ON THE MORPHOLOGICAL DISTINCTIVENESS OF *CALLITHRIX HUMILIS* VAN ROOSMALEN *ET AL.*, 1998

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Abstract

The dwarf marmoset, described as *Callithrix humilis* by van Roosmalen *et al.* (1998), is an anomaly among Amazonian marmosets for its size, morphology and behavior. We compare cranial and mandibular characters of the dwarf marmoset with representatives of four other callitrichid genera. *C. humilis* displays qualitative differences in skull morphology when compared to other callitrichids, and a discriminant analysis of quantitative characters suggests that the dwarf marmoset is strongly distinct from all other Amazonian genera, including *Callithrix*. These differences are most pronounced in the morphology of the lower jaw and may reflect specialized feeding adaptations, although little is known of the dwarf marmoset's behavior in the wild.

Key Words – Primates, Callitrichidae, marmosets, *Callithrix humilis*, dwarf marmoset, *Callibella*, morphology, morphometrics, Amazonia.

Resumo

O sagüi-anão, previamente descrito como *Callithrix humilis* van Roosmalen *et al.,* 1998, é uma anomalia entre os sagüis da Amazônia por causa de tamanho, comportamento e morfologia. Comparamos carácteres cranianos e mandibulares do sagüi-anão com exemplares dos quatro outros gêneros de calitriquídeos. *C. humilis* exibe diferenças qualitativas na morfologia do crânio em comparação aos outros calitriquídeos, e uma análise discriminante dos carácteres quantitativos sugere que o sagüi-anão é marcadamente distinto de todos outros gêneros da Amazônia, incluindo *Callithrix*. Estas diferenças são mais acentuadas na morfologia da mandibula, e talvez refletam adaptações especializadas para alimentação, apesar de que o comportamento do sagüi-anão na natureza ainda ser pouco conhecido.

Palavras-Chave – Primatas, Callitrichidae, sagüis, *Callithrix humilis*, sagüi-anão, *Callibella*, morfologia, morfometria, Amazônia.

Introduction

The dwarf marmoset, first described as *Callithrix humilis* van Roosmalen *et al.*, 1998, is by far the most unusual of the seven new marmosets discovered in the Brazilian Amazon during the past decade. Its small size and atypical behavior make it an anomaly among classic marmosets; yet *C. humilis* is clearly both phenotypically and geographically distinct from *Cebuella pygmaea* as well. The original description offered several plausible alternatives for its taxonomic status, ranging from another species of *Cebuella* to a new genus of its own. Recent taxonomic reviews of the marmosets have elevated the two major species groups, the Amazonian and Atlantic Forest clades, to subgeneric (Groves, 2001) or full generic status (Rylands *et al.*, 2000), as *Mico* and *Callithrix* respectively—in each case recognizing that, given *Cebuella*'s closer relationship with the Amazonian clade, the latter must be considered as a full genus in order for *Cebuella* to be retained. Although van Roosmalen *et al.* (1998) originally described *C. humilis* as a conventional marmoset, albeit a peculiar one, further observation has convinced them that it deserves recognition as a novel monotypic genus (van Roosmalen, 2002; van Roosmalen and van Roosmalen, 2003).

The dwarf marmoset is exceptionally difficult to observe in the wild—one reason why it remained unnamed until the close of the twentieth century—and the most detailed observations have been made on a very limited number of captive specimens (van Roosmalen and van Roosmalen, 2003). This original group has since died from a variety of causes, including an outbreak of yellow fever (van Roosmalen, pers. comm.), but the type specimen (MPEG 24769) and two paratypes (INPA 4090, INPA 4091) have been cleaned and preserved at the Museu Paraense Emílio Goeldi (Belém, Pará) and the mammal collections of the Instituto Nacional de Pesquisas da Amazônia (Manaus, Amazonas), respectively. These three specimens, each consisting of skin and skull, represent the only material yet available for making direct morphological comparisons with other callitrichids. A comparative analysis of cranial and mandibular morphology is essential to evaluate the distinctiveness of this new species, and may also generate useful predictions concerning its ecology and feeding behavior in the wild.

Methods

As part of a larger project on callitrichid morphometrics and biogeography, we examined the three extant specimens of *Callithrix humilis* and compared them with other specimens of *Callithrix* and *Cebuella* held at MPEG and INPA, plus additional material representing *Callithrix*, *Saguinus* and *Leontopithecus* at the following institutions: the United States National Museum of Natural History (Smithsonian) in Washington, D.C.; the American Museum of Natural History in New York; the Rijksmuseum van Natuurlijke Historie in Leiden, the Netherlands; the Museu Nacional do Rio de Janeiro, Brazil; the Museu de Zoologia da Universidade de São Paulo, Brazil; the Swedish Museum of Natural History in Stockholm, Sweden; and the Humboldt Museum für Naturkunde in Berlin, Germany.

We measured all specimens to the nearest 0.01 mm with Mitutoyo Digimatic digital calipers, series/model 500-196. We measured a total of 32 characters from each specimen, except where precluded by damage; we did not take partial measurements on damaged features. (A list of measurement codes and descriptions is included in Appendix I.) To avoid issues of ontogenetic size change, we only examined adult specimens; our primary criteria for adulthood were fully fused cranial sutures and fully descended upper canines, supplemented by the presence of sharply defined superior temporal ridges. We log-transformed and analyzed the data using the Discriminant Analysis module of SPSS 11.0, running through Windows 2000 on a Dell XPS-R400 Pentium computer.

Results

Statistical Analyses

We compared the morphology of *C. humilis* with representatives of four other callitrichid genera: *Cebuella pygmaea*, *Callithrix chrysoleuca*, *Saguinus midas midas*, and one specimen each of the four species of *Leontopithecus*. (See Appendix II for a complete list of accession numbers.) The primary purpose of the initial morphological assessment was to evaluate the classification probabilities of the five genera. In an overall discriminant analysis of 17 cranial and mandibular characters, all four genera plus *C. humilis* were sorted into well-defined clusters differing markedly in both size and shape. All groups returned a 100% correct classification. Figure 1a shows a clear gradient of size along the axis of Function 1, with a secondary gradient of shape widely dividing *Callithrix* and *Saguinus* on Function 2. A similar pattern obtains in a comparison of cranial dimensions alone, using eight characters (Fig. 1b); in both cases *C. humilis* is closely allied to *Cebuella pygmaea*, yet is classified as entirely discrete.

When features of the mandible are compared separately (nine characters), a different pattern emerges which fur-

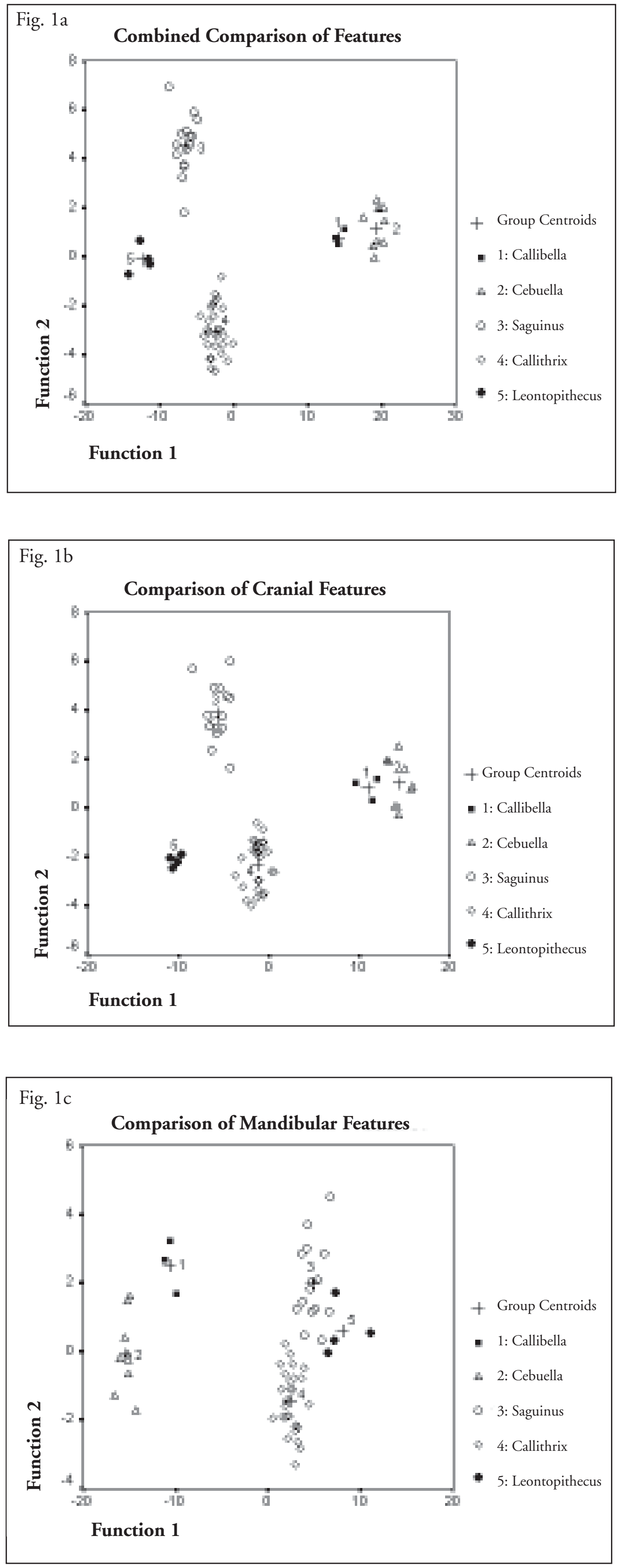

Figure 1. Discriminant plots of representative callitrichid taxa along gradients of size (Function 1) and shape (Function 2): a. combination of cranial and mandibular characters (17 total); b. cranial characters analyzed separately (8); c. mandibular characters analyzed separately (9).

ther separates *C. humilis* from *Cebuella* (Fig. 1c). The three larger genera—*Callithrix*, *Saguinus* and *Leontopithecus*—form a continuum of jaw shape, with a clear boundary between the exudate-gouging form of *Callithrix* and the non-gouging forms of *Saguinus* and *Leontopithecus*. There is also a recognizable gradient of size, with the latter two genera plainly larger than *Callithrix*. The dwarf and pygmy marmosets, meanwhile, are at an exceptional remove from the other callitrichids, isolated by their smaller size; yet *C. humilis* is further set apart on the dimensions of both size and shape. As expected from the visual examination, *C. humilis* separates out as slightly larger than *Cebuella*, and occupies a discrete subregion of morphospace. Intriguingly, *C. humilis* plots toward what might be considered the non-gouging axis, which might suggest that the dwarf marmoset is less reliant on active exudate-feeding than *Cebuella*, which is an extreme gum specialist (Soini, 1988).

Visual Examination

In his monumental description of the callitrichids, Hershkovitz (1977) gave the size of *Cebuella*—"smallest of known platyrrhines and absolutely smaller than all other callitrichids"—as its main diagnostic character, aside from a list of its ostensibly primitive features. Of marmosets, he admitted that "no single cranial character consistently separates *Callithrix* from *Cebuella* or *Saguinus*." Similarly, *C. humilis* shows no definitive cranial features which might easily distinguish it from classic *Callithrix* or *Cebuella*; the skull is significantly smaller than *Callithrix*, and visibly larger than *Cebuella*, but there are no structures or assemblies which are clearly unique. The mandible of *C. humilis*, however, is visually distinct from any other callitrichid, and is the focus of the comparative descriptions below.

When describing the shapes of callitrichid jaws, Hershkovitz (1977) concentrated on several key features: the height of the coronoid and condylar processes; the shape of the sigmoid notch between them; the depth of the angular process; and the overall shape of the ascending ramus (Fig. 2). When observed firsthand, these features combine to produce a gestalt impression of the characteristic jaw shape for each genus. The lower jaws of *Saguinus*, for instance, typically have a high, curving coronoid process with a "wavecrest" tip, above a compact, oval sigmoid notch and a mandibular condyle positioned well above the toothrow plane (Fig 3b). *Leontopithecus* has a similar, slightly larger structure (Fig. 3a), and both tamarin genera display a nearly flat jaw base, with virtually no lower projection of the angular process.

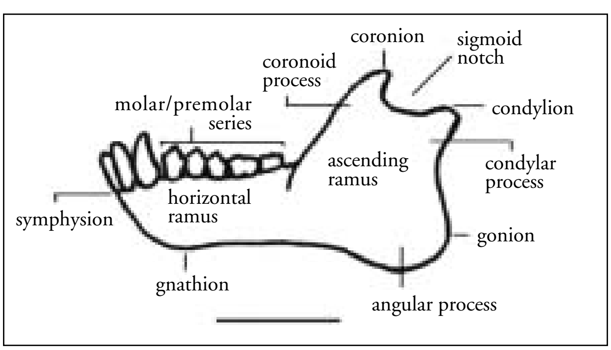

Figure 2. A generalized callitrichid jaw, showing major features. Drawn from a specimen at the Smithsonian National Museum of Natural History. Scale bar = 1.0 cm.

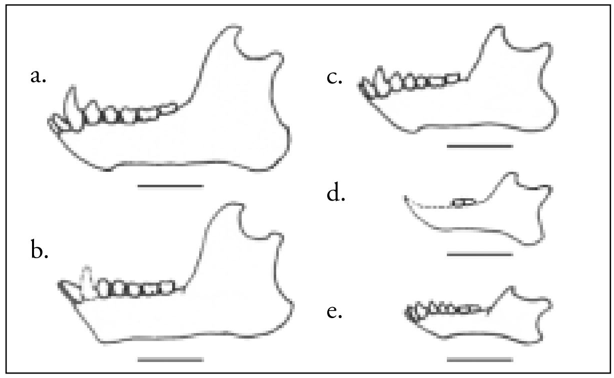

Figure 3. Jaws of representative callitrichid genera: a. *Leontopithecus*; b. *Saguinus*; c. *Callithrix*; d. *Callibella* (*sensu* van Roosmalen and van Roosmalen, 2003); e. *Cebuella*. Drawn from specimens at the Smithsonian National Museum of Natural History (a-c, e) and from a photograph by Stephen Nash (d). Scale bar = 1.0 cm.

The ascending ramus of a typical *Callithrix* jaw, by contrast, has a much lower coronoid process; there is a wider lateral separation between coronoid and condylar processes, with the sigmoid notch usually more of an open oval or a long, inclined fish-hook (Fig. 3c). The condyle is comparatively closer to the plane of the toothrow (though not quite as close as Hershkovitz implied, on p. 488) and the angular process is often a deep, rounded lobe beneath the jawline. *Cebuella* represents the extreme culmination of these trends: the coronoid process is modest, brief and shallow, with the most delicate of points; the sigmoid notch is wide open, more of a hyperbolic segment; and the condyle rides directly at or just above the molar plane (Fig. 3e). In *Cebuella* the angular process is sharp, lean and projects well below the baseline; the entire ascending assembly gives the impression of having been compressed and tilted from a *Saguinus*-like starting point, elongated and rotated downwards and aft. Following the genera in reducing size, the trend is for a lower and less arcuate coronoid; an increasingly wide and open sigmoid notch; a shallower condylar process, descending to meet the molar plane; and an angular process which extends ever deeper, creating an increasingly recurved jawline.

In this context, the jaw of *C. humilis* is intermediate in shape between *Callithrix* and *Cebuella* (Fig. 3d). The mandibular condyle is just barely above the occlusal plane, the coronoid just above that, with a shallow "fish-hook" sigmoid notch. The angular process, however, projects much lower than that of either *Cebuella* or *Callithrix*, and the composite of these features is immediately recognizable as a singular morphological package. In contrast with the *Cebuella* jaw, which is gracile and delicate, the jaw of *C. humilis* is comparatively robust, with lower canines that are visibly much larger than in *Cebuella*. The symphysial prow is not strongly procumbent as in *Cebuella*, but rather more vertical as in *Callithrix*; and in general the ascending ramus of *C. humilis* is not quite so angled and compressed as that of *Cebuella*.

In addition, *Cebuella* possesses another feature apparently unique to its genus: a strong, slender ridge on the inner face of each ramus, arising from the slight shelf interior to the gonion and running horizontally to just below each of the mandibular foramina. (This feature is distinct from the mylohyoid line, which originates from the inner edge of the mandibular condyle.) This feature is apparently unnamed (C. Groves, pers. comm.) and here we label it as the inner gonial flange. Although faint inner gonial flanges are frequently found in *Saguinus*, and often in *Callithrix*, they are never so exaggerated as in *Cebuella*—and *C. humilis* shows no trace of one.

Thus the mandible of *C. humilis* is set apart from that of *Cebuella* by several important features: the higher coronoid and condyle, the more vertical symphysial prow, the notably deeper angular process, the absence of any inner gonial flange, and a generally heavier aspect. If Hershkovitz were to write a description of the *C. humilis* mandible today, it might read something like this:

> "…ascending ramus broad, more or less oblong; average coronoidal height about 52% of condyloincisive length of mandible; coronoid process low, the rounded tip extending slightly above condyle; sigmoid notch broad and shallow; articular surface of condylar process hardly above the plane of molar crowns; inferior border of angular process deflected radically below basal plane of horizontal ramus."

Discussion

The dwarf marmoset, *Callithrix humilis*, was described as one among many new marmoset species discovered in the 1990s. Although the number of species-level taxa had more than doubled in the prior decade, this was almost entirely a result of the stepwise elevation of subspecies to full species status. Hershkovitz (1977) originally recognized only two species of marmosets from the Amazon basin: *Callithrix humeralifer* and *C. argentata*, with three subspecies apiece. Initially accepted without alteration (e.g., Mittermeier and Coimbra-Filho, 1981), this arrangement persisted throughout much of the 1980s. The first major change was the reassertion of *C. emiliae* by Mittermeier *et al.* (1988), a species which had been described by Thomas (1920) but later subsumed within *C. argentata* by Hershkovitz (1977). Earlier, de Vivo (1985) had noted the presence of a form of *Callithrix* in Rondônia, which he identified as *emiliae*; and following a morphometric survey of the genus, he treated *all* marmoset taxa as full species (de Vivo, 1991), which had the effect of more than tripling the recognized diversity of Amazonian marmosets—from the two species recognized by Hershkovitz (1977) to a total of seven.

Immediately afterwards, the first pair of new marmoset species was described: *Callithrix nigriceps* from Rondônia (Ferrari and Lopes, 1992) and *C. mauesi* from the Amazonian floodplain (Mittermeier *et al.,* 1992), the latter description adopting de Vivo's (1991) arrangement. Then Alperin (1993) described the new subspecies *C. argentata marcai*, later treated as a full species (Rylands *et al.*, 2000; Groves, 2001); and in 1998 two more new species were described, the distinctive *C. saterei* (Sousa e Silva and Noronha, 1998) and the singular *C. humilis* (van Roosmalen *et al.*, 1998). A final pair of *species novae*, *C. acariensis* and *C. manicorensis*, was described by van Roosmalen *et al.* (2000)—closing a decade of unexpected discoveries and bringing the complement of known Amazonian marmosets to a total of 14 species. Rylands *et al.* (2000) and Groves (2001), following de Vivo's (1991) lead, upheld the practice of considering all new taxa as de facto species. In addition, many researchers now believe the Rondônian *Callithrix*, which de Vivo (1985) had considered "*C.* cf. *emiliae*," to be another distinct species (L. Sena, pers. comm.), and the potential exists for additional discoveries in other, underexplored regions of the central Amazon.

In this rather heady context, the appearance of a new marmoset species unlike any other stimulated less discussion than it might otherwise have. *Callithrix humilis*, as it was originally described, is much closer in size to *Cebuella* than to other marmosets, but is set off from the pygmy marmoset by its bare ears, lack of full mane and a smoother, more even coloration. *C. humilis* is reported exclusively from a small region between the Rios Aripuanã and Manicoré, south of the Rio Madeira (van Roosmalen *et al.*, 1998; van Roosmalen and van Roosmalen, 2003). Wild sightings have been made principally along the western bank of the Rio Aripuanã, close to its convergence with the Madeira, which has led van Roosmalen *et al.* (1998) to consider its range "by far the smallest distribution of any primate in the Amazon" and of potential conservation concern.

When van Roosmalen *et al.* (1998) originally described the dwarf marmoset, they chose to include it within the genus *Callithrix*, but indicated that its unusual appearance and behavior had prompted them to consider a variety of taxonomic options—considering it either a form of *Cebuella*, or a separate species of *Callithrix*, or perhaps even a representative of a previously undescribed genus. After further explorations in the field, and prolonged observations of a captive group, van Roosmalen and van Roosmalen (2003) are now convinced it merits recognition as a new platyrrhine genus, for which they propose the name *Callibella*.

On purely morphological grounds, we would consider this to be appropriate. *Callibella*'s exceptionally small size clearly argues against combining it with other marmosets; and the distinctive features of its pelage and cranial morphology—in particular its unique mandibular design—separate it just as completely from *Cebuella*. Given this strong morphological differentiation from both *Cebuella* and the Amazonian marmosets, the case for a new genus appears promising—although we recognize that a genus must be defined by its status as a monophyletic group (Groves, 2001) and that the separation of *Callibella* would be invalid if the remaining Amazonian marmosets (*Mico*, *sensu* Rylands *et al.*, 2000) were shown to be paraphyletic as a result. At present, however, we have no reason to suspect this, owing in part to a general scarcity of information on most aspects of its biology. Its remarkably elusive nature makes it difficult to locate and observe in the field (J. M. Aguiar, pers. obs.), and a long-term field study would help clarify our understanding of its distribution and behavior.

In the meantime, lacking comprehensive field data, can we generate predictions about its behavior from the morphological information now available? A range of studies have used cranial and mandibular characteristics to examine ecological trends in both extinct and extant organisms. The advantage of the latter is that their behavior may be observed in the field and directly correlated with morphological features, allowing for attempts at synthesis between ecological and morphological studies (e.g., Anapol and Lee, 1994; Dumont, 1997; Monteiro-Filho *et al.*, 2002). Although a number of studies have employed a deductive approach to explore the interaction of cranial morphology and ecological specialization (e.g., Hylander, 1979; Dumont, 1997; Vinyard *et al.*, 2003), some recent research has begun to integrate morphometrics and field ecology (Sicuro and Oliveira, 2002; Aguirre *et al.*, 2002), and cross-taxon comparisons may generate predictions which may be tested against both theoretical models and observations from the field (e.g., Williams and Wall, 1999; Aguirre *et al.*, 2003; Vinyard *et al.* 2003).

Although the jaw morphology of callitrichids is often quite variable within species (Aguiar and Lacher, 2002), certain trends may be seen between those marmoset species which rely heavily on exudate-feeding and those which do not. Amazonian marmosets such as *Callithrix humeralifer*, which feed more on fruits and insects and less on exudates (Stevenson and Rylands, 1988; Ferrari and Lopes Ferrari, 1989), often display a straighter, less arcuate jaw base, with the lobe of the angular process extending only minimally below the gnathion (Fig. 3c). Marmoset species from the Atlantic Forest clade, such as *C. jacchus* and *C. penicillata*, spend a greater proportion of their time parasitizing exudate sources (Lacher *et al.*, 1984; Kinzey, 1997); these species typically demonstrate a deeper angular lobe and a more strongly recurved inferior margin of the jaw. *Cebuella* likewise bears a strongly descending angular lobe, though more gracile in form, corresponding with the rest of the lightweight mandible. *Callibella humilis* also shows a prominent angular lobe—deeper than that of *Cebuella*—which by itself might suggest an emphasis on intensive exudate-gouging.

Another major feature differentiating callitrichid jaws is the position of the mandibular condyle in relation to the coronoid process, the sigmoid notch and the occlusal plane of the molars. In the larger-bodied callitrichids, the coronoid-condylar assembly rises high above the toothrow; the sigmoid notch is tightly oval or nearly circular, and the coronoid process extends high above the condyle. (This reaches an extreme in *Saguinus bicolor*, whose coronoid blades sweep up and back like slender scimitars.) In the smaller, actively gouging *Callithrix*, however, the coronoids are much lower, closer to the level of the condyles, and the sigmoid notch opens out into a fish-hook shape. The condyle itself is still positioned above the toothrow, but lower than in the tamarins.

In *Cebuella*, the condyle is on a direct line with the occlusal surface of the lower molars, a dramatically different shape which seems to occupy the endpoint of a continuum beginning with the tamarins. In this context, *Callibella* is remarkable, as its coronoid-condylar assembly is intermediate between the sturdy, nearly level pattern of *Callithrix* and the gracile, sharply angled shape of *Cebuella*. If *Callibella* were merely another species of *Cebuella*, as its discoverers had once imagined, the mandible should show a similar morphology. That it does not, but rather displays a third, intermediate design, argues for a distinct ancestry and dietary habit which should be recognized taxonomically.

The distinctly lower condylar position of *Cebuella* and *Callibella* is congruent with the pattern of several other small, gum-feeding primates, notably *Phaner furcifer* and *Euoticus elegantulus*. In a new study on the morphology of exudate-eaters, Vinyard *et al.* (2003) examined the crania and mandibles of both gouging and non-gouging primates, including *Callithrix*, *Phaner*, *Euoticus*, *Galago* and *Cheirogaleus*. Although Vinyard *et al.* found virtually no morphological evidence for special strengthening in the skulls of gouging primates, they did detect a correlation between the height of the mandibular condyle and dietary reliance on gouging. According to their predictions, lower condyles should reduce the stretching of muscle fibers in the masseter and pterygoid, minimize the aft displacement of the jaw in motion, and increase the moment arm of the temporalis—the combination of which, according to Vinyard *et al.*, would help a gouging primate to produce more force in its bite, and presumably improve the efficiency of the gouging process.

This correlation between lower condyle position and active exudate-gouging is easily seen in callitrichids; the genera *Callimico*, *Saguinus* and *Leontopithecus*, which feed on available gum but do not stimulate its flow, all have mandibular condyles borne high above the occlusal plane of the teeth. Gouging marmosets—*Cebuella*, *Callithrix* and *Callibella*—bear condyles which are notably lower, and in both *Cebuella* and *Callibella* the occlusal plane passes through or directly beneath the condylar bulb. As noted above, this latter condition is also visible in *Phaner furcifer* and *Euoticus elegantulus*, which are well-established as archetypal exudate-feeders (Charles-Dominique, 1971; Hershkovitz, 1977; Nash, 1986). The extreme shift of the condyles and associated structures in *Cebuella* is almost certainly correlated with that species' reliance on gums as a staple food resource (Soini, 1988; Garber, 1992), and a similar condition in *Callibella* may correspond to a parallel but less-pronounced focus on exudate-feeding.

Conclusions

The marmoset formerly known as *Callithrix humilis*, which van Roosmalen and van Roosmalen (2003) propose as the new genus *Callibella*, is morphologically distinct from all other marmoset and tamarin taxa. Discriminant analyses of cranial and mandibular characters all returned a 100% separation of groups. These differences are apparent on visual inspection, especially in the mandibular morphology, and aspects of the jaw structure appear to fit into general trends across the Callitrichidae. The dwarf marmoset is morphologically distinct from both *Callithrix* and *Cebuella* (presumably its nearest relatives) to an equal degree, and we consider its elevation to the genus *Callibella* to be an appropriate recognition of its exceptional nature.

Callibella's suite of craniomandibular traits, in turn, suggests a lifestyle somewhat similar to that of *Cebuella*, but perhaps with less of an emphasis on exudate-feeding. Van Roosmalen *et al*. (1998) reported a number of social, ecological and behavioral traits which seem unique to this genus, and which might imply a correspondingly unprecedented foraging niche. The dwarf marmoset's reported heavy reliance on a single tree species, *Didymopanax morototoni*, together with its restricted and potentially relict distribution, might suggest a closer coevolutionary link with a specific host tree than reported from any other marmoset; but only a full field study will provide the necessary ecological context for these initial speculations.

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Appendix I:
Baseline Morphometric Measurements

Code	Name	Description
CL	cranial length	Prosthion to rearmost point of cranium
OCP	occipital condyle-prosthion	Rear of left occipital condyle to prosthion
ZAZ	zygomatics at zygions	Width of zygomatic arches at zygions
SKW	skull width	Maximum skull width, at temporal ridges
OWC	orbital width at cyclosions	Maximum orbital width at cyclosions
BL	bregma-lambda	Distance from tripoint bregma to tripoint lambda
CONW	condylar width	Distance across base of occipital condyles
MW	molar width	Maximum width of upper molars, M1L-M1R
CW	canine width	Maximum width of upper canines, C1L-C1R
MSL-L	molar series length, left	Length of left upper molar/premolar row
MSL-R	molar series length, right	Length of right upper molar/premolar row
BN	bregma-nasion	Distance from tripoint bregma to tripoint nasion
PBG	prosthion-bregma	Distance from prosthion to tripoint bregma
NP	nasion-prosthion	Distance from prosthion to tripoint nasion
NL	nasion-lambda	Distance from tripoint nasion to tripoint lambda
PL	prosthion-lambda	Distance from prosthion to tripoint lambda
MWJ	molar width, jaw	Maximum width of lower molars, M2L-M2R
CWJ	canine width, jaw	Maximum width of lower canines, C1L-C1R
MSLJ-L	molar series length, jaw, left	Length of left lower molar/premolar row
MSLJ-R	molar series length, jaw, right	Length of right lower molar/premolar row
SGL-L	symphysion-gonion, left	Distance from symphysion to rearmost left gonial point
SGL-R	symphysion-gonion, right	Distance from symphysion to rearmost right gonial point
CJB-L	condylion-jaw base, left	Height from condylar knob to base of left jaw flange
CJB-R	condylion-jaw base, right	Height from condylar knob to base of right jaw flange
COR-L	coronion-jaw base, left	Height from coronion tip to base of left jaw flange
COR-R	coronion-jaw base, right	Height from coronion tip to base of right jaw flange
SCN-L	symphysion-condylion, left	Distance from symphysion to rearmost left condylion
SCOR-L	symphysion-coronion, left	Distance from symphysion to left coronial tip
SCN-R	symphysion-condylion, right	Distance from symphysion to rearmost right condylion
SCOR-R	symphysion-coronion, right	Distance from symphysion to right coronial tip
JWCR	jaw width, coronia	Maximum width between outer coronial tips
JWCY	jaw width, condylia	Maximum width between outer condylar knobs

Appendix II:
Specimens Examined

Callithrix chrysoleuca: AMNH: 91833, 91834, 91835, 91836, 91838, 91839, 92296; FMNH: 50821, 50822, 50828; MNRJ: 5947, 5948, 5950; MZUSP: 4886, 4892, 4976, 5008, 5022, 5028, 11410, 13466, 13467; SMNH: A611502, A611497, A611520, A611579. *Callithrix humilis:* MPEG: 24769; INPA: 4090, 4091. *Cebuella pygmaea:* AMNH: 74056, 74369, 75280, 76327, 76328, 182943, 182944; MPEG: 382, 26367. *Leontopithecus caissara:* MNRJ: 28861. *Leontopithecus chrysomelas:* MNRJ: 24573. *Leontopithecus chrysopygus:* HMNK: 304. *Leontopithecus rosalia:* NMNH: 337334. *Saguinus midas midas:* MPEG: 15269; RMNH: 20566, 20568, 20569, 20582, 20571, 20574, 20575, 20577, 20578, 20580, 22562, 22572, 24089, 22546.