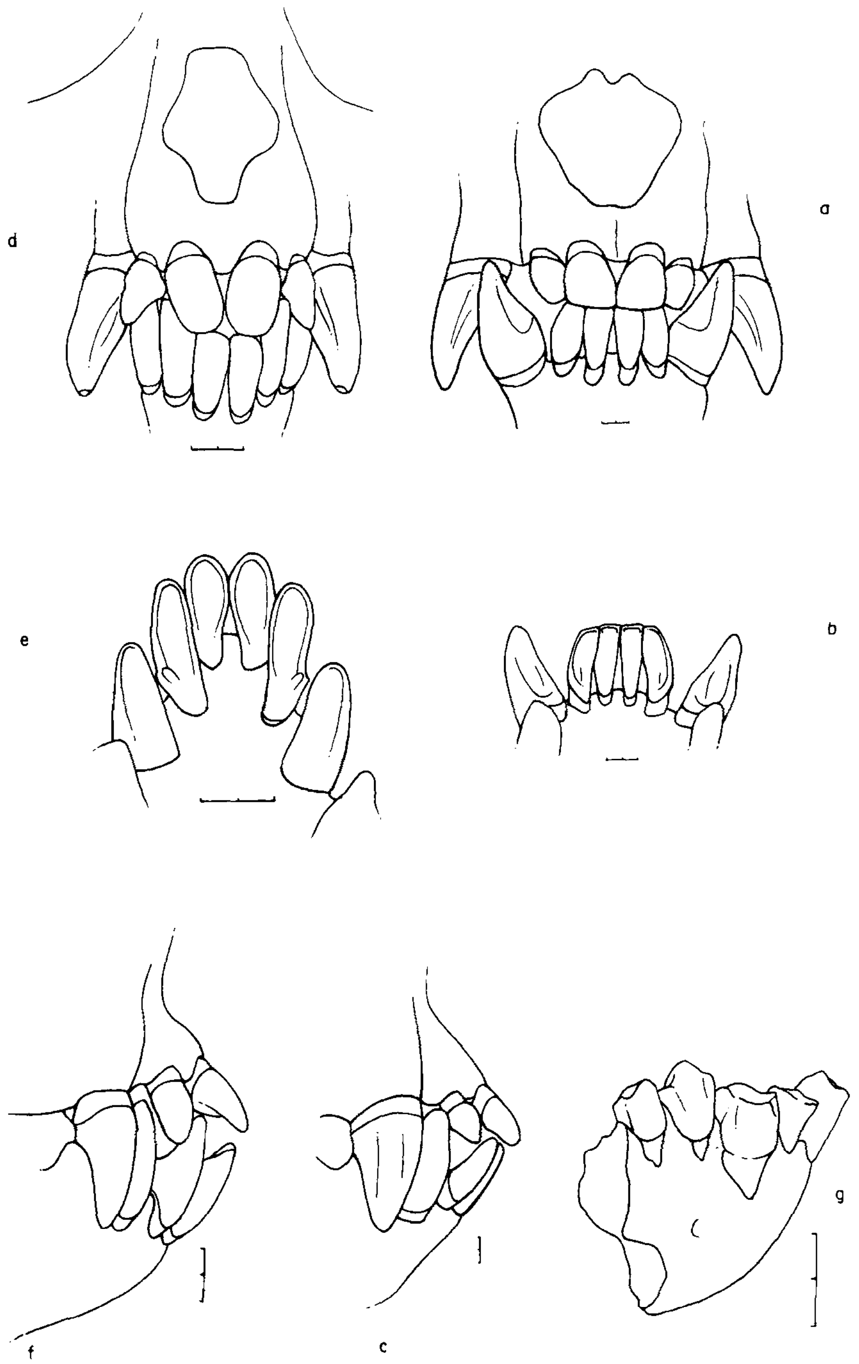

Figure 7. Anterior dentitions of *Pithecia pithecia* (*a,b,c*) and *Callithrix jacchus* (*d,e,f*) compared with a lateral view of *Soriacebus ameghinorum* (*g*). Scale divisions represent 1 mm. Drawings show frontal (*a,d*) and lateral views (*c,f*) of occluded anterior teeth, and lingual (*b,e*) and lateral (*g*) views of lowers. Note the non-recurved, slender incisors of *Pithecia*; the back-tilted, enlarged P_2, massive C_1 and anteriorly deep jaw of *Soriacebus*; the huge diastemata and distinct entocristid on C_1 of *Pithecia* (frontal and lingual views).

incisors with large, deep roots, the latter almost certainly being functionally continuous with those of pitheciinans.

On the lower molars, the development of distinct hypoconids and entoconids in the talonid is quite unlike callitrichines, where the cusps are inconspicuous, as previously mentioned. These relate to occlusion with an expanded talon basin on the uppers, as found among pitheciinans and in *Soriacebus*, which, at first glance, appear to have small hypocones but actually have large talon basins, as do pitheciinans. The lingually large, squared upper premolars also align *Soriacebus* with pitheciinans, resembling *Cebupithecia* in retaining the cingulum but also modern saki-uakaris in the incipient development of a large distal fovea. In callitrichines, of course, the talon region of the molars (Figure 6) is usually inconsequential, as the hypocone tends to be reduced to a distal cingulum.

In our view, *Soriacebus* is more closely related to pitheciinans than to any other group, which justifies placing them all in a monophyletic tribe, Pitheciini (Table 1). *Soriacebus*, comprising a primitive subtribe of the pitheciins, Soriacebina, represents the first branch of this monophyletic taxon and retains a number of ancestral dental features that later became modified in the last common ancestor of the other subtribe, Pitheciina. Although bark prising for wood-boring insects and/or gums, and a callitrichine-like diet containing many invertebrates as well as fruit and possibly exudate (see Fleagle *et al.*, 1987) cannot be ruled out for *Soriacebus*, there are no living ecological analogs of exudate eaters that occur at the body size Fleagle *et al.* estimated for *Soriacebus ameghinorum*, 1500–2000 g. The morphological continuities spanning the other pitheciinans, on the other hand, make it more likely that a pitheciin-like feeding adaptation prevailed, but without the fruit-husking lower canines.

Branisella boliviana

Because it is the oldest fossil platyrrhine, approximately 26 Ma (e.g., MacFadden, 1990), this Deseadan form from La Salla, Bolivia, earned much attention since the type maxilla was described by Hoffstetter (1969). In total there are five primate specimens from the Salla deposits (Hoffstetter, 1969; Rosenberger, 1981; Wolff, 1984; MacFadden, 1990), all at least provisionally allocated to *B. boliviana*. However, Rosenberger *et al.* (in preparation) are currently describing some of these as a second genus whose morphology has relevance to the topic of callitrichine evolution. In dental dimensions, all the Salla material is similar in size to *Leontopithecus chrysomelas* and *Callimico goeldii*, although both of these modern species differ from the Deseadan primates in exhibiting more posterior dental reduction.

There are a number of important differences distinguishing the newer specimens reported by Wolff (1984) from those previously described (Figure 8). Clearly, these specimens do not belong to the same individual, as some (e.g., Fleagle, 1988) have thought. For example, the upper molars are more triangular in shape, producing larger interproximal embrasures, and their mandibles are far shallower and more gracile despite the fact that molar size is similar. The lingual aspect of the upper molars of this new form appears to be reduced, with a small hypocone, a reduced protocone (possibly), no more than a sidewall sulcus to offset protocone and hypocone, and more gracile molar roots.

Although *Branisella* appears to be quite primitive in its morphology (e.g., Rosenberger, 1981), and perhaps outside of the monophyletic cebid–atelid clade, this new Deseadan form, especially because of its rather triangular upper molars, suggests the possibility of a relationship with callitrichines. Before considering this point, it is important to clear up a misperception that has crept into the literature regarding the phenetics and homologies of

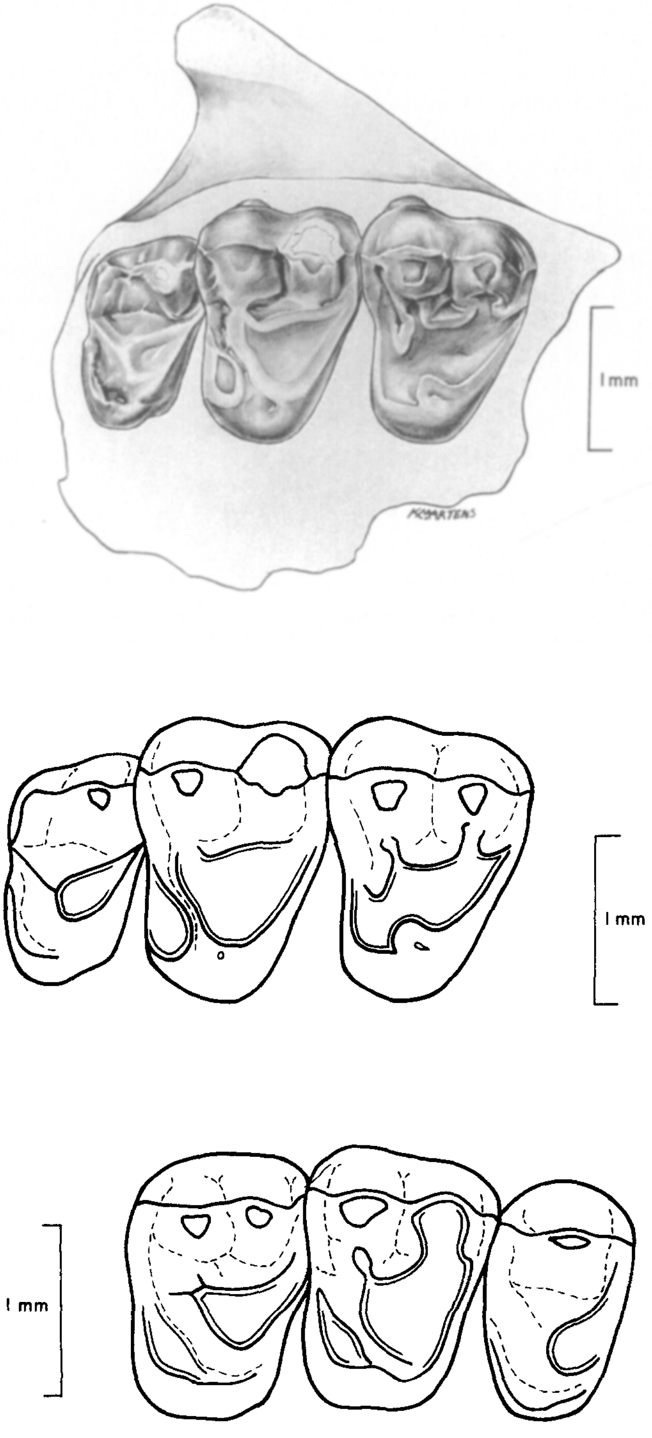

Figure 8. Occlusal views of Deseadan primates. Right M^{1-3} of UF (Univ. of Florida) 27887 (middle) compared with P^4–M^2 of *Branisella boliviana* holotype photographically reversed.

Branisella. Several workers (e.g., Rosenberger, 1977, 1979*b*; Hershkovitz, 1977), have compared the molars of *Branisella* with *Samiri* (see Figure 6), implying that they are structurally similar and, to an extent, indicative of a *Saimiri*-like ancestral platyrrhine molar morphotype. These generalities might be misleading. The hypocone and lingual region of all *Saimiri* are secondarily enlarged. What remains primitive about its morphology is the low position of the cusp relative to the trigon. In *Branisella* the hypocone is much smaller, roughly comparable in size to that of *Dolichocebus* among extinct forms and to *Callimico* among the living. Thus the *small* and *low* hypocone pattern of *Branisella* is the morphotypic pattern.

The upper first and second molars of the new material, especially UF 27887, are intriguingly "triangular" in crown view (Figure 8). On the M^2, the hypocone is hardly differentiated from the lingual cingulum. Although (mainly) neontological studies have suggested that a small to moderate hypocone is ancestral in platyrrhines (e.g., Rosenberger, 1977, 1979*b*), a view that seems to be achieving consensus (e.g., Ford, 1986*b*; Kay, 1980), this model still does not simplify the problem of distinguishing between the morphotype anatomy of the cebid–atelid common ancestor and that of platyrrhines generally. This difficulty is especially confounding if one assumes that *Branisella* is dentally more primitive than all the post-Deseadan taxa, such as *Dolichocebus* and *Tremacebus* (e.g., Rosenberger *et al.*, in preparation). This means that the triangular occlusal structure of UF 27887 may be interpreted as either more primitive than *Branisella* or more derived. If the latter, UF 27887 may represent a stage in hypocone *reduction* that is postulated to have occurred in the origins of the callitrichines (e.g., Rosenberger, 1977 *et seq.*).

On the basis of the limited data, it is difficult to refute this hypothesis completely. It is generally consistent with some characters of the lower molars. For example, in most primitive primates with a small hypocone, such as the omomyids, either the paraconid or a small trigonid occludes into the maxillary interproximal molar embrasures during centric occlusion. In *Callimico*, as in other platyrrhines, the paraconid is typically absent but there is a relatively large trigonid which replaces it. Its function is to occlude with the talon region of the preceding upper molar, now occupying the space of the archaic ambrasure. This is one of the significant reasons why hypocone loss is suspected to have occurred in callitrichines: the embrasure is large but the paraconid is missing and the trigonid is large. In the new Deseadan species, the quadrate, relatively well developed trigonid seems to resemble other platyrrhines in its proportions, indicating that a platyrrhine occlusal pattern obtained in conjunction with the triangular upper molars; occlusion in this species may have been callitrichine-like.

Several points argue against this interpretation, however. (1) The uppers of both Deseadan primates retain primitive features, such as a metaconule fused into the base of the metacone that is lost in all later platyrrhines and would not have been present in the callitrichine morphotype. (2) As MacFadden (1990) pointed out, the lowers of the new species are rather high-crowned and also have strongly conical cusps, unlike the poorly differentiated cusps of callitrichines. (3) M_2 and M_3 are subequal in length, and there are no functional signs of the M_3 reduction that is to occur later in cebines as a derived preadaptation to the strongly reduced M_3 of ancestral callitrichines.

Thus it is unlikely that the triangular molars of the new Deseadan primate are homologous with callitrichines as a stage of posterior dental reduction. Still, it remains a challenge to distinguish between a small hypocone that has undergone reduction from a small hypocone that has not yet enlarged, which is presumably the case in *Branisella*.

Finding direct evidence for such important transformations will bedevil us until the paleontology of platyrrhines is much better known.

Summary and conclusions

A surprisingly large number of fossil New World monkeys have been connected with callitrichines. Some have been classified as members of the subfamily, others promoted as potential relatives linking them with other platyrrhines, still others seen as confusing taxa that share (derived) callitrichine-like features but do not align them convincingly.

The possibility that callitrichines inhabited the Caribbean during the Pleistocene, a hypothesis based on cladistic analyses of postcranial remains as well as the presence of the two-molared *Xenothrix* (Ford, 1986*a*; see Williams & Koopman, 1952), is not supported by dental evidence (Rosenberger, 1977). *Xenothrix* is probably a pitheciine (see Table 1) most closely related to *Callicebus* among the living forms. "*Saimiri*" *bernensis* is a cebine (Rosenberger, 1978*b*; MacPhee & Woods, 1982; see also Ford, 1990).

There are indications, however, that callitrichines existed on the continent at the Colombian Miocene site of La Venta, 12–15 Ma. *Micodon*, a poorly represented fossil, is a very small form approximately the size of *Callithrix aurita* of eastern Brazil. Small size favors its interpretation as a callitrichine, and there is nothing in its morphology that implies an alternative genealogical hypothesis (Setoguchi & Rosenberger, 1985). However, the most relevant specimen is a single upper molar, with a low, moderate-sized hypocone. If *Micodon* is a callitrichine, this implies that the loss of hypocones in platyrrhines was not rigidly controlled by body size reduction (see Hershkovitz, 1977). Losses and gains, enlargements and reductions are to be expected, given the amount and style of variation seen in living callitrichines and cebines.

Also from La Venta is *Mohanamico*, first described as a possible primitive pitheciine (Luchterhand *et al.*, 1986) and recently claimed to be the senior synonym (Kay, 1988, 1990) of *Aotus dindensis* (Setoguchi & Rosenberger, 1987). The differences between these forms are here clarified, with an emphasis upon their contrasting anterior teeth and mandibular morphologies. *Mohanamico* shares strong resemblances with callitrichines that are probably synapomorphic. Most significant is the large-caliber, tall lower canine that is combined with an unmodified P_2 canine occlusion/honing platform (for the inferred, correspondingly tall upper canine). It is important to note that a large C_1 is rare in omomyids and is not expected in the ancestral platyrrhine.

Regardless of the sex of this specimen, this pattern is evidence of callitrichine affinities, for they are the only platyrrhines of this size class to have enlarged canines in either or both sexes without a correlatively modified P_2 honing structure. If one assumes that the type of *Mohanamico* is female, then the morphology closely matches the phenetics of callitrichines, the only platyrrhines in which females of the same approximate body size have enlarged lower canines of this sort. Pitheciin females may also have large lower canines, but they are much larger in body size and have a radically different morphology. If the specimen is male, then the canine/premolar complex of a male *Mohanamico* was entirely unlike that of other platyrrhines. The other relevant patterns are: (1) large-canined, dimorphic cebines or atelines, which involve honing specializations on P_2; (2) large-canined, monomorphic pitheciines, which have another set of specializations on P_2; or (3) small- and moderate-canined, monomorphic forms like *Aotus* and *Callicebus*, which also lack modified honing premolars. In either case, tall lower canines associated with a relatively simple anterior premolar seems to be derived for callitrichines, including *Mohanamico*. The mesially flaring lower canine and slender, moderately tall lateral incisor also reflects a combination found among modern *Callimico*.

Neosaimiri, a third La Venta primate historically connected with callitrichines (Stirton, 1951), is a very close relative of *Saimiri* (Stirton, 1951; Hershkovitz, 1970; Delson & Rosenberger, 1984), a cebine. *Dolichocebus*, also mentioned as a possible callitrichine (Kraglievich, 1951) on the basis of an erroneous interpretation of its dental formula (Hershkovitz, 1970), is phyletically aligned with the *Neosaimiri–Saimiri* stock. It is far too distinct to provide much insight into the morphological evolution of callitrichines. However, in keeping with the hypothesis that cebines and callitrichines are a monophyletic group (Rosenberger, 1979*a,b*, 1981, 1984), it suggests that other relatives of the callitrichines were in existence by then. The branch which gave rise to callitrichines must have appeared prior to the 18–19 Ma Colhuehuapian Land Mammal Age (MacFadden, 1990) associated with *Dolichocebus*, but not necessarily the callitrichine lineage *per se*; a persistently conservative cebid species could have lived on past the differentiation of *Dolichocebus* before differentiating into callitrichines. The Deseadan mammal fauna (26 Ma) from La Salla, Bolivia, includes at least two primate species. New fossils described by Wolff (1984; see also MacFadden, 1990) differ morphologically from material allocated to *Branisella boliviana* and resemble callitrichines in having relatively triangular upper molars. However, this similarity appears to be convergent with, rather than homologous to, the callitrichine pattern.

The possibility that callitrichines had a relatively early origin within the radiation of New World monkeys is in accordance with the view that several of the platyrrhine lineages emerged early and were long-lived (Rosenberger, 1979*a*; Delson & Rosenberger, 1984; Setoguchi & Rosenberger, 1987). It does not however, alter the prevailing opinion (e.g., Rosenberger, 1977, 1983; Ford, 1980; Kay, 1980) that callitrichines are a modified stock rather than a retentitive one (e.g., Hershkovitz, 1977).

Thus, callitrichines may be represented by two species in the 12–15 Ma La Venta fauna, *Micodon kiotensis* and *Mohanamico hershkovitzi*. The morphology of the latter suggests that it may be a member of the callimiconin lineage, which retains three molars and the best developed hypocones (although this is possibly secondary). The small body size of *Micodon*, and some aspects of premolar form, are weaker links with callitrichines. If *Micodon* is not a callitrichin but of another lineage, it indicates that a wide range of body sizes existed among other platyrrhines by the middle Miocene. Little can be said of the dietary adaptations of either *Micodon* or *Mohanamico*, other than gross categorizations of their dentitions as being of the frugivorous-insectivorous pattern, the primitive feeding strategy for callitrichines (Rosenberger, 1980).

The fossil record still provides no historical evidence for body size reduction (see Sussman & Kinzey, 1984) in the origin of the subfamily, although we suspect that it was important in the adaptive radiation of callitrichins (e.g., Rosenberger, 1977, 1983) and even central to the callitrichinans (see Rosenberger, in press), especially *Callithrix* and *Cebuella*. The "dwarfism" issue is still largely a matter of speculation, with few indications of the *scale* of body size reduction that would have been involved. The earliest known platyrrhine, *Branisella*, currently our best indicator of body size for ancestral platyrrhines, has dental dimensions comparable to the largest callitrichins, such as *Leontopithecus chrysomelas* (Rosenberger & Coimbra–Filho, 1984). Among the modern callitrichines, the first-branching clade, represented by *Callimico goeldii*, is smaller in size than callitrichins, such as *Saguinus* and *Leontopithecus*. It is also the most primitive dentally, in retaining a three-molar dental formula. But, is the body size of *Callimico* (ca. 500 g) ancestral for the subfamily, or has this lineage also reduced in size from a larger common ancestor (without attendant loss of M3)? Thus, it is not clear that proto-callitrichines were larger than extant members of the radiation, nor how many times body size decreased or increased during callitrichine evolution.

The notion that hypocone reduction was an intrinsic aspect of the size reduction process linked with callitrichine origins (see Ford, 1980; Rosenberger, 1977, 1983; Sussman & Kinzey, 1984) is also unsupported by the dental evidence. If *Micodon* indeed proves to be a callitrichine, it would represent one of the smallest of the known forms, yet its hypocone is far less reduced than in any of the modern species. Furthermore, since other possibly dwarfed platyrrhines, such as *Saimiri* (note the pattern of enlarged relative brain size, inclined ectotympanics, abbreviated face, vaulted/rounded neurocranium, etc.), have rather enlarged hypocones, this type of "simplification" of platyrrhine molars is not necessarily linked with body size reduction. The new Deseadan primate also appears to have independently evolved hypocone reduction without wholesale reduction in the proportions of the molar battery. Thus there are different functional patterns that can be associated with the loss of this cusp.

We should not be surprised to find more callitrichine lineages uncovered as the fossil record grows. What is most apparent from this review is that callitrichines will remain an enigmatic group of New World monkeys until their fossil record improves considerably, and that neontological and paleontological data need to be combined without emphasis on either source if we are to untangle their evolutionary history.

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