Laventiana annectens, new genus and species: Fossil evidence for the origins of callitrichine New World monkeys

(Platyrrhines/La Venta/marmosets/Miocene)

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ABSTRACT A previously unidentified middle Miocene primate from the La Venta deposits of Colombia is intermediate between squirrel monkeys (Saimiri) and callitrichines (marmosets and tamarins) in the morphology of the lower molars, mandible, and talus. Laventiana annectens is closely related to Saimiri and to Cebus (capuchin monkeys) yet resembles the probable callitrichine morphotype, demonstrating that archaic relatives of a Saimiri-like stock were suitable structural ancestors for the enigmatic callitrichines. Laventiana is also more primitive than Saimiri (= Neosaimiri) fieldsi from the same fauna, further increasing the likelihood that the latter is a lineal ancestor of modern squirrel monkeys.

Less is known about the evolution of the small-bodied, clawed marmosets and tamarins—the callitrichines—than any other major group of extant anthropoids (1). Incongruous morphological (2–4) and biochemical studies (5) and a poor fossil record (1, 6) have left uncertain their phylogenetic position among New World monkeys. A newly discovered fossil from the Miocene of Colombia, represented by a lower jaw and talus, pertains to the question of callitrichine origins. Although cladistically related to extant cebines (Cebus and Saimiri), it is intermediate between callitrichines and Saimiri in molar, mandibular, and talus morphology and demonstrates that archaic relatives of squirrel monkeys are suitable structural ancestors for this enigmatic radiation of miniature anthropoids.

Anatomists such as T. H. Huxley (7), Beattie (8), Le Gros Clark (9, 10), and their followers (2), impressed by the seemingly primitive features of most modern callitrichines (Callithrix, Cebuella, Leontopithecus, Saginus, Callimico), including small body size, three-cusped upper molars, clawed and nonopposable digits, plural litter sizes, poorly convoluted brains, and reliance on olfaction, related the origins of callitrichines to tarsioids (8) or to a basal anthropoid stock (9). After a long period during which callitrichines were considered separate from the other platyrhines, Oldfield Thomas (ref. 11, see p. 132–133) erased the perceived morphologic and taxonomic barriers by demonstrating that a newly discovered Amazonian form, Callimico goeldii, was an intermediate link between the two groups:

It is to be noted that the difference in structure between molars with hypocones and those without is not so abrupt as it sounds, for there is almost a perfect series of gradations from (1) the marmosets, which have no trace of hypocone, through (2) Callimico, which has a slight rise in the cingulum that might be called a potential hypocone, to (3) Saimiri, which has small and simple hypocones, and is itself again separated from (4) Cebicus and other monkeys which have complicated square molars with large hypocones and connecting commissures.

In arranging the dental character states of platyrhines into a morphocline, Thomas laid the groundwork for new evolutionary interpretations. Diagnostic callitrichine features are now considered derived rather than primitive conditions, based upon comparative anatomy (12, 13) and allometric (14, 15), ecological (3, 16, 17), and cladistic analyses (4, 18) of the living forms. This, in turn, has led to a variety of hypotheses regarding the phylogenetic origins (1, 18, 19) of callitrichines from within a monophyletic Platyrhini.

The new species described here presents a morphological pattern not seen among living platyrhines. It appears to be the first record to our knowledge of an intact lower tooth row of primitive cebine design. The morphology of its lower molars completes a morphocline parallel to Thomas’ arrangement of the upper molars. In doing so, it provides fossil evidence corroborating the hypothesis that callitrichines are the sister group of cebines (20).

The fossil material, discovered in 1988, derives from the La Venta badlands of the Magdalena River Valley in west central Colombia. La Venta has produced the largest fossil vertebrate assemblage from northern South America (21) and the continent’s richest record of Tertiary primates (22–25). The specimens were discovered in the upper redbeds of the Villavieja Formation, which is overlain unconformably by the Mesa Formation. Radiometric dates for the latter provide a minimal geochronological age of >7.8 ± 0.5 meganannum (Ma; 10⁶ years) (Ma) (26) or >8.5 ± 0.4 Ma. A conservative age estimate of the other primate-bearing beds at La Venta is 12–15 Ma (27), although recent discoveries are reported to be slightly older (23).

SYSTEMATICS

Order Primates Linnaeus, 1758
Suborder Haplorhini Pocock, 1918
Infraorder Platyrhini E. Geoffroy, 1812
Superfamily Ateloida Gray, 1825
Family Cebidae Bonaparte, 1831
Subfamily Cebinae Bonaparte, 1831
Laventiana, gen. nov.
Laventiana annectens, sp. nov.

Type specimen. IGM-KU (Instituto Nacional de Investigaciones Geologico-Mineras/Kyoto University) 8801a, a young adult mandible preserving perfectly the right and left C–M₂ (canines through lower second molars) and alveoli for the incisors (I₁ and I₂) and third molars (M₃) (Fig. 1); IGM-KU 8801b, a right talus found in association with the mandible, presumably of the same individual.

Age and locality. Middle Miocene (Friarian land-mammal age) of the La Venta area; the Masato Site, in the upper redbeds (28) of the Villavieja Formation.
Etymology. *Laventiana*, after La Venta (the wind); *annectens*, L. ad-, towards + *nectens*, tying or connecting, in reference to the fossil's phylogenetic implications.

Diagnosis. A *Saimiri*-sized cebine characterized by the combination of acutely cusped postcanine crowns, relatively large broad P₂ (second premolar), and shallow mandibular corpus, differing from all known platyrhines in having a postentoconid notch on M₁,2, and further distinguished from *Saimiri* by a narrower P₃ and relatively longer and narrower M₁,2 (approximately 15%), the latter with incipiently developed buccal cingulids.

DESCRIPTION AND COMPARISONS

The morphology of C-P₄ (Fig. 1) strongly resembles the modern species of *Saimiri* and a Miocene species, also from La Venta, that has been synomnized recently into the same genus, *S.* (= *Neosaimiri*) *fieldsi* (29). As with all *Saimiri*, the lower canine of *Laventiana* is high-crowned, vertical, robust, and slightly recurved. P₂ is relatively massive, with a laterally canted protoconid apex, elongate canine honing blade, strong lingual cingulid, and distolingual cristid; P₃ is similar to P₂, only smaller and without the honing extension; P₄ is premo-

lariform, with a small metaconid and a short talonid heel. In contrast to the premolars, the molars of *Laventiana* lack the defining occlusal pattern of genus *Saimiri*. For example, the crown sidewall does not flare from cusp tip to cervix; the ectoflexid is small as the cristid obliquis is not sharply angled; the buccal cingulid is very small on M₁ and is only a tiny remnant on M₂. Measurements are given in Table 1. The molars of *Laventiana* are also slightly longer than in *Saimiri*; mandibular dimensions are somewhat smaller (29).

Like the premolar morphology, the talus of *Laventiana* is similar to modern cebines, especially *Saimiri*, in all features

<table>
<thead>
<tr>
<th>Table 1. Linear measurements (mm) of <em>Laventiana annectens</em></th>
<th>mandible* teeth</th>
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<tr>
<td></td>
<td>P₄</td>
</tr>
<tr>
<td></td>
<td>P₃</td>
</tr>
<tr>
<td>Length</td>
<td>2.7</td>
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<tr>
<td>Breadth</td>
<td>3.3</td>
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* tri, trigonid; tal, talonid.
* Mandible depth (below M₂) = 7.6 mm; mandible breadth (below M₂) = 2.9 mm.
The pattern appears to be of a functionally generalized type, indicating quadrupedalism with a substantial leaping element. It clearly lacks the derived pattern of traits characterizing the more scansional callithricines and climbing atelines or other individual genera, including the exceptionally long talar neck that characterizes living Saimiri. Thus, the phe- notypes of the talus of Laventiana are consistent with molar dentition in its nonderived structural intermediary with respect to cebines and callithricines.

**DISCUSSION**

The detailed resemblances of premolar pattern shared by Laventiana and Saimiri, which are not seen elsewhere among platyrrhines, make it highly likely that these genera are closely related. On the other hand, the fossil’s molars are more primitive than either Saimiri or Cebus. For example, they lack the derived thick-enamed bunodonty of Cebus and the broad trigonids, large eocotifexis, angular cristid obliquids, and prominent buccal cingulids of Saimiri. The one oclusal feature that argues against Laventiana being ancestral to Saimiri is the postentocindice notch. This is a unique specialization of the species. It does not appear in any other fossil platyrrhines, nor could we identify anything similar to it in a survey of 150 individuals representing the 16 modern New World monkey genera.

In lacking the major derived features of cebine ocluscal anatomy, Laventiana approximates the dental pattern of callithricines. Like marmosets and tamarins and unlike other platyrrhines of this size class, such as Callicebus, the fossil’s cu{sp}s are acute, the trigonids are elevated relative to the talonid, and the mandible is relatively shallow posteriorly. Additionally, Laventiana retains a third molar, and $M_2$ is relatively shorter mesiodistally (13%) than $M_3$. This suggests a reduction of the molar series from behind. Posterior reduction is characteristic of cebines, where $M_3$ is especially reduced in size, and of the dentally primitive callithricine Callimico, where $M_3$ is shorter still (Fig. 2).

Two other species from La Venta have been interpreted as callithricines, Micodon kiotensis and Mohanamico hershkovitzi (1), but neither have any evident implications for callithrinic origins. La Venta has preserved a remarkable and still expanding diversity of middle Miocene platyrhines, including one representative of each of the four extant subfamilies and, among them, at least two species congeneric with modern forms, Aotus dundens and Saimiri fieldisi (24, 29). The discovery of this new species represents to our knowledge the first linking of any two of these subfamilial clades with fossil evidence. Laventiana annectens empirically demonstrates that a morphology suitable to cebine ancestry is also suitable to callithrinic ancestry (Fig. 2), lending a certain taxonomic truth to the elegant cebine–callithrinic morphcline of Oldfield Thomas. Callithricines, whose ancestral affinities have remained anonymous despite extensive comparative research, probably evolved from a cebine relative prior to the middle Miocene.

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