

A Mandible of *Branisella boliviana* (Platyrrhini, Primates) from the Oligocene of South America

A. L. Rosenberger¹

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*A mandibular specimen from the Bolivian Early Oligocene is provisionally assigned to *Branisella boliviana*. The crown anatomy of the single preserved tooth, an M_2 , indicates platyrrhine affinities and several details of the broken jaw are suggestive of symphyseal fusion. Like the African Oligocene parapithecids, *Branisella* contrasts with extant anthropoids in the relative shallowness of its mandible. *Branisella* is the most ancient, and seemingly the most primitive, fossil platyrrhine monkey, lacking any of the derived features of the two major clades of modern ceboids. Taxonomically, it is best regarded as family incertae sedis.*

KEY WORDS: *Branisella*; platyrrhines; fossil; South America; dentition.

The significance of *Branisella boliviana*, the most ancient South American fossil primate, needs no special elaboration. This species is best known from a maxillary fragment containing P^4 , $M^{1,2}$, and at least partial alveoli for $P^{2,3}$ and M^3 (Hoffstetter, 1969). A second specimen which probably represents *Branisella* has also been briefly mentioned (Rosenberger, 1978; Szalay and Delson, 1979), but it has not been adequately described and compared until now. The specimen is a fragmentary mandible, P. U. 21861, which preserves much of the M_2 crown and alveoli and/or roots for P_2 - M_1 and M_3 . It represents the first example of the mandibular morphology of an Oligocene platyrrhine primate. This individual is presumed to come from the same early Oligocene (Deseadan) locality as

¹Department of Anthropology, University of Illinois at Chicago Circle, Chicago, Illinois 60680.

the original specimen, having been retrieved from the La Salla faunal collections of the Museum of Natural History, Princeton University, and collected by L. Branisa, who found the maxilla.

The size of the Princeton mandible is comparable to the size of the type maxilla. Bivariate regression of sex-pooled, mean upper versus lower molar lengths of 13 platyrrhine species representing eight or nine genera [$\alpha = 0.727$, $\beta = 1.27$ mm, $r = 0.976$; see Rosenberger (1979) for details] predicts an M^2 length of 3.03 mm for the new jaw, essentially identical to the observed length of the known M^2 , 3.0 mm (Hoffstetter, 1969). Other morphological features, such as the contour and orientation of the sidewall supporting the hypoconid, which suggests an extreme reduction of the M^1 metaconule (the posthypocristid would presumably have occluded into the sulcus running obliquely across the base of the metacone), and the relatively narrow talonid, implying a constricted trigon basin and a narrow M^2 distal width, are also consistent with the occlusal anatomy of the type specimen. Thus it seems justified to refer the mandible provisionally to *B. boliviana*.

The morphology of the Princeton mandible, which is roughly the size of a *Saimiri* mandible, is shown in Fig. 1. The occlusal surface of the single molar crown is essentially devoid of all details save for a small island of enamel which probably marks the division between trigonid and talonid. A shallow pit in the center of the latter represents the foveal depression of the talonid basin. The low relief of this remnant, together with the high convexity of the buccal sidewall of the crown, implies that the M_2 was a bunodont rather than cristodont tooth. The position of the fovea (just lingual to the apex of the ectoflexid) also suggests that the talonid was relatively short in mesiodistal length; in primates having comparatively elongate $M_{1,2}$ talonids, the deepest point of the talonid is generally displaced distally. Buccally there are no indications of cingulum in the ectoflexid or below it. Although the crown is chipped mesiolingually, its maximum length can be accurately measured as 3.3 mm. The approximate greatest breadth of the trigonid is 3.0 mm; the talonid breadth is 2.7 mm. Judging by the lengths of the stumps of M_1 and M_3 , each of these teeth would have measured slightly over 3 mm. This suggests that M_3 was neither highly abbreviated nor elongate.

The overall morphology of the jaw is suggestive of a shorter-faced primate, i.e., by comparison to typical strepsirrhines. The inferior border of the corpus is ventrally concave; the ascending ramus arises immediately behind M_1 , preempting the space for a retromolar fossa and possibly tilting M_1 forward; the preserved portion of the anterior (coronoid) margin of the ramus is relatively vertical and situated lateral to M_3 ; the toothrow conspicuously arches toward the midline and the medial surface of the body turns inward rather sharply at the level of $P_{2/3}$; and P_2 is

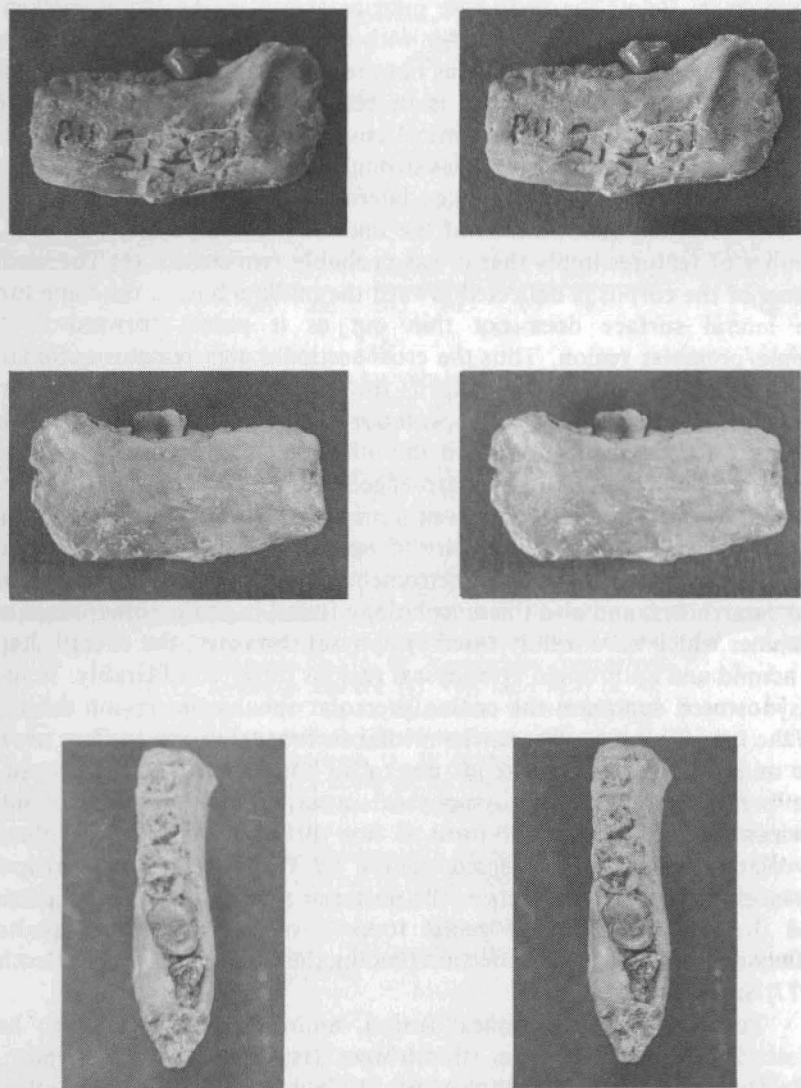


Fig. 1. Stereophotographs of lower jaw referred to *Branisella boliviana*. Lateral (top), medial (middle), and occlusal (bottom) views. Maximum length of specimen = 18.2 mm.

much reduced and P_3 transverse. Posteriorly, the anteroinferior margin of the masseteric fossa is very well delineated and is marked by a lateral prominence. Below the fossa, the inferior aspect of the jaw is thickened and inflected medially. By analogy with other primates, this morphology suggests that the gonial region was not greatly enlarged nor was the gonial angle prolonged ventrad, as it is in certain omomyids (Szalay, 1976). However, the thickness of the vertical cross section through the masseteric fossa indicates that this region was strongly built.

Anteriorly, the jaw is broken lateral to the midline, so there is no decisive evidence of the status of the mandibular symphysis. However, a number of features imply that it was probably synostosed: (1) The medial aspect of the corpus is deflected toward the midline but, at the same time, the lateral surface does not thin out as it passes forward in the canine/premolar region. Thus the cross-sectional area remains quite large (or is enhanced) as the body "turns the corner." (2) There is a distinct retromental (superior) torus. Its posterior aspect overhangs the depression leading into the genial fossa and the inflected mandibular border below the fossa is blunt rather than sharp-edged. (3) The broken cross section is primarily vertical and the convex retromental torus appears to grade superiorly into a planum alveolare of opposite curvature. This combination of features resembles the retromental morphologies of platyrrhines and catarrhines, and also the morphology found in those notharctines and adapines which have solidly fused symphyses; however, the overall shapes of adapid and anthropoid symphyseal regions differ considerably. In most unsynostosed dentaries, the canine/premolar subalveolar region thins out on the lateral aspect, whereas the medial surface tends not to flare toward the midline; the toothrow tends not to be both arched *and* thickened in the premolar region; the symphyseal cross section is generally more horizontal; the retromental torus is not differentiated from a planum alveolare, which is represented merely by the superior, extraarticular surfaces of the joint, but acts as the posterior part of the symphysis itself; and the border below the genial fossa is often sharp-edged, perhaps reflecting a ligamentous connection binding the joint from behind (Beecher, 1977; Szalay, 1976).

Together with symphyseal fusion, anthropoids also tend to have relatively deeper jaws than strepsirhines (Hylander, 1979). A plot of mandibular depth below M_1 versus M_2 length (Fig. 2) bears out this relation for certain strepsirhines as well as anthropoids, but with some qualifications. Compared with that of modern anthropoids, the corpus of *Branisella* is relatively shallow; on the plot *Branisella* falls near various strepsirhines and the haplorhine *Microchoerus*, which have open symphyses. However, the corpora of the Fayum parapathecids, *Apidium* and *Parapithecus*, are similarly shallow but do have completely fused

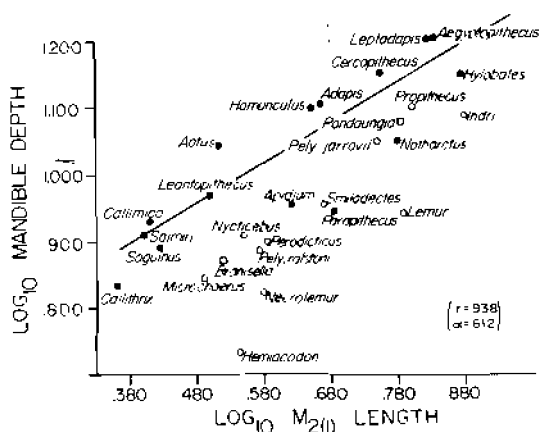


Fig. 2. A plot of mean mandibular corpus depth in the region of M_2 versus mean M_2 length, or M_1 , in callitrichines. Least-squares regression line fitted for modern anthropoids only. Symbols denote the condition of the mandibular symphysis: filled circles, fused; open circles, unfused (although *Propithecus* and *Indri* reportedly (Beecher, 1977) show signs of fusion); open squares, symphyses unknown. Identifications and sample sizes (molars, jaws): *Adapis parisiensis* (5, 5); *Aegyptopithecus zeuxis* (11, 10); *Aotus trivirgatus* (5, 5); *Apidium phiomense* (11, 8); *Callimico goeldii* (4, 4); *Callithrix jacchus* (14, 13); *Cercopithecus denti* (14, 14); *Hemicacodon gracilis* (16, 9); *Homunculus patagonicus* (1, 1); *Hylobates hoolock* (15, 16); *Indri indri* (4, 4); *Lemur macaco* (5, 5); *Leontopithecus rosalia* (21, 11); *Leptadapis magnus* (3, 3); *Microchoerus erinaceus* (1, 1); *Necrolemur antiquus* (3, 3); *Notharctus tenebrosus* (6, 6); *Nycticebus coucang* (5, 5); *Parapithecus grangeri* (7, 4); *Pelycodus jarrowii* (7, 7); *Pelycodus ralstoni* (20, 14); *Perodicticus potto* (5, 5); *Pondaungia cotteri* [1, 1 (Type)]; *Propithecus verreauxi* (5, 5); *Saguinus geoffroyi* (10, 9); *Saimiri sciureus* (6, 4); *Smilodectes gracilis* (4, 4). Sources: Ba Maw *et al.* (1979); Fleagle, J. G. (personal communication); Gingerich and Simons (1977); Rosenberger, 1979, personal observations; Kay *et al.* (1981); Szalay (1976).

symphyses (Simons, 1972). There is also considerable variation in the absolute depth of parapithecoid lower jaws, which is obscured by the sex-pooled sample plotted in Fig. 2; male jaws may be up to 40% deeper than those of females (Kay, personal communication). If my previous inferences regarding the affinities of the Princeton specimen and the status of its symphysis prove correct, these data may indicate that the earliest anthropoids commonly had relatively shallower jaws than their

modern relatives. This further implies that symphyseal fusion may have been attained prior to the selection demands leading to the development of deepened jaws and requires certain modifications in Hylander's evolutionary explanation for the development of anthropoid mandibular form.

In conclusion, the Princeton mandible is probably referable to *Branisella boliviana* and reaffirms Hoffstetter's (1969) original recognition of this species as a platyrrhine, which has recently been criticized (Hershkovitz, 1977). Despite the very limited nature of the material, such features as the relatively broad trigonid, short talonid and bunodont design of the M_2 crown, subequal $M_{2/3}$, a possibly fused symphysis, and a foreshortened rostrum all point to its anthropoid affinities. Furthermore, the lack of a basal buccal cingulid, characteristic of ancestral catarrhines (Szalay and Delson, 1979) and widespread among Paleogene primates generally, may be a shared derived feature of the platyrrhines, including *B. boliviana*. Cingular shelves and like structures occur only sporadically on lower molars of extant ceboids and are most common among callitrichines and *Saimiri* (Kinzey, 1973). But their restricted location in the hypoflexid and/or below the protoconid, among other things (Rosenberger, 1979), suggests that platyrrhine cingulids are not homologous with the conspicuous basal ledges which tend to rim the molars of more archaic primates and Fayum catarrhines. Since such cingulids are likely to represent the primitive morphology of anthropoids as well as the euprimates of modern aspect, their postulated absence in the ceboid morphotype may be an important indicator of this group's monophyletic origin.

As far as it is now known, *Branisella boliviana* appears to lack any of the derived signatures of either of the two major platyrrhine clades (Rosenberger, 1979; Szalay and Delson, 1979), e.g., highly abbreviated third molars and enlarged P2 (Cebidae) or expanded gonial regions and well-developed hypocones (Atelidae). I therefore prefer to regard it as family *incertae sedis*. The inferred smallness of its P2 and retention of a tiny M^2 metaconule (and correlative lack of a continuous crista obliqua) are also primitive conditions relative to later New World monkeys (Rosenberger, 1979; Kay, 1981). It remains possible, then, that the modern forms shared a common ancestry after the appearance of *Branisella*, and that the early Oligocene South American fossil record will someday reveal the existence of a third sister group of platyrrhines.

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