

New Fossil Materials of the Earliest New World Monkey, *Branisella boliviiana*, and the Problem of Platyrrhine Origins

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ABSTRACT *Branisella boliviiana*, from the Late Oligocene of Salla, Bolivia, is the oldest fossil platyrrhine monkey discovered. To date, several fossil specimens of *Branisella* have been obtained, but most of them are fragmentary dentitions, so the animals craniodental morphology is still obscure. During the 1996 field season a pair of upper and lower jaw fragments and another nearly complete mandible were recovered. These new fossil materials reveal the following morphological features in *Branisella*: 1) P² is much smaller than P^{3,4}, whereas P₂ is relatively small but probably sexually dimorphic; 2) the zygomatic arch protrudes smoothly posterolaterally from the maxillary bone, as in extant *Callicebus*; 3) the mandibular arcade is nearly V-shaped and the symphyseal angle, which is formed by the horizontal plane and the anterior face of mandibular symphysis, is about 40°, i.e., it neither leans as far anteriorly as in callitrichines nor does it stand as vertically as *Cebus*; 4) upper and lower molars wore down rapidly in life, suggesting a herbivorous diet and the possibility of terrestriality; and 5) dental eruptive sequence is the same as in extant *Aotus*.

As a whole, the dentition of *Branisella* is very similar to that of *Proteopithecus* from the Late Eocene of Fayum, Egypt, except in the lower canine morphology, suggesting a close phyletic relationship between them. The origin and early diversification of platyrrhine monkeys might have occurred on the African continent before crossing the Atlantic Ocean. Am J Phys Anthropol 111:263–281, 2000. © 2000 Wiley-Liss, Inc.

Branisella boliviiana is a Late Oligocene fossil platyrrhine, discovered in the Salla-Luribay basin of northwestern Bolivia (Fig. 1). The first specimen, a fragmentary maxilla, was recovered in the 1960s (Hoffstetter, 1969), and an additional mandibular specimen was described by Rosenberger (1981). After a long interval, several new specimens were recovered from the same Salla beds (e.g., Rosenberger, 1981; Wolff, 1984). All these specimens, however, are fragmentary jaws, most with well-worn teeth, and so the morphological characteristics of this species have not yet been established.

Some workers have emphasized *Branisella*'s morphological resemblance to living squirrel monkeys, *Saimiri* (Hoffstetter, 1969, 1974; Szalay and Delson, 1979; Gingerich, 1980; Orlosky, 1980; Wolff, 1984; Conroy, 1990), and others to omomyids or callitrichines (e.g., Gingerich 1980; McKenna, 1980;

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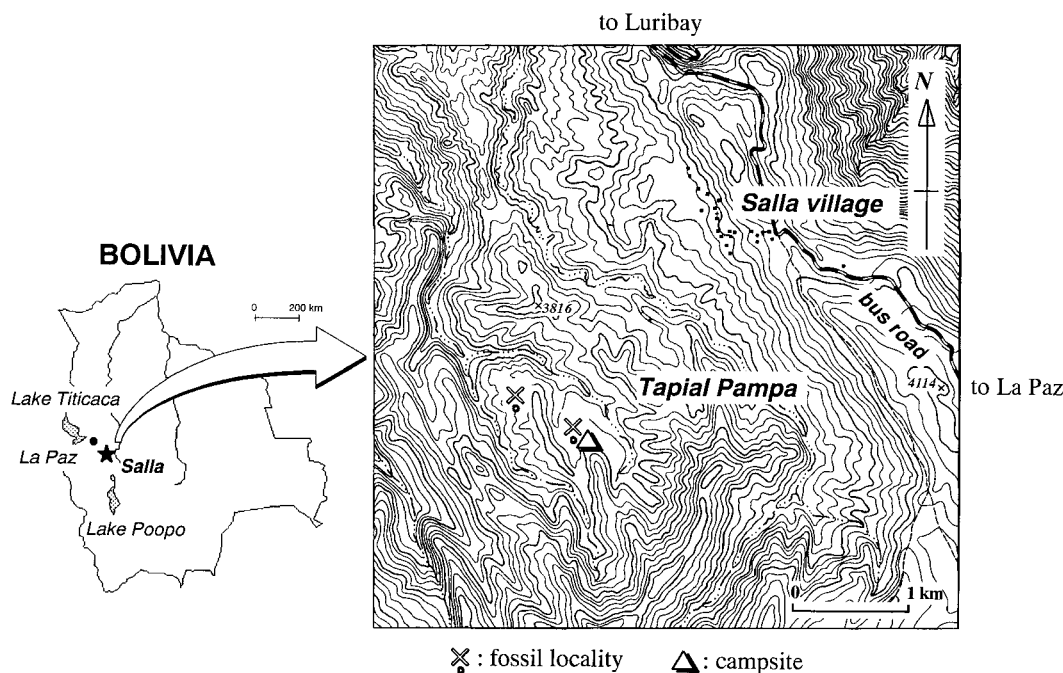


Fig. 1. Index map of Salla, indicating localities of new primate fossils and campsite for the Japanese expedition in 1996.

Rosenberger et al., 1991). Some researchers, moreover, reexamined these fossil Salla primates and concluded that they should be classified into two taxa, *B. boliviana* and "*Szalatavus attricuspis*," on the basis of several minute dental features (Rosenberger et al., 1990, 1991).

Recently, several paleontological excavations were carried out at Salla by Kyoto University and Duke University, respectively, in cooperation with the Museo Nacional de Historia Natural, Bolivia (MNHN). These excavations were successful in discovering many primate fossils (e.g., Kay and Williams, 1995; Takai and Anaya, 1996), and it was demonstrated that all fossil primates recovered from Salla belong to the same taxon, *B. boliviana*. Takai and Anaya (1996), moreover, advocated that *Branisella* is more closely related to extant callitrichines than to other noncallitrichine platyrrhines on the basis of dental morphology, though Rosenberger et al. (1990, 1991) had already suggested the possible relationships between callitrichines and "*Szalatavus*" (not including *Branisella* in their sense). The

phyletic position of *Branisella* is still obscure, yet it appears to be not the ancestral species for all platyrrhines but rather for the callitrichine clade.

During the 1996 field season, several new specimens of *Branisella* were recovered by the Kyoto University-MNHN joint expedition team. The new specimens are two nearly complete mandibles, two mandibular fragments, and a fragmentary maxilla. Of these, the maxillary specimen is of the same individual as one mandible, so the exact occlusal pattern between upper and lower jaws can be observed.

GEOLOGICAL SETTING AND THE MATERIALS

The new fossil specimens discussed in this paper are listed in Table 1. All these specimens were obtained from almost the same horizon, known as the *Branisella* zone of Unit 5 of the Salla beds (MacFadden et al., 1985; MacFadden, 1990; Kay et al., 1999). The Salla fauna is assigned to the Deseadan Land Mammal Age based on detailed comparisons of mammal faunas (MacFadden et

TABLE 1. List of new fossil specimens of *Branisella boliviana*

Specimen no., MNHN-Bol-V	Description
5310 (upper)	Left isolated upper canine and maxillae, with root of P ² , P ³ –M ³
5310 (lower)	A nearly complete mandible with right roots of right I _{1,2} , C (tip broken), P ₂ –M ₁ , and left root of I ₁ , I ₂ , and C (tip broken), P ₂₋₃ , M ₁₋₃
5311	A nearly complete mandible with right roots of I _{1,2} , badly worn C–P ₃ , badly worn M ₁ , and labial half of M ₂ , left roots of I ₁ –P ₃ , and badly worn M ₁₋₃
5312	Left fragmentary mandible with dP ₄ and M ₁
5314	Left fragmentary mandible with M ₃

al., 1985). The results of the calculation of radioisotopic ages suggest a Late Oligocene to Early Miocene date for the Salla deposits, and the absolute age for the *Branisella* zone is estimated at about 25–26 Ma (MacFadden et al., 1985; Naeser et al., 1987; Hayashida and Danhara, 1985; McRae, 1990). Recently, Kay et al. (1998) revised the age of the Salla beds, concluding that the *Branisella* zone should be placed in the Chron C8 (25.82–27.02 Ma) of the Late Oligocene, and suggested that the geological age of the Salla beds might be slightly younger than that of the Deseadan beds in Patagonia.

MNHN-Bol-V 5310 is an isolated left upper canine, fragmentary left maxilla, and nearly complete mandible (Figs. 2a, 3, 4). Though the root of the upper canine is lost, one third of the crown (Fig. 4c) is preserved completely. The maxillary fragment preserves a root of P² and complete P³–M³. The anterior zygomatic root is well-preserved. The lingual half of M¹, the protocone and hypocone, is strongly worn, whereas in M² the protocone is less worn. There is an obvious crack at the bone surface between M¹ and M², but the overall morphology of the maxillozygomatic part seems to be well-preserved.

The almost complete mandible retains intact right P₂–M₁, left P₂₋₃ and M₁₋₃, damaged right and left canines and left I₂, and the roots of right I₁₋₂ and left I₁. M₁ and M₂ of both sides are moderately worn. Though the ascending ramus is not preserved, the mandibular corpus is nearly complete, and so the mandibular arcade is in the natural condition.

These three fossil materials were collected together by Mr. Tarqui and other staff members of MNHN from the same spot, so they most probably belong to the same individual. The maxilla and mandible, in fact, occlude with each other, and their teeth are moderately worn in the same way.

MNHN-Bol-V 5311 is also a nearly complete mandible with well-worn or badly damaged lower teeth (right C₁–P₃ and M₁₋₂, left M₁₋₃) and with roots of the right and left incisors and left canine (Fig. 2b). This mandibular specimen was recovered by F.A. just near the campsite. As in MNHN-Bol-V 5310, the mandibular ramus is not preserved, but the nearly complete mandibular arcade seems to appear in its original shape. Judging from the degree of dental wear, this animal was a very old individual.

The specimens of extant platyrrhines used in this study for comparisons with *Branisella* are housed in the American Museum of Natural History (AMNH), Field Museum of Natural History (FMNH), Museo Nacional de Historia Natural, La Paz, Bolivia, and Primate Research Institute, Kyoto University, Japan.

DESCRIPTIONS AND COMPARISONS

Intraspecific variation in upper dentition

Morphological variation in the upper dentition of *Branisella* has been discussed by many researchers since the second specimens were discovered in the 1980s (Wolff, 1984; Rosenberger et al., 1991; Takai and Anaya, 1996). As mentioned, some authorities once divided the Salla primates into two taxa, *Branisella boliviana* and “*Szalatavus attricuspis*,” mainly on the basis of the morphological differences in the upper molars (Rosenberger et al., 1991). Takai and Anaya (1996), however, argued that all the Salla primates should be classified into a single taxon, *Branisella*, explaining that the morphological differences between *Branisella* and “*Szalatavus*” are intraspecific variation due to the degree of development of the hypocone or distolingual cingulum.

The new specimen, MNHN-Bol-V 5310, also supports their conclusion (Fig. 4): M¹ and M² are nearly triangular in occlusal view, with a small but distinct hypocone on the distolingual cingulum. M³ is basically

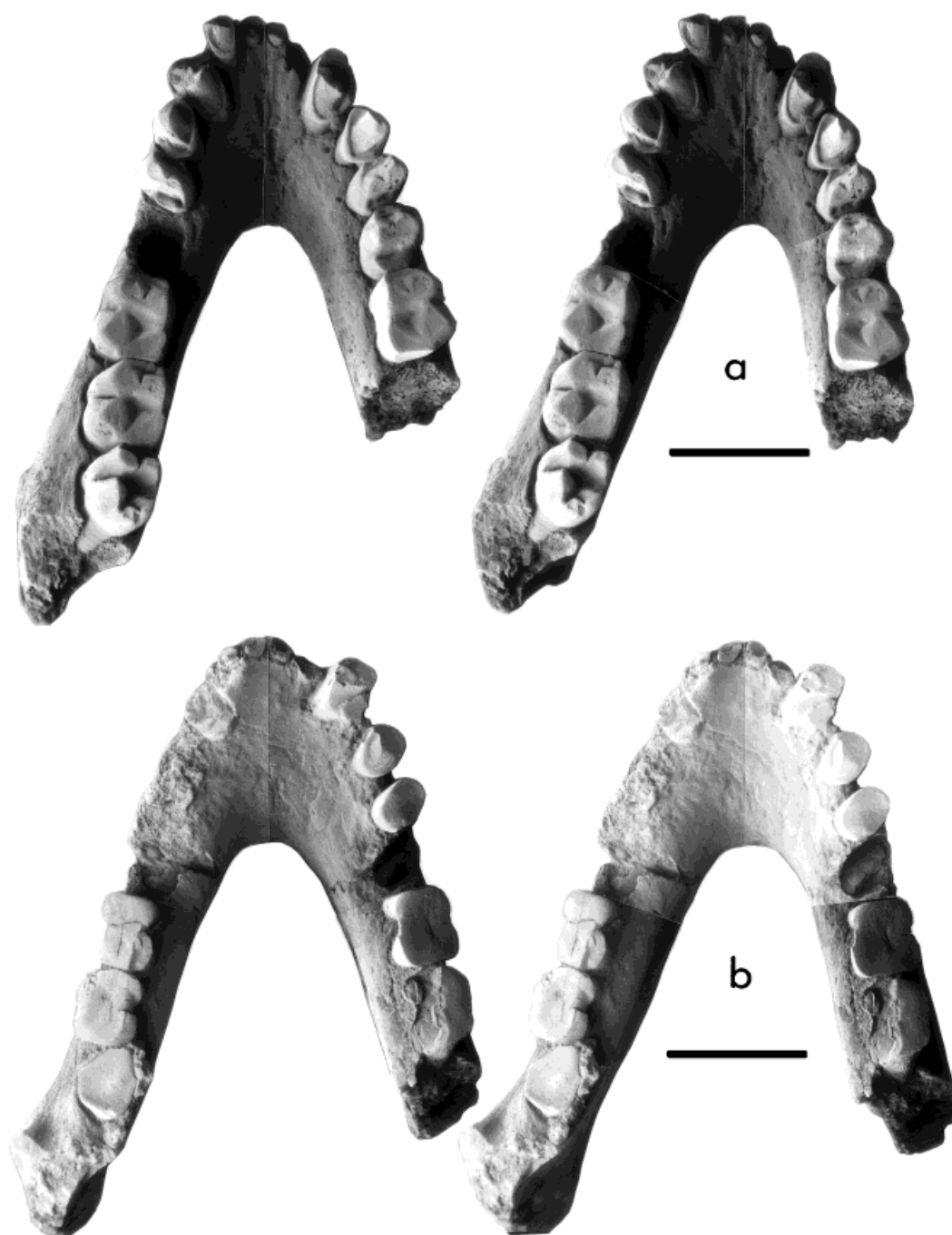


Fig. 2. Scanning electron micrographs (stereopair) of new specimens of *Branisella boliviana*: occlusal view of mandibular specimens, MNHN-Bol-V 5310 (a), and 5311 (b). Scale bar = 5 mm.

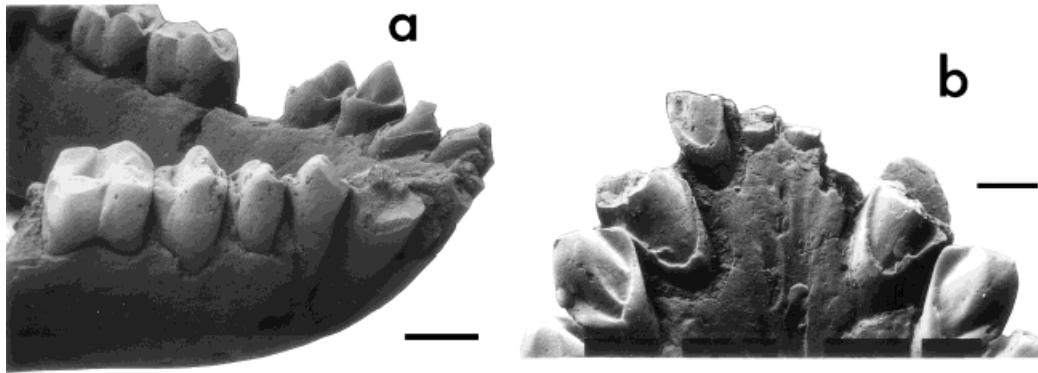


Fig. 3. Scanning electron micrographs of the mandibular specimen of *Branisella*, MNHN-Bol-V 5310. **a:** Right lateral view of the anterior part. **b:** Lingual view of anterior dentitions. The lower incisors are not procumbent anteriorly but rather are vertical. Scale bar = 1 mm.

bicuspid (paracone and protocone), with a well-developed lingual cingulum. Thus, the basic structure of upper molars in *Branisella* is not so discretely variable as to justify division into plural taxa. Though in *Branisella* there are some variations in the development of the hypocone and the distolingual cingulum on M^1 and M^2 , and in the development of the metacone on M^3 , such differences often occur in extant species as intraspecific variation (e.g., Natori, 1986a,b) (Tables 2 and 3).

Takai and Anaya (1996) also discussed the structural difference between the distolingual cingulum on P^4 of the holotype and on P^3 of MNHN-Bol-V 3466: the former has a postprotocrista and a distolingual cingulum, which are completely separated from each other by a deep sulcus, while the latter has a distocrista without the distolingual cingulum. Takai and Anaya (1996) named the former structure as the E type and the latter as the B type. After comparing these teeth with the premolars of the extant platyrrhines, they predicted that the B type is likely the normal condition of *Branisella* upper premolars, and the E type of the holotype was an individual variation. In MNHN-Bol-V 5310, neither P^3 nor P^4 retain a postprotocrista, and a distocrista runs around the protocone lingually (Fig. 4a,b). This form is the B type of Takai and Anaya (1996).

The size and structure of P^2 are also very interesting in *Branisella*. The root of P^2

preserved in the type specimen and in MNHN-Bol-V 5310 suggests that in *Branisella*, P^2 is very much smaller than the posterior premolars, P^3 and P^4 . Though Hershkovitz (1974, 1977) has already discussed that the tiny root of P^2 in the type specimen eliminates *Branisella* from the platyrrhine lineage, the later mandibular specimens demonstrated that *Branisella* actually belongs to platyrrhine monkeys. Kay and Williams (1995) reported an upper jaw specimen with an extremely small, unicusped P^2 , which is nearly half the size of P^3 . If the extremely small P^2 is the natural condition in *Branisella*, is it the primitive condition in platyrrhine phylogeny? Recent discoveries of primitive anthropoid fossils from the Late Eocene to Early Oligocene sediments of Fayum, Egypt, may provide the key to this question.

Among Fayum primates, parapithecids have been considered a possible ancestral group for platyrrhines, but at least two parapithecoid taxa, *Parapithecus* and *Apidium*, have a large P^2 and more specialized cusp pattern, such as many accessory conules, in molars (Simons, 1995). *Proteopithecus*, however, one of the primitive anthropoids recently discovered in the Fayum, appears to retain an extremely small P^2 and a very primitive dentition (Miller and Simons, 1997; Simons, 1997).

Since the first specimen was described in 1989, *Proteopithecus* had been included in the Propliopithecidae, because they were

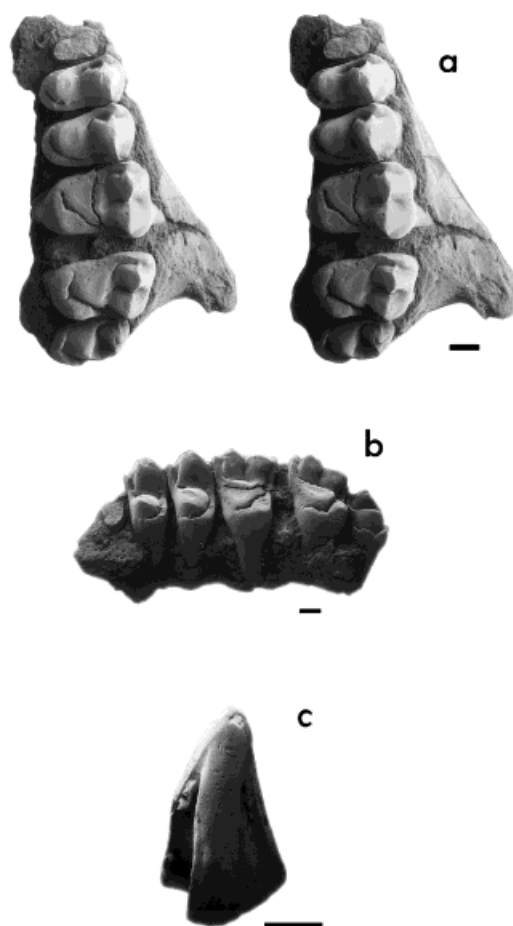


Fig. 4. Scanning electron micrographs of the new maxillary specimen of *Branisella*, MNHN-Bol-V 5310: occlusal (a, stereopair) and lingual (b) views of a left maxillary fragment with P^3 – M^3 and root of P^2 , and a lingual view (c) of an isolated left upper canine. Scale bar = 1 mm.

wrongly presumed to have only two premolars (Simons, 1989; Simons et al., 1994; Kay and Williams, 1995). A new maxillary specimen of *Proteopithecus*, however, has a small but distinct P^2 , which is about half the size of P^3 and P^4 , just as in *Branisella*, suggesting a possible phyletic relationship between them. The morphological similarity and possible relationship between *Proteopithecus* and *Branisella* will be further elaborated in the Discussion.

On the other hand, does the extremely small P^2 seen in *Proteopithecus* and *Branisella* suggest a successive loss of the sec-

ond premolar in their clades? In neither *Proteopithecus* nor *Branisella* does P^2 show any sign of reduction as marked as in P^2 . Though the detailed process of the loss of the second premolars in catarrhine monkeys has not yet been determined, it is presumed that the reduction and loss of the upper and lower second premolars occurred simultaneously in primitive catarrhines. The size discordance between P^2 and P^2 seen in *Proteopithecus* and *Branisella* suggests that the size reduction of their P^2 was not a prelude to the loss of the second premolars but a unique character which occurred in these two taxa.

Structure of the maxilla and zygomatic arch

To date, seven maxillary fragments of *Branisella* have been discovered from the Salla deposits: the type specimen (Hoffstetter, 1969), UF 27887 (Wolff, 1984), two undescribed specimens (Kay and Williams, 1995), MNHN-Bol-V 3460, 3467 (Takai and Anaya, 1996), and the new material, MNHN-Bol-V 5310. Among these specimens, the newly discovered one is most informative because of the retention of five complete teeth (P^3 – M^3), one root (P^2), and an isolated canine (Fig. 4).

M^2 is located somewhat more lingually than M^1 , and M^3 is situated more lingually than M^2 , so the buccal margins of upper postcanine teeth form a slightly convex curve in the occlusal view, and the widest point of the upper dental arcade is located about M^1 . Therefore, though the complete upper dental arcade has not yet been reconstructed, we predict that in *Branisella* the upper dental arcade should be oval-like, with the posterior part curving lingually more acutely than does the anterior part.

Among living platyrrhines, this posteriorly acutely narrowing upper dental arcade is observed in callitrichines and medium-sized genera, *Aotus*, *Callicebus*, *Saimiri*, and *Cebus*, probably corresponding to the reduction of the third molars. In *Callicebus* and *Aotus*, however, M^2 is not so distorted as in *Branisella* but rather square in occlusal view. In *Saimiri*, the anterior tooth row is rather divergent, with the upper canine protruding laterally, so that the dental arcade forms an S-shape curve. In atelines, the

TABLE 2. Dental measurements of the upper dentition of the new *Branisella* specimens¹

Specimen no., MNHN-Bol-V	Side	C		P ²		P ³		P ⁴		M ¹		M ²		M ³	
		MAX	MIN	MD	BL	MD	BL	MD	BL	MD	BL	MD	BL	MD	BL
5310	Left	(2.19)	(1.90)			1.92	3.26	2.19	3.61	2.92	4.36	2.6	4.13	1.72	3.18

¹ MD, mesiodistal length (mm); BL, buccolingual width (mm); MAX, maximum diameter; MIN, minimum diameter; trd, trigonid width; tad, talonid width. Measurements in parentheses are unreliable because of being badly damaged or worn.

upper dental arcade is almost parabolic, with the posterior tooth row diverging laterally.

In *Branisella* the zygomatic arch smoothly protrudes posterolaterally from the maxillary body (Fig. 4a). The anterior margin of the arch begins smoothly from P⁴, and the posterior one begins from between M² and M³. Among small to medium-sized platyrrhines, *Aotus* and *Callicebus* have a similar smoothly protruding zygomatic arch, as in *Branisella*, whereas in *Saimiri* and *Cebus* the zygomatic arch stands more anteriorly and protrudes more perpendicularly from the maxilla than in *Branisella*. In callitrichines the zygomatic arch also protrudes at a more obtuse angle than in *Branisella*.

Although in all maxillary specimens of *Branisella* the zygomatic arch is broken off within 5 mm from the upper teeth, the cross section of the arch shows that it was rather thin and fragile (Fig. 4a, 5). In *Saimiri* and the callitrichines, the zygomatic arch is even more thin and fragile than in *Branisella*. In *Callicebus*, the root of the zygomatic arch is as thin as that of *Branisella*, but there is a prominent protuberance at the ventral margin of the anterior root of the zygomatic arch. In *Cebus*, the zygomatic arch is very robustly constructed. In MNHN-Bol-V 5310 there is no sign of enlargement of the orbit as seen in *Aotus*, though the dorsal part of this specimen is slightly eroded. In atelines a relatively thin zygomatic arch protrudes from a more posterior position than in *Branisella*. In pitheciines the angle between the zygomatic arch and the tooth row is more obtuse than in *Branisella* because the postcanine tooth rows of both sides are nearly parallel, and the zygomatic arch is much higher dorsoventrally than in *Branisella*.

As a whole, the structure of the zygomaticomaxillary part of *Branisella* is most similar to that of extant *Callicebus* in the ventral aspect, but they do not resemble each other in the lateral view because *Branisella* lacks

a ventral protuberance at the base of zygomatic arch. Rosenberger (1979) argued that a robust zygomatic arch was probably the primitive state for primates and for anthropoids (and also for atelids in platyrrhines). The rather robust zygomatic arch in *Branisella* is likely to retain this primitive state for platyrrhines.

Structure of lower premolars and sexual dimorphism in P₂

As already reported in Takai and Anaya (1996), P₂ of *Branisella* (MNHN-Bol-V 3465; Figs. 6a, 8a) is unicusped with a complete lingual cingulum, which is a typical pattern seen in living callitrichines. The newly discovered P₂ specimen, MNHN-Bol-V 5310 (Fig. 6b), shows the same callitrichine characteristics as the previous specimen, but it is very notable that the P₂ of the former is significantly smaller than that of the latter (Figs. 6–8), which suggests the existence of sexual dimorphism in *Branisella*. Size differences between the dentitions of MNHN-Bol-V 3460 and 5310, however, are also observed on other teeth, such as M₁ and M₂ (Fig. 8d,e), so the former is likely to have been a much larger individual than the latter. This size dimorphism can be interpreted in two ways: as intraspecific variation in body size, or as sexual dimorphism present in *Branisella*. At present we cannot resolve this problem because there are too few specimens known. However, compared with extant platyrrhines, the size difference in P₂ between MNHN-Bol-V 3460 and 5310 is as large as the interspecific variation observed in extant genera, but the size-variation on the upper and lower molars of *Branisella* is not as large as that of extant genera. Therefore, it seems natural to interpret the size difference between the two *Branisella* P₂ specimens as evidence of sexual dimorphism in P₂ (and probably also in the canine) in *Branisella*.

TABLE 3. Dental measurements of the lower dentition of the new *Branisella* specimens¹

Specimen no., MNHN-Bol-V	Side	I ₁		I ₂		C		P ₂		P ₃		P ₄		M ₁		M ₂		M ₃		dP ₄		
		MD	BL	MD	BL	MAX	MIN	MD	BL	MD	BL	MD	BL	MD	BL	MD	trd	tad	MD	trd	tad	BL
New specimens																						
5310	Left	(0.74)		(1.01)		(2.46)	(1.72)	1.92	1.65	1.69	2.02			2.91	2.58	2.63	2.93	2.69	2.62	2.82	2.31	2.11
5310	Right					(2.51)	(1.75)	1.90	1.67	1.72	2.04	2.14	2.28	2.98	2.60	2.68						
5311	Left													(2.74)			(2.76)			(2.68)		
5311	Right					(2.26)	(1.56)	(1.87)	(1.73)	(1.68)	(2.06)			(2.86)	(2.24)	(2.61)						
5312	Left													2.89	2.56	2.64						
5314	Left																			(3.04)	2.45	2.29
																					2.58	1.89
																						2.04

¹ MD, mesiodistal length (mm); BL, buccolingual width (mm); MAX, maximum diameter; MIN, minimum diameter; trd, trigonid width; tad, talonid width. Measurements in parentheses are unreliable because of being badly damaged or worn.

Among extant platyrrhines, medium- to large-sized monkeys usually show a significant sexual dimorphism in upper and lower canines and even in P₂, which occludes against the upper dimorphic canine. In smaller-sized marmosets, such sexual dimorphism is not as distinct, but in *Saimiri* it is clearly observed on upper and lower canines and P₂. Miller and Simons (1997) reported sexual dimorphism in the lower canine of *Proteopithecus*, but did not mention P₂.

Complete P₃ and P₄ of *Branisella* were discovered for the first time (Figs. 2a, 3a,b). Both are bicuspid (with a protoconid and metaconid), and have a distinct, lower talonid and a small precingulid. Among the lower premolars of MNHN-Bol-V 5310, possibly a female specimen, P₂ is most projecting, P₃ is second, and P₄ is lowest in height, while in occlusal view P₄ is largest and P₂ is smallest. There is neither a buccal cingulum nor a distinct entoconid on P₃ or P₄. On P₃, the protoconid is much higher and more anteriorly located than the metaconid, so there is a mesiolingual slope at the trigonid, which is almost completely closed by the lingual cingulum. On P₄, the protoconid and metaconid are almost the same size and stand side by side; thus, the trigonid is closed mesially by the anterior cingulum. The talonid is much larger and the precingulid is less developed than those of P₃, and hence P₄ is the more molarized tooth.

MNHN-Bol-V 5310 retains the basal part of left I₂ and the roots of other lower incisors (Fig. 3a,b). Judging from these fragmentary roots, I₂ is obviously larger than I₁, but much smaller than the lower canine in mesiodistal and buccolingual dimensions. I₁ is slightly more anteriorly located than I₂ (Fig. 3a). I₂ is not as compressed bilaterally nor does it protrude anteriorly as in *Soriacebus* (Early Miocene, Patagonia, Argentina; Fleagle et al., 1987; Fleagle, 1990), while I₁ may be more compressed than I₂. I₂ is not symmetrical and has a basal lingual cingulum.

The occlusal outline of the lower canine is almost oval, being mesiodistally compressed. There is a complete basal lingual cingulum, which continues until the distobuccal side of the canine (Fig. 3b). The distostylid is so prominent that there is a deep sulcus inside the lingual cingulum. It must be remembered that,

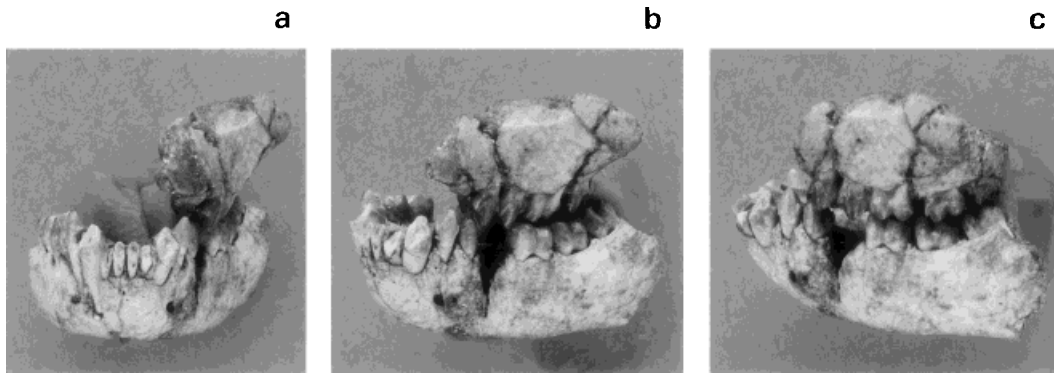


Fig. 5. Photographs of *Branisella*, with upper and lower jaws occluded (MNHN-Bol-V 5310), from frontal (a), frontolateral (b), and lateral (c) views. Scale bar = 10 mm.

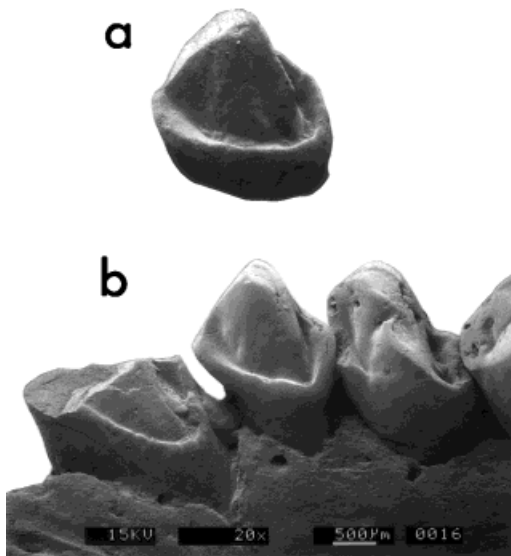


Fig. 6. Scanning electron micrographs of right P_2 of MNHN-Bol-V 3465 (a, lingual view) and right C_1 , P_{2-3} of MNHN-Bol-V 5310 (b, lingual view). Note the morphological similarity and size difference between two specimens, suggesting a probable sexual dimorphism in P_2 . Scale bar = 0.5 mm.

judging from P_2 size, this specimen should be female, and so the lower canine should not protrude as far laterally as in the male.

Mandibular arcade and symphyseal fusion in *Branisella*

The mandibular arcade of two new mandibular specimens, MNHN-Bol-V 5310 and 5311, is nearly V-shaped (Fig. 2a,b). Among

extant and extinct platyrrhines, such a V-shaped mandible is seen in callitrichines only, especially in *Cebuella*, and in some Early Miocene forms from Patagonia, such as *Homunculus* and *Soriacebus* (Fleagle et al., 1987). Hershkovitz (1977, p. 188) regarded the most acute V-shaped mandible of *Cebuella* as the primitive condition, and the more arcuate or U-shaped arcade of *Callithrix* or *Saguinus* as the more derived condition in platyrrhine phylogeny. The V-shaped mandible of *Branisella*, the oldest fossil platyrrhine, seems to support his hypothesis superficially. However, much evidence obtained from morphology, molecular biology, and physiology suggests that *Cebuella* is the most derived form among extant callitrichines. Rosenberger (1979) has already argued this evolutionary polarity on the shape of the mandibular arcade, and concluded that U-shaped arcades are ancestral for platyrrhine monkeys. We agree with his conclusion: if the V-shaped mandibular arcade seen in *Branisella* or some Patagonian forms is the primitive condition, the mandible of *Cebuella* should have secondarily become V-shaped via the condition of a more arcuate arcade, as seen in extant *Callithrix* or *Saguinus*.

Only in the occlusal view are the mandibular arcades of *Cebuella* and *Branisella* very similar. Their mandibular corpora are very different from each other. Hershkovitz (1977, p. 190) calculated the mean values of the

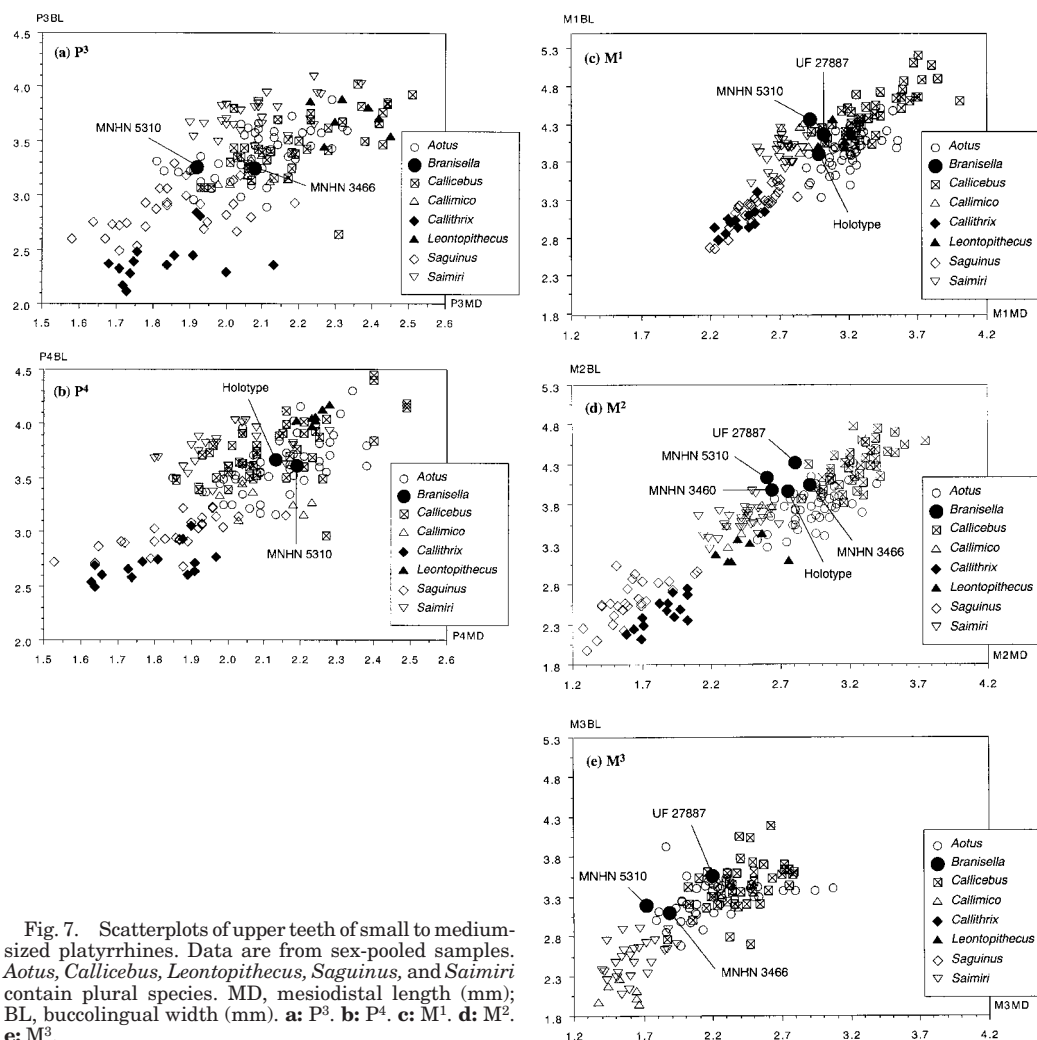


Fig. 7. Scatterplots of upper teeth of small to medium-sized platyrrhines. Data are from sex-pooled samples. *Aotus*, *Callicebus*, *Leontopithecus*, *Saguinus*, and *Saimiri* contain plural species. MD, mesiodistal length (mm); BL, buccolingual width (mm). a: P³. b: P⁴. c: M¹. d: M². e: M³.

symphyseal angle, which is formed by the horizontal plane and the anterior face of the symphysis, in several platyrrhines (Table 4): the symphyseal angle of *Cebuella* is 28° (the mean value of 61 specimens), while that of two mandibles of *Branisella* is about 40°, which is very close to the symphyseal angles of *Callicebus* and *Leontopithecus*. (The value of the symphyseal angle in *Branisella* is not a strict one, because the posterior parts of fossil mandibles are broken and lost, and so they cannot be placed as accurately as the extant complete specimens.) That is, in *Cebuella*, the symphyseal part leans much more anteriorly than in *Branisella*. In *Homunculus* and *Soriacebus*, the symphysis does not

lean as anteriorly as in *Cebuella*, but resembles that of *Branisella* in the symphyseal angle (Herskovitz, 1977; Fleagle et al., 1987; Fleagle, 1990). On the other hand, in *Branisella* the mandibular corpus is rather robust and wide and the ventral margin is flat or slightly convex inferiorly below M₁, whereas in *Cebuella* the corpus is very gracile and the ventral margin is concave superiorly. The mandible of *Cebuella* is likely to have become reduced in conjunction with reduction of body size.

In *Branisella*, one large and some smaller mental foramina are present at about half the height of the mandible below P₂ and P₃. The anterior margin of the ascending ramus

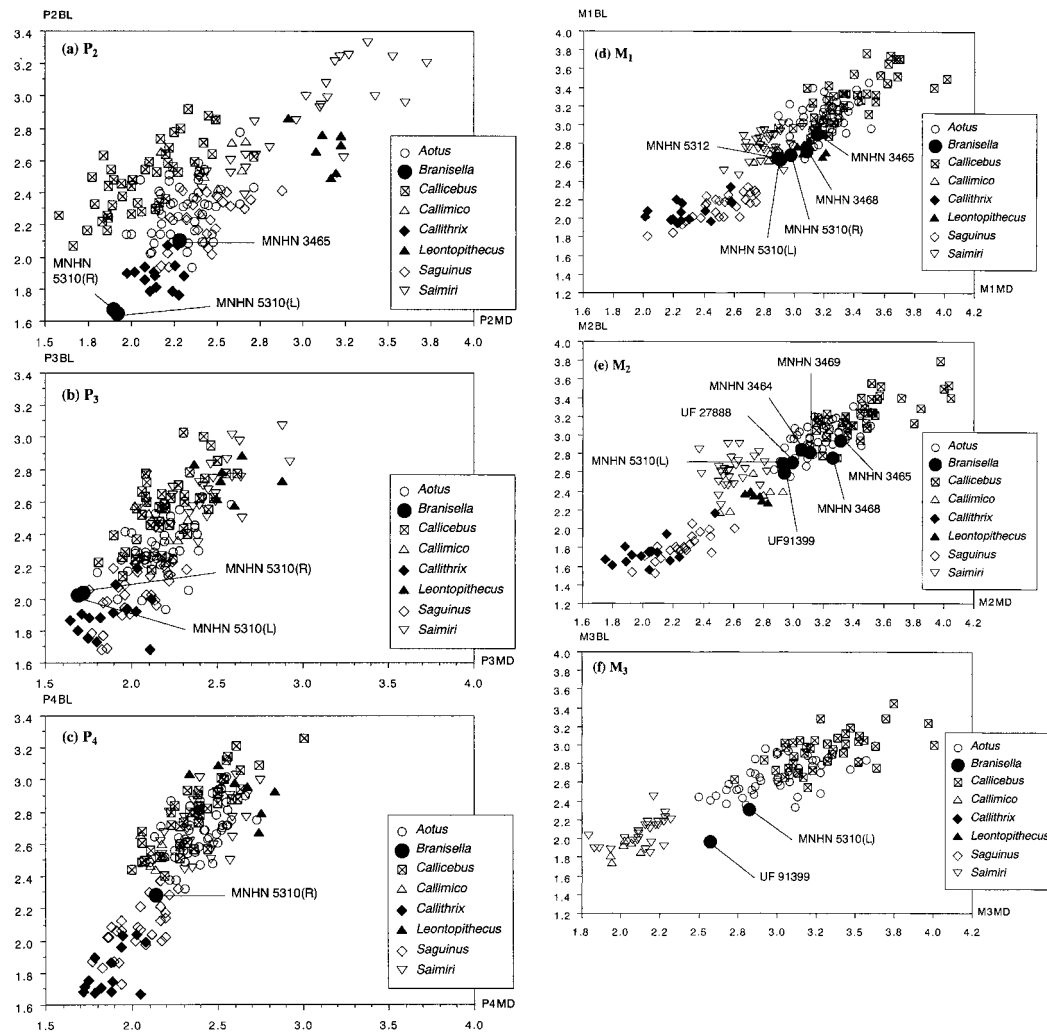


Fig. 8. Scatterplots of lower teeth of small to medium-sized platyrrhines. Data are from sex-pooled samples. *Aotus*, *Callicebus*, *Leontopithecus*, *Saguinus*, and *Saimiri* contain plural species. MD, mesiodistal length (mm); BL, buccolingual width (mm). **a:** P₂. **b:** P₃. **c:** P₄. **d:** M₁. **e:**

M₂. **f:** M₃. Buccolingual width of the lower molars is taken as the maximum width. Note the small size of P₂ of MNHN-Bol-V 5310 (possible female), compared with that of MNHN-Bol-V 3465 (possible male) and other platyrrhines.

starts just posterolateral to M₃, which is usually seen in most extant platyrrhines, while in *Homunculus*, an Early Miocene form from Patagonia, there is a large diastema between M₃ and the ascending ramus. The superior marginal line of the mandibular corpus rises posteriorly, so that posterior molars are situated higher than the anterior teeth.

An enigmatic feature among the new mandibular specimens is the presence of a "su-

ture line" at the symphysis in MNHN-Bol-V 5311 (Fig. 9a; Takai et al., 1998). This vertical line on the anterior face of the symphysis is so straight and located just at the sagittal line as to be presumed a real "suture line," but there is no line observed at the posterior face of the symphysis (Fig. 9b). Moreover, an X-ray photograph shows complete synostosis of right and left mandibles, suggesting a symphyseal fusion in MNHN-Bol-V 5311. The other mandibular specimen, MNHN-

TABLE 4. Symphyseal angle of extant platyrrhines and *Branisella*

Genus (n) ¹	Symphyseal angle
<i>Cebuella</i> (61)	28°
<i>Callithrix</i> (80)	36°
<i>Branisella</i> (2)	40°
<i>Callicebus</i>	41°
<i>Leontopithecus</i> (7)	42°
<i>Saguinus</i> (255)	49°
<i>Callimico</i> (10)	55°
<i>Aotus</i>	56°
<i>Cebus</i>	57°
<i>Saimiri</i>	69°

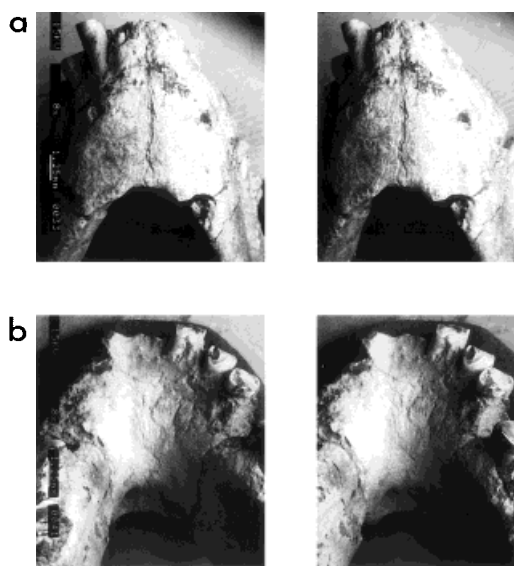
¹n, sample number.

Fig. 9. Scanning electron micrographs (stereopair) of MNHN-Bol-V 5310. Surface of mandibular symphyseal region from anterior (a) and posterior (b) views. Note that there is a straight "suture line" at the anterior surface of the symphysis, but not at the posterior surface.

Bol-V 5310, does not retain such a "suture line" at either the anterior or posterior face. At present, therefore, this "suture line" seen in MNHN-Bol-V 5311 may be only a lineal crack, which has occurred only at the anterior surface of the mandibular symphysis during fossilization.

At the posterior side of the mandibular symphysis there is a well-developed superior transverse torus, and a genioglossal fossa present below it. There is no obvious inferior transverse torus. The sagittal sec-

tion of the mandibular symphysis of *Branisella* is very similar to that of *Apidium*, an Early Oligocene form from Fayum, Egypt (Fig. 14.3 in Fleagle, 1998).

DISCUSSION

Diet and positional behavior

One of the most notable features of *Branisella* dentition is that most upper and lower molars show a tendency towards heavy wear. In all M^{1,2} specimens, the lingual half, the protocone and hypocone, are so worn as to form a flat plane, while in the lower molars, such as MNHN-Bol-V 3469, 5311, and UF 27888, all cusps are heavily worn, exposing a flat dentine surface. The combination of these excessively worn upper and lower molars suggests that *Branisella* fed on very abrasive food.

Based on the size and bunodonty of the teeth, many researchers have considered *Branisella* a frugivorous (e.g., Fleagle, 1998; Conroy, 1990) or an unspecialized omnivorous animal (Takai and Anaya, 1996). Among extant platyrrhines, heavily-worn, flat molars are sometimes seen in *Callicebus* and *Aotus*, both of which feed mainly on fruits, and supplementally eat flowers, young leaves, and insects (e.g., Wright, 1994). However, these frugivorous platyrrhines do not have such high-crowned molars as *Branisella*. In general, the high-crowned lower teeth in *Branisella* are considered an adaptation to the diet of abrasive foods, such as silica-rich leaves or grasses.

The suite of high-crowned lower molars and heavily worn teeth suggests that the diet of *Branisella* was not simply frugivory but included more abrasive foods, such as grasses on the ground, pointing to terrestrial behavior rather than strict arboreality. It is also notable that the mandible of *Branisella* is not so gracile as in extant callitrichines but is rather robustly constructed, suggesting more powerful masticatory movements of the mandible.

However, as is well-known, all living platyrrhines are arboreal quadrupeds, and hypothetical ancestral platyrrhines have also been regarded by many researchers as arboreal quadrupeds (e.g., Ford, 1988; Fleagle, 1998). The hypothetical terrestriality of *Branisella* argues against this traditional view,

but no postcranial fossils have been discovered so far which would demonstrate their locomotor pattern directly. Notably, however, MacFadden (1990) pointed out that the dominant environment at Salla was not humid, dense forest but a semiarid environment. Paleontological data, for example, the presence of many high-crowned, grazing mammals, such as notoungulates and rodents, and sedimentological data, such as the presence of the pedogenic carbonate nodules at the *Branisella* zone, suggest a semiarid or arid environment of deposition. Kay et al. (in press) also concluded that *Branisella* is a terrestrial animal by demonstrating a correlation between the high molar crowns, heavy tooth wear, and terrestriality in primates.

Dental eruption sequence

The wear pattern in the lower dentition of MNHN-Bol-V 5311 provides us with several interesting clues about the sequence of dental eruption in *Branisella*. In this specimen all lower molars, including M_3 , are strongly worn and P_2 is obviously less worn than the posterior premolars, $P_{3,4}$, which suggests that P_3 and P_4 erupted much earlier than P_2 , and that M_3 also erupted relatively early, probably earlier than did the premolars.

The sequence of dental eruption in extant platyrrhine monkeys has been studied by several researchers (e.g., Serra, 1952; Swindler, 1976; Byrd, 1981). According to Swindler (1976), among middle- to large-sized extant platyrrhines, only in *Aotus* and *Brachyteles* does P_3 erupt earlier than P_2 , and especially in *Aotus* M_3 erupts much earlier than in other platyrrhine monkeys. The dental eruption sequence in *Branisella* may have been the same as in *Aotus*. Interestingly, Serra (1952) regards this *Aotus* pattern as the primitive condition in platyrrhines.

In small-sized platyrrhines, the callitrichines, the dental eruptive sequence is more complex than in larger monkeys. Serra (1952) reports that P_2 erupts earlier than P_3 in *Saguinus* and *Leontopithecus*, but in *Callithrix* the reverse is true. Byrd (1981) supports his results in *Saguinus* and *Leontopithecus*, but pointed out variation in *Callithrix*. In *C. jacchus* and *C. argentata*, P_2

erupts later than P_3 , whereas in *C. humeralifer*, P_2 erupts earlier than P_3 and P_4 .

Therefore, in the sequence of dental eruption *Branisella* is not similar to extant callitrichines, but exhibits a hypothetical primitive condition as seen in extant *Aotus*, i.e., the third molar erupts relatively early and P_2 erupts later than other premolars.

Comparison with *Proteopithecus* from Fayum

As already mentioned, *Branisella* has several intriguing resemblances to *Proteopithecus*, one of the oldest fossil anthropoids discovered from the Late Eocene of Fayum, Africa. The first specimen of *Proteopithecus*, a left maxillary fragment, was discovered in 1987 and originally regarded as a member of the Oligopithecinae, Propitopithecidae (Simons, 1989; Simons et al., 1994). In 1997, however, it was redescribed on the basis of new materials, including mandibles, and was moved to a new, as yet unnamed family (Miller and Simons, 1997).

Simons (1997) and Miller and Simon (1997) described *Proteopithecus* as differing substantially from propitopithecids and oligopithecids, both Fayum primates, in having three premolars. This suggests that *Proteopithecus* is more primitive than these other two families. *Proteopithecus* also differs from parapithecids, another Fayum primate with three premolars, in having much better defined trigon/ids and talon/talonid, which are far less bulbous, and in displaying little occlusal elaboration in the form of extra conules/ids and styles/ids other than the occurrence of a prominent metaconule on M^1 (Miller and Simons, 1997; Simons, 1997).

On the other hand, Miller and Simons (1997) suggested that *Proteopithecus* resembles several living platyrrhines, especially *Saimiri*, *Saguinus*, and *Callimico*, in having a large P_2 and a much smaller P^2 than P^3 , and in the occlusal morphology of upper molars. (All these characters are also observed in *Branisella*.) They also pointed out the following morphological differences between *Proteopithecus* and living platyrrhines: 1) in living platyrrhines, P^2 is not so reduced as in *Proteopithecus*; 2) in platyrrhines, premolars and molars are not so transversely expanded as in *Proteopithecus*;

TABLE 5. List of morphological similarities and differences seen in *Proteopithecus* and *Branisella*, with a comparison to extant callitrichines¹

	<i>Proteopithecus</i>	<i>Branisella</i>	Callitrichines
Similarities			
Dental formula	2.1.3.3	2.1.3.3	2.1.3.2(3)
C ¹ mesial groove	Distinct	Very deep	Very shallow
P ²	Unicusped	Unicusped	Unicusped
P ² and P ³	P ² << P ³	P ² << P ³	P ² < P ³
P ^{3,4} outline	Oval	Oval	Rather waisted
M ^{1,2} outline	Triangular	Triangular	Triangular
M ^{1,2} hypocone	Crestiform	Crestiform	Absent/vestigial
M ³	Bicusped	Bicusped	Lost
M ^{1,2} and M ³	M ^{1,2} >> M ³	M ^{1,2} >> M ³	M ³ lost
C ₁ sexual dimorphism	Present	Present	Absent/very weak
M _{1,2} outline	Square	Square	Waisted
Differences			
P ⁴ -M ³ buccal cingulum	Complete	Vestigial	Absent/vestigial
M ^{1,2} protocone	Not inflated	Inflated*	Not inflated
C ₁ outline	Almond-like	Oval	Rather oval
C ₁ long axis	Mesiodistal	Oblique	Oblique
P ₂ and P ₃	P ₂ > P ₃ **	P ₂ < P ₃ in female	P ₂ = P ₃
P ₄ -M ₂ buccal cingulid	Indistinct	Only buccal conules	Undeveloped
M ₁ paraconid	Present	Absent	Absent
M _{1,2} hypoconulid	Small but present	Absent	Absent
M ₃ width	Narrower	Broader	M ₃ lost
M ₃ talonid	Protrudes distally	Not so long	M ₃ lost

¹ The features with one or more asterisks are somewhat doubtful, and are discussed in detail in the text.

* Not inflated? See text.

** Male sample? See text.

and 3) the long axis of the lower canine in *Proteopithecus* is oriented to the cheek tooth row rather than being set obliquely as in extant platyrrhines (Miller and Simons, 1997). Among these three discriminating characters, the first two are not seen in *Branisella*. The last one, the lower canine orientation and morphology, will be discussed below in more detail.

Miller and Simons (1997) compared *Proteopithecus* with *Branisella*, pointing out that *Proteopithecus* has broader upper molars and lacks an inflated protocone. However, a direct comparison of the specimens of these two genera reveals that upper molars of *Proteopithecus* are not much broader than those of *Branisella*, and the protocone of *Branisella* is not significantly inflated. In contrast to earlier deductions, there are many morphological similarities in the dentition of these two genera: 1) the dental formula is 2 (?)/2.1/1.3/3.3/3; 2) P² is basically unicusped and much smaller than bicusped P^{3,4}; 3) M¹ and M² are rather wide buccolingually and triangular in occlusal outline, with a moderately large, crestiform hypocone on the distolingual cingulum; 4) the metaconule often occurs on M¹; 5) M³ is bicusped, with a lingual cingulum and much

smaller than M^{1,2}; 6) the upper canine has a distinct mesial vertical groove; 7) sexual dimorphism is present in the lower canine (and probably on P₂); and 8) on M_{1,2} the occlusal outline is basically square.

Thus, *Branisella* and *Proteopithecus* closely resemble each other in the basic structure of the upper dentition (Table 5). Their only substantial difference in the upper dentition occurs in the buccal cingulum. *Proteopithecus* retains a complete buccal cingulum, whereas in *Branisella* there are only vestigial ones at the mesial and distal buccal corners. Nevertheless, a complete buccal cingulum/cingulid is generally regarded as a primitive character usually seen in fossil prosimians. The presence of the complete lingual cingulum in *Proteopithecus*, which is geochronologically much older than *Branisella*, does not negate the possibility of the phyletic relationship between *Proteopithecus* and *Branisella*. Moreover, the following shared features of both taxa, such as a distinctly small P², oval outline of P³ and P⁴, and buccolingually wide, triangular M¹ and M² with a crestiform hypocone on the distolingual cingulum, can be a synapomorphy among them. The combination of these features is not seen in other Fayum

primates or in other South American monkeys.

In the lower dentition, however, these two genera are not as similar as in the upper one (Table 5): in *Proteopithecus*, 1) an occlusal outline of the lower canine is almond-like, being bilaterally compressed, while in *Branisella* it is oval-like, being mesiodistally compressed; 2) P_2 is larger than P_3 (Miller and Simons, 1997), whereas in *Branisella*, P_2 is slightly smaller than P_3 in MNHN-Bol-V 5310, which is probably a female specimen; 3) P_4 and $M_{1,2}$ have an indistinct buccal cingulum, but in *Branisella*, a buccal conule is occasionally present; 4) M_1 has a paraconid; 5) M_1 and M_2 often have a small hypoconulid twinning with the entoconid; and 6) M_3 is much narrower buccolingually and its talonid protrudes more distally than in *Branisella*.

By these morphological differences, *Branisella* and *Proteopithecus* can be easily distinguished from each other taxonomically, but are these features sufficient to negate the possibility of a phyletic relationship between them? Can features seen in *Proteopithecus*, such as the occurrence of the buccal cingulum, paracone, hypoconulid-entoconid twinning, and tapering of the M_3 talonid, be regarded as primitive characters in anthropoid evolution? As in the upper dental characters, most of these features suggest the primitiveness of *Proteopithecus*, with the exception of two characters: P_2/P_3 size ratio and lower canine morphology.

In one new specimen of *Branisella* (MNHN-Bol-V 5310), P_2 projects further but is slightly smaller in occlusal view than P_3 (Figs. 2a, 6b), but in another specimen (MNHN-Bol-V 3465) the size of P_2 (unfortunately, $P_{3,4}$ were not discovered) is much larger than the P_3 of MNHN-Bol-V 5310 (Fig. 6a,b). As already mentioned, if MNHN-Bol-V 5310 is a female and 3465 is a male specimen, then a male individual P_2 should not be smaller than P_3 . On the other hand, although in *Proteopithecus* P_2 is larger and more projecting than P_3 , as shown in a stereopair photograph of CGM 42209 (Miller and Simons, 1997), sexual dimorphism in the canine is reported by the same authors. Therefore, if CGM 42209 (whose P_2 is larger than P_3) is a male specimen, a female speci-

men of *Proteopithecus* might have a smaller P_2 than P_3 . In short, MNHN-Bol-V 5310 may be a female *Branisella*, and CGM 42209 be a male *Proteopithecus*, and so the direct comparison of P_2 morphology may be meaningless at present. Only more detailed analysis of sexual dimorphism in *Branisella* and *Proteopithecus* will resolve this problem.

The morphology of the lower canine is more enigmatic. Such a bilaterally compressed canine as seen in *Proteopithecus* is never seen in either extant or extinct platyrrhines. In platyrrhine monkeys, the lower canine is generally compressed mesiodistally with the distolingual heel protruding posteriorly, so that the occlusal outline is nearly oval-like. If the shape of the lower canine of *Proteopithecus* is really almond-like as in the photograph of CGM 42209 (its lower canine was reversed from a micrograph of another specimen, DPC 15416), it is very strange feature, unique to *Proteopithecus*.

In conclusion, *Proteopithecus* and *Branisella* show more similarity to each other in dental morphology, except for the lower canine, than to any other extinct or extant primates, and, moreover, the former obviously shows a more primitive condition than the latter (Table 5). Therefore, it is very natural to hypothesize a phyletic relationship between them, i.e., *Proteopithecus* may be a member of the ancestral group for *Branisella*.

Where and when did platyrrhine monkeys originate?

The problem of platyrrhine origins has been debated for a long time by many researchers. During this decade, the African origin hypothesis has been favored over the North American one on the basis of paleontological evidence, such as fossil records of primates and rodents (Hoffstetter, 1980; Lavocat, 1980). One of the candidates for a hypothetical African ancestral stock for living South American monkeys was the parapihthecid group from the Early Oligocene of Fayum, Egypt (e.g., Hoffstetter, 1980). However, the phyletic position of parapihthecids is currently regarded as "a specialized side-branch of anthropoid evolution which split

off from the combined platyrrhine/catarrhine stem" (Fleagle and Kay, 1987).

The dental morphology of parapithecids is actually too specialized to be a model for the ancestral condition of the platyrrhine dentition, whereas the dentition of *Proteopithecus* is basically more primitive than that of the platyrrhines. Miller and Simons (1997) and Simons (1997) suggested the phyletic relationships between *Proteopithecus* and platyrrhines. Kay and Williams (1995) and Fleagle (1998) also pointed out the morphological suitability of *Proteopithecus* as an example of the platyrrhine ancestral condition in dental, cranial, and postcranial features. The morphological similarity between *Proteopithecus* and *Branisella* supports the idea that *Proteopithecus* is the ancestral taxon for platyrrhines.

If there is some phyletic relationship between *Proteopithecus* and *Branisella*, can they qualify as ancestral stock for all platyrrhine monkeys? Rosenberger et al. (1990, 1991) have already argued for callitrichine ancestry in Salla primates, on the basis of upper molar similarities, though they classified the Salla primates into the two taxa *Branisella* and "*Szalatavus*." They concluded that upper molar similarities between "*Szalatavus*" (not including *Branisella* in their sense) and callitrichines are unlikely to be homology (Rosenberger et al., 1991). On the other hand, Takai and Anaya (1996) suggested that *Branisella* is likely to be a morphotype, not for all platyrrhines, but only for the callitrichine clade. Other nonmarmoset platyrrhines, pitheciines and atelines, exhibit much larger body-size, quadricusped, square-outlined upper molars, more robustly constructed canines, and narrow spatulate, protruding incisors (pitheciines), or wide spoon-like incisors (atelines). Neither *Branisella* nor *Proteopithecus* shares these derived characters with pitheciines and atelines. On the contrary, *Soriacebus* and *Carlocebus*, both Early Miocene primates from Patagonia, share these derived features with nonmarmosets (Fleagle et al., 1987; Fleagle, 1990). *Chilecebus* from the Early Miocene of Central Chile also retains quadricusped, square-outlined upper molars, and does not show any special resemblance to *Branisella* (Flynn et al., 1995).

The hypothetical *Proteopithecus-Branisella* clade never shows nonmarmoset features but indicates an initial evolution towards the marmoset group. Moreover, other slightly younger fossil taxa from the Early Miocene of Southern South America, such as *Soriacebus*, *Carlocebus*, and *Chilecebus*, show nonmarmoset features. Thus, the initial diversification of platyrrhine monkeys, such as the marmoset/nonmarmoset dichotomy, might have begun much earlier than ever presumed, i.e., during the Late Eocene or Early Oligocene on the African continent. The ocean drifting and invasion of several land mammals, at least rodents and primates, from the African continent to South America might have been a more inevitable event than imagined by many researchers. During the Middle Oligocene, when the sea level was lowest during the Paleogene, there should have been island connections with ideal currents from Africa to South America. There seems no compelling reason to assume that only a single primate taxon was successful in crossing the Oligocene (?) Atlantic Ocean. A hypothetical *Proteopithecus-Branisella* clade suggests the possibility and probability of the invasion of South America by other groups that were ancestral to nonmarmoset monkeys (Fig. 10b).

Recently, on the other hand, several molecular or immunological studies provide divergence times among the platyrrhine lineages. Schneider et al. (1993) and Porter et al. (1997) calculated the divergence dates between Cebidae (including callitrichines, *Cebus*, *Saimiri*, and *Aotus* in their sense) and Atelidae (including atelines, pitheciines, and *Callicebus* in their sense) at 20.1 million years ago (Ma) or 21.3 Ma, respectively, using sequences of the ϵ -globin gene. Both of these papers adopted 35 Ma for the platyrrhine-catarrhine split of the primate fossil record set by Fleagle (in 1988, which was revised in 1998) as the basis of the calculation, and they discussed that the presence of *Branisella*, the oldest platyrrhine fossil (26 Ma), is compatible with their estimation of the cebid-atelid divergence time (20.1 or 21.3 Ma). As mentioned above, however, *Branisella* is unlikely to be a basal ancestor of all platyrrhines. About 20 mil-

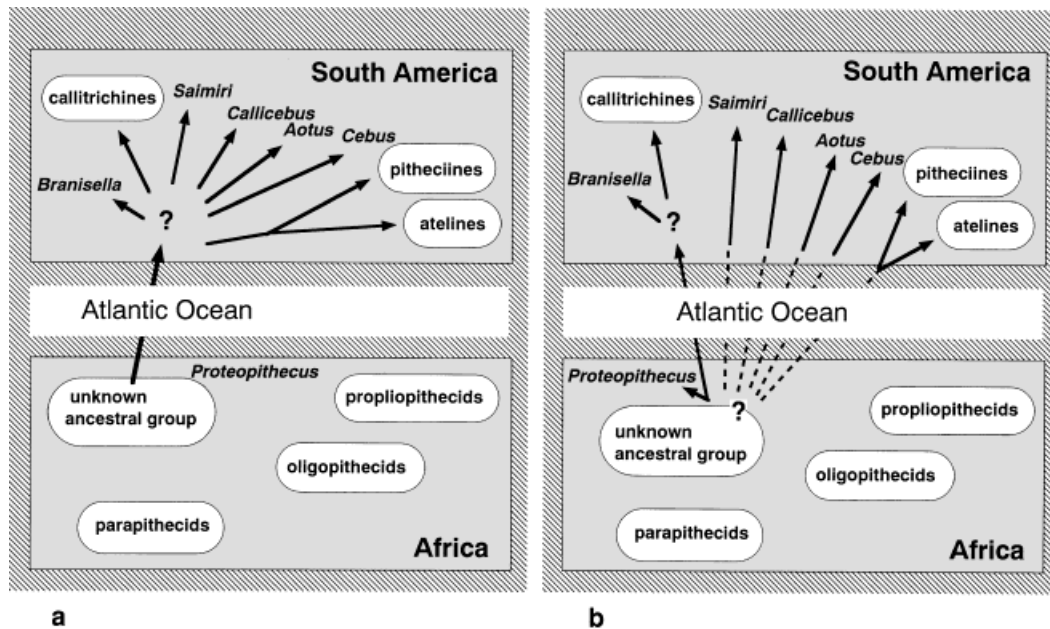


Fig. 10. Schematic diagram of two hypotheses of platyrrhine origins. **a:** Traditional view. **b:** The early diversification hypothesis of this paper. Early platyrrhines may have diversified on the African continent before invading South America. Dotted areas mean the continents.

lion years ago there were at least two other fossil platyrrhines: *Chilecebus*, which retains far more quadrate upper molars and moderate-size P^2 (Flynn et al., 1995), and unnamed primates from Gran Barranca (Kay et al., 1999). It is very unlikely that *Branisella* produced *Chilecebus* and other Early Miocene Patagonian platyrrhines, such as *Soriacebus* or *Carlocebus* (Fleagle et al., 1987; Fleagle, 1990). Therefore, if these divergence times estimated by ϵ -globin gene sequences are correct and *Branisella* is not a basal ancestor for all platyrrhines, *Branisella* should be a side branch of the extant platyrrhines, and there must have been another ancestral taxon for *Branisella* and all later extinct/extant platyrrhines before 25 Ma. If this evolutionary scenario is correct, the morphological similarities observed among *Proteopithecus*, *Branisella*, and living callitrichines should be convergence.

Bauer and Schreiber (1997), however, in contrast to Fleagle (1998), estimated the platyrrhine divergent data as 52.5 Ma based on the comparative determinant analysis (CDA) of serum proteins of several anthropoids. Their data indicate double invasions

of ancestral platyrrhines to South America, and a platyrrhine paraphyly. Though their serum samples for platyrrhines are only of *Cebus* and *Lagothrix* and their assumption for primate origin is too old (80 Ma), it should be noted that their estimation of platyrrhine origins is much older than ever presumed by many authors. Supposing that 65 Ma were adopted for the emergence of primates, their estimation of platyrrhine divergence would be 42.7 Ma, which is still far older than other estimates, such as by Schneider et al. (1993) and Porter et al. (1997). As Bauer and Schreiber (1997) insist, it is not necessary to assume that platyrrhine monkeys originated on the South American continent. It may be more natural to infer that the earliest platyrrhines arose and diverged on the African continent during the Eocene or Early Oligocene, and some of them successfully cross the Atlantic Ocean to a new paradise, a neotropical forest, which provided an adequate habitat for them.

Our "early diversification hypothesis," however, does not mean a platyrrhine paraphyly as Bauer and Schreiber (1997) said. Our hypothesis is a preliminary proposal on

the origin and evolution of early platyrrhine monkeys, which rests only upon morphological similarity in dentition between *Proteopithecus* and *Branisella*. In order to examine this hypothesis, we need more complete fossil specimens of these taxa. Fortunately, the new findings in Africa and South America have stimulated us to examine the possibility of the early diversification and multiple invasions of ancestral platyrrhine monkeys into South America without preconceptions.

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