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 talar 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, Saguinus, 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 platyrrhines, 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) *Callicebus* and other monkeys which have complicated

square molars with large hypocones and connecting commissures.

In arranging the dental character states of platyrrhines 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 Platyrrhini.

The new species described here presents a morphological pattern not seen among living platyrrhines. 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 uncomformably by the Mesa Formation. Radiometric dates for the latter provide a minimal geochronological age of >7.8 ± 0.5 megannum (Ma; 10^6 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 Platyrrhini E. Geoffroy, 1812
Superfamily Ateloidea 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–M_2 (canines through lower second molars) and alveoli for the incisors (I_1 and I_2) and third molars (M_3) (Fig. 1); IGM-KU 8801b, a right talus found in association with the mandible, presumably of the same individual.

Age and locality. Middle Miocene (Friasian land-mammal age) of the La Venta area; the Masato Site, in the upper redbeds (28) of the Villavieja Formation.
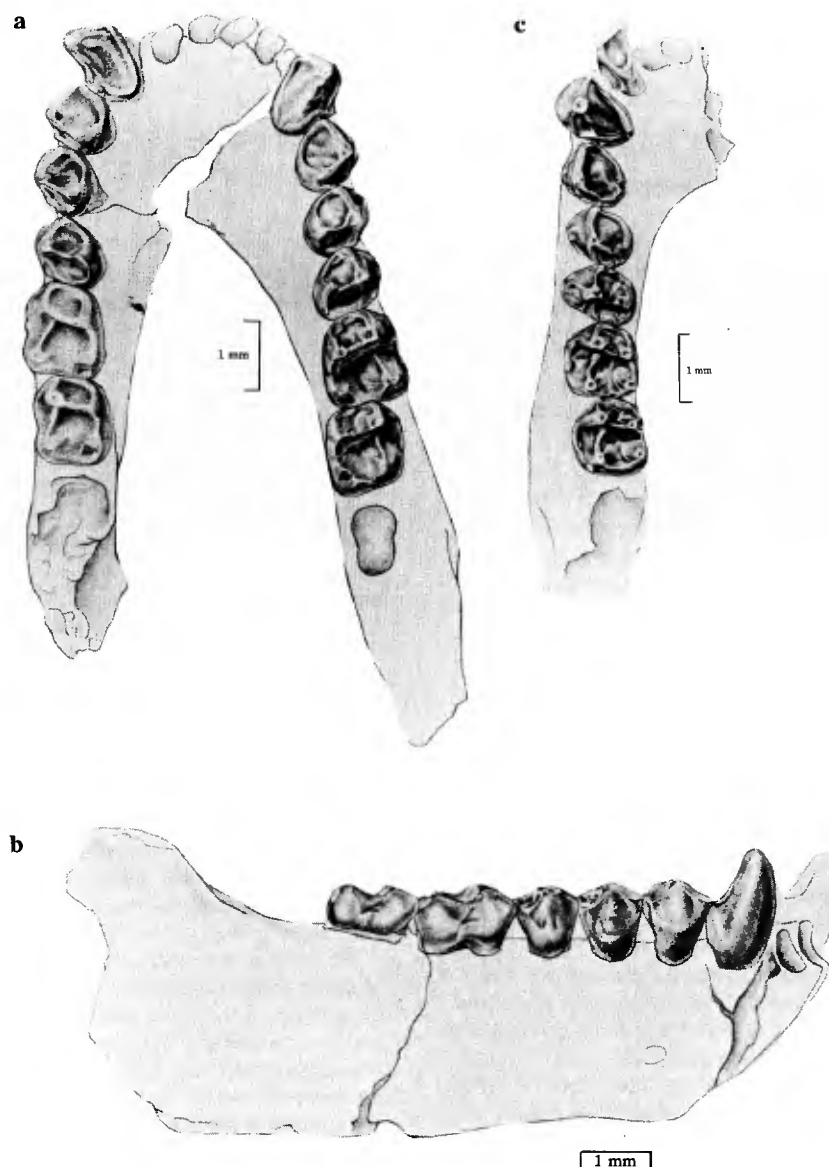
FIG. 1.   Occlusal (*a*) and lateral (*b*) views of IGM-KU 8801a, type specimen of *Laventiana annectens*. The mandible retains C–M$_2$, with preserved alveoli for I$_{1-2}$ and M$_3$. Note the postentoconid notch present on the molars. (*c*) Occlusal view of the left half of UCMP 39205, *Saimiri* (= *Neosaimiri*) *fieldsi*, also from La Venta, is included for comparison.

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 P$_2$ (second premolar), and shallow mandibular corpus, differing from all known platyrrhines in having a postentoconid notch on M$_{1-2}$, and further distinguished from *Saimiri* by a narrower P$_4$ and relatively longer and narrower M$_{1-2}$ (approximately 15%), the latter with incipiently developed buccal cingulids.

DESCRIPTION AND COMPARISONS

The morphology of C-P$_4$ (Fig. 1) strongly resembles the modern species of *Saimiri* and a Miocene species, also from La Venta, that has been synonomized 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. P$_2$ is relatively massive, with a laterally canted protoconid apex, elongate canine honing blade, strong lingual cingulid, and distolingual cristid; P$_3$ is similar to P$_2$, only smaller and without the honing extension; P$_4$ 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 obliquid is not sharply angled; the buccal cingulid is very small on M$_1$ and is only a tiny remnant on M$_2$. 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 1.   Linear measurements (mm) of *Laventiana annectens* mandible* teeth

	C	P$_2$	P$_3$	P$_4$ tri	P$_4$ tal	M$_1$ tri	M$_1$ tal	M$_2$ tri	M$_2$ tal
Length	2.7	2.4	2.2	1.4	0.8	1.4	2.0	1.1	1.9
Breadth	3.3	2.4	2.5	2.7		2.8	2.9	2.7	2.5

tri, trigonid; tal, talonid.
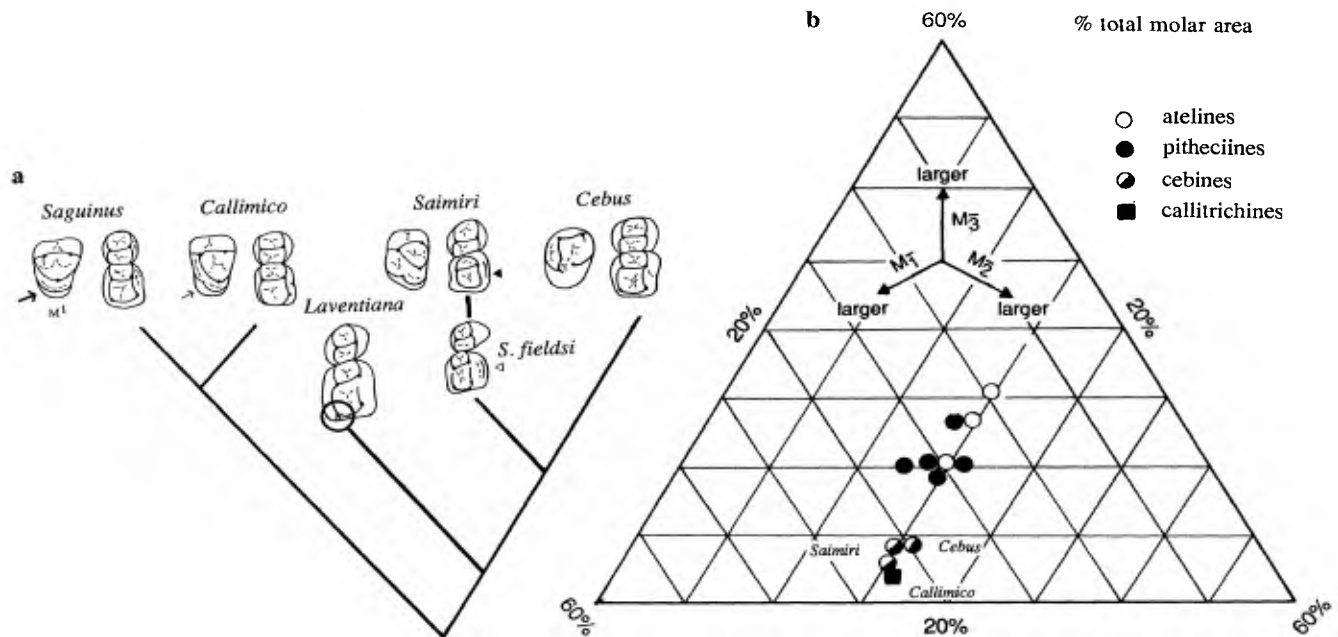*Mandible depth (below M$_2$) = 7.6 mm; mandible breadth (below M$_2$) = 2.9 mm.

FIG. 2. (a) Phylogenetic relationships of the fossils *Laventiana annectens* and *Saimiri fieldsi* and selected cebines and callitrichines. The most conservative position for *Laventiana* is shown. Schematics of right-cheek teeth illustrate the location of the postentoconid notch (*) in *Laventiana* and morphoclines in hypocone development and cingulid structure. Only a small hypocone cusp occurs in *Callimico* (thin arrow), reflecting the derived callitrichine pattern of cusp reduction that culminates in hypocone loss (*Saguinus*, thick arrow), opposite to the cebine trend toward hypocone enlargement. *Saimiri fieldsi* and modern *Saimiri* are shown as an ancestral–descendant lineage, highlighting the transformational enlargement of the buccal cingulid (arrowheads). (b) The ternary diagram plots the area (length × breadth) of each lower molar relative to the total molar area for three-molared platyrrhines. Like the callitrichine *Callimico, Saimiri* and *Cebus* have reduced third molars, a derived state foreshadowing complete loss of this tooth in the remaining callitrichines.

(30). 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 scansorial callitrichines and climbing atelines or other individual genera, including the exceptionally long talar neck that characterizes living *Saimiri*. Thus, the phenetics of the talus of *Laventiana* are consistent with molar dentition in its nonderived structural intermediacy with respect to cebines and callitrichines.

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-enameled bunodonty of *Cebus* and the broad trigonids, large ectoflexids, angular cristid obliquids, and prominent buccal cingulids of *Saimiri*. The one occlusal feature that argues against *Laventiana* being ancestral to *Saimiri* is the postentoconid 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 occlusal anatomy, *Laventiana* approximates the dental pattern of callitrichines. Like marmosets and tamarins and unlike other platyrrhines of this size class, such as *Callicebus*, the fossil's cusps 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_1. 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 callitrichine *Callimico*, where M_3 is shorter still (Fig. 2).

Two other species from La Venta have been interpreted as callitrichines, *Micodon kiotensis* and *Mohanamico hershkovitzi* (1), but neither have any evident implications for callitrichine origins. La Venta has preserved a remarkable and still expanding diversity of middle Miocene platyrrhines, including one representative of each of the four extant subfamilies and, among them, at least two species congeneric with modern forms, *Aotus dindensis* and *Saimiri fieldsi* (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 callitrichine ancestry (Fig. 2), lending a certain taxonomic truth to the elegant cebine–callitrichine morphocline of Oldfield Thomas. Callitrichines, 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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