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© 1991 S. Karger AG, Basel  
0015-5713/91/0564-0225\$2.75/0***Szalatavus atricuspsis*, an Early Platyrrhine Primate**Alfred L. Rosenberger<sup>a</sup>, Walter Carl Hartwig<sup>b</sup>, Ronald G. Wolff<sup>c</sup><sup>a</sup> Department of Anthropology University of Illinois at Chicago, Ill.;<sup>b</sup> Laboratory for Human Evolutionary Studies, Department of Anthropology, University of California, Berkeley, Calif.; Department of Zoology, University of Florida, Gainesville, Fla., USA**Key Words.** Paleontology · Evolution · Platyrrhines · Salla deposits · Cebidae · *Szalatavus* · Anthropoid**Introduction**

The Salla beds of west central Bolivia contain the earliest representatives of the platyrrhine radiation. Since primates were first discovered there in the 1960s [1], when the biostratigraphically-determined land mammal age (Descadan) of these deposits was considered to be basal Oligocene (35 million years) [2, 3], Salla has been valued as a locality that potentially could shed light on the origins of New World anthropoids [1, 4-9]. Recently, however, radiometric dates of  $26 \pm 1$  million years have been obtained and independently confirmed for the Salla deposits, thus reducing the once-accepted age by some 10 million years [10-12]. This chronological revision, coupled with the recognition of a second primate species diagnosed here, based largely on a re-evaluation of material previously published [13], indicates that this stage of platyrrhine evolution was considerably more complex than previously believed.

**Type Specimen**

UF (University of Florida) 27887, a right maxillary fragment with a portion of the P<sup>4</sup> root, moderately worn M<sup>1-3</sup> (length, width in mm = 3.1, 4.3; 3.0, 4.3; 2.1, 3.7, respectively) and part of the lateral orbital floor and face (fig. 1); UF 27888, a mandibular fragment of the same individual (fig. 2) preserving the posterior wall of the M<sub>1</sub> alveolus, M<sub>2</sub> (3.0, 2.7) and roots of M<sub>3</sub> (depth below M<sub>2</sub> = 5.5).

*Szalatavus atricuspsis*, sp. nov.*Szalatavus*, gen. nov.

Subfamily Branssellinae Hershkovitz, 1977

Family Cebidae Bonaparte, 1831

Superfamily Ateloidea Gray, 1825

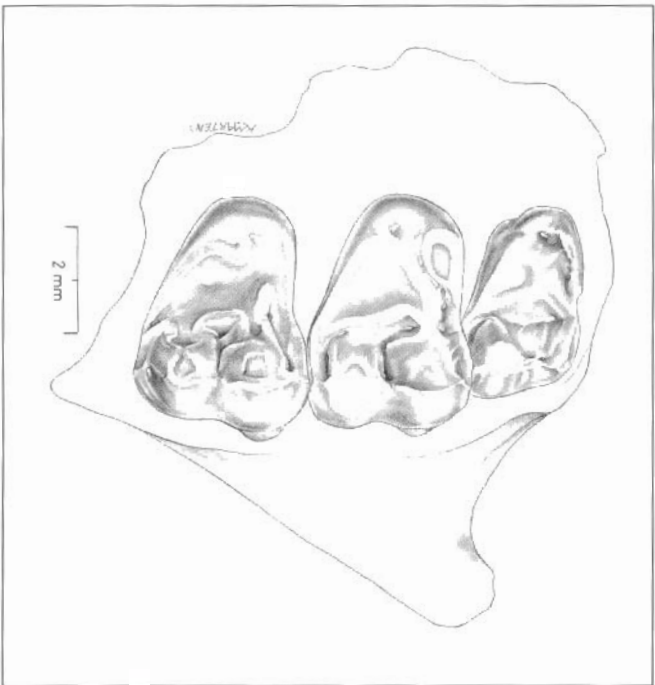
Infraorder Platyrrhini E. Geoffroy, 1812

Semisuborder Anthropoidea Mivart, 1864

Suborder Haplorhini Pocock, 1918

Semiother Euprimates Hoffstetter, 1977

Order Primates Linnaeus, 1758



1a

#### Referred Specimen

UF 91399 (Fig. 2), a partial subadult right posterior mandible (depth = 5.2) with  $M_2$  (3.0, 2.5) and erupting  $M_3$  crown (length = 3.2), found in stratigraphic association with the type specimen.

#### Locality

The *Brantissella* zone, approximately 260 m above the base of the composite section of the Salla beds, Salla-Lurtbay basin, about 90 km southeast of La Paz, Bolivia.

#### Age

Late Oligocene/early Miocene, Desadan land mammal age,  $26 \pm 1$  million years [10–12].

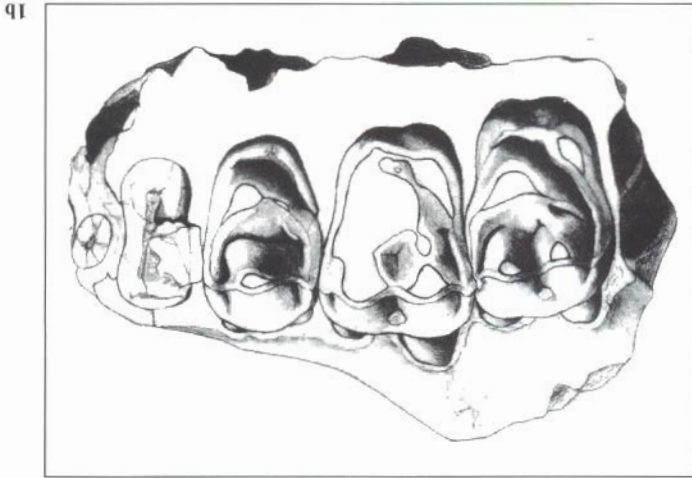
#### Diagnosis

A *Leontopithecus*-sized cebid with relatively small hypocones on  $M_{1-2}$ ; high-crowned lower molars with columnar cusps and deep, constricted talonid basins; no hypocoenulid on  $M_{2-3}$ ;  $M_3$  as long mesiodistally as  $M_2$  but with tapered talonid, and a relatively very shallow posterior mandibular corpus. The upper dentition differs from the type specimen of *Brantissella boliviana* in the following combination of characters: upper

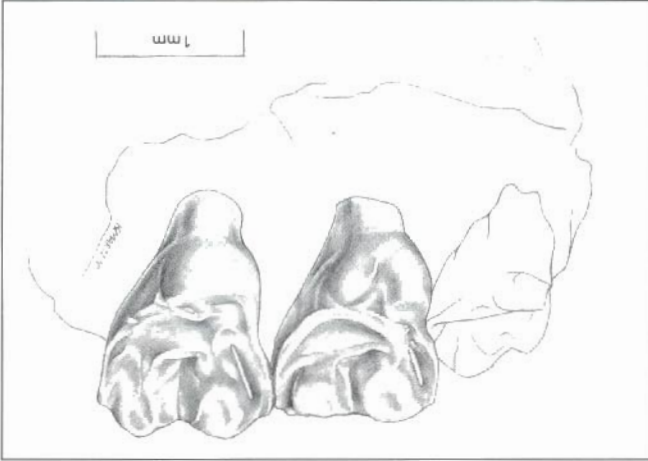
#### Etymology

*Szalavus* (pronounced zuh-lá-ta-vus), from Szalay, after Dr. Frederick S. Szalay, in honor of his contributions to the understanding of primate phylogeny, and *L. alta* vs. ancestor.

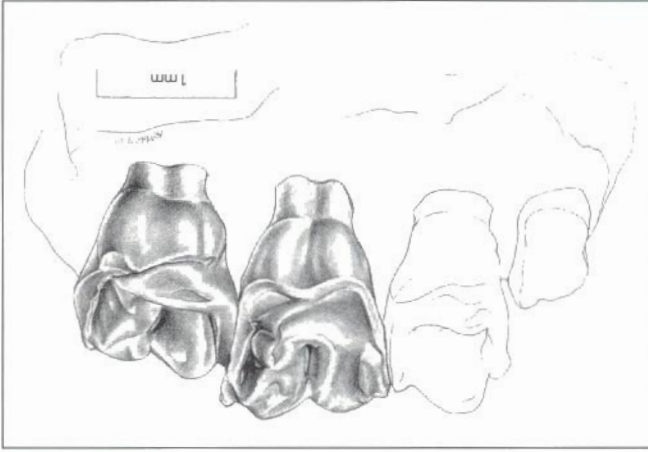
Fig. 1. Occlusal views of *S. attricusps* (a), holotype maxilla (UF 27887),  $RM^{-3}$ , and *B. boliviana* (b), mirror image of holotype maxilla<sup>1</sup>,  $LP^2-M^2$ ; three-quarter lingual views of *S. attricusps* (c) and *B. boliviana* (d), mirror image. Note the reduced lingual morphology and greater maxillary contour of *S. attricusps*.



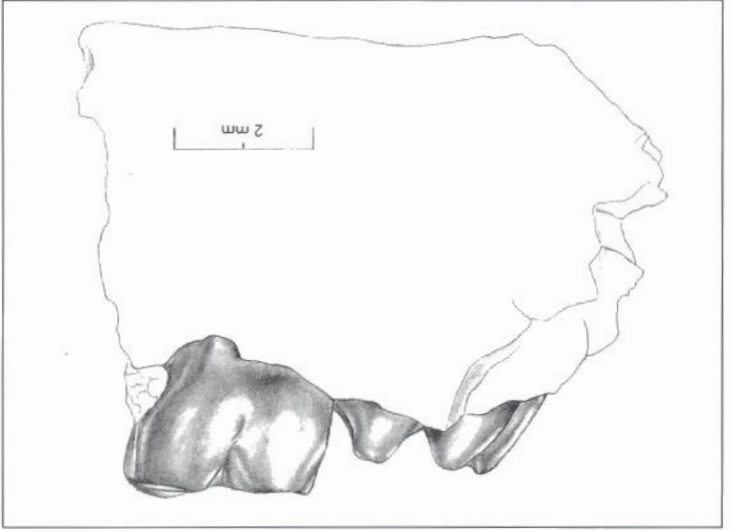
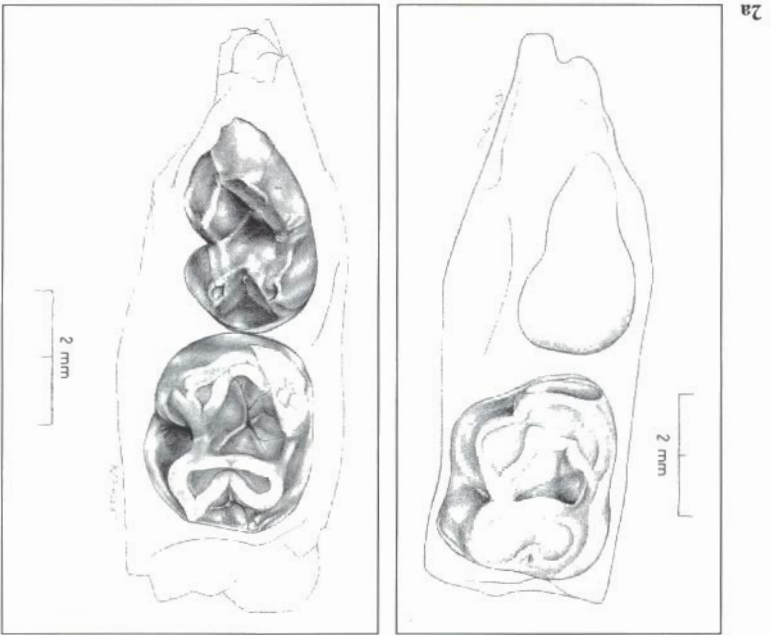
1b



1c

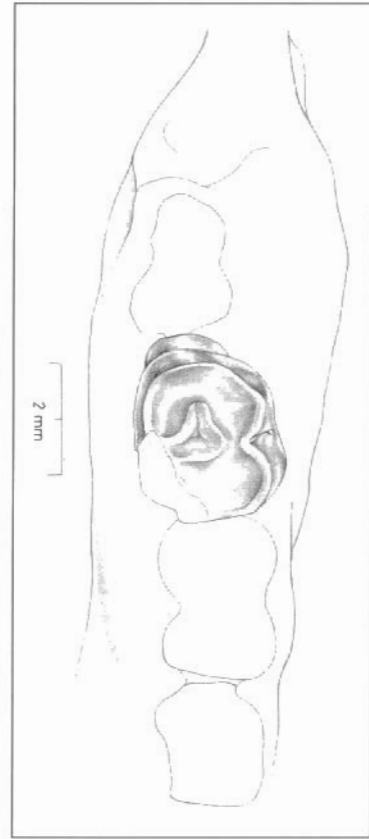


1d

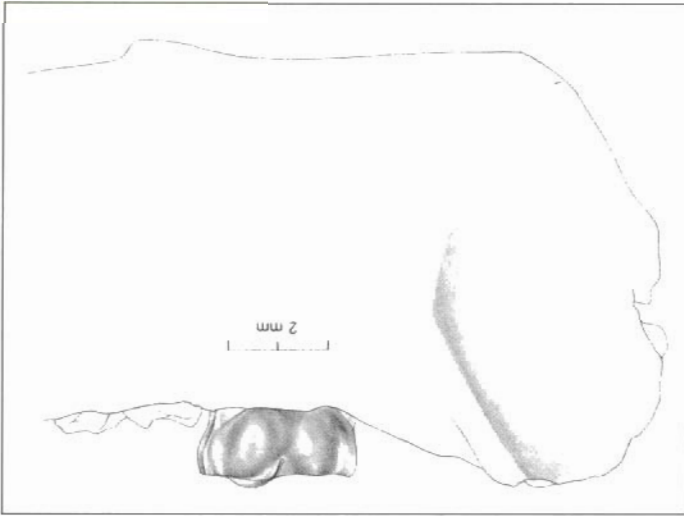


molar crowns more triangular, with relatively small hypocone on  $M1-2$ , strongly oblique mesial margin (preprotocrista) and S-shaped distal margin (postcrista), producing larger interproximal embrasures; vertical sulcus along the lingual sidewall of crown and root.

lingual cingulum reduced to a remnant fovea separating protocone and hypocone and no



**Fig. 2.** Occlusal views of *S. attricusps* (a), holotype mandible (UF 27888) with RM<sub>2</sub>, and referred mandible (b) (UF 91399) with RM<sub>2-3</sub>; lateral view of UF 91399 (c), showing M<sub>3</sub> emerging from its crypt; occlusal (d) and lateral (e) views of RM<sub>2</sub> molar region of the Princeton mandible (PU 21861), photographically reversed and scaled to equal approximately the M<sub>2</sub> length of *Szalaiavus*. Note that no hypocondylid is visible on either M<sub>2</sub> or M<sub>3</sub> of *Szalaiavus* and the interaxonal constrasts in mandibular depth and thickness.



***Szalaiavus attricusps***

*Etiymology*

*Attricusps*, L. *ad-*, towards + *tri-*, three + *cusps*, pointed; in reference to the three prominent cusps and reduced hypocone of the upper molars.

*Diagnosis*

Same as for genus.

*Description and Discussion*

The Salla beds contain the earliest known representatives of the platyrrhine radiation. The first primate identified from Salla was

designated *B. boliviana*, the type specimen of which preserves P<sub>4</sub>-M<sub>2</sub> of the right maxilla, roughly comparable to *Szalaiavus*. A partial mandible (Princeton University 21861) reportedly from the same locality, but of uncertain provenance, was later identified as a primate and provisionally assigned to *B. boliviana* [8]. The holotype of *S. attricusps* was discovered in 1981 [13] at Salla in the level designated the *Branisella* zone [10]. Wolf [13] described this material, which includes upper and lower partial dentitions, and assigned it to *Branisella*, although recognizing that it may belong to another primate. The referred mandibular specimen

(UF 91399) [12] is described here for the first time.

M<sup>1</sup> and M<sup>2</sup> in *Szalaiavus* are triangular in the occlusal outline, a distinctive morphology resulting from reduced lingual features (fig. 1). The crowns are characterized by small hypocones that are barely differentiated from the cingular region. The hypocone is offset by a slight sidewall sulcus. The molars are more flared and less blocky than the relatively quadrate morphology of *Brant-sella*, in which the hypocone is larger. In *Szalaiavus* there is little or no evidence of buccal cingula on either M<sup>1</sup> or M<sup>2</sup>, although there are short cingulum-derived supports for the styler cusps. The third molar has a simpler crown pattern, with a relatively small metacone and no hypocone on the distal cingulum. The preserved portion of the zygomatic region of the face is strongly curved in both anteroposterior and transverse contour. The infraorbital foramen is located relatively posteriorly, immediately anterior to the zygomatic root and directly above M<sup>1</sup>.

The referred jaw fragment is a subadult specimen and therefore not as heavily worn as the type mandible, but nearly identical in all other features. The molar are high-crowned, with tall trigonids and low, but steeply walled, talonid basins (fig. 2). The talonid central foveae are impressively deep, with robust, conical and steep-sided cusps. The hypoconids are large, the entoconids lobe-like, and there are no traces of buccal cingulids on either molar. In both specimens M<sup>2</sup> presents a very short cristid obliqua that runs mesially and unequivocally lacks a hypoconulid.

The four-cusped M<sub>3</sub>, with a moderately tapering distal talonid, is subequal to M<sub>2</sub> in length. There is no hypoconulid. Along the

*Szalaiavus* is relevant to a number of important systematic issues in the early evolutionary history of platyrrhine primates. Foremost is its relevance to the diversity of the earliest known platyrrhine fauna. Two or three species may be represented at Salla, depending upon the allocation of the

same body size class. *Brant-sella* and *Szalaiavus* are different from one another morphologically as are several modern platyrrhine genera of the same body size class.

The preserved portion of the muzzle in *Brant-sella* indicates a flattened rostrum, whereas in *Szalaiavus* the maxilla is strongly contoured dorsoventrally and anteroposteriorly. The difference in mandible construction suggests a strong functional difference analogous to the robust build of *Saimiri* mandibles and the gracile pattern of *Saginus*. Thus, although they are similar in molar size, *Brant-sella* and *Szalaiavus* are as different from one another morphologically as are several modern platyrrhine genera of the

provisionally-assigned, anatomically robust Princeton mandible (fig. 2) [8]. It is highly unlikely that this specimen is attributable to *S. attricuspsis* (fig. 3). Although having similar molar dimensions, the mandible is more than 30% deeper and thicker below  $M_2$  than *Szalaiavus*. On the other hand, it may not be referable to *B. boliviana* either, if the mandibular structure of the latter resembles *Szalaiavus* to the extent that their maxillary dentitions imply.

*Szalaiavus* clarifies several important points regarding the morphology of early platyrrhines. The lower molars have relatively elevated trigonids and no signs of either a paracoid or discrete hypoconulid cusp on  $M_2$  or  $M_3$ , apart from the heel-like extension on  $M_3$ . This resolves the initial ambiguity [13, 14] concerning the occurrence of a hypoconulid on the type specimen and in the very similar and heavily worn second lower molar of the Princeton mandible. The third molar is neither reduced nor elongated compared with  $M_2$  length, and the mandible is very shallow relative to molar length (fig. 3).

The triangular upper molars of *Szalaiavus* resemble those of the small-bodied, clawed callitrichine primates, such as the marmoset *Callithrix*. Fossil platyrrhines that have been proposed as callitrichines [15, 16] come from the younger La Venta beds of Colombia (approx. 15–16 million years [12]) and suggest an earlier ancestry for the lineage, but upper dentitions of the putative callitrichines are poorly represented in the fossil record. Among modern marmosets and tamarins, only the relatively primitive *Calimico* [17, 18] retains a differentiated hypocone cusp, on  $M^1$ , roughly comparable to that of *Szalaiavus* in size. Most workers now agree that hypocone reduction is a derived

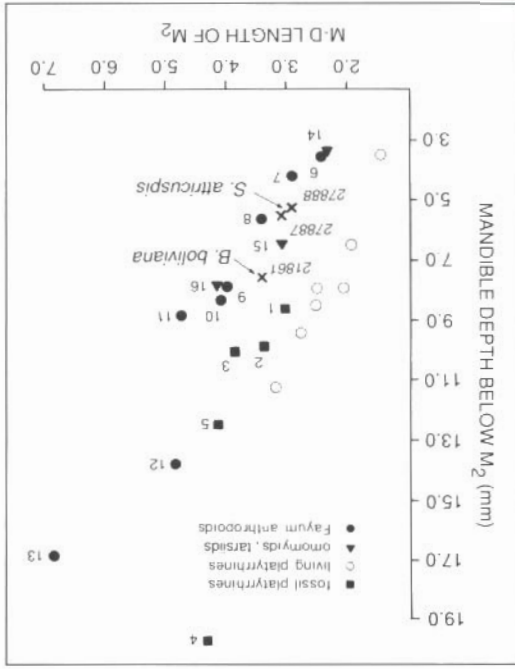


Fig. 3. Plot of  $M_2$  mesiodistal length against mandible depth below  $M_2$  for various living and fossil primates. *Szalaiavus* has the shallowest mandible of known fossil platyrrhines, and, like the Princeton mandible (21861), is shallower than in any living platyrrhine except the pygmy marmoset. 1 = *Saimiri (= Neosaimiri) fieldsi*; 2 = *Mohanamantico hershkovitzii*; 3 = *Aotus dindensis*; 4 = *Soriatcebus ameghinorum*; 5 = *Homunculus patagonicus*; 6 = *Qatrania wingi*; 7 = *Qatrania fleaghi*; 8 = *Apidium phiomense*; 9 = *Parapiithecus fraasi*; 10 = *Apidium phiomense*; 11 = *Parapiithecus fraasi*; 12 = *Propliopithecus haeckeli*; 13 = *Aegyptopithecus zeuxis*; 14 = *Afrotarsius charvati*; 15 = *Necrolemur antiquus*; 16 = *Microchoeris erina-cens*.

condition in New World monkeys [18–20]. But the presence of an early fossil platyrrhine with reduced hypocones might be read as evidence that tricuspid molars are primitive instead, as some have advocated [21]. We consider this unlikely. *Szalaiavus* molars show no signs of the advanced degree of size

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polarity and mammalian biostratigraphy of the

reduction that is a callitrichine hallmark,  
and the lower molars are unusually high-  
crowned and cuspidate, contrasting with the  
low-crowned, undifferentiated cusps of calli-  
trichines. Thus, the similar triangular crown  
outlines of *Szalavus* and callitrichines oc-  
cur within different functional contexts and  
are unlikely to be homologous.

Given their temporal position some 6-8  
million years [12] earlier than the next known  
appearance of fossil platyrrhines, *Szalavus*  
and *Branisella* are a preferred source of em-  
pirical evidence for the platyrrhine morpho-  
type. Their resemblances to omomyids [1, 7,  
8, 22] confirm this status and further imply  
that these features are also primitive for an-  
thropoids. For example, the hypocones on  
upper first and second molars are relatively  
small in *Szalavus* and *Branisella*, and hypo-  
conids are absent on lower molars, as in  
omomyids. On the other hand, in the early  
catarrhines *Apidium*, *Aegyptioptihicus* and  
*Propliopithecus*, the hypocones are large,  
raised relative to the level of the molar trigon,  
combined with large, basally flaring proto-  
cones and strong lingual cingula to form lin-  
gually massive crowns, and occlude with well-  
developed hypoconulids on M<sub>1</sub> and M<sub>2</sub>.  
Hence, Old World anthropoids have, seem-  
ingly from the beginning, been more derived  
than the earliest platyrrhines discovered thus  
far [23], and resemblances emphasized be-  
tween the upper molars of *Aegyptioptihicus*  
and the latest Oligocene/earliest Miocene pla-  
tyrrhine *Dolichocebus* [24, 25] are unlikely to  
be of phylogenetic significance.

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