Mandibular Specimens of *Stirtonia victoriae* from the La Victoria Formation, La Venta, Colombia

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ABSTRACT

The earliest evidence for the alouattine clade, howler monkeys, can be found at the Middle Miocene site of La Venta in Huila Department, Colombia. La Venta has yielded over 100 vertebrate species including 12 primates representing all extant platyrrhine families and is notable as the site that provides the earliest evidence of a proto-Amazonian primate community. Currently, two alouattine species have been described: *Stirtonia victoriae* and *Stirtonia tatacoensis. Stirtonia victoriae* is found in the older La Victoria Formation and was previously known only from maxillary and cranial fragments. *Stirtonia tatacoensis* has been recovered from sediments in the younger Villavieja Formation and is primarily known from isolated teeth and partial mandibular remains. Here, we report the first mandibular specimens of *S. victoriae*, which preserve canines, premolars, and molars, as well as the mandibular symphysis and portions of the mandibular ramus. We use three-dimensional geometric morphometric (3DGM) analysis of second lower molars to reconstruct diet as well as 3DGM analysis of mandibular shape to examine *S. victoriae* morphology within the evolutionary context of the platyrrhine radiation. Our dental analyses indicate that *S. victoriae* likely consumed leaves as a substantial portion of its diet. Its mandibular shape is broadly similar to that observed among atelids and howler monkeys, genus *Alouatta*, more specifically. Body mass reconstruction using lower first molar area and a phylogenetic least squares regression approach indicate that *S. victoriae* was around 6.6–8.7kg. New body mass estimates using this method are also provided for other extinct platyrrhine species. The fossil evidence of *S. victoriae* described here provides the earliest example of committed leaf-eating among platyrrhines.

INTRODUCTION

The oldest fossil evidence associated with the lineage that gave rise to howler monkeys (genus *Alouatta*) comes from the Middle Miocene paleontological site of La Venta, Colombia (Kay et al. 1987; Stirton 1951). La Venta also provides evidence for the earliest known ecologically and dietarily diverse platyrrhine community, with species exhibiting a wide range of body masses and dietary adaptations comparable to those present in modern Amazonian primate communities (Cooke 2011; Kay and Madden 1997a; Wheeler 2010). This contrasts sharply with the more constrained diets and body masses observed among the extinct Caribbean (*Antillothrix bernensis, Insulacebus toussaintiana, Paralouatta varonai, Xenothrix mcgregori*) and Patagonian (*Soriacebus ameghinorum*, *Soriacebus adrianae*, *Homunculus patagonicus*, *Dolichocebus gaimanensis*, *Carlocebus carmanensis*) primates. The La Venta fauna is crucial for examining the earliest stages of dietary niche differentiation among platyrrhines, as the divergence of many extant primate lineages likely occurred during the Middle Miocene. As dietary shifts often lie at the base of speciation events, understanding the evolution of dietary adaptations within this primate paleocommunity can provide essential insight into the evolution of dietary diversity and niche differentiation across the extant platyrrhine radiation.

Howler monkeys are currently distributed throughout Central and South America in a wide variety of ecosystems including rainforests, tropical dry forest, deciduous, and semi-deciduous forests (Doyle et al. 2021) and have been well-studied across their geographic range (e.g., Chaves and Cesar Bicca-Marques 2013; Chiarello 1994; Garber et al. 2015; Julliot and Sabatier 1993; Pavelka and Knopff 2004; Pinto and Setz 2004; Rosenberger and Strier 1989). Their wide distribution and adaptability have been attributed to a combination of dietary flexibility (including the possibility of relying on large proportions of leaves in their diets) and behavioral strategies associated with minimizing energetic expenditure (Milton 1980; Rosenberger and Strier 1989). Morphological features associated with these adaptations include a relatively small brain, dentition with well-developed shearing crests capable of processing a leafy diet, and a proportionally long digestive tract capable of hind-gut fermentation (Anapol and Lee 1994; Milton 1980, 1981; Milton and McBee 1983; Milton et al. 1980; Rosenberger et al. 2015). Among platyrrhines, howlers are unique in this combination of traits.

The wooly spider monkey (genus *Brachyteles*) has been reported to consume comparable quantities of leaves (Milton 1984; Strier 1992) in some parts of its range but has important behavioral and morphological differences from *Alouatta*. *Brachyteles* has a suspensory and brachiating locomotor pattern with associated long limbs, reduced thumb, and dorsally placed scapulae. In contrast to *Alouatta*, *Brachyteles* also has a relatively large brain size (Erikson 1963). Finally, a more recent ecological study in a non-fragmented habitat indicated a much higher consumption of fruit than previously reported (de Carvalho et al. 2004), potentially indicating more dietary flexibility than the older literature reports.

Molecular data indicate howler monkeys diverged from other members of the family Atelidae in the Middle Miocene (Beck et al. 2023; Doyle et al. 2021; Perelman et al. 2011). The divergence patterns of *Ateles, Lagothrix,* and *Brachyteles* have not been fully resolved with *Brachyteles* most commonly returned as sister taxon to *Lagothrix* (Chatterjee et al. 2009; Doyle et al. 2021; Opazo et al. 2006; Perelman et al. 2011; Schrago et al. 2013; Wildman et al. 2009), but *Ateles* has also been posited as its sister taxon (Beck et al. 2023). All studies are consistent that these divergences occurred in the Late Miocene. This makes fossil evidence from this time period especially important for understanding the development of niche partitioning and dietary specialization among atelids broadly and howlers specifically.

Members of the howler monkey lineage at La Venta include *Stirtonia tatacoensis* (Hershkovitz 1970; Stirton 1951) and *Stirtonia victoriae* (Kay et al. 1987). *Stirtonia* is consistently recovered as the sister group to extant *Alouatta* (Beck et al. 2023; Kay 2015), with some authors suggesting an ancestor descendent relationship (Delson and Rosenberger 1984; Rosenberger et al. 2015). The first specimen of *S. tatacoensis*, a partial mandible (UMPC 38989), was recovered in 1949 by Robert Fields and Diego Henao-Londoño (Stirton 1951). It was published two years later by Stirton (1951), who included the fossil in the Patagonian genus *Homunculus* (Ameghino 1891) as a new species, *Homunculus tatacoensis*, based on "marked similarity of dental patterns" (Stirton 1951: 332). He noted that the species bore resemblance to *Alouatta* particularly in the morphology of the M_1 and M_2 and listed the species under Alouattinae in subsequent publications (Stirton 1953; Stirton and Savage 1951). At the time of the species description, Stirton did not have access to the Patagonian *Homunculus* specimens and made comparisons using Bluntschli's figures (Bluntschli 1931)—many of which were of worn dentition. Hershkovitz took up the problem of *H. tatacoensis* again in 1970 and named a new genus, *Stirtonia*, based on the La Venta material. Hershkovitz did not support Stirton's assessment of alouattine affinities and suggested that *S. tatacoensis* was part of an early stock of platyrrhines unrelated to the modern forms (Hershkovitz 1970, 1984). At the time of his 1970 reassessment, only three species had been named from La Venta, *Cebupithecia sarmientoi, Neosaimiri fieldsi*, and *S. tatacoensis* (Stirton 1951; Stirton and Savage 1951).

Research at La Venta from the mid-1970s through the early 1990s recovered many additional primate specimens including representatives from each of the platyrrhine families, Pitheciidae, Atelidae, Callitrichidae, Cebidae, and Aotidae (Gebo et al. 1990; Hershkovitz 1984; Kay 1994; Kay and Meldrum 1997; Kay et al. 1987; Lutcherhand et al. 1986; Madden et al. 1989; Meldrum and Kay 1997; Meldrum and Lemelin 1991; Nakatsukasa et al. 1997; Rosenberger et al. 1991a; Setoguchi 1985; Setoguchi and Rosenberger 1987; Setoguchi et al. 1981; Takai 1994; Takai et al. 2001). During this period, in total, ten new species were described, though, some have argued not all of these are valid (e.g., Fleagle et al. 1997; Kay et al. 1987; Takai 1994). Of relevance here, is the status of *Kondous laventicus* (Setoguchi 1985), which was initially described as sharing a close relationship with the spider monkey, *Ateles*. This was rejected by Kay et al. (1987) who attributed the specimens to *S. tatacoensis*, a position we accept here. Among these discoveries were more specimens of *S. tatacoensis* including the first maxillary premolars and molars (Setoguchi et al. 1981) as well as 35 isolated teeth (Kay et al. 1987). During this period, *S. victoriae* was also described (Kay et al. 1987; Madden et al. 1989).

Kay et al. (1987) described *S. victoriae* from two maxillary fragments from the same individual—Duke/INGEOMINAS 85-400, which preserves the right dP^2–dP^4 and M^1–M^2, and Duke/INGEOMINAS 86-534, which preserves left dC–dP^4; the accession number 85-400 is now used to refer to both specimens. An adult right maxilla with C–M^1 well-preserved and a partial M^2 (Duke/INGEOMINAS 86-057) is referred to the hypodigm (Kay et al. 1987). During the 1987–1988 field season, a fully adult left maxillary fragment preserving P^3–M^3 (Duke/INGEOMINAS 87-200) and an isolated M_2 (Duke/INGEOMINAS 88-450) were recovered (Madden et al. 1989). In their descriptions of these specimens, Kay, Madden, and colleagues noted the overall larger size of *S. victoriae* relative to *S. tatacoensis* and the somewhat more developed shearing crests of the molars. Additionally, 86-057 preserves parts of the lateral nasal aperture, maxillary sinus, floor of the orbit, and anterior root of the zygomatic, and Kay et al. (1987) note this morphology is reminiscent of that of *Alouatta*. Geologically, *S. victoriae* is confined to the older La Victoria Formation while *S. tatacoensis* is largely found in the younger Villavieja Formation with most specimens retrieved from the Monkey Beds and Fish Beds (Kay et al. 1987; Setoguchi 1985; Setoguchi et al. 1981), though one specimen has been recovered from the Chunchullo Beds. To date, the two *Stirtonia* species are temporally separated. *Stirtonia* has also been recovered from the Late Miocene Rio Acre fauna of Peru (Kay and Frailey 1993). The specimen (LACM 117501) is a lower right M_1 or M_2 with some wear and chipping of enamel. It is notable as being the only record of *Stirtonia* outside of La Venta and recovered from Late Miocene sediments.

Additional fossil evidence related to the howler monkey lineage includes the Pleistocene taxa, *Cartelles coimbrafilhoi* (Halenar and Rosenberger 2013; Lund 1838; Rosenberger et al. 2015) and *Alouatta mauroi* (Tejedor et al. 2008) as well as, more controversially, *Paralouatta varonai* (Horovitz and MacPhee 1999; Rivero and Arredondo 1991). *Cartelles coimbrafilhoi* (formerly *Protopithecus brasiliensis)* was one of the largest platyrrhines ever recorded—estimated to be 20–25kg (Cartelle and Hartwig 1996; Halenar 2011)—and known from a single skeleton. Its molars are poorly preserved, constraining descriptive and comparative dietary analyses, but incisor proportions indicate it may have relied on leaves as a substantial portion of its diet (Rosenberger et al. 2015). Cranially, it is small-brained and airorhynchous, features which are also shared with extant *Alouatta* (Rosenberger et al. 2015). *Paralouatta varonai* possesses a combination of morphological features, some of which suggest alouattine affinities (i.e., small cranial capacity, airorhynchy) (Halenar-Price and Tallman 2019; Rosenberger et al. 2015), while other aspects of its dental and skeletal morphology do not (i.e., short phalanges, dental morphology including small canines, upper molar lingual cingulum). Its phylogenetic relationships remain unresolved with studies allying *P. varonai* with pitheciids (Beck et al. 2023; Horovitz and MacPhee 1999; MacPhee and Meldrum 2006; MacPhee et al. 1995), stem platyrrhines (Kay 2015), or alouattines (Rosenberger et al. 2015). Finally, the Late Miocene platyrrhine, *Solimoea acrensis*, known from a few teeth, has been argued to be either an alouattine (Rosenberger et al. 2015) or a stem ateline (Kay and Cozzuol 2006), though available morphological evidence is not sufficient to thoroughly evaluate its phylogenetic affinities. *A. mauroi* is from the Late Pleistocene of Bahía, Brazil, and is known only from its type specimen, a rostral fragment. The specimen does provide strong support for its inclusion within the alouattine clade (Tejedor et al. 2008), though, given the paucity of fossil evidence for this species, it is mentioned here only for completeness.

Here, we describe the first mandibular specimens recovered from *S. victoriae* from the Middle Miocene of La Venta, Colombia. We employ a three-dimensional geometric morphometric (3DGM) analysis of dentition and mandibular shape to examine *S. victoriae* within the evolutionary context of the platyrrhine radiation. We use phylogenetically informed methods to provide new body mass estimates for *S. victoriae* as well as other extinct platyrrhines. Finally, we provide an amended diagnosis of the species *S. victoriae*.

MATERIALS AND METHODS

GEOLOGICAL SETTING

The Middle Miocene fossiliferous deposits of La Venta in Colombia have yielded over 100 vertebrate species including 12 platyrrhine species (Kay and Madden 1997b; Madden et al. 1997; Mora-Rojas et al. 2023). The La Venta sediments are divided into two formations, the La Victoria Formation with sediments dating from ~16 (mega-annum; Ma) to 12.58 Ma and the Villavieja Formation with sediments from 12.58 to 10.52 Ma (Anderson et al. 2016; Montes et al. 2021; Mora-Rojas et al. 2023) (Figure 1). Primates have been recovered throughout the sequence, but the Monkey Beds in the lowest part of the Villavieja Formation have been most intensively sampled.

The specimens described here were recovered from the La Repartidora locality (3°22′11.99″N, 75° 8′56.29″W) in the La Victoria Formation, municipality of Villavieja, Huila Department, Colombia. The two individuals were found near each other. The site is located northeast from the center of the small town of La Victoria. Stratigraphically, it is in the San Alfonso Beds in the lower section of the La Victoria Formation, in the same sediments as the recently collected and described turtle species, *Mesoclemmys vanegasorum* (Cadena et al. 2020). These sediments have been dated to be between 13.3±0.1 Ma and 13.6±0.2 Ma (Cadena et al. 2020).

SAMPLE

Sampling of extant platyrrhines aimed for ecological and phylogenetic breadth. We sampled members of the platyrrhine families, Atelidae, Pitheciidae, Cebidae, and Aotidae and most dietary categories (Supplementary Online Material [SOM] Table S1). The extant specimens used in our analyses were from the collections of the American Museum of Natural History, New York, New York, United States, the Smithsonian National Museum of Natural History, Washington D.C., United States, the Field Museum, Chicago, Illinois, United States, and the Museu Nacaional (the National Museum of Brazil), Rio de Janeiro, Brazil. For descriptive comparisons, we examined at least five male and five female individuals. For metric analyses, the species sampled and the sample sizes are shown in SOM Tables S1–S4.

The fossil platyrrhine sample included species from the Early Miocene through the Holocene from sites in Patagonia (Miocene), Brazil (Pleistocene), and the Caribbean (Pleistocene/Holocene) (see SOM Table S1) including some stem platyrrhines as well as members of extant platyrrhine families. Of the 38 species of extinct platyrrhines that have been described, we sampled 17—including virtually all species for which appropriate fossil material is available. Our goal in including this broad sample was to situate *S. victoriae* within the broader context of the platyrrhine radiation with a particular emphasis on examining the dietary breadth of the faunal community in which it existed. Detailed information about the fossil sample including specimen numbers and the museums where specimens are curated can be found in SOM Text 1.

LINEAR MEASUREMENTS

For descriptive purposes, linear measures were taken of the dentition (Table 1) using a digital caliper. Length and width measures of teeth were taken at the maximum dimension of the tooth. To examine dental row divergence, the ratio of toothrow width at P_2 to toothrow width at M_1 was taken. Toothrow width measurements were taken on the lingual side of each corresponding pair of teeth, P_2 and M_1, (SOM Table S5).

THREE-DIMENSIONAL DENTAL ANALYSES

Three dimensional analyses of dentition were conducted using surface scans of lower second molars (M_2) of 31 extant and 17 extinct platyrrhine species (see SOM Table S1); detailed methods are described in SOM Text 2. For 3DGM analyses, 23 x, y, z coordinate landmarks were placed on molars using Landmark Editor (Wiley et al. 2005) or Checkpoint (Stratovan 2018). Landmarks were chosen for their repeatability and functional significance and included major dental features including cusp tips, basin low points, crest intersections, the mesial- and distal-most points on the crown surface, points of greatest curvature on the tooth sidewall, and the boundary of the cemento-enamel junction (CEJ) (Figure 2; SOM Table S6). Landmarks were exported and aligned using generalized Procrustes analysis (GPA) (Gower 1975; Rohlf and Slice 1990) to remove variation due to scale, location, and rotation so that only variation in shape remained. GPA-aligned points were analyzed using principal component (PC) analysis to examine tooth shape across species. See Cooke (2011) for further details on the methods and previous results related to this landmark set.

We used principal component scores from the 3DGM analyses in conjunction with lower molar length as a body size proxy to classify extinct primates by diet (Cooke 2011). Dietary categories for living primates were taken from the literature (see SOM Table S1). Using SPSS 28.0 (IBM Corporation 2021), a discriminant function analysis was run with ‘leave-one-out’ cross validation. The following settings

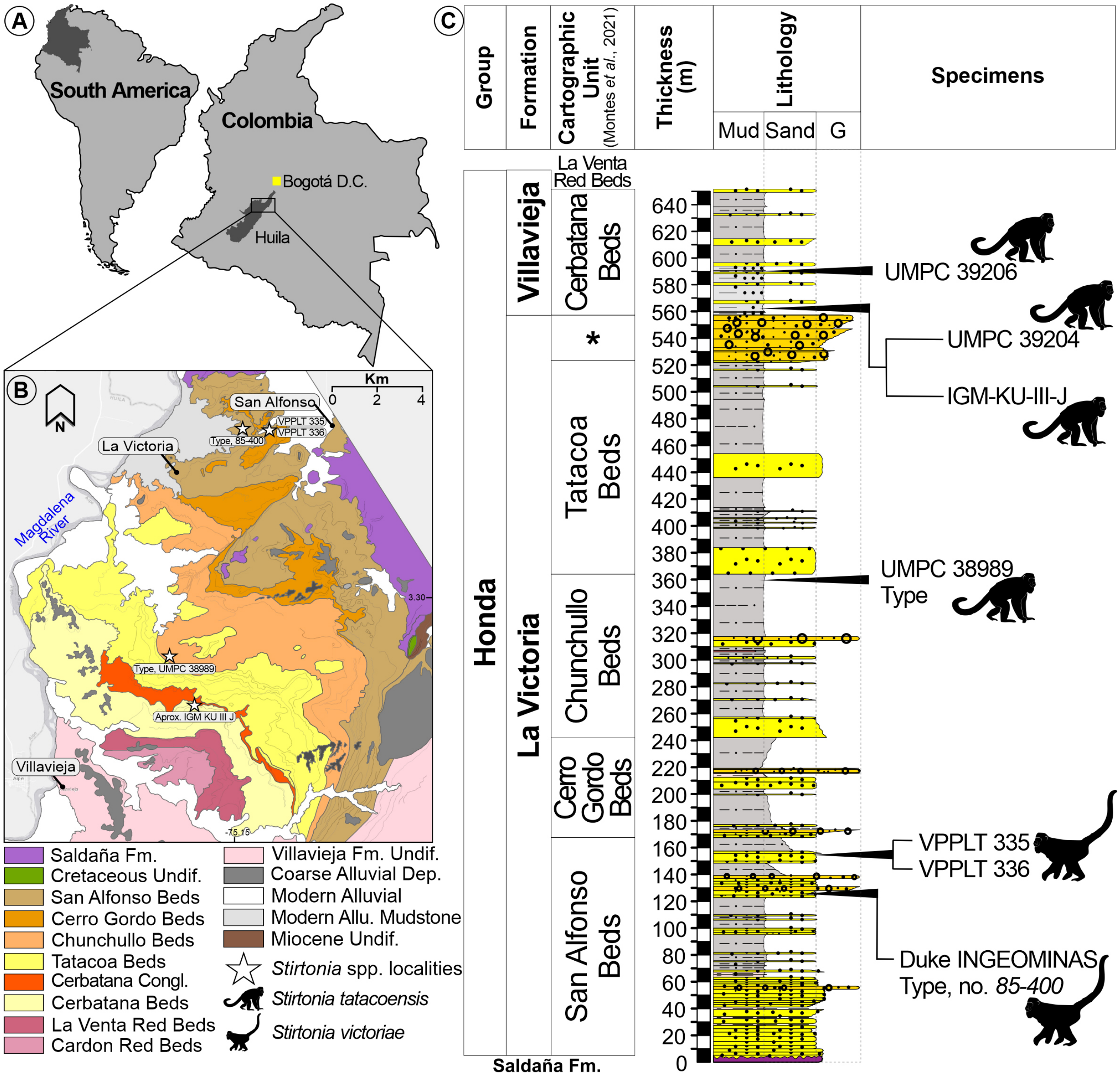

Figure 1. Map and stratigraphy of La Venta (modified from Montes et al. 2021; Mora-Rojas et al. 2023). A) shows the location of La Venta within South America and Colombia; B) shows the geology of the site of La Venta with Stirtonia *specimens indicated with stars; C) shows the statigraphic column of La Venta with the location of* Stironia *specimens indicated with stars.*

were used: 1) grouping variable was diet; 2) independents were entered together; and, 3) prior probabilities were entered together. All data used in these analyses are available for download (see Data Availability Statement).

THREE-DIMENSIONAL MANDIBULAR ANALYSES

The mandible sample included 21 extant platyrrhine species of 15 genera and 3 extinct platyrrhine species including *A. bernensis*, *P. varonai*, and *S. victoriae* (see SOM Table S1). Due to small sample sizes, all titi monkeys, which have somewhat recently been divided into three genera, *Plecturocebus*, *Callicebus*, and *Cheracebus* (Byrne et al. 2016), were analyzed together as *'Callicebus' sensu lato*. Surface scans for each specimen were collected using a Breuckmann SmartSCAN structured white-light scanner or accessed from the MorphoSource website (www.morphosource.org) (Copes et al. 2016). A set of 16 three-dimensional landmarks representing the morphology of the left-side mandibular corpus and mandibular symphysis were collected on each speci-

TABLE 1. DENTAL MEASUREMENTS OF *STIRTONIA VICTORIAE* SPECIMENS VPPLT 335 AND VPPLT 336.

VPPLT 335				
	Right		**Left**	
	MD length	**BL width**	**MD length**	**BL width**
P_3	4.97	6.38	4.9	6.74
P_4	5.3	7.37	5.67	7.28
M_1	8	6.15	8.09	6.32
M_2	8.83	7.02	8.76	6.79
VPPLT 336				
	Right		**Left**	
	MD length	**BL width**	**MD length**	**BL width**
P_2	6.18	7.52	6.31	7.69
P_3	5.98	6.1	5.77	6.73
P_4	6.12	6.32	5.76	6.35
M_1	x	x	7.85	6.33

Abbreviations: MD=mesiodistal; BL=buccolingual; P_2, P_3, and P_4 refers to the first, second, and third premolars in the platyrrhine mandible; the mammalian P_1 has been lost in platyrrhines; M_1 and M_2 refer to the first and second molars in the platyrrhine mandible.

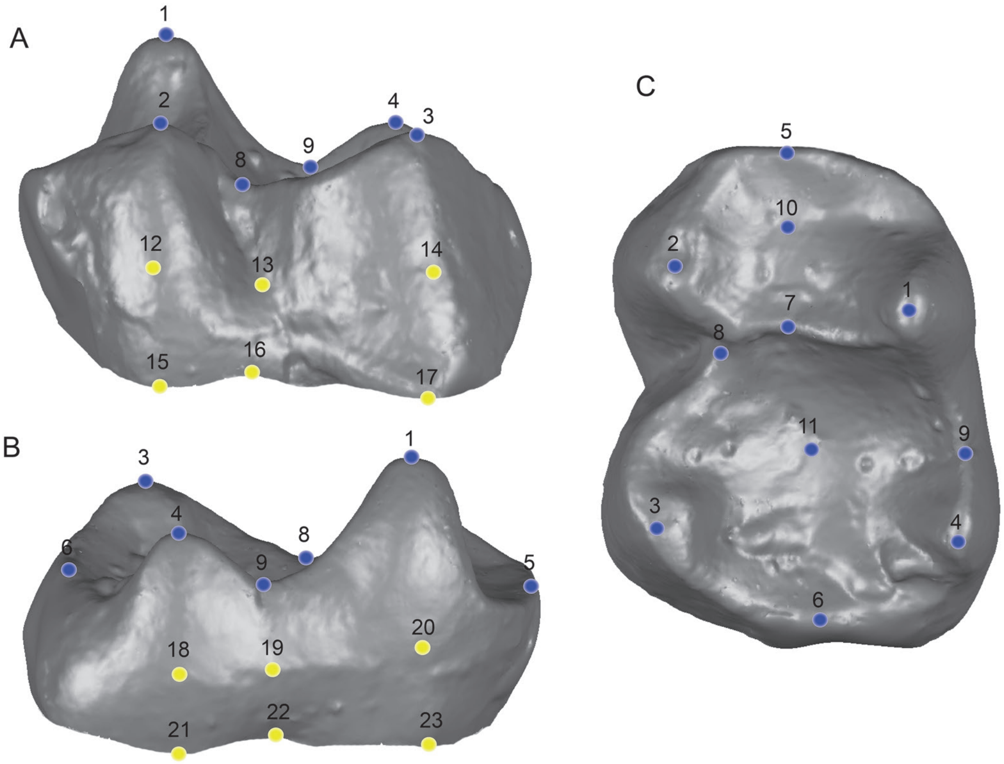

Figure 2. Dental landmarks used in this study shown on an Alouatta palliata *molar (after Cooke 2011). Blue dots show occlusal landmarks and yellow dots show sidewall landmarks in buccal (A), lingual (B), and occlusal (C) views. Landmark definitions can be found in SOM Table 2.*

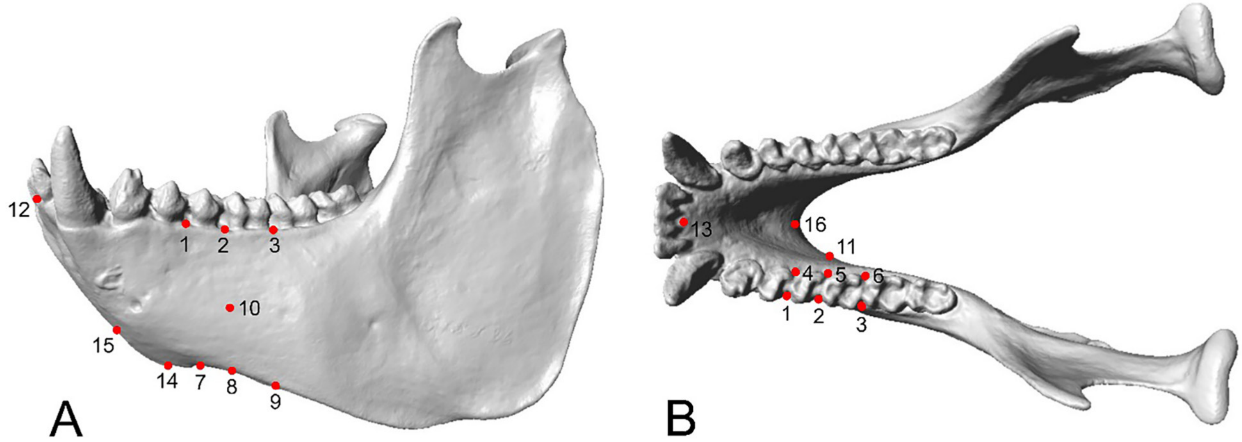

Figure 3. Mandibular landmarks (red) used in this study depicted on a Alouatta palliata *mandible in lateral (A) and superior (B) views. Landmark definitions can be found in SOM Table 3.*

men (Figure 3; SOM Table S7) using Checkpoint software (Stratovan 2018). The number and placement of landmarks were limited to the anterior mandible based on the morphology preserved across fossil specimens.

The following analyses were performed in R using the package Morpho (Schlager 2017). Mandible landmark configurations were aligned by generalized Procrustes analysis using the procSym() function. Principal component analysis (PCA) of the aligned landmark coordinates was used to characterize major patterns of mandibular shape variation across the sample and to reduce the dimensionality of the dataset by generating new variables represented by principal component axes (PCs). The resulting PC scores were subject to two canonical variates analyses (CVA) with extant specimens grouped first by genus and second by dietary category. The number of PCs included in the CVAs was determined using the function getMeaningfulPCs(). This function utilizes the likelihood ratio between the geometric and arithmetic means of consecutive eigenvalues to determine which PCs are distinct in their direction and should be evaluated (see Bookstein 2014). Group affiliation for each extant specimen was tested using leave-one-out cross-validation, and morphological affinities of each fossil specimen to extant groups were determined by calculating both Procrustes and Mahalanobis distance to each group mean.

BODY MASS ESTIMATION

Proposed body masses for extinct taxa were calculated using phylogenetically-corrected least squares regression (PGLS) (Grafen 1989; Martins and Hansen 1997; Pagel 1997; Rohlf 2001; Symonds and Blomberg 2014) with the natural log of M_1 area and the natural log of wild caught body mass as the independent variable. The buccolingual breadth and the mediodistal length of M_1 was measured in 49 species of platyrrhine primates (n=998) and then multiplied to create an area measurement. Lower first molar area has previously been shown to correlate strongly with primate body mass (Conroy 1987); but previous publications have not used PGLS in as extensive a sample as presented here. Body masses from primates living in the wild were taken from Ford and Davis (1992). The data were partitioned so that three PGLS regression equations were calculated: 1) averaged male and female data (n=998 individuals; n=49 species); 2) female data (n=444; n=46 species); and, 3) male data (n=463; n=43 species). In the combined dataset, specimens whose sex could not be identified were also included (see SOM Tables S2–S4). All data used in these analyses are available for download (see Data Availability Statement).

To generate the PGLS equations, we downloaded three consensus trees from 10K Trees (https://10ktrees.nunn-lab.org/; Arnold et al. 2010) for taxa in each of the three datasets (the combined-sex dataset, the female dataset, and the male dataset). The PGLS regression equations were generated in R Version 2024.04.1+748 (R Core Team 2024) using the following packages: phytools (Revell 2024), ape (Paradis and Schliep 2019), nlme (Pinheiro et al. 2023), geiger (Pennell et al. 2014), and caper (Orme et al. 2023).

To estimate the body masses of extinct platyrrhine species we used the natural log of M_1 area. For some species only one M_1 was available, but when more than one M_1 was available, we averaged the molar area for the analysis.

RESULTS

FOSSIL DESCRIPTION

The two specimens described here are the first known mandibles of *S. victoriae* and include the only known mandibular dentition of the species. The left and right portions of the mandible of VPPLT 335 were collected separately (in 2012 and 2014) and reconstructed along the mandibular symphysis (Figure 4; see Table 1). There was some abrasion along the symphysis, and the fit is offset. The tooth roots of the left and right incisors and canines are preserved as are the left and right P_3–M_2. The premolars and molars are relatively unworn with small points of dentin exposure on

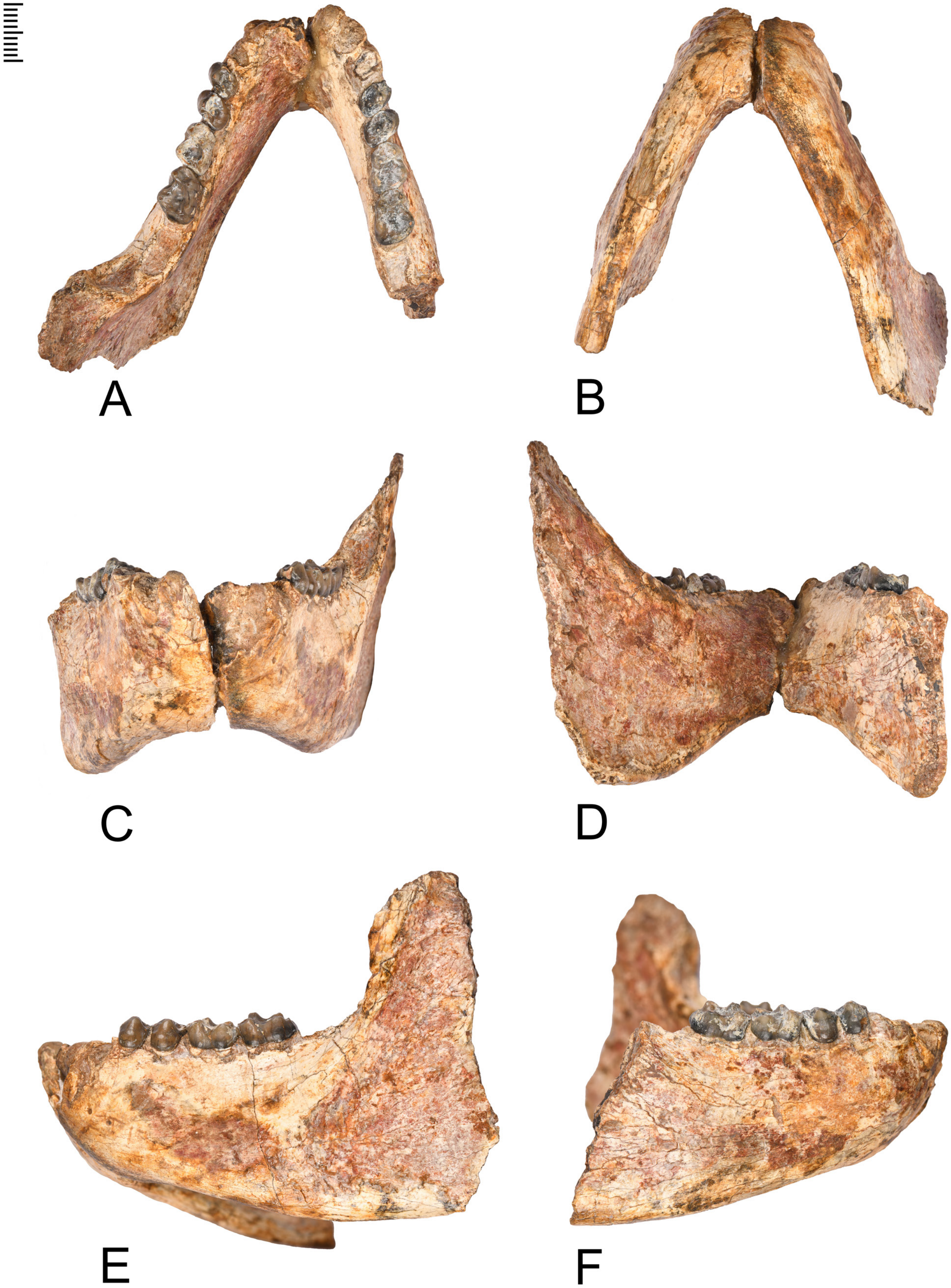

Figure 4. The mandible of Stirtonia victoriae, *VPPLT 335 in occlusal (A), inferior (B), anterior (C), posterior (D), left lateral (E), and right lateral (F) views.*

the cusp tips. The right mandibular corpus is broken vertically at the mid-point of the M_3 alveolus. The left corpus is largely intact with a small portion of the gonial angle broken. The left ramus is partially preserved with an intact coronoid process; the mandibular condyle and posterior portion of the mandibular ramus is missing. The mandible deepens posteriorly.

VPPLT 336 preserves the mandibular symphysis with the roots of the left and right incisors, part of the mandibular corpus with the left and right P_2–P_4, part of the right M_1 root, left M_1, and part of the left M_2 mesial root (Figure 5; see Table 1). The right side of the specimen is broken through the M_1 alveolus, and the left side is broken halfway through the M_2 alveolus. The dentition of the specimen is also only lightly worn.

The P_2 has a single cusp, is robust relative to P_3, and shows significant development of the lingual cingulum, which extends to the mesial edge of the tooth. There is a strong crest extending distolingually from the protoconid and a small distal basin. The pronounced robusticity of P_2 relative to P_3 in VPPLT 336 may indicate that this was a male individual if similar dental proportions existed in this species as in extant atelids (SOM Figure 1). P_3 has a protoconid and metaconid with a crest connecting them; there is some development of small basins mesially and distally. P_4 shows some molarization in both specimens; there is an expanded distal basin and a third distolingual cusp present, though it is variably developed. The mesial basin is somewhat rounded and centrally placed. Few premolars of *S. tatacoensis* have been published limiting comparisons between the two species; however, apart from size, the P_3 and P_4 are broadly similar between the two taxa. The premolars of *S. victoriae* are similar to those of extant *Alouatta* (*A. palliata*, *A. caraya*, *A. seniculus*, *A. belzebul*, *A. pigra*, and *A. guariba* were examined), except for the prominent lingual cingulum on P_2, which extant species generally lack, though it does occasionally occur. Molarization of the P_4 can also be found among extant species with an inconsistent presence of a third cusp.

The molars of *S. victoriae* have well-developed crests and cusps with large round trigonid basins and large talonid basins. The protoconid and metaconid are of equal height with a protocristid connecting the cusps on both $M_{1–2}$. The hypoconid and entoconid are widely spaced; there is incipient development of a hypoconulid on M_2, but not on M_1. The cristid obliqua connects with the trigonid somewhat lingually thus forming a prominent ectoflexid on the buccal side of the molars. There is a prominent notch distal to the entoconid on M_{1-2} such that the talonid basin opens disto-lingually. This feature is more prominent in *S. victoriae* than in *S. tatacoensis* and is variably developed in the extant *Alouatta* species examined. *Stirtonia victoriae* also has a more buccally placed metaconid than *S. tatacoensis* resulting in a more open trigonid, and a large trigonid basin. Crests are more prominent, and cusps are higher above the basin in *S. victoriae* than in *S. tatacoensis*, as previously noted by Kay et al. (1987). Overall, *S. victoraie* has a similar molar size and morphology to extant *Alouatta*.

Both specimens also provide additional data about the mandibular morphology of *S. victoriae*. The symphysis is fully preserved in VLPPT 336. The anterior aspect of the symphysis in this specimen angles posteriorly with the symphyseal shelf ending at the level of P_4–M_1. In VLPPT 335, the symphysis appears to end in the premolar region, but given damage to the specimen in this area, the morphology cannot be fully evaluated. Among extant alouattines, the symphysis generally ends in the premolar P_2–P_3 region; however, *A. palliata* tends to have a somewhat longer symphysis than other species observed with it more frequently ending in the P_3–P_4 region. In *Ateles* and *Lagothrix,* the symphysis generally ends between P_2 and P_3. A single mental foramen is present in VLPPT 336 while two appear to be present in VLPPT 335; variability of this foramen is common in atelids.

The tooth rows diverge posteriorly in both specimens, but the extent of this cannot be fully determined given the distortion of the symphysis of VLPPT 335. To capture the extent of toothrow divergence, the ratio of P_2 toothrow width (taken lingually) to M_1 toothrow width (see SOM Table S5) shows that *S. victoriae* falls within the range of extant atelids; in this measure, there is considerable overlap among living forms with the average ratio of the P_2/M_1 toothrow width equaling 0.76. In contrast, the type specimen of *S. tatacoensis* (UMPC 38989) has a notably V-shaped symphysis with more divergent dental rows that do not fall within the range of extant atelids for this metric; its P_2/M_1 ratio is 0.61. Since there is only one complete mandible known for *S. tatacoensis*, it cannot be determined if this is an unusual individual or a species wide morphology, but minimally, it falls outside of the range of variation of the extant atelids sampled and is a different morphology than that seen in VLPPT 335.

The mandibular corpus deepens posteriorly in VLPPT 335 as in extant *Alouatta*, though the shape of the inferior edge of the mandibular body differs (see Figures 4–5). In *S. victortiae*, the mandibular body has a slightly convex inferior margin from the symphysis to ramus. In extant *Alouatta*, there is a slight upward curvature at the symphysis (note points 7, 8, and 14 in Figure 3) followed by a straight descent to the gonial region where the mandible greatly expands—more so in males than in females. This morphology cannot be fully evaluated in *S. tatacoensis* as the mandibular body is poorly preserved along the margin, but it does appear to lack the slight upward anterior curvature of *Alouatta*. In *S. victoriae* there is a slight medial inflection of the inferior border of the corpus anterior to the gonial region; this is the distal attachment site of the medial pterygoid muscle. Medial inflection is common in *Alouatta* and is most prominent among males; in some individuals, the bone is also thicker in this region. Among atelids, medial inflection just anterior to the gonial angle is also seen in *Lagothrix* males and can be quite substantial; it exists to a much lesser extent in *Lagothrix* females. In *Ateles,* medial inflection is slight if present at all.

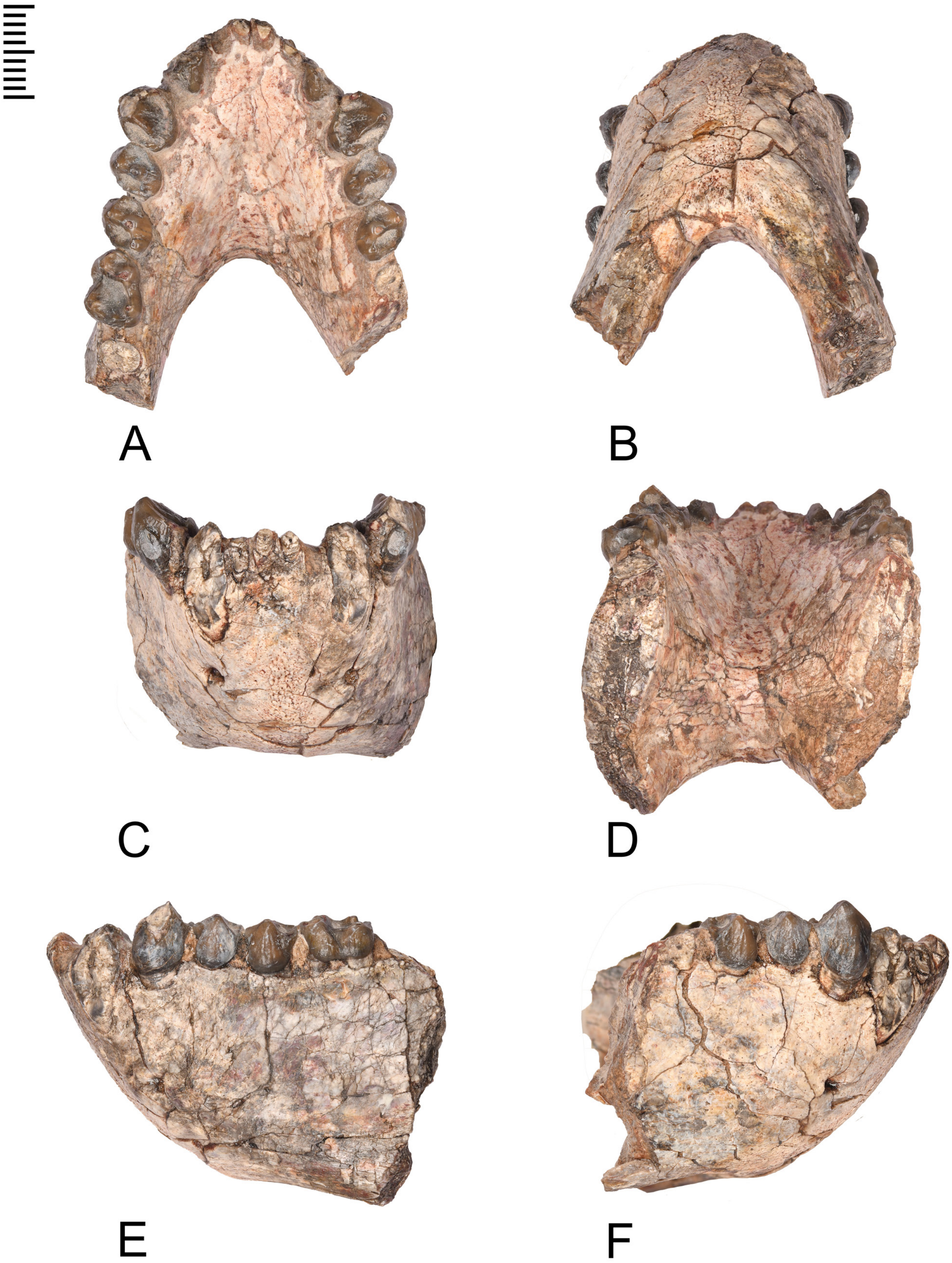

Figure. 5. The mandible of Stirtonia victoriae*, VPPLT 336 in occlusal (A), inferior (B), anterior (C), posterior (D), left lateral (E), and right lateral (F) views.*

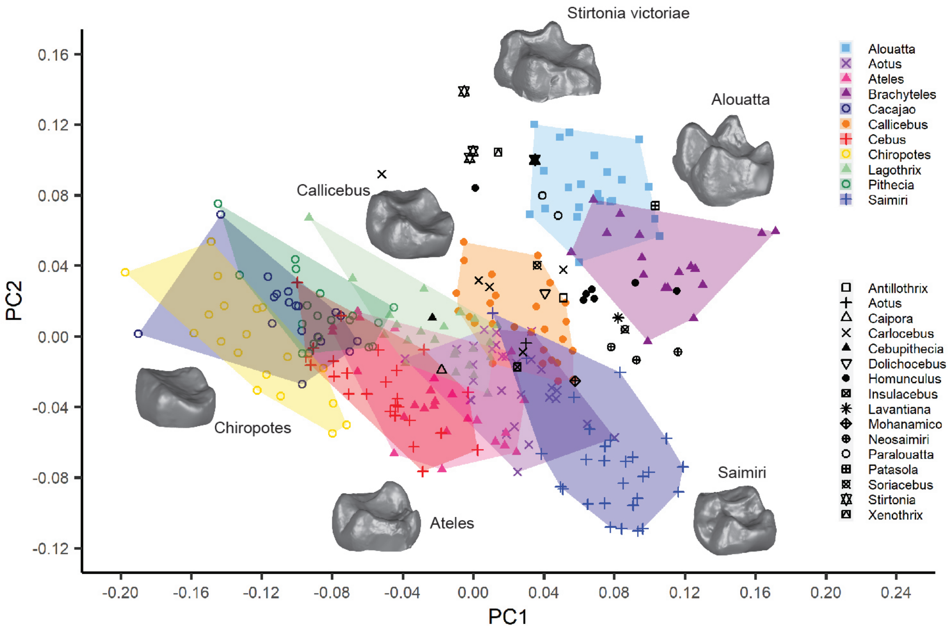

Figure 6. Plot of a principal components analysis showing PC 1 and PC 2. PC 1 has 27.53% and PC 2 has 11.86% of total variance. Stirtonia tatacoensis *is shown as an open star and* S. victoriae *(VLPPT 335) as a filled star.*

The shape of the gonial angle in VLPPT 335 cannot be fully evaluated due to poor preservation, but the mandible of *S. victoriae* does appear to expand towards the angle, thought to a lesser degree than observed in extant *Alouatta* species. In comparison to other atelids, alouattines have a more expanded gonial angle, and greater corpus depth to accommodate the greatly inflated hyoid. *Ateles* has the least expansion of the gonial region with *Lagothrix* and *Brachyteles* having greater expansion.

The ramus of the mandible in VLPPT 335 rises vertically and is thickened posterior to the alveolus of M_3. Between the anterolateral and anteromedial edges of the ramus, there is a triangular depression in *S. victoriae*. While this region is thickened somewhat in *Alouatta*, a similar depression was not observed in the species sampled; however, this depression is present in most male *Lagothrix* as well as some females and was present in the one female *Brachyteles arachnoides* available for study. The depression was absent in *Ateles.* Schön (1968) notes that fibers of the temporalis and buccinator muscle insert in this region in *Alouatta seniculus*. The coronoid process of the mandible is incompletely preserved, but a clear line of insertion of the temporalis muscle is visible medially as in other atelids.

Systematics

Order Primates
Family Atelidae
Subfamily Alouattinae
Genus *Stirtonia* Hershkovitz, 1970
Species *victoriae* Kay et al., 1987

AMENDED DIAGNOSIS, *STIRTONIA VICTORIAE*

Stirtonia victoriae is distinguished from *S. tatacoensis* by its larger size, more buccally placed metaconid concomitantly with a relatively larger trigonid basin, greater development of shearing crests, and less divergence of the tooth rows. *Stirtonia victoriae* has a mandibular symphysis that slopes posteriorly, a mandibular corpus that deepens posteriorly with an inferior mandibular margin that is slightly convex in outline, a slight medial inflection of the inferior mandibular margin approaching the gonial angle, a vertical mandibular ramus, and prominent insertion sites for the buccinator and temporalis muscles.

THREE-DIMENSIONAL ANALYSES OF DENTITION

In the principal component analysis of GPA-aligned dental landmarks, the first four principal components account for 27.53%, 11.86%, 8.28%, and 5.7% of total variance respectively (Figure 6); the remaining PCs each account for less than 5% of the remaining variance. PC 1 is largely a measure of cusp height and relative molar length. In this analysis, folivorous primates and the insect-consuming *Saimiri* have higher PC 1 scores, while soft fruit frugivores and hard-object eating have lower scores. Variation along PC 2 is largely governed by the position of the cusps relative to the molar width at the cementoenamel junction (CEJ) and the relative mesiodistal length of the trigonid. There is substantial overlap among platyrrhine species on PC 2, but it does separate the genera *Alouatta*, *Stirtonia*, and *Paralouatta* from other platyrrhine taxa. More positive PC 2 values are associated with a relatively longer trigonid, and cusp tips more closely approximated on the occlusal surface. On PC 3 and PC 4 there is substantial overlap across species. On PC 3, only *Cebus* pulls away from the other platyrrhines; all *Stirtonia* species fall within the *Alouatta* range on PC 3, but it must be noted that so do other extinct and extant taxa.

Overall, *S. victoriae* falls within the *Alouatta* morphospace while *S. tatacoensis* falls within or slightly outside of it. *S. tatacoensis* has slightly lower cusps relative to basin height than *S. victoriae* and extant *Alouatta.* Features aligning *Stirtonia* species with extant *Alouatta* include a wide talonid basin, a trigonid that is slightly higher than the talonid, a well-developed cristid obliqua, and a prominent protocristid. Interestingly, the Cuban species, *P. varonai*, falls within the *Alouatta* distribution. Other La Venta primates included in the analysis also tend to fall at the more positive end of PC 1 indicating a fauna with few species adapted to soft-fruit frugivory (i.e., an *Ateles*-like niche) or hard object eating (i.e., pitheciine-like niche) with the notable exception of *C. sarmientoi*; however, even this taxon does not attain the very open basins and low cusp height of the extant pitheciines, *Chiropotes* and *Cacajao.* The Patagonian primates included in this analysis, *Carlocebus, Humunculus, Soriacebus,* and *Dolicocebus* largely fall in the positive regions of PC 1 indicating a moderate or tall cusp height.

A discriminant function analysis using PC 1 and molar length to classify all primates by diet achieved a cross validated correct classification rate of 84.8% (see SOM Table S7). Most errors of classification occurred for the frugivore/omnivore, *Cebus capucinus*, as well as among frugivores and seed predators. *Stirtonia victoriae* was classified as a folivore/frugivore as were two of three specimens of *S. tatacoensis* and all specimens of *P. varonai.* The classification results of the remaining fossil platyrrhines are comparable to Cooke (2011) (Table 2).

3DGM ANALYSES OF MANDIBULAR MORPHOLOGY

The first principal component of the PCA on the aligned mandibular landmarks account for 40.2% and 20.4% of the total variance, respectively (Figure 7). *Alouatta* occupies a distinct area of morphospace located at the negative ends of PC 1 and PC 2 relative to other platyrrhines. Pitheciids are centrally located along PC 1 but tend to cluster together towards the positive end of PC 2 and slightly overlap with other platyrrhines. The remaining platyrrhines, in addition to *Ateles* and *Lagothrix*, have overlapping distributions located at the positive end of PC 1 but centrally along PC 2. PC 1 describes variation in the height of the corpus and symphysis and the width of the mandibular arch. Negative values of PC 1 are associated with a taller corpus that deepens posteriorly, an elongated symphysis, and a narrower mandibular arch. PC 2 is driven by the cross-sectional shape of the symphysis and the contour of the inferior margin of the corpus. Negative values of PC 2 describe a sloping lingual symphyseal surface that is thickest inferiorly with a concave inferior margin of the corpus under the premolars.

Among fossil specimens, *S. victoriae* and *P. varonai* fall just outside, but nearest to, the *Alouatta* distribution (see Figure 7). *Stirtonia victoriae* exhibits both an elongated symphysis and a corpus that deepens posteriorly, characteristic of *Alouatta*. *Paralouatta varonai* shares aspects of corpus morphology with *Alouatta* but exhibits a symphyseal morphology more similar to pitheciids that is less elongated and labiolingually thickest midway through the length of the symphysis. *Antillothrix bernensis* plots among the overlapping distributions of other platyrrhine genera but nearest to *Callithrix* and *Lagothrix*. In lateral view, *A. bernensis* has a concave inferior margin of the corpus beneath the premolars, which resembles the morphology found in *Lagothrix* and *Alouatta*.

The first seven PCs (89.3% of the total variance) were considered “meaningful” and met the criteria for inclusion in the canonical variates analyses. When grouped by genus, CV1 clearly distinguishes *Alouatta* from other platyrrhines, and CV2 primarily distinguishes *Cebus* from *Callicebus* (Figure 8A). The associated leave-one-out cross-validation yielded a 90.6% correct reclassification rate overall for extant taxa (see SOM Table S7). *Lagothrix* had the lowest reclassification rate (69.2%) perhaps due to having a generalized morphology that overlapped with many different taxa (e.g., *Ateles* and *Saimiri*).

The morphology of the anterior mandible of *S. victoriae* most closely resembles that of *Alouatta* based on both Procrustes and Mahalanobis distances (SOM Table S8). *Antillothrix bernensis* is nearest to *Lagothrix* for both measures. *Paralouatta varonai* is nearest to *Alouatta* by Procrustes distance and *Callicebus* by Mahalanobis distance, likely indicating a unique combination of morphological characteristics in this taxon. The classification of fossil specimens to extant platyrrhine genera does not necessarily indicate that they belong to those specific genera, but instead that they have closer morphological affinities to those groups relative to others.

When grouped by dietary category, CV1 separates folivore/frugivores (consisting only of *Alouatta*) from other categories (Figure 8B). CV2 separates gummivore/insectivores at the positive end with most other categories overlapping across the middle and negative end of the axis. The cross-validation based on dietary category yielded an overall correct reclassification rate of 89.7% (see SOM Table S8). The lowest reclassification rate was observed in the frugivore/insectivore group (76.9%) with misclassified specimens grouped with either the frugivore or gummivore/insectivore/frugivore categories. The folivore/frugivore category had 100% correct reclassification. Based on Procrustes and Mahalanobis distances (SOM Table S9), both *S. victoriae* and *P. varonai* were classified as a folivore/frugivore, and *A. bernensis* was classified as frugivore.

BODY MASS

Three PGLS equations were calculated from M_1 area and

TABLE 2. DISCRIMINANT FUNCTION ANALYSIS DIETARY CLASSIFICATION OF FOSSIL PLATYRRHINE TAXA USING PC 1 AND M_2 LENGTH.

Species	Specimen number	PC 1, M_2 length
Pleistocene Brazil		
Caipora bamborium	IGC-IFMG 05	fol./frug.
Pleistocene–Holocene, Caribbean		
Antillothrix bernensis	MHD 01	frug.
Insulacebus toussaintiana	UF 11417	frug.
Paralouatta varonai	MHNH Cueva Alta 1996	fol./frug.
Paralouatta varonai	MHNH V123	fol./frug.
Xenothrix mcgregori	AMNH 148198	frug.
Middle Miocene, La Venta, Colombia		
Aotus dindensis	IGM-KU 8601	frug.
Cebupithecia sarmientoi	UCMP 38762	frug.
Laventiana annectens	IGM-KU 8801a	frug./ins.
Mohanimico hershkovitzi	IGM 181500	frug.
Neosaimiri fieldsi	UCMP 39205	frug./ins.
Neosaimiri fieldsi	IGM-KU 89002	frug./ins.
Neosaimiri fieldsi	IGM-KU 89034	frug./ins.
Patasola magdalenae	IGM 184332	frug./ins.
Stirtonia tatacoensis	IGM-KU 8102	fol./frug.
Stirtonia tatacoensis	IGM-KU 8215	fol./frug.
Stirtonia tatacoensis	UCMP 38989	frug.
Stirtonia victoriae	VPPLT 335	fol./frug.
Early Miocene, Patagonia, Argentina		
Carlocebus carmenensis	MACN-SC 63	frug.
Carlocebus carmenensis	MACN-SC 43	frug.
Carlocebus carmenensis	MACN-SC 250	frug.
Dolichocebus gaimanensis	MPEF 5146	frug.
Homunculus patagonicus	MACN 1149	frug.
Homunculus patagonicus	MACN 2918	frug.
Homunculus patagonicus	MACN 5969	frug.
Homunculus patagonicus	MACN-SC 336	frug.
Homunculus patagonicus	MACN-SC 339	frug.
Homunculus patagonicus	MPMPV 3708	frug.
Soriacebus ameghinorum	MACN-SC 379	frug.
Soriacebus ameghinorum	MACN-SC 2	frug.

Abbreviations: PC 1=principal component 1; M_2=second mandibular molar; fol.=folivore; frug.=frugivore; ins.=insectivore

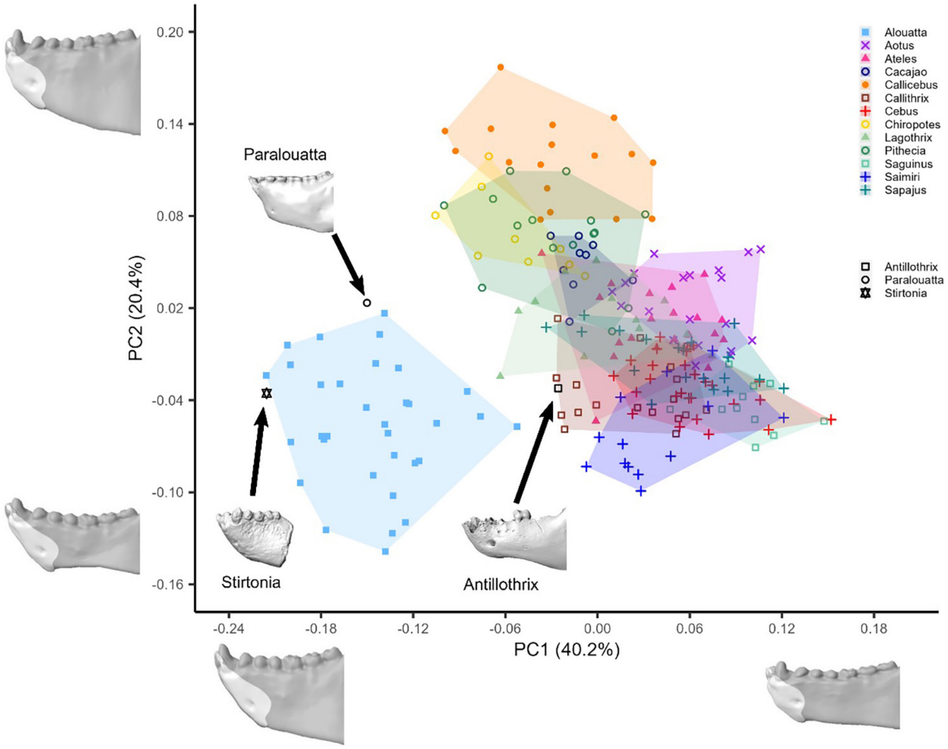

Figure 7. Plot of PC1 and PC2 of a principal component analysis of the aligned landmark coordinates. Visualization of shape change described along each axis is from -0.15 to 0.15. Shape depictions are semi-transparent to visualize the outline of the mandibular symphysis.

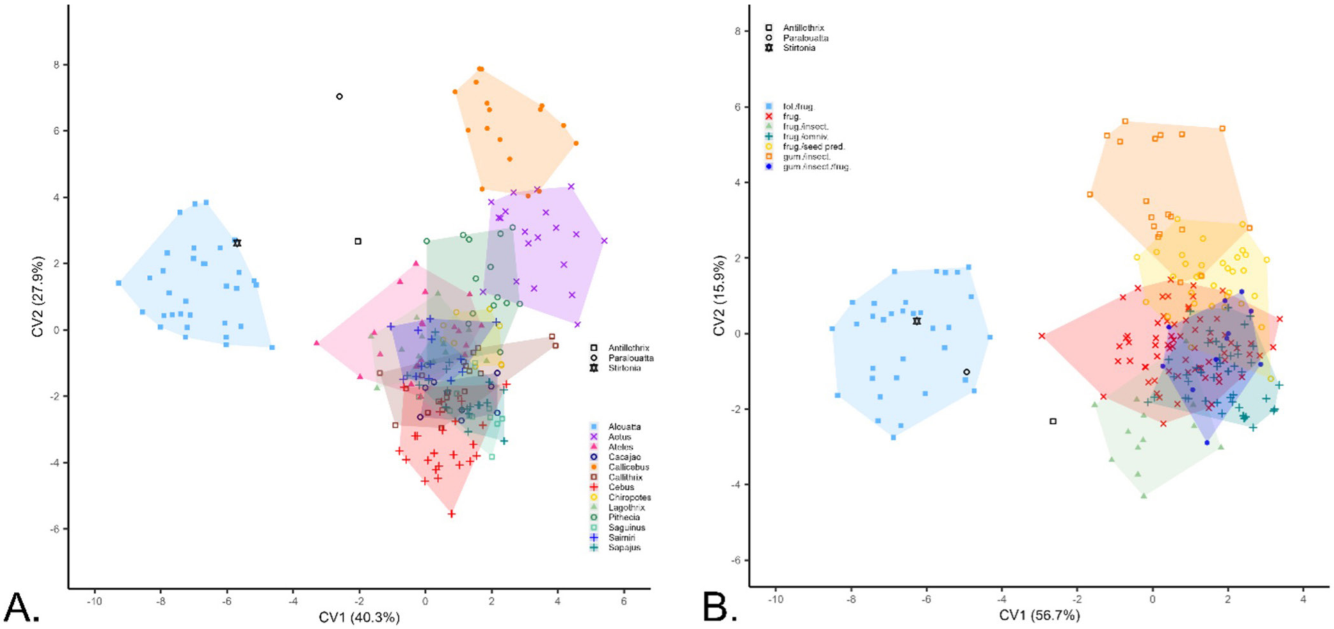

Figure 8. Plot of CV1 and CV2 of the canonical variates analyses using the first seven principal components grouped by genus (A) and dietary (B).

body mass taken from the literature (Ford and Davis 1992) in a sample of extant platyrrhine primates; three regression equations were produced:

Combined male and female sample
$\text{Ln Body Mass}=1.181069 (\text{Ln } M_1 \text{ Area})+4.402993$
Female sample
$\text{Ln Body Mass}=1.084285 (\text{Ln } M_1 \text{ Area})+4.571255$
Male sample
$\text{Ln Body Mass}=1.189507 (\text{Ln } M_1 \text{ Area})+4.420231$

Using these regressions, we estimated body masses for fossil platyrrhines found throughout South America and the Caribbean (Table 3; Figure 9). *Stirtonia victoriae* is estimated to have weighed between 6605–8658 grams. The lower estimate was derived from the female platyrrhine regression and the higher from the male regression. The combined dataset produced an estimated weight of 8138–8234 grams. This falls within the higher end of the range of the extant *Alouatta* sample and overlaps with the range of *Ateles* and *Brachyteles* (Ford and Davis 1992). *Stirtonia victoriae* is the largest platyrrhine found at La Venta and the largest definitively Miocene platyrrhine currently known. In contrast, *S. tatacoensis* is estimated to be 3928–4839 grams. Other platyrrhines at La Venta have body masses around ca. 700 grams for the smallest species, *Patasola magdelanae*, to around 1800–2200 grams for the pitheciids *C. sarmientoi* and *N. rubricae*. The Patagonian primates have a more constrained body mass range with the smallest species, *S. adrianae* estimated to be ca. 1100 grams and the largest *C. carmanensis* ca. 3200 grams. In the Caribbean, platyrrhines are larger with body mass for three species (*X. mcgregori, A. bernensis,* and *I. toussaintiana*) ca. 3200–4300 grams and for *P. varonai* 6400 grams.

DISCUSSION

MORPHOLOGICAL ANALYSES

The description and analyses of *S. victoriae* presented here indicate that an *Alouatta*-like dental pattern was in place by the Middle Miocene—very shortly after molecular evidence suggests divergence of Alouattinae from the other atelid species (Beck et al. 2023; Perelman et al. 2011). Shearing crest development, tall cusp height, and relatively large molars are adaptations for grinding and shearing structural carbohydrates (i.e., leaves). *Stirtonia tatacoensis*, however, does not have as extreme development of cusp and crown height (as indicated by PC 1 scores) as extant howler monkeys do, and *S. victoriae* falls just within extant *Alouatta* range on PC 1. *P. varonai* falls within the *Alouatta* morphospace indicating similarity in overall shape; this result is in accordance with what Cooke (2011) previously found. The age of *P. varonai* is uncertain, but some evidence exists for dispersal of primates into Cuba by 18–16 Ma (MacPhee et al. 2003) suggesting the potential for an early radiation of primates adapted to consuming leaves. At the base of the atelid clade, leaf consumption predominates—including *P. varonai*, if considered part of the howler clade. Though, extant *Ateles* and to a lesser extent *Lagothrix* are committed soft-fruit frugivores (Rosenberger 1992), compared with other frugivorous platyrrhines, they have relatively high relief values for their dental crowns (Allen et al. 2015; Winchester et al. 2014)—a feature associated with resistance to wear experienced by consuming abrasive foods—potentially indicating an ancestral diet for atelids that included a substantial component of leaves or other structural carbohydrates.

Overall, howler monkeys have a distinct mandibular shape among platyrrhines, notably the extreme expansion of the ramus and gonial region. However, our analysis also finds a unique combination of features of the anterior mandible of *Alouatta* including an elongated symphysis with a low, projecting symphyseal shelf and a tall mandibular corpus with a concave inferior margin beneath the premolars. Even though neither of the newly discovered mandibular specimens (VPPLT 335 or VPPLT 336) preserve the entirety of the ramus and posterior mandible, a howler monkey-like shape of the anterior mandible was present in *S. victoriae* as evidenced by morphometric analyses thus adding to our understanding of the evolution of this unique morphology. In all our analyses, *S. victoriae* consistently falls near extant *Alouatta* morphologically. Though the type specimen of *S. tatacoensis* is a partial mandible, the mandibular corpus and ramus are not preserved, and the posterior depth of the mandible cannot be fully evaluated; interestingly, it has a more v-shaped mandible than *S. victoriae* or extant *Alouatta* species. Whether this is an unusual individual or characteristic of this younger species cannot be fully evaluated with current fossil evidence. Although assessing the evolutionary relationships of *Paralouatta* was not a primary goal of this study, it is interesting that the Cuban *P. varonai* exhibits an anterior mandible most similar to either *Alouatta* (Procrustes distance) or *Callicebus* (Mahalanobis distance, although the next closest taxon is *Alouatta*) depending on the analysis. Both phylogenetic positions are supported by character-based analyses (Beck et al. 2023; Horovitz and MacPhee 1999; Rosenberger et al. 2015).

Mandibular morphology in howler monkeys is also tied to their unique vocalization. Extant *Alouatta* has a greatly inflated hyoid that acts as a resonating chamber, requiring a deep mandibular corpus to accommodate this bone (Dunn et al. 2015; Rosenberger et al. 2015; Youlatos et al. 2015). Across *Alouatta*'s geographic range, there is substantial variation in hyoid and mandibular shape as well as vocalization behavior, but all extant taxa howl to some degree (Dunn et al. 2015). While we cannot know with current evidence the degree of hyoid inflation in fossil taxa, the mandibular morphology suggests that the mandible of *S. victoriae* would likely have accommodated a larger hyoid, but additional fossil evidence is needed to confirm this hypothesis.

This study includes separate analyses of dental and mandibular shape to assess dietary adaptations for *Stirtonia*, both finding support for a folivorous diet. Although more direct dietary inferences can be made based on dental morphology, associations between diet and mandibular

TABLE 3. BODY MASS ESTIMATES OF *STIRTONIA VICTORIAE* AND SELECTED EXTINCT PLATYRRHINE SPECIES BASED ON M_1 AREA (mesiodistal length x buccolingual breadth) USING A PGLS REGRESSION.*

				Body Mass (grams)			
				PGLS Regression			OLS Regression
Region	**Species**	**Specimens included in analysis**	**N**	**Female**	**Male**	**Female & Male**	**Female & Male**
Brazil	*Caipora bamborium*	IGC-IFMG 05	1	6866	8929	8490[a]	12584
Hispaniola	*Antillothrix bernensis*	MHD 01, MHD 21, FOS 25.1113, FOS 25.1129, FOS 25.1141	5	3176	3832	3666	4223
Hispaniola	*Insulacebus toussaintiana*	UF 114714	1	3561	4345	4152	4966
Cuba	*Paralouatta varonai*	MNHNCu 76.1213–1217[b]	5	5262	6669	6354	8634
Jamaica	*Xenothrix mcgregori*	AMNH 148198	1	4018	4960	4736	5893
La Venta	*Stirtonia tatcoensis*	UCMP 38989, IGM-KU III 1	2	3928	4839	4621	5707
La Venta	*Stirtonia victoriae*	VPPLT 335	1	6605	8556	8138	11910
La Venta	*Stirtonia victoriae*	VPPLT 336	1	6676	8658	8234	12093
La Venta	*Aotus dindensis*	IGM-KU 8601	1	1245	1372	1322	1122
La Venta	*Laventiana annectens*	IGM-KU 8801a	1	847	899	869	650
La Venta	*Neosaimiri fieldsi*	IGM-KU 90019, IGM-KU 89033, IGM-KU 89140, IGM-KU 90036, IGM-KU 89121, IGM-KU 89029, IGM-KU 89039, IGM-KU 89006, IGM-KU 89080, IGM-KU 90036, IGM-KU 88001, UCMP 39205	12	1015	1097	1059	840
La Venta	*Patasola magdalenae*	IGM 184332	1	722	755	730	519
La Venta	*Lagonimico conclucatus*	IGM 184531	1	837	888	858	640
La Venta	*Mahanamico hershkovitzi*	IGM 181500	1	1035	1120	1081	863
La Venta	*Cebupithecia sarmientoi*	UMCP 38762	1	1664	1886	1813	1692
La Venta	*Nuciruptor rubricae*	IGM 251074	1	1886	2163	2077	2019

TABLE 3. BODY MASS ESTIMATES OF *STIRTONIA VICTORIAE* AND SELECTED EXTINCT PLATYRRHINE SPECIES BASED ON M_1 AREA (mesiodistal length x buccolingual breadth) USING A PGLS REGRESSION.* (continued)

				Body Mass (grams)			
				PGLS Regression			**OLS Regression**
Region	**Species**	**Specimens included in analysis**	**N**	**Female**	**Male**	**Female & Male**	**Female & Male**
Patagonia	*Dolichocebus gaimanensis*	MPEF 5146	1	1595	1800	1731	1593
Patagonia	*Carlocebus carmenensis*	MACN-SC 266, MACN-SC 1, MACN-SC 286, MACN-SC 99, MACN-SC 104, MACN-SC 264, MACN-SC 382, MACN-SC 370, MACN-SC 250	9	2742	3262	3124	3430
Patagonia	*Homunculus patagonicus*	MACN-SC 5757, MACN-SC 10403, MACN-SC 336, MACN-SC 339, MLP 11-121, MLP-55-XII-13-151	6	1845	2112	2029	1957
Patagonia	*Soriacebus ameghinorum*	MACN-SC-2	1	1576	1776	1708	1565
Patagonia	*Soriacebus adrianae*	MACN-SC 251; MACN-SC 344	2	1074	1166	1125	910

*Regression equations are as follows: 1) female body mass, Ln Body Mass=1.084285 (Ln M_1 Area)+4.571255; 2) male body mass, Ln Body Mass=1.189507 (Ln M_1 Area)+4.420231; 3) female and male body mass; Ln Body Mass=1.181069 (Ln M_1 Area)+4.402993.

[a] Estimates from PGLS regressions for this taxon are likely a substantial underestimation.

[b] Measurements from Meldrum and MacPhee (2006).

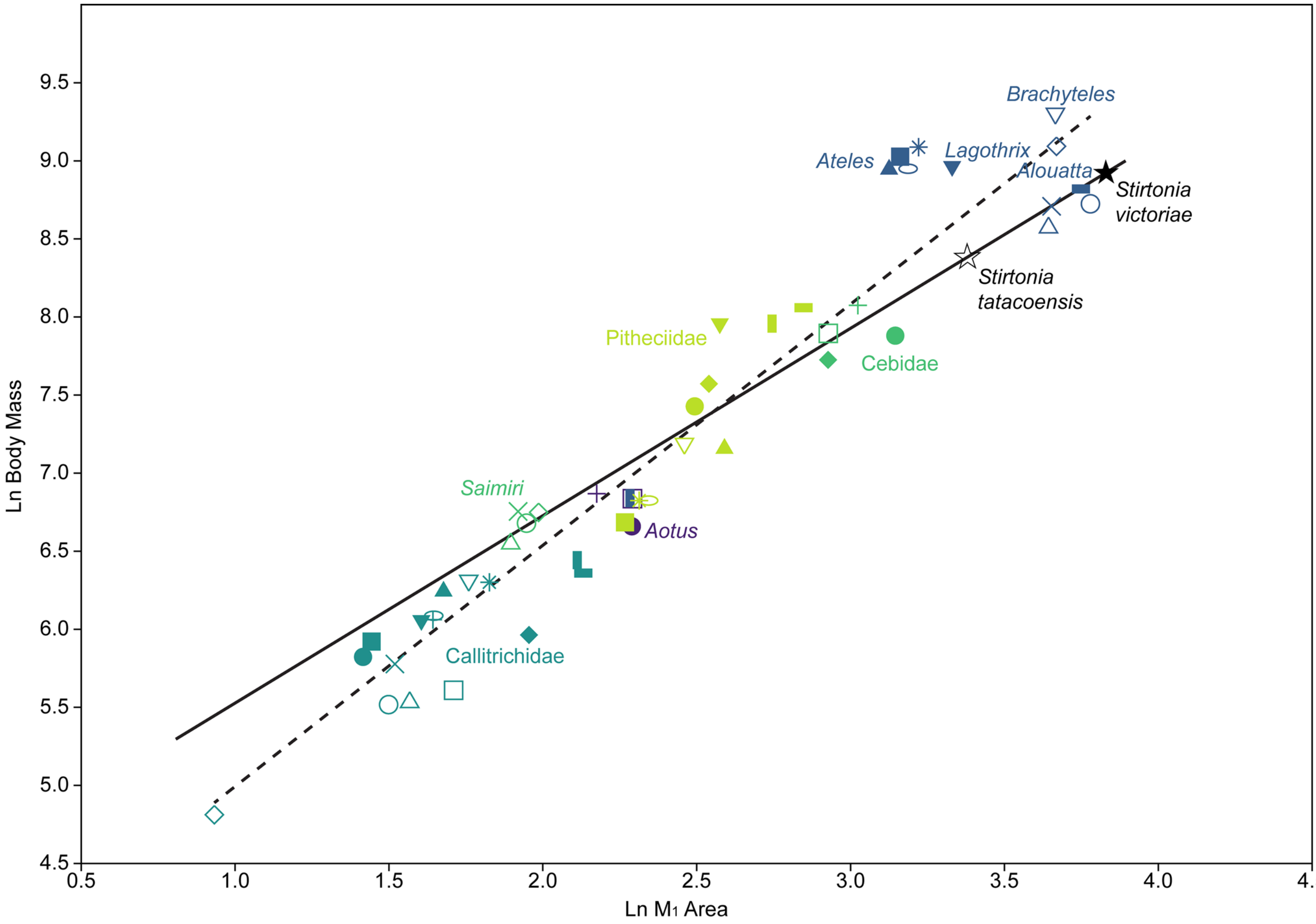

Figure 9. Plot of the natural log of species averages of lower molar area and the natural log of body mass; n=49 species; n=998 individuals sampled. Solid line is a phylogenetically-corrected least squares regression line (PGLS) with the equation y=1.181069(x)+4.402993; the dashed line is an ordinary least squares regression line with the equation y=1.5353(x)+3.4038. Stirtonia victoriae *is shown with a filled star and* S. tatacoensis *is shown with a white star.*

shape are stronger within platyrrhines compared to other primate clades (Meloro et al. 2015). The cross-validations of dietary groups in this study find comparable results between dental and mandibular morphology overall (85% and 90%, respectively). However, dental morphology was not successful in reclassifying the frugivore/omnivore group (consisting of only *Cebus*), which had only a 24% success rate. *Cebus* was alternatively classified as either a frugivore or seed predator based on dental morphology which may reflect the dietary diversity of *Cebus* that includes some hard object feeding. Interestingly, mandibular morphology was able to better distinguish the frugivore/omnivore group (including both *Cebus* and *Sapajus*) with a 93% success rate. Although it may initially seem that mandibular morphology is a good indicator of this dietary group, most dietary categories in this study divide along clade lines. Therefore, the morphological similarities of *Cebus* and *Sapajus* that distinguish them from the other groups may be more related to phylogeny than dietary adaptations. It is notable, however, that the folivore group, which is most phylogenetically diverse (six genera from three platyrrhine families), is recovered with an 86% success rate based only on mandibular shape. The frugivore/insectivore group has the lowest reclassification rate (77%) and only included *Saimiri*. Future work may benefit from integrating dental and mandibular data to distinguish dietary groups in order to make dietary inferences for extinct taxa.

BODY MASS ESTIMATES

We used a PGLS regression to estimate the body mass of *S. victoriae* as well as a sample of other platyrrhine primates (see Table 3; see Figure 9). In comparison to the OLS regression equation, the PGLS regression has a slightly lower slope resulting in the PGLS line passing through the cluster of sampled extant *Alouatta* species. If an ordinary least squares (OLS) regression were used, predicted body masses of *Alouatta* taxa would be somewhat overestimated given their relatively larger molars. Consequently, previous estimates using standard regression approaches (e.g., Cooke et al. 2011) likely overestimated the body mass of *S. tatacoen-*

sis. However, caution should be used when applying these equations in estimating body masses of ateline species, as the PGLS approach will underestimate body mass in these taxa. This is certainly the case for the very large-bodied *C. bamborium*. Its molar measures are within the range for extant *Alouatta* and *Brachyteles* species, but skeletal material indicates a much larger body size; Cartelle and Hartwig (1996) provide an estimate of 20,500 grams based on femoral head volume. Using dental metrics with an OLS regression, we estimate body mass of *C. bamborium* to be ca. 12,500 grams while the PGLS regression returns estimates of 6800–8900 grams, certainly incorrect. We would recommend that any future attempts to estimate the body masses of fossil atelines from molar area do not include *Alouatta* in the sample if the taxon of interest is definitively non-alouattine. Conversely, our PGLS equations also likely overestimate the body mass of smaller-bodied Callitrichines to various degrees (see Table 3; see Figure 9). For example, the small-bodied taxon *P. magdalena* was previously estimated to have a body mass of 480 grams using a least squares regression of molar area and female platyrrhine body mass (Kay and Meldrum 1997) and ca. 350–550 grams by Cooke et al. (2011) using least squares equations from Conroy (1987). The PGLS presented here provides a body mass of ca. 730 grams—substantially larger. Consequently, when estimating body mass in extinct platyrrhine primates, we recommend careful selection of the sample used to generate equations and consideration of how PGLS versus OLS approaches will affect results.

Stirtonia victoriae is the earliest known larger-bodied platyrrhine primate. Taxa from the Early Middle Miocene and before consistently fall at or below ca. 3000 grams. Atelidae as a group, have body masses generally above 5000 grams with the largest known fossil atelids, *C. bamborium, Ca. coimbrafilhoi,* and *P. brasiliensis* (Ford and Davis 1992; Halenar 2011; Halenar and Rosenberger 2013) considerably larger. *Paralouatta varonai* also falls within the atelid body mass range at the higher end of the distribution. Together these data provide further evidence for the evolution of lager body mass at the base of the atelid clade.

CONCLUSION

The platyrrhine faunal diversity present at La Venta, Colombia, is unique in the fossil record of South America and provides the earliest evidence of levels of species richness comparable to extant Amazonian primate communities (Cooke 2011; Wheeler 2010). At La Venta, there is evidence for two folivore/frugivore species, three frugivore/insectivores, five frugivores, and potentially one seed predator (see Table 2). Older fossil assemblages have more restricted niches and a lower species diversity. The oldest South American primates (late Eocene to mid-Oligocene) were largely small-bodied (400–700g) and likely consumed insects and/or fruit (Bond et al. 2015; Hoffstetter 1969; Kay et al. 2002; Rosenberger et al. 1991b; Seiffert et al. 2020; Takai and Anaya 1996). Early Miocene sites yielding primate remains exist in Patagonia. These taxa are larger in body mass than the oldest species (see Table 3) and largely appear to be frugivorous or generalist feeders (Cooke 2011; Perry et al. 2018). These sites lack small-bodied insect-consuming taxa as well as folivores. Species diversity is restricted at these Patagonian sites potentially due to their extremely southern latitude and concomitant seasonality, so they do not make a perfect comparison to the lower latitudes of La Venta. Nevertheless, they do provide a window into the morphological variation present at this point in platyrrhine evolutionary history.

In sum, the mandibular specimens described here provide evidence for the evolution of leaf-eating adaptations by the Middle Miocene shortly after molecular evidence indicates the divergence of alouattines from the other atelids. In broader platyrrhine context, these species were part of an increasingly dietarily diverse platyrrhine community evolving in the context of the formation of the Amazonian Basin (Hoorn et al. 2010; Montes et al. 2021; Shephard et al. 2010).

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DATA AVAILABILITY

Linear measurements of platyrrhine mandibular first molars are available as an excel file from Zenodo under the DOI 10.5281/zenodo.14907406. Linear measures of cheek tooth divergence are available as an excel from from Zenodo under the DOI 10.5281/zenodo.17087510. Surface scans of cropped second mandibular molars are available as a downloadable zip file from Zenodo under the DOI 10.5281/zenodo.14907494. All Zenodo data may be used freely with appropriate attribution. The surface scans of the mandibles of *Stirtonia victoriae* are available for download on Morphosource under the DOI 10.17602/M2/M774745 (VLPPT 335) and the DOI 10.17602/M2/M774765 (VLPPT 336). These data may be used freely. Surface scans of extant platyrrhine mandibles are available upon request from Ryan Knigge.

AUTHOR CONTRIBUTIONS

Siobhán B. Cooke: Conceptualization; Data curation; Formal analysis; Funding acquisition; Investigation; Methodology; Project administration; Supervision; Visualization; Writing – original draft; Writing – review and editing; Ryan P. Knigge: Data curation; Formal analysis; Investigation; Methodology; Visualization; Writing – original draft; Writing – review and editing; Melissa Tallman: Conceptualization; Funding acquisition; Investigation; Project administration; Supervision; Andrés F. Vanegas: Data curation; Investigation; Resources; Laura K. Stroik: Funding acquisition; Investigation; Project administration; Supervision; Writing – review and editing; Brian Shearer: Investigation; Project administration; Supervision; Savannah Cobb: Formal analysis; Investigation; Stephanie M. Palmer: Formal analysis; Investigation; Zana R. Sims: Formal analysis; Investigation; Luis G. Ortiz-Pabón: Formal analysis; Visualization; Andrés Link Ospina: Conceptualization; Data curation; Funding acquisition; Investigation; Project administration; Supervision; Writing – original draft; Writing – review and editing

CONFLICTS OF INTEREST

The authors have no conflicts of interest.

STATEMENT ON GENERATIVE AI

The authors did not use generative AI in the writing of this manuscript.

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Supplement 1 to Mandibular Specimens of *Stirtonia victoriae* from the La Victoria Formation, La Venta, Colombia

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SUPPLEMENTARY ONLINE MATERIAL 1

This supplement contains: SOM Text 1 and 2, SOM Figure 1, SOM Tables 1–10, and SOM References.

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SOM Text 1. Detailed information about the fossil sample.

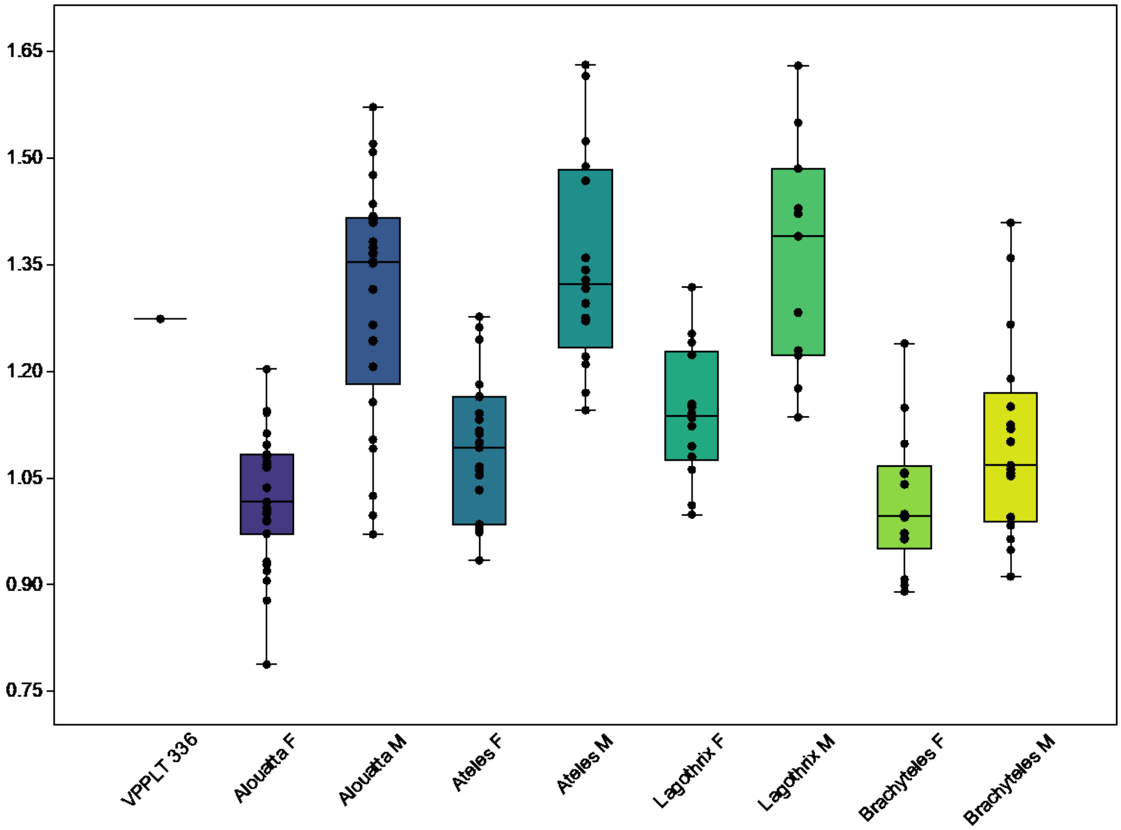
The sample of primate fossils includes the two specimens of *S. victoriae* (VPPLT 335, VPPLT 336) described here. These specimens are curated at the Museo de Historia Natural La Tatacoa, La Victoria, Huila, Colombia. Other specimens from La Venta examined here are curated at several different museums and universities outside of Colombia. These include the University of California Museum of Paleontology, Berkeley, California, United States, (*S. tatacoensis* UCMP 38989; *Neosamiri fieldsi*, UMCP 39205; *Cebupithecia sarmientoi* UMCP 38762), the Primate Research Institute of Kyoto University, Kyoto, Japan (*S. tatacoensis* IGM-KU 8102, 8215, and III 1; *N. fieldsi* IGM-KU 88001, 89002, 89006, 89029, 89034, 89033, 89039, 89080, 89121, 89140, 90019, and 90036; *Aotus dindensis* IGM-KU 8601; *Laventiana annectens* IGM-KU 8801a), and the Duke Lemur Center Museum of Natural History, Durham, North Carolina, United States (*S. victoriae* IGM 85-400; *Patasola magdalenae* IGM 184332; *Lagonimico conclutatus* IGM 184531; *Nuciruptor rubricae* IGM 251074). *Mohanamico hershkovitzi* (IGM 181500) is in the collections of Servicio Geológico Colombiana (SGC) in Bogotá, Colombia.

Specimens of *A. bernensis* are curated at the Museo del Hombre Dominicano (MHD 01, MHD 21) and the Museo Nacional de Historia Natural "Prof. Eugenio de Jesús Marcano" (FOS 25.1113, 25.1129, and 25.1141); both museums are in Santo Domingo, the Dominican Republic. *Insulacebus toussaintiana* (UF 11417) is curated at the Florida Museum of Natural History, Gainesville, Florida, United States. *Xenothrix mcgregori* (AMNH 148198) is curated at the American Museum of Natural History, New York, New York, United States. *Paralouatta varonai* (MNHNCu V123; Cueva Alta 1996; MNHNCu 76.1213–76.1217) is curated at the Museo Nacional de Historia Natural de Cuba (National Museum of Natural History of Cuba), Havanna, Cuba. *Caipora bamborium* (IGC-IFMG 05) is in the Instituto de Geociencias – Universidade Federal de Minas Gerais (Institute of Geosciences – Federal University of Minas Gerais), Belo Horizonte, Brazil.

The fossil primates from the Early Miocene of Patagonia are curated at three separate museums. The Museo de Ciencias Naturales Bernardino Rivadavia, Buenos Aries, Argentina has specimens of *S. ameghinorium* (MACN-SC 2 and 379), *S. adrianae* (MACN-SC 251 and 344), *C. carmanensis* (MACN-SC 1, 43, 63, 99, 104, 250, 264, 266, 286, 370, and 382), and *H. patagonicus* (MACN-SC 336, 339, 5757, and 10403). *Homunculus patagonicus* (MLP 11-121, MLP 55-XII-13-151 and MLP XXII 13156) specimens are also curated the Museo de La Plata, La Plata, Provincia de Buenos Aires, Argentina. *Dolichocebus gaimanensis* (MPEF 5146) is curated at Museo Paleontológico Egidio Feruglio, Trelew, Chubut, Argentina.

SOM Text 2. Description of dental scanning protocols.

To create surface scans, epoxy casts were made of original specimens and coated with a non-reflective spray (e.g., Helling 3D Laser Scanning Spray). They were then scanned using either an LDI Surveyor AM-66RR laser scanner with a RPS 120 sensor or an HDI R4X white light scanner. The scans were edited to crop out the M_2 using Geomagic Wrap 2020 (Oqton; Cary, NC). The resolution was standardized using the 'decimate' function so that models had interpoint distances of approximately 25μm. The three-dimensional geometric morphometric analysis (3DGM) included 285 specimens.



SOM Figure 1. Box and jitter plot showing area of P_2 to P_3 index; calculated as mesiodistal length x buccolingual breadth x 100. The sample includes *Stirtonia victoriae* (VPPLT 336) n=1, *Alouatta* females n=27, *Alouatta* males n=25; *Ateles* females n=23, *Ateles* males n=16; *Lagothrix* females n= 14, *Lagothrix* males n=11; *Brachyteles* females n=14, *Brachyteles* males n=17.

SOM Table 1. Sample used in morphometric analyses with dietary information from Cooke (2011), Norconk et al. (2009), and Rowe and Myers (2016). Species marked with: *only used in the 3DGM analysis; †only used in the mandibular analysis.

Species	**n** **3DGM analyses**	**n** **Mandible analyses**	**Diet of extant species**
EXTANT			
Atelidae			
Alouatta caraya		7	Folivore/Frugivore
Alouatta palliata	14	7	Folivore/Frugivore
Alouatta seniculus	8	19	Folivore/Frugivore
Brachyteles arachnoides	17		Folivore/Frugivore
Lagothrix cana	8		Frugivore
Lagothrix lagotricha	13	13	Frugivore
Lagothrix lugens	1		Frugivore
Lagothrix poeppigii	2		Frugivore
Ateles geoffroyi	21	20	Frugivore
Ateles paniscus	3		Frugivore
Ateles chamek	1		Frugivore
Cebidae			
Cebus capucinus	25	10	Frugivore/Omnivore
Cebus albifrons		16	Frugivore/Omnivore
Sapajus apella		19	Frugivore/Omnivore
Saimiri oerstedii		5	Frugivore/Insectivore
Saimiri sciureus		8	Frugivore/Insectivore
Saimiri boliviensis	28		Frugivore/Insectivore
Callithrix argentata		7	Gumivore/Insectivore
Callithrix jacchus		12	Gumivore/Insectivore
Saguinus fuscicollis		11	Gumivore/Insectivore /Frugivore
Aotus lemurinus	4		Frugivore
Aotus trivirgatus	4	20	Frugivore
Aotus vociferans	9		Frugivore
Aotus azarae	1		Frugivore
Aotus nigriceps	4		Frugivore
Aotus brumbacki	1		Frugivore
Aotus infulatus	5		Frugivore
Pitheciidae			
Plecturocebus caligatus	2		Frugivore

Plecturocebus cupreus	5		Frugivore
Plecturocebus moloch		10	Frugivore
Plecturocebus discolor	9		Frugivore
Plecturocebus ornatus	9		Frugivore
Callicebus personatus	2	3	Frugivore
Cheracebus torquatus		4	Frugivore
Pithecia pithecia	7	10	Seed predator
Pithecia irrorata	10		Seed predator
Pithecia aequitorialis	2		Seed predator
Pithecia monachus		5	Seed predator
Chiropotes albinasus	4		Seed predator
Chiropotes satanas	15	9	Seed predator
Cacajao melanocephalus	8	9	Seed predator
Cacajao calvus	10		Seed predator

EXTINCT			
Caribbean (Pleistocene-Holocene)			
Antillothrix bernensis MHD 01	1	1	
Insulacebus toussaintiana UF 11417	1		
Xenothrix mcgregori AMNH 148198	1		
Paralouatta varonai MHNHCu Cueva Alta 1996 MHNHCu V123	2	1	
Brazil (Pleistocene)			
Caipora bambuiorum IGC-IFMG 05	1		
La Venta (Middle Miocene)			
Stirtonia victoriae VPPLT 335	1	1	
Stirtonia tatacoensis IGM-KU 8102 IGM-KU 8215 UCMP 38989	3		
Aotus dindensis IGM-KU 8601	1		
Laventiana annectens IGM-KU 8801a	1		
Neosaimiri fieldsi UCMP 39205 IGM-KU 89002 IGM-KU 89034	3		

Mohanamico hershkovitzi IGM 181500	1		
Patasola magdalenae IGM 184332	1		
Cebupithecia sarmientoi UCMP 38762	1		
Patagonia (Early Miocene)			
Soriacebus ameghinorum MACN-SC 379 MACN-SC 2	2		
Homunculus patagonicus MACN 1149 MACN 2918 MACN 5969 MACN-SC 336 MACN-SC 339 MPMPV 3708 MLP 55 XXII 13156*	7		
Dolichocebus gaimanensis MPEF 5146	1		
Carlocebus carmanensis MACN-SC 63 MACN-SC 43 MACN-SC 250	3		

SOM Table 2. Species averages for M_1 measures and body mass for a combined male and female platyrrhine sample. Molar measures were collected by Cooke and body mass data was taken from Ford and Davis (1992). Molar measures are in millimeters and body mass is in grams. Raw data are deposited at Zenodo under the DOI 10.5281/zenodo.14907406.

Genus species	**N**	**Min M1 Area**	**Max M1 Area**	**Mean M1 Area**	**Body Mass***	**Ln M1 Area**	**Ln Body Mass**
Alouatta belzebul	27	28.57	51.17	38.60	6056	3.65	8.71
Alouatta caraya	26	29.58	47.37	38.21	5372	3.64	8.59
Alouatta palliata	29	38.13	48.78	43.79	6153	3.78	8.72
Alouatta pigra	29	32.56	45.24	39.22	8893	3.67	9.09
Alouatta seniculus	31	31.66	52.50	42.46	6767	3.75	8.82
Aotus azarae	7	8.96	10.59	9.87	780	2.29	6.66
Aotus lemurinus	39	7.75	10.66	8.80	961	2.18	6.87
Aotus nancymaae	10	8.33	11.35	9.89	931	2.29	6.84
Aotus trivirgatus	17	8.97	11.12	9.81	934	2.28	6.84
Ateles belzebuth	23	19.54	28.56	23.60	8322	3.16	9.03
Ateles fusciceps	30	17.57	33.44	25.05	8845	3.22	9.09
Ateles geoffroyi	28	17.55	32.15	24.22	7704	3.19	8.95
Ateles paniscus	7	19.83	26.06	22.76	7803	3.13	8.96
Brachyteles arachnoides	30	33.23	47.28	39.08	10788	3.67	9.29
Cacajao calvus	11	16.03	18.52	17.24	3165	2.85	8.06
Cacajao melanocephalus	19	13.45	17.83	15.56	2858	2.74	7.96
Callicebus donacophilus	11	7.89	11.21	9.65	800	2.27	6.68
Callicebus hoffmannsi	31	7.96	12.66	10.11	920	2.31	6.82
Callicebus moloch	18	9.04	11.72	10.42	920	2.34	6.82
Callicebus personatus	11	11.79	14.87	13.33	1305	2.59	7.17
Callicebus torquatus	13	10.24	13.07	11.71	1303	2.46	7.17
Callimico goeldii	17	5.60	8.47	7.06	389	1.96	5.96
Callithrix aurita	1	5.17	5.17	5.17	429	1.64	6.06

Callithrix geoffroyi	1	5.53	5.53	5.53	273	1.71	5.61
Callithrix jacchus	6	4.51	5.61	4.79	257	1.57	5.55
Callithrix penicilatta	20	3.43	6.11	4.48	249	1.50	5.52
Cebuella pygmaea	30	1.98	3.18	2.54	123	0.93	4.81
Cebus albifrons	31	14.94	25.46	18.67	2265	2.93	7.73
Cebus capucinus	30	18.47	23.97	20.57	3212	3.02	8.07
Cebus olivaceus	27	14.90	23.09	18.68	2684	2.93	7.90
Chiropotes satanas	31	11.35	16.02	13.13	2810	2.58	7.94
Lagothrix lagotricha	24	23.13	33.81	27.94	7695	3.33	8.95
Leontopithecus chrysomelas	2	7.62	9.23	8.43	578	2.13	6.36
Leontopithecus rosalila	23	7.19	9.52	8.26	628	2.11	6.44
Mico argentata	27	3.61	4.75	4.12	338	1.42	5.82
Mico humeralifer	12	4.20	5.06	4.57	323	1.52	5.78
Pithecia irrorata	12	11.76	14.48	12.68	1943	2.54	7.57
Pithecia pithecia	27	9.80	13.80	12.10	1682	2.49	7.43
Saguinus fuscicollis	4	3.82	4.52	4.24	373	1.44	5.92
Saguinus geoffroyi	28	5.13	7.32	6.21	545	1.83	6.30
Saguinus leucopus	22	4.07	5.84	5.19	440	1.65	6.09
Saguinus midas	18	4.26	6.30	5.35	523	1.68	6.26
Saguinus mystax	11	4.69	6.65	5.81	542	1.76	6.30
Saguinus oedipus	14	4.32	5.46	4.98	420	1.61	6.04
Saimiri boliviensis	36	5.57	8.46	6.82	858	1.92	6.75
Saimiri oerstedii	17	6.02	7.44	6.66	710	1.90	6.57
Saimiri sciureus	29	6.05	8.76	7.01	796	1.95	6.68
Saimiri ustus	20	5.98	8.65	7.29	853	1.99	6.75
Sapajus apella	31	17.43	27.98	23.23	2645	3.15	7.88
TOTAL	**998**				***Ford & Davis, 1992**		

SOM Table 3. Species averages for M_1 measures and body mass for a combined female platyrrhine sample. Molar measures were collected by Cooke and body mass data was taken from Ford and Davis (1992). Molar measures are in millimeters and body mass is in grams. Raw data are deposited at Zenodo under the DOI 10.5281/zenodo.14907406.

Genus species	N	Min M1 Area	Max M1 Area	Mean M1 Area	Body Mass*	Ln M1 Area	Ln Body Mass
Alouatta belzebul	13	28.57	40.34	35.67	5525	3.57	8.62
Alouatta caraya	12	29.58	38.45	33.56	4605	3.51	8.43
Alouatta palliata	13	38.13	48.39	42.64	5350	3.75	8.58
Alouatta pigra	15	33.41	43.81	38.86	6434	3.66	8.77
Alouatta seniculus	17	31.66	51.26	39.55	5600	3.68	8.63
Aotus azarae	3	8.96	9.95	9.58	780	2.26	6.66
Aotus lemurinus	12	7.91	9.72	8.76	968	2.17	6.88
Aotus nancymaae	5	8.44	11.35	9.80	940	2.28	6.85
Aotus trivirgatus	9	8.97	11.12	9.78	950	2.28	6.86
Ateles belzebuth	13	21.66	28.56	24.23	8112	3.19	9.00
Ateles fusciceps	16	21.72	30.28	25.79	8800	3.25	9.08
Ateles geoffroyi	16	21.67	32.15	25.32	7456	3.23	8.92
Ateles paniscus	5	19.83	26.06	22.63	8750	3.12	9.08
Brachyteles arachnoides	14	33.23	42.85	38.41	9450	3.65	9.15
Cacajao calvus	5	16.15	18.30	16.99	2880	2.83	7.97
Cacajao melanocephalus	10	13.45	17.51	15.20	2740	2.72	7.92
Callicebus hoffmannsi	17	7.96	12.66	10.16	920	2.32	6.82
Callicebus moloch	9	9.36	11.72	10.53	860	2.35	6.76
Callicebus personatus	3	12.69	14.24	13.40	1285	2.60	7.16
Callicebus torquatus	3	11.88	12.09	11.98	1307	2.48	7.18
Callimico goeldii	4	7.29	8.47	7.97	355	2.08	5.87
Callithrix geoffroyi	1	5.53	5.53	5.53	190	1.71	5.25
Callithrix jacchus	3	4.55	4.73	4.65	326	1.54	5.79

Callithrix penicilatta	10	3.67	6.11	4.42	182	1.49	5.20
Cebuella pygmaea	16	2.10	3.18	2.58	126	0.95	4.84
Cebus albifrons	15	15.15	22.60	18.54	1814	2.92	7.50
Cebus capucinus	12	18.57	23.65	20.78	2666	3.03	7.89
Cebus olivaceus	13	15.72	23.09	18.64	2395	2.93	7.78
Chiropotes satanas	15	11.52	14.73	12.74	2600	2.54	7.86
Lagothrix lagotricha	13	25.33	33.81	28.55	5750	3.35	8.66
Leontopithecus chrysomelas	1	7.62	7.62	7.62	535	2.03	6.28
Leontopithecus rosalila	9	7.74	8.85	8.37	578	2.12	6.36
Mico argentata	15	3.80	4.75	4.21	320	1.44	5.77
Mico humeralifer	6	4.24	5.06	4.62	310	1.53	5.74
Pithecia irrorata	4	12.10	12.92	12.40	1875	2.52	7.54
Pithecia pithecia	9	9.80	13.57	11.93	1515	2.48	7.32
Saguinus fuscicollis	2	4.09	4.52	4.30	403	1.46	6.00
Saguinus geoffroyi	8	5.13	7.32	6.31	544	1.84	6.30
Saguinus midas	8	4.55	6.12	5.37	432	1.68	6.07
Saguinus mystax	3	6.16	6.49	6.28	560	1.84	6.33
Saguinus oedipus	6	4.80	5.36	4.94	430	1.60	6.06
Saimiri boliviensis	16	5.57	7.21	6.62	700	1.89	6.55
Saimiri oerstedii	8	6.39	7.44	6.79	695	1.91	6.54
Saimiri sciureus	13	6.22	7.75	6.83	675	1.92	6.51
Saimiri ustus	10	6.43	7.81	7.24	795	1.98	6.68
Sapajus apella	14	17.43	26.08	22.64	2385	3.12	7.78
TOTAL	**444**				***Ford & Davis, 1992**		

SOM Table 4. Species averages for M_1 measures and body mass for a combined male platyrrhine sample. Molar measures were collected by Cooke and body mass data was taken from Ford and Davis (1992). Molar measures are in millimeters and body mass is in grams. Raw data are deposited at Zenodo under the DOI 10.5281/zenodo.14907406.

Genus species	**N**	**Min M1 Area**	**Max M1 Area**	**Mean M1 Area**	**Body Mass***	**Ln M1 Area**	**Ln Body Mass**
Alouatta belzebul	14	34.64	51.17	41.33	7270	3.72	8.89
Alouatta caraya	14	33.24	47.37	42.20	6800	3.74	8.82
Alouatta palliata	16	40.59	48.78	44.73	7150	3.80	8.87
Alouatta pigra	14	32.56	45.24	39.60	11352	3.68	9.34
Alouatta seniculus	14	39.71	52.50	46.00	7200	3.83	8.88
Aotus lemurinus	23	7.75	10.66	8.88	955	2.18	6.86
Aotus nancymaae	5	8.33	10.99	9.98	923	2.30	6.83
Aotus trivirgatus	8	8.99	10.92	9.84	920	2.29	6.82
Ateles belzebuth	9	19.57	24.90	23.14	8532	3.14	9.05
Ateles fusciceps	12	17.57	33.44	24.91	8890	3.22	9.09
Ateles geoffroyi	12	17.55	28.25	22.74	8210	3.12	9.01
Ateles paniscus	1	25.72	25.72	25.72	7460	3.25	8.92
Brachyteles arachnoides	16	33.56	47.28	39.67	12125	3.68	9.40
Cacajao calvus	6	16.03	18.52	17.45	3450	2.86	8.15
Callicebus donacophilus	6	7.89	11.21	9.60	800	2.26	6.68
Callicebus moloch	8	9.04	11.26	10.21	1000	2.32	6.91
Callicebus personatus	5	11.79	14.87	13.25	1325	2.58	7.19
Callicebus torquatus	7	10.24	12.57	11.52	1300	2.44	7.17
Callimico goeldii	7	5.60	7.36	6.63	278	1.89	5.63
Callithrix jacchus	2	4.51	4.69	4.60	256	1.53	5.55
Callithrix penicilatta	9	3.43	5.24	4.54	182	1.51	5.20
Cebuella pygmaea	12	1.98	2.82	2.48	130	0.91	4.87
Cebus albifrons	15	14.94	20.79	18.35	2480	2.91	7.82

Cebus capucinus	18	18.47	23.97	20.43	3868	3.02	8.26
Cebus olivaceus	14	14.90	20.64	18.72	2974	2.93	8.00
Chiropotes satanas	14	11.83	16.02	13.48	3200	2.60	8.07
Lagothrix lagotricha	10	23.13	33.12	27.39	8335	3.31	9.03
Leontopithecus chrysomelas	1	9.23	9.23	9.23	620	2.22	6.43
Leontopithecus rosalila	14	7.19	9.52	8.20	607	2.10	6.41
Mico argentata	12	3.61	4.28	4.00	357	1.39	5.88
Mico humeralifer	6	4.20	4.87	4.52	280	1.51	5.63
Pithecia irrorata	8	11.76	14.48	12.81	2010	2.55	7.61
Pithecia pithecia	16	10.86	13.80	12.33	1732	2.51	7.46
Saguinus fuscicollis	2	3.82	4.52	4.17	387	1.43	5.96
Saguinus geoffroyi	20	5.55	7.06	6.17	546	1.82	6.30
Saguinus midas	10	4.26	6.30	5.34	586	1.68	6.37
Saguinus mystax	8	4.69	6.65	5.63	577	1.73	6.36
Saguinus oedipus	7	4.32	5.46	5.01	411	1.61	6.02
Saimiri boliviensis	20	5.85	8.46	6.98	1015	1.94	6.92
Saimiri oerstedii	5	6.05	6.73	6.52	829	1.87	6.72
Saimiri sciureus	16	6.05	8.76	7.15	852	1.97	6.75
Saimiri ustus	10	5.98	8.65	7.34	910	1.99	6.81
Sapajus apella	17	19.66	27.98	23.71	3050	3.17	8.02
TOTAL	**463**				***Ford & Davis, 1992**		

SOM Table 5. Averages of toothrow width measurements taken lingual to each corresponding pair of teeth, P_2 and M_1 for twelve atelid species as well as VPPLT 335 and UMPC 38989.

Genus species	**n**	**Mean P2/M1**
Alouatta belzebul	F n=5; M n=5	0.75
Alouatta caraya	F n=4; M n=4	0.75
Alouatta guariba	F n=4; M n=5	0.75
Alouatta nigerrima	F n=1; M n=1	0.77
Alouatta palliata	F n=5; M n=5	0.80
Alouatta pigra	F n=6; M n=6	0.76
Alouatta seniculus	F n=5; M n=6	0.74
Ateles chamek	F n=4; M n=5	0.77
Ateles fusciceps	F n=5; M n=6	0.74
Ateles geoffroyi	F n=5; M n=5	0.73
Ateles paniscus	F n=5; M n=2	0.74
Lagothrix lagotricha	F n=8; M n=7	0.78
Stirtonia victoriae (VPPLT 335)	n=1	0.77
Stirtonia tatacoensis (UMPC 38989)	n=1	0.61

SOM Table 6. Landmarks used in the dental analyses (Cooke et al. 2011). See Figure 2.

Occlusal Surface Landmarks	
Number	**Landmark description**
1	Metaconid apex
2	Protoconid apex
3	Hypoconid apex
4	Entoconid apex
5	Mesial-most point on occlusal surface
6	Distal-most point on occlusal surface
7	Lowest point on the protocristid - usually at the midline
8	Lowest point on the cristid obliquid
9	Point at which the preentocristid and postmetacristid meet
10	Lowest point in the trigonid basin
11	Lowest point in the talonid basin
Sidewall Landmarks	
12	Point of maximum curvature directly below the protoconid
13	Point of intersection of the ectoflexid with the buccal wall
14	Point of maximum curvature directly below the hypoconid
15	The cemento-enamel junction (CEJ) directly below the protoconid
16	The CEJ directly below the intersection of the ectoflexid with the buccal wall
17	The CEJ directly below the hypoconid
18	Point of maximum curvature directly below the entoconid
19	Point of maximum curvature directly below where the preentocristid and postmetacristid meet
20	Point of maximum curvature directly below the metaconid
21	The CEJ directly below the entoconid
22	The CEJ directly below the below where the preentocristid and postmetacristid meet
23	The CEJ directly below the metaconid

SOM Table 7. Landmarks used in the mandible analysis. Landmarks 1–3, 7–9 were developed by Robinson (2012) See Figure 3.

Landmark Definitions

Number	**Landmark description**
1	Medial alveolus interdental point: p3-p4
2	Medial alveolus interdental point: p4-m1
3	Medial alveolus interdental point: m1-m2
4	Lateral alveolus interdental point: p3-p4
5	Lateral alveolus interdental point: p4-m1
6	Lateral alveolus interdental point: m1-m2
7	Basal margin point directly inferior to p3-p4 interdental points
8	Basal margin point directly inferior to p4-m1 interdental points
9	Basal margin point directly inferior to m1-m2 interdental points
10	Maximum curvature of the lateral corpus between points 2 and 8
11	Maximum curvature of the medial corpus between points 5 and 8
12	Infradentale
13	Mandibular orale
14	Gnathion
15	Maximum curvature of the anterior symphysis between points 12 and 14
16	Most projecting point of the superior transverse torus

SOM Table 7. Table showing the results of the discriminant function analysis using PC 1 and molar length as classification variables. With leave-one-out-cross-validation, there was an 84.8% correct classification rate.

		PREDICTED GROUP					
	DIET	**Folivore/ Frugivore**	**Frugivore**	**Frugivore / Insectivore**	**Seed Predator**	**Frugivore/ Omnivore**	**TOTAL**
COUNT	**Folivore/ frugivore**	38	0	0	0	0	38
	Frugivore	0	87	2	0	6	95
	Frugivore/ Insectivore	0	2	24	0	0	26
	Seed Predator	0	0	0	41	6	47
	Frugivore/ omnivore	0	11	0	8	6	25
PERCENTAGE	**Folivore/ frugivore**	100	0	0	0	0	100
	Frugivore	0	91.6	2.1	0	6.3	100
	Frugivore / Insectivore	0	7.7	92.3	0	0	100
	Seed Predator	0	0	0	87.2	12.8	100
	Frugivore/ omnivore	0	44	0	32	24	100

SOM Table 8. Reclassification results from the CVA with jackknife cross-validation for each extant specimen using the first 7 PCs and grouping by genus.

ACTUAL GENUS	**PREDICTED GENUS**														
	Alouatta	***Aotus***	***Ateles***	***Cacajao***	***Callicebus***	***Callithrix***	***Cebus***	***Chiropotes***	***Lagothrix***	***Pithecia***	***Saguinus***	***Saimiri***	***Sapajus***	**Total correct**	**% Correct**
Alouatta	33	0	0	0	0	0	0	0	0	0	0	0	0	33/33	100.0
Aotus	0	20	0	0	0	0	0	0	0	0	0	0	0	20/20	100.0
Ateles	0	0	19	0	0	0	0	0	1	0	0	0	0	19/20	95.0
Cacajao	0	0	0	9	0	0	0	0	0	0	0	0	0	9/9	100.0
Callicebus	0	1	0	0	16	0	0	0	0	0	0	0	0	16/17	94.1
Callithrix	0	0	0	0	0	18	0	0	0	0	1	0	0	18/19	94.7
Cebus	0	0	0	0	0	0	22	0	0	0	2	0	2	22/26	84.6
Chiropotes	0	0	0	0	0	0	0	8	0	1	0	0	0	8/9	88.9
Lagothrix	0	0	3	0	0	0	0	0	9	0	0	1	0	9/13	69.2
Pithecia	0	0	1	0	0	0	0	1	0	12	0	0	1	12/15	80.0
Saguinus	0	0	0	0	0	0	0	0	0	0	10	1	0	10/11	90.9
Saimiri	0	0	0	0	0	0	0	0	0	0	3	10	0	10/13	76.9
Sapajus	0	0	0	0	0	0	1	0	1	0	0	0	17	17/19	89.5

SOM Table 9. Classification and morphological affinities of each fossil specimen to extant specimens grouped by genus and by dietary category using Procrustes distance (PD) and Mahalanobis distance (MD). Smallest distance in each column is bolded for both genus and diet categories.

		Antillothrix		***Paralouatta***		***Stirtonia***	
		PD	**MD**	**PD**	**MD**	**PD**	**MD**
BY GENUS	***Alouatta***	0.15	5.98	**0.14**	7.54	**0.12**	**3.81**
	Aotus	0.14	6.4	0.23	7.88	0.3	10.05
	Ateles	0.13	5.15	0.24	8.97	0.29	8.46
	Cacajao	0.16	8.64	0.22	11.22	0.25	9.54
	Callicebus	0.17	6.55	0.18	**6.17**	0.26	9.84
	Callithrix	0.14	8.26	0.24	10.76	0.27	9.58
	Cebus	0.14	7.08	0.26	11.25	0.29	9.58
	Chiropotes	0.17	7.85	0.18	9.66	0.21	8.53
	Lagothrix	**0.11**	**4.99**	0.21	9.01	0.25	8.18
	Pithecia	0.15	6.48	0.18	8.07	0.23	8.2
	Saguinus	0.16	6.91	0.29	10.82	0.33	10
	Saimiri	0.12	5.47	0.23	8.83	0.27	8.28
	Sapajus	0.15	6.74	0.24	10.27	0.28	9.27
BY DIET	**folivore/frugivore**	0.15	5.01	**0.14**	**3.15**	**0.12**	**2.21**
	frugivore	**0.11**	**4.18**	0.21	5.90	0.27	7.94
	frugivore/insectivore	0.12	4.37	0.23	5.97	0.27	7.37
	frugivore/omnivore	0.14	5.82	0.25	8.08	0.28	8.76
	frugivore/ seed predator	0.15	6.89	0.19	7.39	0.23	8.04
	gumivore/insectivore	0.14	7.09	0.24	8.06	0.27	8.25
	gumivore/ insectivore/frugivore	0.16	5.20	0.29	7.40	0.33	8.61

SOM Table 10. Reclassification results from the CVA with jackknife cross-validation for each extant specimen using the first 7 PCs and grouping by dietary category.

	PREDICTED GROUP								
ACTUAL GROUP	**folivore/ frugivore**	**frugivore**	**frugivore/ insectivore**	**frugivore/ omnivore**	**frugivore/ seed predator**	**gumivore/ insectivore**	**gumivore/ insectivore/frugivore**	**Total correct**	**% Correct**
folivore/frugivore	33	0	0	0	0	0	0	33/33	100.0
frugivore	1	60	1	3	2	0	3	60/70	85.7
frugivore/insectivore	0	2	10	0	0	0	1	10/13	76.9
frugivore/omnivore	0	0	0	42	0	0	3	42/45	93.3
frugivore/seed predator	0	3	0	1	29	0	0	29/33	87.9
gumivore/insectivore	0	0	0	1	0	17	1	17/19	89.5
gumivore/insectivore/frugivore	0	0	1	0	0	0	10	10/11	90.9

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