Paleobiology of *Protopithecus brasiliensis*, a Plus-Size Pleistocene Platyrrhine from Brazil

by

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A dissertation submitted to the Graduate Faculty in Anthropology in partial fulfillment of the
requirements for the degree of Doctor of Philosophy, the City University of New York

2012

This manuscript has been read and accepted for the Graduate Faculty in Anthropology in satisfaction of the dissertation requirement for the degree of Doctor of Philosophy.

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Abstract

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This dissertation tested several hypotheses concerning the paleobiology of the extinct platyrrhine *Protopithecus brasiliensis* in order to fill in many of the gaps in our knowledge of this fossil and the evolutionary history of its ateline relatives. Both cranial and postcranial morphology were examined using three-dimensional geometric morphometric (3DGM) techniques to investigate the body size, basicranial shape, and locomotor repertoire of the fossil.

Regression equations based on platyrrhine postcranial dimensions support the hypothesis that *Protopithecus* belonged to a size class of platyrrhines that no longer survives, yielding an average estimate of 23 kg. This large body mass led to a previous suggestion that *Protopithecus* would have traveled on the ground, but detailed observations of the skeleton found no adaptations to terrestriality. Instead, the original hypothesis of a suspensory mode of locomotion was supported, particularly based on analyses of the elbow and phalanges. The femur and pelvis exhibit robust muscle markings, suggesting that *Protopithecus*, like *Alouatta*, also used hindlimb suspension and climbing.

A phylogenetic link between *Protopithecus* and *Alouatta* was originally proposed based on suggested synapomorphies of the cranial base and mandible, traditionally related to opening subbasal space for the howler's uniquely enlarged hyoid. These features were examined in more detail to test the hypothesis that *Protopithecus* also had an enlarged hyoid. Based on the landmark dataset analysed here, the *Protopithecus* cranial base and mandible were more similar to the generalized, potentially primitive, condition seen in *Lagothrix*. The occipital region, however, was similar to *Alouatta* in shape and orientation, a potential phylogenetic link but a neutral feature with respect to the question of hyoid enlargement. The large body size of *Protopithecus* needs to be considered here as well, since it is possible that at 23 kg the fossil had sufficient space in the throat to accommodate a relatively large hyoid without extreme cranial base modifications comparable to those of the much smaller *Alouatta*.

Protopithecus demonstrates derived alouattin, primitive ateline, and autapomorphic traits. Based on the fossil hip and thigh morphology, as well as the modified occipital region and small brain size, a provisional phylogenetic position as a basal alouattin is supported.

Acknowledgements

First, this dissertation would not have been possible without generous funding from several agencies. Data collection for the initial pilot studies (2006) was funded by the NYCEP NSF IGERT, grant #0333415. Without the results of those pilot studies, I would not have been able to procure my NSF Doctoral Dissertation Improvement Grant #0925704, which enabled the travel and equipment purchases necessary to finish my data collection (2009-2011). Funding for one of my data collection trips to the National Museum of Natural History in Washington, DC was also provided by a CUNY Doctoral Student Research Grant (2008).

No less important to these data collection trips was the wonderful museum staff who provided specimen access. I would not have been able to assemble the comparative sample of extant primates that forms the basis of this work without help from Eileen Westwig at the American Museum of Natural History in New York, Linda Gordon at the National Museum of Natural History in Washington, Bill Stanley at the Field Museum of Natural History in Chicago, and Leandro Salles at the Museu Nacional in Rio de Janeiro, Brazil. Profound thanks also go to Drs. Castor Cartelle in Belo Horizonte, Brazil and Kim Aaris in Copenhagen for allowing me to study some of the most beautiful fossil primates ever discovered.

Throughout my entire graduate school experience, I have received invaluable help and support from my advisor Alfie Rosenberger. This dissertation truly would not have been possible without him. The same could be said of Eric Delson, who has been so generous with both intellectual and monetary support for the last eight years. Thanks also go to the other two members of my dissertation committee, John Fleagle and Jeff Laitman, whose insightful comments helped me greatly improve the manuscript. Others who have offered their time and advice towards the successful completion of this project include Michelle Singleton, Marian

Dagosto, Jeff Meldrum, Walter Hartwig, Susan Ford, and the late Elizabeth Harmon, who is sorely missed. Special thanks go to Cliff Jolly and Pam Crabtree, my undergraduate mentors at NYU who started me down this path in the first place.

As a graduate student, nobody else knows what you're going through quite like other graduate students. Without the support of my academic peers here in New York and elsewhere, I would not have been able to survive my time at CUNY. In particular, I would like to thank my fellow Ladies, Melissa Tallman, Siobhán Cooke, Jessica Brinkworth, Mary Blair, Jenna Lawrence, Danielle Whittaker, and Stephanie Spehar for providing hours of much needed distraction (and sometimes even academic collaboration). Lindsey Smith and Julia Zichello belong on that list as well for their intimate knowledge of the perils of making a living as a CUNY adjunct. I also thank Sergio Almècijá, Jason Organ, Claire Terhune, Justin Gladman, Zach Klukkert, and Tom Rein for participating in important intellectual discussions over the years. Last but certainly not least, without Cristiane Cäsar, I quite literally would not have been able to survive my first trip to Brazil and subsequently would have needed to start over on a totally different project.

While having a graduate student support network is vital, so is being able to step outside the academic realm to participate in social activities with people who live and work in the real world. All of my high school and college friends who I have seen on a regular basis over the last eight years in the city and in New Jersey deserve just as much thanks as those mentioned so far. In the last several years, Ted Price's unwavering confidence in my abilities to become the best PhD that has ever lived has helped get me through some particularly rough patches. And, it should go without saying, the support of my family throughout my entire academic career has been integral to my success. This is for you. I hope it makes you proud.

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CHAPTER 1

BACKGROUND

History of discoveries

Remains of *Protopithecus brasiliensis* were first discovered in 1836 by the Danish naturalist Peter Wilhelm Lund. A left proximal femur and right distal humerus were found in the Lagoa Santa cave system in Minas Gerais, Brazil, and despite their large size and robusticity, Lund recognized the fossils as belonging to a New World monkey (Lund, 1838). These fossils were the first to be correctly recognized as a primate at the time of their discovery and were included in Darwin's brief discussion of the evolution of South American monkeys in *On the Origin of Species* (1859). As Lund was writing well before natural selection became an accepted mechanism for evolutionary change, his interpretations of the mammalian remains came from a catastrophist point of view that traditionally saw monkeys, apes, and humans as all being created very recently after the Great Deluge (Hartwig, 1995b; Holten and Sterll, 2000). This, however, did not stop him from including *Protopithecus* on the "Fossil" side of his specimen list as separate from the several representatives of extant genera of platyrrhines that he also discovered in the caves. Lund's publications do not include any further analysis of the *Protopithecus* material.

The next major publication to focus any attention on *Protopithecus* was a monograph by Winge (1895) which summarizes the mammalian remains collected by Lund in the Lagoa Santa caves over his many years of excavations. Winge includes the provenance of Lund's discoveries and discusses the fossils within a relatively modern-sounding comparative context. He notes that the distal humerus and proximal femur were found in the same cavern, but not on the exact same site, and concludes that they are "probably" from the same individual. Unfortunately, without more of the skeleton to inform his interpretations, Winge attributes the *Protopithecus* material to a larger species of what we now know as *Brachyteles*. This relatively uninteresting conclusion relegated the fossils to scientific obscurity for over 150 years (Hartwig, 1995a, 1995b). The situation was not helped by the Hill (1962) volume on New World monkeys which incorrectly reported the size of the *Protopithecus* femur as just 1.5 mm larger than that of a *Brachyteles*.

Then, in 1992, a nearly complete skeleton of a very large platyrrhine was discovered in the Toca da Boa Vista caves in the neighboring state of Bahia, approximately 1200 km away (Fig. 1.1); it was included in the hypodigm of *Protopithecus brasiliensis* based on its comparable

Figure 1.1. Map showing fossil mammal localities in Brazil.
Modified from Auler et al. (2006).

Table 1.1. Preserved elements of *Protopithecus brasiliensis*.[1]

Element	**Condition**
Cranium	Complete except for broken zygomatic arches, pterygoids, and right postglenoid process – calcite deposition obscures some sutures and surface anatomy, especially on the posterior basicranium
Mandible	Anterior portion only (broken behind the M3 on each side, some right ascending ramus present)
Dentition	Upper: incisors (central covered in calcite), canines (tips broken, especially the right), P4, M1-3 (left M3 plastered back in place, right M1 missing anterior portion) Lower: incisors (central and right lateral are broken at the crown tips), canines (broken more than uppers), P2-4
Vertebrae	11 caudal, 13 thoracic and lumbar (some too fragmentary to distinguish type)
Ribs	At least 9 partial
Clavicle	Left: complete except for the medial epiphysis
Scapula	Left: acromion process and base of the glenoid fossa connected by partial spine, no blade Right: partial glenoid, acromion process, and spine, no blade
Humerus (TBV + LS right distal)	Left: broken about midway down the shaft, only distal end is present – brachioradialis flange, medial and lateral epicondyles are slightly eroded Right: complete except for the head which is eroded away, especially the posterior portion
Radius	Proximal end only (broken just below the radial tuberosity) – head and shaft are eroded, obscuring morphology
Ulna	Left: nearly complete (posterior border of radial facet is slightly eroded), distal epiphysis is missing Right: shaft is broken in thirds with approximately 1-2 cm missing of the middle portion, epiphyses are complete except for the posterior portion of the radial facet
Phalanges	At least a full set from one cheiridium
Pelvis	Right: nearly complete, missing ischiopubic ramus and superior border of the ilium
Sacrum	Superior half only (two vertebral bodies preserved with calcite deposits obscuring details of the transverse and spinous processes, left auricular surface is eroded)
Femur (TBV + LS left proximal)	Left: complete, posterior and inferior surfaces of head are slightly eroded Right: complete, lesser trochanter is slightly eroded and medial half of the medial condyle is missing
Patella	Right: complete with slight erosion around the circumference
Tibia	Left: complete but the anterior surface of the tibial plateau is heavily eroded as is the anterior portion of the medial malleolus Right: complete, medial portion of the medial malleolus is eroded
Tarsals	Calcaneus (right and left), talus (right and left), and right navicular, cuneiforms, and cuboid
Metatarsals	I – V (right and left)

[1] See Chapters 3 and 4 for images of most of this material.

size (Hartwig and Cartelle, 1996; Table 1.1). The femoral head volume of both the Lagoa Santa (LS) and Toca da Boa Vista (TBV) specimens yielded a body size estimate for the fossil of around 25 kg (Hartwig, 1995a; Hartwig and Cartelle, 1996). Depending on the source, either *Brachyteles* or *Ateles* is cited as the largest living New World primate at approximately 10-12 kg (e.g., DiFiore and Campbell, 2007). The large body size estimate plus new morphological information from the skull and more complete postcranial remains made *Protopithecus* a fossil of interest once again; it seems to be a genus that exhibits a mosaic of atelin and alouattin characters (Hartwig and Cartelle, 1996; Jones, 2008) which are usually seen as opposite ends of a morphocline within the Atelinae (Rosenberger and Strier, 1989). A whole host of hypotheses regarding the sequence of evolutionary changes within this subfamily can now be investigated.

Dating, taphonomy, and paleoenvironment

Mass spectronomic U-series dating of speleothem calcite deposits from Lagoa Santa and Toca da Boa Vista suggest a late Pleistocene date for the fossils, but the skeletal elements have not been dated directly. Samples from the caves range from 359,890 ±23,373 ya to 10,276 ±2001 ya with a cluster of dates around 15-20 kya for material associated with some of the non-primate fossils (Auler et al., 2006). Unfortunately, none of those samples come from the exact *Protopithecus* localities so a more precise age estimate is not possible at this time. Fossils found in cave deposits are notoriously hard to date directly, partially because there is no way to calculate the time lag between the death of the organism on the surface, its deposition in the cave, and the buildup of the calcite layer on top of its remains (Auler et al., 2004).

With no way to pinpoint an exact date for the fossils, making inferences about the paleoclimate or microhabitat that existed around the caves at the time *Protopithecus* was roaming eastern Brazil becomes even more speculative than usual. Various lines of evidence suggest mixed habitat types in alternating climates for the region through the late Pleistocene. Carbon isotopes from teeth of the notoungulate *Toxodon* in the Toco dos Ossos cave, approximately 50 km away from Toca da Boa Vista in Bahia, indicate habitats including C_3 woody plants, possibly more arid-adapted CAM photosynthesis plants, and some C_4 grasslands during this time period (MacFadden, 2005). Mammalian fauna from the late Pleistocene found in other sites in both the Lagoa Santa and Toca da Boa Vista cave systems suggest ground cover of low vegetation and available grazing material for "megaherbivores" (Cartelle, 1994). Cartelle and Hartwig (1996), however, infer the presence of a more prominent and diverse forest habitat in the area as well in order to support the large biomass of *Protopithecus* and its contemporaneous ateline relative, *Caipora*. This reconstruction is also supported by more recent work that points to the presence of fossil tropical bat species in the caves that would have necessitated a wetter, more forested environment than exists around Toca da Boa Vista today (Auler et al., 2006).

Due to the nearly complete nature of the many articulated skeletons of large bodied mammals found in the caves, Auler et al. (2006) also conclude that the remains found in Toca da Boa Vista most likely came from animals that entered the cave of their own accord, as opposed to being washed in by floodwaters or carried in by predators. Remains in the Lagoa Santa caves are more fragmented and were most likely deposited by runoff during a dry period before the calcite deposits formed on top of the bones during a subsequent moist climate period (Auler et al., 2006). These alternating wet and dry periods last throughout the late Pleistocene, providing a connection between the Amazon and the Atlantic Coastal Forest that became permanently dry approximately 11,700 years ago (Auler et al., 2004). This has important biogeographic implications for the ateline primates, as *Brachyteles* is currently restricted to the Atlantic Coastal Forest and it has been suggested that *Alouatta* has evolutionary roots outside the Amazon basin (Rosenberger et al., 2009). Evidence from the fossil's more primitive craniodental morphology and its potentially more forested paleohabitat suggest that *Protopithecus* represents a much older "stage" of ateline evolution than the Pleistocene cave deposit dates suggest (Rosenberger et al., 2009). This would make the known fossil individuals late-surviving members of a ghost lineage.

Relationship to the living atelines

The four genera of living ateline primates, *Ateles, Lagothrix, Brachyteles,* and *Alouatta*, comprise a monophyletic group, unique among the platyrrhines in their relatively large body size and possession of a prehensile tail. There are several syntheses focusing on the behavioral and ecological adaptations of this radiation based on the modern forms (e.g., Rosenberger and Strier, 1989; Strier, 1992; DiFiore and Campbell, 2007). This body of literature revolves around the relatively well-studied *Ateles* and *Alouatta* as the two extreme ends of a morphocline of morphology and behavior and the convergences between members of this clade and the living apes (Erikson, 1963; Douglas and Marcellus, 1975; Rosenberger and Strier, 1989; DiFiore and Campbell, 2007).

Spider monkeys are characterized by a "lanky" body plan, sexual monomorphism, a large globular brain, highly frugivorous diet, small molars and mandibles compared to the other atelines, highly energetic suspensory locomotion, and a fission-fusion social system (e.g., Rosenberger et al., 2008). Howler monkeys, like the spiders, are a speciose genus with a wide geographic distribution throughout Central and South America, but in many ways are their complete opposite. Where spider monkey crania are rounded and globular, howlers are long and drawn out with an airorynchous face and rugose posteriorly facing occipital region. Howler monkeys are considered to be the most folivorous of the New World monkeys and this is reflected in their small incisors, long molar shearing crests, and small relative brain size (Rosenberger, 1992; Anthony and Kay, 1993; Rosenberger et al., 2011). Sexual dimorphism, slow deliberate quadrupedalism, and a more cohesive social group structure than the other atelines round out the howler monkey gestalt (see DiFiore and Campbell, 2007 for review of the literature). Howler monkeys are also the only platyrrhines in which both males and females have trichromatic vision (Jacobs and Deegan, 2001). While both spider monkeys and howler monkeys use long calls to communicate, only the eponymous howler monkeys possess a greatly enlarged and pneumatized hyoid bone that is said to act as a resonating chamber during their howling bouts (Chapman, 1929; Kelemen and Sade, 1960; Schön, 1971; Fitch and Hauser, 1995; Hewitt et al., 2002). The unique cranial and mandibular morphology of the howler monkey could be functionally related to either opening the subbasal space to make room for this enlarged hyoid, or to their folivorous diet, although this is certainly more complicated than these two main hypotheses would suggest (Biegert, 1963; Watanabe, 1982; Halpern, 1987; see Chapter 3).

The two genera that fall “in between” the spider and howler extremes, *Lagothrix* and *Brachyteles*, have only begun to be understood by detailed research on both captive and wild populations. These genera are more restricted in geographic range and habitat types and are each known by only one or two species. *Brachyteles* populations in the Atlantic Coastal Forest of Brazil consist of highly endangered primates who seem to share social grouping and locomotor patterns with the spider monkeys and a more folivorous diet and dentition with the howler monkeys, although not to the extreme degree found in either of the other taxa (e.g., Strier, 1999; Strier and Boubli, 2006). Woolly monkeys, the two species of the genus *Lagothrix*, show a different mosaic of characters, sharing a frugivorous diet with the spider monkeys and slower more deliberate locomotion and cohesive social behavior with the howler monkeys (Rosenberger and Strier, 1989; Turnquist et al., 1999; Dew, 2005; DiFiore and Fleischer, 2005; Schmitt et al., 2005). A fifth genus, *Oreonax*, resurrected for the Yellow-tailed woolly monkey by Groves (2001), will not be recognized here and those monkeys will continue to be referred to as *Lagothrix flavicauda* (see Matthews and Rosenberger, 2008; Rosenberger and Matthews, 2008).

Despite the Pleistocene age of the fossil material, *Protopithecus* as a taxon could potentially reflect a more primitive element of the Miocene radiation of atelines (Rosenberger et al., 2009). Therefore, neither its morphology nor its behavior is expected to closely match any of the living species and it could be argued that comparison should be made instead to the ancestral morphotype of the ateline subfamily. Based on analyses of the living genera alone, Rosenberger and Strier (1989) suggested that *Lagothrix*, with craniodental and postcranial morphology intermediate between the extremely derived alouattin and atelin character states, is the best model for this hypothetical ancestor (but see below). This genus may well be best for comparison with the fossil in attempting to reconstruct aspects of its paleobiology.

The postcrania of *Ateles* and *Brachyteles* are very specialized for suspensory locomotion while both the postcranial and cranial morphology of *Alouatta* show their own unique set of specializations for more deliberate quadrupedalism and loud howling. With the publication of the relatively complete skeleton of *Protopithecus,* it became clear that the fossil exhibits a combination of traits that were not expected to be seen together in one individual; the skull was described as very similar to that of an *Alouatta* but with frugivorous teeth, and the postcranial skeleton seemed to be adapted for the more acrobatic locomotion of *Ateles* and *Brachyteles* (Hartwig and Cartelle, 1996). However, none of the traits that are usually discussed as being derived in terms of their polarity are quite as derived as those found in extant *Alouatta* or *Ateles*. Putting *Protopithecus* within the context of the living ateline radiation cannot be done by simple comparisons to animals we can see in the South American forests today.

Ateline phylogeny

Neither the species-level nor the genus-level phylogeny of the ateline subfamily has been resolved without controversy. As in other primate groups, most notably the papionins (see review in Gilbert, 2011), molecular and morphological data sets recover different phylogenies. The most commonly reported results are a sister-taxa grouping of *Brachyteles* and *Ateles*, based on their shared postcranial adaptations for acrobatic suspensory locomotion and increased brain size (Rosenberger and Strier, 1989; Rosenberger, 1992; Cole, 1995), or *Brachyteles* and *Lagothrix*, which is supported by most of the molecular evidence [ε-globin and karyotype (Schneider et al., 1993; Meireles et al., 1999); IRBP (Harada et al., 1995); combined mtDNA and morphology (Horovitz et al., 1998); G6PD (von Dornum and Ruvolo, 1999); β-microglobulin (Canavez et al., 1999); and more recently, non-coding intergenic regions (Wildman et al., 2009)].

The results of both morphological and molecular studies vary depending on the taxa included in the sample, which molecules or bones are being used to build the data matrix, and whether parsimony-based algorithms or character analysis are used as the tree-building method. For example, character matrices based only on dental morphology link *Brachyteles* and *Alouatta* (Kay et al., 1987 and subsequent publications), but despite a shared cristodont surface, detailed inspection of the molars show differences in morphology that suggest convergent evolution due to dietary similarities (Rosenberger and Strier, 1989). A sister-group pairing of *Lagothrix* and *Ateles* has been recovered by analyses based on both postcranial (Ford, 1986) and cranial

(Groves, 2001) data matrices. Some molecular studies suffer from repeated use of previously published data sets making for a false sense of strong support (Harada et al., 1995) and the *Brachyteles/Lagothrix* pair is sometimes the least supported in the analysis (e.g., Von Dornum and Ruvolo, 1999; Wildman et al., 2009). Both molecular and morphological studies, however, do agree on the distinction between *Alouatta* and the other three genera (*Ateles, Lagothrix*, and *Brachyteles*), with *Alouatta* as the most basal member of the clade.

This inconclusive evidence has caused some to throw up their hands and use an unresolved trichotomy for the atelins (e.g., Collins, 2004). It has been suggested that these three genera, as well as the other commonly recognized platyrrhine clades, underwent a very rapid adaptive radiation which is why their phylogeny can be so hard to resolve (Schneider et al., 1993; Schrago, 2007; Wildman et al., 2009). However, it has also been pointed out that these inconsistencies could also be related to flaws inherent in the phylogenetic methods being used (Rosenberger, 2011). For example, several studies have shown the importance of taxon sampling and repeatable character coding when using software like PAUP (e.g., Matthews and Rosenberger, 2008; Rosenberger, 2010), as is commonly done in both morphological and molecular studies. It is likely that more reliable phylogenetic methods are needed, but it also could be worth taking a page out of the papinion book; perhaps the ateline situation is analogous to the baboons, and a rethinking of the informative morphological traits will find those that support the molecular trees (i.e., Gilbert, 2011).

As *Protopithecus* has been suggested to be more closely related to *Alouatta* than to the other atelines, a look at howler monkey species-level phylogeny and taxonomy is warranted. As mentioned above, *Alouatta* is generally placed in its own tribe within the ateline subfamily, the Alouattini (e.g., Schneider and Rosenberger, 1996; Goodman et al., 1998; Rylands et al., 2000), that consists of extant *Alouatta* and its fossil relatives (see below). The species-level taxonomy within *Alouatta* has been discussed based on various lines of morphological and, more recently, genetic evidence (Elliot, 1913; von Ihering, 1914; Lonnberg, 1941; Hershkovitz, 1949; Cabrera, 1958; Hill, 1962; Bonvicino et al., 1995; Rylands et al., 1995; Rylands et al., 2000; Groves, 2001; Cortes-Ortiz et al., 2003; Gregorin, 2006). The number of species recognized ranges from five (Cabrera, 1958) to fourteen (Gregorin, 2006). Currently, six species names are most commonly used, and these will be used in subsequent chapters: *A. belzebul, A. caraya, A. guariba, A. palliata, A. pigra,* and *A. seniculus*. (*A. guariba* is sometimes referred to as *A. fusca* – see Gregorin (2006) for discussion of the complex taxonomic arguments involved). *A. palliata* and *A. pigra* are sister taxa with a Central American distribution and they shared a common ancestor with South American species approximately 7 Ma (Smith, 1970; Meireles et al., 1999; Cortes-Ortiz et al., 2003; Fig. 1.2). *A. belzebul* and *A. seniculus* have the broadest geographic distributions and are the most diverse species groups with many subspecies designated for each, some of which are elevated to the species level by various authors. For example, Groves (2001) recognizes ten species of *Alouatta,* the six listed above plus *A. nigerrima* (a subspecies of *A. belzebul*), *A. macconnelli* and *A. sara* (subspecies of *A. seniculus*), and *A. coibensis* (a subspecies of *A. palliata* restricted to Coiba Island off the coast of Panama).

Most species and subspecies are identified by pelage color, ranging from tan to auburn to black with sexual dichromatism in *A. caraya* and *A. guariba*. In most cases, species distributions are defined by rivers, but hybrid zones exist in areas of home range overlap in Mexico for *A. palliata* and *A. pigra* and in Brazil for *A. guariba* and *A. caraya* (Aguiar et al., 2007; Cortes-Ortiz et al., 2007; Bicca-Marques et al., 2008). Differences in chromosome number and arrangement between many of the species could be too complex for hybrid zones to exist in other

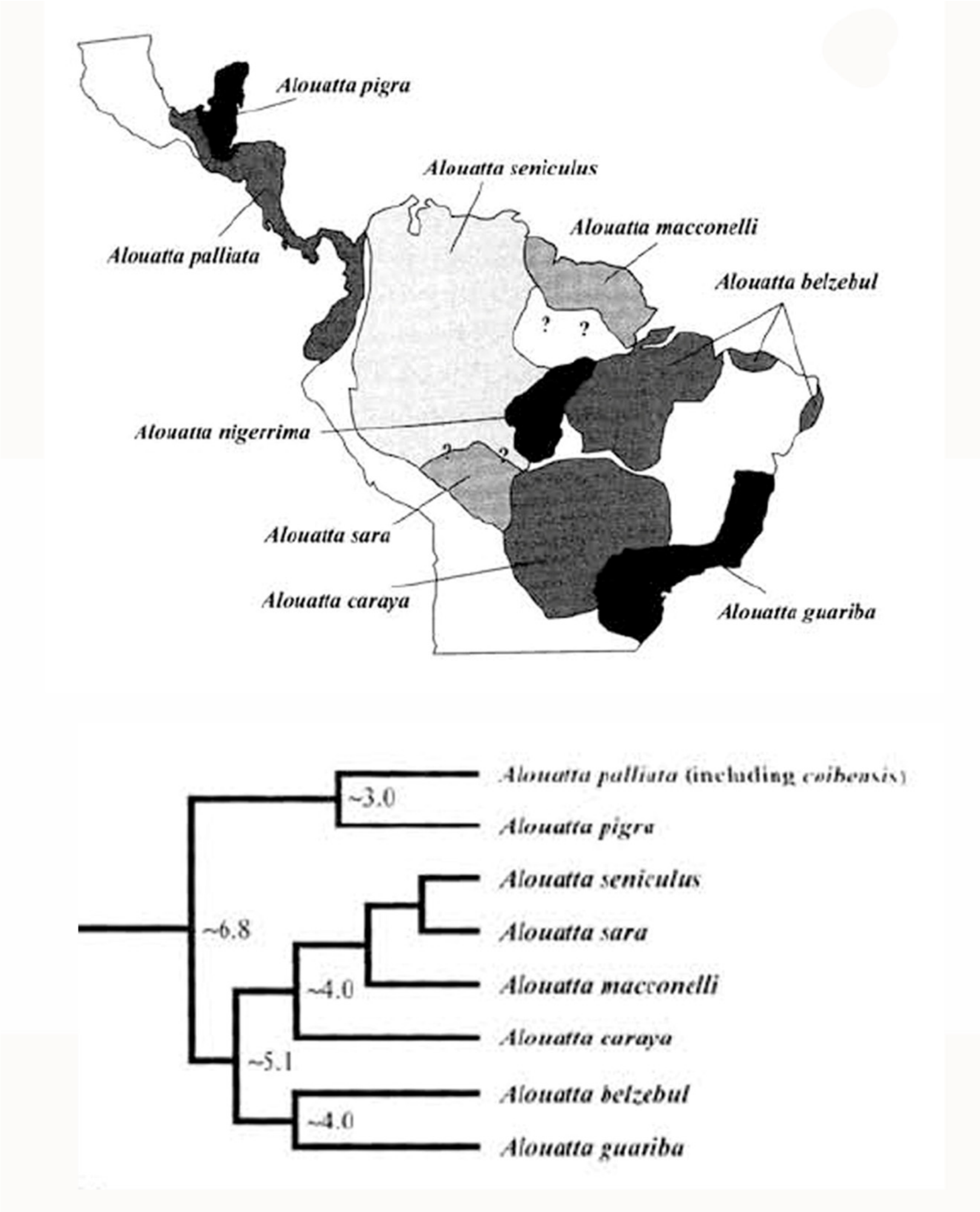

Figure 1.2. Geographic distribution and phylogenetic relationships amongst species of extant *Alouatta*. Both map and phylogeny are labeled using the Groves (2001) taxonomy. Molecular phylogeny and divergence dates are from Meireles et al. (1999) and Cortes-Ortiz et al. (2003). Figure modified from DiFiore and Campbell (2007).

areas of sympatry (de Oliveira et al., 2002).

Given the unique morphology of the genus, the hyoid bone and the skull have also been used by several authors for taxonomic and phylogenetic purposes (von Ihering, 1914; Lonnberg, 1941; Hershkovitz, 1949; Hill, 1962; Gregorin, 2006; see Chapter 3). There are also behavioral differences between the species, most importantly in diet and the use of long calls, that are important for understanding the evolutionary history of the group (see Chapter 3).

Place within platyrrhine paleontology

The fossil evidence pertaining to the evolution of the four living ateline genera is relatively sparse (Table 1.2). Thus the stunning completeness of the *Protopithecus* fossil material has important implications for testing hypotheses of ateline evolution and the morphotype of their last common ancestor, which have heretofore been based largely on neontology (e.g., Rosenberger and Strier, 1989; Rosenberger, 2002). So far, only the lineages of *Alouatta* and *Ateles* are linked to extinct genera by good fossil material; fossil relatives pertaining to the genera *Lagothrix* and *Brachyteles* are not known. *Stirtonia* from the Miocene of La Venta, Colombia and Rio Acre, Brazil (Stirton, 1951; Hershkovitz, 1970; Setoguchi et al., 1981; Kay et al., 1987; Kay and Frailey, 1993), the late Pleistocene fossil genus *Protopithecus* from Brazil (Lund, 1838; Hartwig, 1995a, 1995b; Hartwig and Cartelle, 1996), and the Cuban genus *Paralouatta* from Quaternary cave deposits (Rivero and Arredondo, 1991; MacPhee and Horowitz, 2002; MacPhee et al., 2003; MacPhee and Meldrum, 2006) have all been proposed to share phylogenetic affinities with the living howler monkeys, although the status of *Paralouatta* is still heavily debated (Horovitz and MacPhee, 1999; Rosenberger, 2002). The Pleistocene genus *Caipora* can best be described as a giant spider monkey (Cartelle and Hartwig, 1996),

Table 1.2. Summary of known fossil atelines.

Genus	Species	Locality	Age	Attributed Material	Body Size	Diet	Locomotion	Major References
Stirtonia	*tatacoensis*	La Venta, Colombia	middle Miocene	Mandible, isolated teeth	6 kg	Folivore	N/A	Stirton (1951), Hershkovitz (1970), Setoguchi (1981)
	victoriae	La Venta, Colombia	middle Miocene	Gnathic-dental (including deciduous teeth)	10 kg	Folivore	N/A	Kay et al. (1987)
	sp.	Rio Acre, Brazil	late Miocene	Isolated lower molar	N/A	N/A	N/A	Kay and Frailey (1993)
Paralouatta	*varonai*	Cueva de Mono Fosil, Cuba	Pleistocene	Craniodental and postcranial	9 kg	Folivore?	Semi-terrestrial?	Rivero and Arredondo (1991), Horovitz and MacPhee (1999), MacPhee and Meldrum (2006)
	marianae	Domo de Zaza, Cuba	early Miocene	Talus	N/A	N/A	AQ	MacPhee et al. (2003)
Protopithecus	*brasiliensis*	Lagoa Santa, Minas Gerais, Brazil; Toca da Boa Vista, Bahia, Brazil	late Pleistocene	Proximal femur, distal humerus; nearly complete skeleton	25 kg	Frugivore	Suspensory? Terrestrial?	Lund (1838), Hartwig (1995), Hartwig and Cartelle (1996), Heymann (1998)
Caipora	*bambuiorum*	Toca da Boa Vista, Bahia, Brazil	late Pleistocene	Nearly complete skeleton	21 kg	Frugivore	Suspensory? Terrestrial?	Cartelle and Hartwig (1996), Heymann (1998)
Solimoea	*acrensis*	Rio Acre, Brazil	late Miocene	Isolated lower molar and maxillary fragment (P3-4)	5 – 6 kg	Frugivore	N/A	Kay and Cozzuol (2006)

although more detailed work needs to be done to confirm this interpretation. The poorly known genus *Solimoea*, reportedly represented by three worn postcanine teeth, may be a basal ateline (Kay and Cozzuol, 2006) or a primitive alouattin (Rosenberger et al., in press).

Stirtonia is represented by dental remains only and includes two species, *S. tatacoensis* and *S. victoriae* (Hershkovitz, 1970; Setoguchi et al., 1981; Kay et al., 1987). Both species share molar shearing characters and a buttressed mandibular symphysis with *Alouatta*; *S. victoriae* is slightly larger with more developed shearing crests. Despite these similarities, neither species was as derived as the living howler monkey in terms of dietary adaptations useful for folivory (Kay et al., 1987). As previous work has suggested that *Protopithecus* is related to howler monkeys, one would expect to find the well-developed shearing crests and small incisors of the howler's folivorous dentition in the fossil. However, these characters are lacking in *Protopithecus*, and it instead seems to have teeth more adapted to a frugivorous diet (Hartwig and Cartelle, 1996; Cooke et al., 2007).

When it was first discovered, the type specimen of *Paralouatta varonai*, a nearly complete cranium, was immediately recognized as sharing many of the unique cranial traits seen in *Alouatta* such as the small brain, posteriorly directed nuchal plane, and long unflexed cranial base (Rivero and Arredondo, 1991). The discoverers noted that these characters were not as developed as in the living genus, but they pointed out that this would be expected in an older, more primitive taxon. As new material was discovered, in the form of both postcranial elements and isolated teeth, new interpretations of *Paralouatta* and the other Antillean primates, *Antillothrix* and *Xenothrix*, suggested that the similarities with *Alouatta* were merely primitive retentions or allometrically induced similarities. Based on a phylogenetic analysis of mostly dental characters, Horovitz and MacPhee (1999) preferred to see *Paralouatta*, *Antillothrix*, and

Xenothrix as a monophyletic group most closely related to *Callicebus* on the South American mainland, making them all pitheciines.

New work on the postcranial material attributed to *Paralouatta* suggests that it might have been semi-terrestrial in its locomotor pattern, a behavior not seen in any living or extinct platyrrhine thus far (MacPhee and Meldrum, 2006). Like *Protopithecus*, *Paralouatta* could be a much older genus than the recent cave deposit dates for *P. varonai* would imply. A talus that has been attributed to a second species, *P. marianae*, comes from the early Miocene Domo de Zaza cave in Cuba (MacPhee et al., 2003). How and when *Paralouatta* and the other Antillean primates colonized the islands from the mainland is still an open question (Iturralde-Vinent and MacPhee, 1999; Hedges, 2001; MacPhee and Horowitz, 2002).

Caipora bambuiorum was discovered at the same time and in the same chamber as *Protopithecus* in the Toca da Boa Vista cave network in Bahia, Brazil (Cartelle and Hartwig, 1996). It is represented by the nearly complete skeleton of a late-stage subadult individual; like *Protopithecus*, the bones of the skeleton are more robust than any living ateline, but the original body size estimates are slightly smaller, at approximately 20 kg. The round globular braincase, a large incisor to molar ratio, molars with rounded cusps, and postcrania adapted for suspensory locomotion indicate a close relationship with *Ateles* (Cartelle and Hartwig, 1996). *Caipora* and *Protopithecus* seem to be part of the larger-bodied mammalian fauna of the Pleistocene found around the globe, but the full importance of their size to other aspects of their paleobiology has yet to be determined (see Chapter 2).

The other relevant fossil taxon, *Solimoea acrensis*, is represented solely by dental remains: a lower first molar and a maxilla fragment containing P3-4. The results of a PAUP analysis run by Kay and Cozzuol (2006) link the fossil teeth with *Ateles,* based mostly on shared low shearing quotients. The authors suggest that this means *Solimoea* would have been a similarly frugivorous animal. However, this adaptive connection does not necessitate a phylogenetic one between the fossil and the extant atelins, and other aspects of its dental morphology suggest that *Solimoea* belongs in the alouattin tribe (Rosenberger et al., in press). Regardless of phylogenetic affinities, the material is dated to approximately 6-9 Ma, making it, and *Acrecebus* from the same locality, the oldest fossil primates in Brazil.

Various molecular studies have calculated divergence dates for the ateline clade, most of which fit well with the available fossil material (e.g., Meireles et al., 1999; Collins and Dubach, 2000; Collins, 2001; Cortes-Ortiz et al., 2003; Fig. 1.2). The exception seems to be *Protopithecus*; its mosaic of morphological traits suggests a more basal position on the ateline tree, closer to the divergence of the alouattin tribe. This split is dated to approximately 16 Ma (Cortes-Ortiz et al., 2003), well before the late Pleistocene date assigned to the known fossil material. Cranially, *Paralouatta varonai* is much more similar to the fully derived *Alouatta* condition, making its Pleistocene date more parsimonious. Differences between *Paralouatta* and *Alouatta* could potentially be attributed, in part, to the fossils' isolation in the Caribbean islands (Whittaker, 1998; MacPhee and Horowitz, 2002). Similarly, the existence of the already dentally-derived *Stirtonia* at approximately 13-14 Ma (Flynn et al., 1997; Hartwig and Meldrum, 2002) suggests that *Protopithecus* is a member of a very old lineage (Rosenberger et al., 2009). Unfortunately, no postcranial material exists for *Stirtonia*; it would be interesting to know where in the spectrum of *Alouatta*-like slow quadrupedalism to *Ateles*-like acrobatic suspension the La Venta species falls, as that data would contribute to a more confident reconstruction of the sequence of evolutionary steps from a more generalized ancestor to the modern forms.

Recent advances

Soon after the discovery of the TBV skeleton in 1992, Hartwig (1995a) published the first modern analysis of the original LS material. This publication includes a more detailed description of the fragmentary femur and humerus and outlines the history of their discovery, dismissal by the field, and subsequent rediscovery. Figures show the *Protopithecus* specimens laid out next to the same elements of the modern atelines and various metrics are compared to those of other platyrrhines. Hartwig concludes that the fossils are "grossly indistinguishable" from *Brachyteles* and *Ateles*, except for their larger size (a mass estimate of 22.7-24.1 kg is derived from the femoral head volume). A closer relationship to *Brachyteles* is suggested because of Lagoa Santa's proximity to the Atlantic Coastal Forest where the woolly spider monkeys currently live in a very restricted distribution.

The publication of the TBV skeleton (Hartwig and Cartelle, 1996) includes a brief description of its most unique and informative features, with similar photographic and biometric comparisons to the living atelines as found in Hartwig (1995a). The skeleton adds evidence from cranial morphology that was suggested to link *Protopithecus* with *Alouatta*, instead of *Brachyteles*. However, instead of simplifying the situation and providing closure to a 150-plus-year old mystery, the publication of this material brought up new questions about the evolutionary history of the atelines in general, and *Alouatta* in particular. The existence of an individual primate with the small brain and elongated cranial base of a folivore like *Alouatta* but with the teeth and postcranial adaptations to the more acrobatic locomotion of a frugivore like *Ateles* was an unexpected find. There are also outstanding questions about the attribution of the TBV material to *Protopithecus brasiliensis*. Hartwig and Cartelle (1996) used the comparable size of the bones to make this taxonomic assumption, but visual inspection of the distal humerus and proximal femur of the two individuals show several morphological differences that could be of some importance (Fig. 1.3; see Chapter 4).

The conclusions of Hartwig and Cartelle (1996) were challenged soon thereafter. Considering the large body size estimates emphasized by Hartwig (1995a) and Hartwig and Cartelle (1996), Heymann (1998) suggested that *Protopithecus* would have been too large to practice *Ateles*-like suspensory locomotion as its main mode of travel and instead would have spent more of its time on the ground. This is an interesting suggestion for several reasons, one of which is that there are no extant platyrrhine primates that are committed to terrestrial locomotion in a way similar to many of the primates in the Old World. The reason for the absence of this adaptation in Central and South America has yet to be adequately explained (see Chapter 4). Interestingly, while Lund never made any inferences about its behavior, he would also have had to assume that *Protopithecus* was terrestrial. As a catastrophist, his explanation for the survival of any monkeys through the Great Deluge was their arboreal habitat which kept them above the flood waters and out of danger (Hartwig, 1995b). Since *Protopithecus* was included in Lund's list of extinct fossil mammals, he must have assumed that it lived on the ground where it was wiped out by the last global catastrophe.

A decade later, Jones (2008) included the fossil as a member of a group of "brachiating" primates while investigating the evolution of "brachiation" in atelines and reconstructing ancestral morphotypes within the clade. Index values for several morphological traits in the forelimb and vertebral column suggested by earlier analyses (i.e., Jones, 2004) to distinguish between brachiating and non- brachiating taxa were used as data. Unfortunately, as noted in the discussion, many of the most informative variables, such as glenoid fossa shape and humeral bituberosity index, are not preserved in the fossil material and so conclusions should be viewed

Figure 1.3. *Protopithecus* femur (left) and humerus (right) from Toca da Boa Vista (pair on the left in each) and Lagoa Santa (pair on the right in each).

with caution. Of the eight indices given for *Protopithecus*, seven are more like the *Ateles* values and one, humeral robusticity, is closer to the value for *Alouatta* (Table 1.3); there are more measurements listed for *Caipora* and they are more evenly distributed between the *Ateles* and *Alouatta* ends of the spectrum.

The results of the ancestral morphotype analyses are equivocal, as Jones (2008) finds support for almost all of the various incarnations of the ateline last common ancestor, i.e., *Ateles*-like, *Lagothrix*-like, or *Alouatta*-like, depending on which base phylogeny, model of evolutionary change, set of morphological characters, and comparative taxa are included in each analysis. As in any algorithmic phylogeny reconstruction, user input has a hand in dertermining software output (see Rosenberger, 2010, 2011). Ultimately, however, the ateline last common ancestor is reconstructed as a *Lagothrix*-like agile quadruped with suspensory abilities, in agreement with previous suggestions (e.g., Rosenberger and Strier, 1989). Hartwig and Cartelle (1996) conclude that the addition of *Protopithecus* to the list of ateline primates suggests that their last common ancestor was more suspensory. This is also suggested by Schön (1968) based on the derived features of the extant *Alouatta* postcranium as well as the potential influence of their enlarged hyoid apparatus on their locomotion (see Chapter 5). These competing hypotheses lend themselves to further testing and more detailed investigation into the fossil's morphology. As mentioned above, they also emphasize the importance of comparing a more primitive taxon to an ancestral morphotype and not expecting a fossil to look exactly like any of its extant relatives.

The different branching patterns recovered by the morphological and molecular phylogenetic evidence discussed above suggests that parallelism is just as likely to have occurred in the ateline postcranial as in the cranial skeleton (Hartwig, 2005); there is no easy answer to

Table 1.3. Summary of previously proposed *Protopithecus* synapomorphies.

Author	**Morphological Trait**	**Phylogenetic/Functional Affinity**
Lund (1838)	Distal humerus and proximal femur shape	New World monkey
Winge (1895)	Distal humerus and proximal femur shape	*Brachyteles*
Hartwig (1995)	Distal humerus and proximal femur shape	*Ateles/Brachyteles*
	Tubercle on posterior femoral neck for insertion of the capsular ligament	*Brachyteles*
	Proximity to Atlantic Coastal Forest	*Brachyteles*
Hartwig and Cartelle (1996) (mostly qualitative character analysis)	Intermembral Index	Atelin
	Long, straight long bone shafts	Atelin
	Reduced olecranon process	Atelin
	Rotational ability at glenohumeral joint	Atelin
	Robust temporal lines that peak above the parietals	Alouattin
	Small, cylindrical braincase	Alouattin
	Flat, posteriorly directed nuchal plane	Alouattin
	Elongated cranial base	Alouattin
	Deep symphyseal shelf	Alouattin
	Lower molar alveoli along the base of the ramus	Alouattin
Heymann (1998) (quantitative bivariate plot)	IMI taking into account large body size	Terrestrial catarrhine
Cooke et al. (2007) (quantitative bivariate plots)	Small relative brain size	Alouattin
	Craniofacial and basicranial anatomy	Alouattin
	Large incisors, small molars	Atelin
Jones (2008) (quantitative index values)	Bicipital Groove Shape	*Ateles*
	Capitulum Shape	*Ateles*
	Caudal Robusticity	*Ateles*
	Caudal Transverse Process Width	*Ateles*
	Humeral Robusticity	*Alouatta*
	Intermembral Index	*Ateles*
	M. Biceps Lever Arm	*Ateles*
	Radial Head Shape	*Ateles*
Rosenberger et al. (in press) (mostly qualitative character analysis)	Large, airorynchous face	Alouattin
	Postorbital constriction	Alouattin
	Compound temporonuchal crest	Alouattin
	Inclined nuchal plane	Alouattin/Ancestral ateline
	Small, posteriorly positioned foramen magnum	Alouattin
	Small, non-globular braincase	Alouattin/Ancestral ateline
	Moderately elongate cranial base	Alouattin/Ancestral ateline
	Large incisors	Atelin
	Low relief molars	Atelin

which tribe *Protopithecus* belongs because of the mosaic nature of the fossil as well as the subfamily as a whole. The previous publications summarized here have all focused on limited aspects of the postcranial skeleton and their implications for the fossil's locomotor repertoire. They also have taken for granted the cranial similarities to *Alouatta* suggested by Hartwig and Cartelle (1996) (Table 1.3) as being phylogenetically difinitive. This is one reason why the ancestral morphotype reconstructions of Jones (2008) are relatively equivocal; character state changes are mapped onto three phylogenies that differ based on the position of *Protopithecus*. The fossil is placed as either a sister-taxon to *Alouatta* (Hartwig and Cartelle, 1996), to the atelins (Fleagle, 1999), or to *Brachyteles* (Hartwig, 1995a). These three hypotheses need to be tested first, before any morphotype reconstruction can be done with certainty.

While the three-dimensional geometric morphometric (3DGM) methods to be used here do not constitute a phylogenetic analysis, the phenetic similarities and differences in shape that they quantify can still be informative about both function and relationships amongst the fossil and extant taxa in the sample. The similarities of some cranial features like relative brain and foramen magnum size that are shared with *Alouatta*, as well as the fossil incisor/molar proportions that suggest frugivory, have been supported by recent quantitative analyes (Cooke et al., 2007; Rosenberger et al., in press), but more aspects of craniomandibular morphology are investigated here for the first time in 3D using new data imaging technology and multivariate statistics. Similarly, when testing hypotheses about the fossil locomotor repertoire, the postcranial skeleton is treated as an unknown and the joint surface morphology of both the forelimb and the hindlimb is allowed to speak for itself without imposition of *a priori* labels.

Subsequent chapters will attempt to integrate cranial and postcranial comparative morphology as well as more detailed descriptions into analyses of this little-studied fossil skeleton. Chapter 2 re-examines body size estimates for *Protopithecus*, making use of new platyrrhine-based regression models developed specifically to test the hypothesis that the fossil belongs to a large-bodied size class of platyrrhines that no longer exists. Chapter 3 investigates the craniomandibular morphology of *Protopithecus* and extant *Alouatta* in an attempt to evaluate the synapomorphies proposed by previous researchers (Table 1.3) and to test the hypothesis that *Protopithecus* is a basal member of the alouattin tribe. Chapter 4 also uses three-dimensional geometric morphometric techniques to compare the postcranial morphology of *Protopithecus* to that of a broad sample of extant primates as a way of addressing Heymann's terrestriality hypothesis. Chapter 5 summarizes the results of the analyses presented here and synthesizes them into a scenario wherein *Protopithecus* is seen as a key to understanding important aspects of the evolutionary history of the atelines.

CHAPTER 2

HOW BIG WAS *PROTOPITHECUS*?

Introduction

One of the most intriguing differences between *Protopithecus* and its living ateline relatives is the large size and robusticity of its long bones. Using a regression equation for estimating body mass based on femoral head volume in catarrhine primates (Ruff, 1990), the original individual discovered by Lund in the 1800s was estimated to have a body weight of 22.7 – 24.1 kg (Hartwig, 1995a). At the time, Hartwig recognized that using catarrhines as a regression model was a fallback approach since comparable data and regression equations for living atelines did not exist. He also noted that *Protopithecus* is so much larger than modern atelines that it would fall outside of the range of any regression plot generated by a more phylogenetically appropriate platyrrhine reference sample (Hartwig, 1995a). Despite these caveats, Hartwig and Cartelle (1996) again used Ruff's (1990) femoral head equation when the more complete *Protopithecus* skeleton was discovered; the new material was estimated at 25 kg, a value approximately twice that of the largest living platyrrhines. Prediction error, measures of estimate consistency and accuracy, and standard error were not provided in either publication.

A vast literature exists on the topic of body mass estimation for fossil hominin and non-human primates. The problems encountered by Hartwig (1995a) in choosing an appropriate reference sample and dealing with fossils of large body size have been discussed at length and solved to varying degrees of satisfaction in more recent publications involving other taxa. For example, in order to estimate the body size of the truly giant subfossil lemurs, extrapolation into body size ranges outside of anything seen in living primates was required (Godfrey et al., 1995; Jungers et al., 2002; Jungers et al., 2008). The best estimates of body size were produced using humeral and femoral midshaft circumferences against a primate reference sample, as well as a mammalian reference sample which represented a wide range of body sizes and positional behaviors (Godfrey et al., 1995). Similarly, Delson et al. (2000) discussed the problem of investigating very large fossils and concluded that it is the estimates for these taxa that come with the most error, regardless of the alternative materials and methods chosen. Other studies estimating the body weights of fossil primates (e.g., Dagosto and Terranova, 1992; Aiello and Wood, 1994) have shown that different regression models and reference samples produce not only different estimates of body mass but also different ranges and confidence intervals.

From a phylogenetic perspective, the appropriate reference sample for estimating body size of *Protopithecus* would include the four genera of ateline primates (*Alouatta, Lagothrix, Ateles,* and *Brachyteles*) because they are very likely to be its closest living relatives (Hartwig and Cartelle, 1996). Platyrrhine-only craniodental regression equations are now available from two studies (Meldrum and Kay, 1997; Sears et al., 2008), although their value in this context remains somewhat limited. The lower molars of *Protopithecus* are not preserved and canine size and temporal line strength suggest the cranium belongs to a male (Hartwig and Cartelle, 1996), so the regression equations of Meldrum and Kay (1997) based on female platyrrhine molar dimensions are not directly useful here. The equations of Sears et al. (2008) come with poor R^2 values and relatively high error sum of squares (ESS) values; of the 80 craniodental variables investigated, the highest R^2 value is 0.636 and the majority of the rest are below 0.5. It could be that there are so many variable cranial morphologies in their reference sample (i.e., callitrichine skulls are very different from *Alouatta* skulls), that those differences are making the scatter around the regression line too diffuse for accurate predictions. These equations were developed to estimate the body mass of *Chilecebus carrascoensis*, a 20 Ma platyrrhine from Chile represented by a well-preserved skull (Flynn et al., 1995). There are several other reasons for caution when applying them to other fossil taxa. For example, the equations produced in that study are not tested for accuracy on individuals of known body mass so there is no evidence for certain variables over- or under-estimating body mass, as the authors discuss.

Despite these issues, the Sears et al. (2008) equations were applied to *Protopithecus* and, not surprisingly, the results beg further investigation. The fossil mandible is incomplete, so data are not available for implementing "mandibular length", their best predictor variable ($R^2 = 0.636$, ESS = 0.117). Ranking second and third, "bizygomatic width" ($R^2 = 0.626$, ESS = 0.166) and "skull length" ($R^2 = 0.537$, ESS = 0.196) of *Protopithecus* give a mass estimate of approximately 12 kg, or about the size of a large male *Alouatta pigra*. This is much lower than either of the original estimates (Hartwig, 1995a; Hartwig and Cartelle, 1996) and seems an unlikely value both because of the relatively low R^2 values of the equations and the fact that the fossil bones themselves are much larger than the bones of an extant 12 kg platyrrhine. For example, mean total skull length of a sample of *Brachyteles* (usually cited as the largest ateline at around 12 kg) is 115 mm while for *Protopithecus* it is 150 mm; in the postcranial skeleton, mean femoral length of *Brachyteles* is 202 mm and in *Protopithecus* is 237 mm (Hartwig and Cartelle, 1996). Attempting to use these newly published equations again serves to highlight the fact that the choice of reference group and predictor variable will affect the final estimate. The development of more accurate platyrrhine-based regression models for application to the fossil record is a necessary step forward.

Body size of an individual or species is related to many other aspects of its biology and behavior. For fossil taxa, reconstructing diet and/or locomotion is most often the focus of studies attempting to estimate body size (e.g., Fleagle, 1978; Jungers, 1984a; Kay, 1985; Fleagle, 1999).

“Kay’s Threshold” of 500 g has long been used to separate small-bodied animals that get the majority of their protein from insects from larger-bodied animals that utilize leaves as a source of this vital nutrient (Kay, 1975; Gingerich, 1981). Similarly, a limit of 10-12 kg has been suggested for the metabolically efficient use of ricochetal brachiation (Preuschoft and Demes, 1985; see below). This chapter provides a new set of regression equations for predicting body weight and linear dimensions of body size based on a large series of New World monkey species and specimens. Focus is placed on the postcranial skeleton as a source of size information, especially joint surfaces that have been shown to be valuable in other studies that estimate fossil body mass in various primate groups (e.g., Jungers, 1990; Godfrey et al., 1995; Delson et al., 2000; Ruff, 2003).

Materials and Methods

A comparative sample across primates was used consisting of adult wild shot, non-pathological individuals from collections at the American Museum of Natural History (AMNH) in New York, the National Museum of Natural History (NMNH) in Washington, DC, and the Museu Nacional do Rio de Janeiro (MN) in Brazil (Table 2.1). In choosing the sample, several factors were considered. Conroy (1987) strongly advises using a restricted sample of only a few related taxa to create predictive equations and also strongly advises against extrapolating outside the size range of that comparative sample. Bracketing the fossil of interest between larger and smaller relatives would seem to adhere to these suggestions; however, Delson et al. (2000) note that using a comparative sample that includes one very large and one very small species leads to a regression line anchored by those points and less influenced by the species in the middle of the range. (The problem of extrapolation will be discussed further below with regard to choosing a

Table 2.1. Taxa involved in calculating regression equations.

				TOTL (mm)		**TrL (mm)**		**Body Weight (g)**
			***n*[1]**	**Average**	**Range**	**Average**	**Range**	**Average[2]**
Alouatta	*belzebul*	M	28	1222	1010 – 1345	583	440 – 700	7270
		F	25	1134	1030 – 1241	516	315 – 735	5525
	caraya	M	7	1183	1030 – 1293	566	480 – 671	6610
		F	7	1029	960 – 1093	466	420 – 490	4468
	guariba	M	4	1106	1065 – 1130	511	476 – 535	6453
		F	5	1030	950 – 1120	478	440 – 520	4450
	palliata	M	12	1136	1046 – 1270	548	466 – 690	7150
		F	7	1093	1000 – 1125	495	425 – 560	5350
	pigra	M	4	1251	1206 – 1315	588	554 – 630	11352
		F	2	1236	1143 – 1329	586	532 – 639	6434
	seniculus	M	38	1171	1030 – 1300	558	465 – 680	6850
		F	41	1103	900 – 1210	495	430 – 550	5120
Lagothrix	*lagotricha*	M	10	1096	994 – 1200	454	414 – 525	8531
		F	9	1095	1030 – 1160	439	390 – 470	5983
Brachyteles	*arachnoides*	M						11139
		F						10111
Ateles	*belzebuth*	M	5	1280	1110 – 1315	465	415 – 510	8317
		F	8	1273	1214 – 1325	481	425 – 555	8089
	geoffroyi	M	5	1126	1034 – 1210	415	332 – 460	8210
		F	15	1129	850 – 1284	433	340 – 540	7700
	paniscus	M	5	1280	1230 – 1360	446	410 – 500	8223
		F	8	1297	1170 – 1400	450	408 – 500	8595
Aotus	*azarae*	M	5	694	600 – 731	305	260 – 330	923
		F	3	673	660 – 689	287	273 – 308	936
Pithecia	*monachus*	M						2610
		F						2110
Chiropotes	*satanus*	M	2	819	788 – 850	412	394 – 430	3000
		F						2770
Cebus	*albifrons*	M	1	880		400		3180
		F	2	794	735 – 853	374	346 – 403	2290
	apella	M	8	859	820 – 920	412	380 – 450	3650
		F	4	742	712 – 780	340	317 – 360	2520
	olivaceous	M	3	923	858 – 960	448	403 – 470	3290
		F	1	865		385		2520
Colobus	*angolensis*	M	3	1451	1407 – 1505	602	560 – 645	9660
		F	1	1390		575		9100
	guereza	M	11	1275	1105 – 1495	606	535 – 660	10222
		F	8	1212	1090 – 1370	564	525 – 617	8043
Lophocebus	*albigena*	M	4	1448	1348 – 1500	568	540 – 590	8250
		F	2	1381	1337 – 1425	534	489 – 580	6021
Macaca	*nemestrina*	M	2	939	930 – 948	709	680 – 738	9450
		F						5700

	brunnescens	M	1	565		530		
		F	2	494	485 – 503	462	450 – 475	
	fascicularis	M	1	1092		500		5360
		F	1	925		390		3590
	thibetana	M						15200
		F						9500
	tonkeana	M						14900
		F						9000
	mulatta	M						7710
		F						5370
	sylvanus	M						14530
		F						10140
Nasalis	*larvatus*	M	4	1393	1383 – 1421	746	730 – 752	20400
		F						9820
Papio	*hamadryas*	M	4	1261	1225 – 1330	690	635 – 780	21857
		F	3	1125	1060 – 1210	615	562 – 660	11906
Presbytis	*pileatus*	M	1	1340		580		12000
		F	1	1240		480		9860
	cristatus	M	1	1248		546		6610
		F	1	1222		532		5760
	johni	M	1	1523		711		12000
		F	1	1530		616		11200
	melalophos	M	1	1136		590		6590
		F	1	1297		587		6470
	obscurus	M	1	1094		389		7900
		F	1	1230		480		6260
	rubicundus	M	2	1216	1215 – 1217	513	507 – 520	5682
		F				480		6137
	frontatus	M	1	1120		490	480 – 500	5560
		F	3	1183	1160 – 1200			5670
	potenziani	M						6170
		F						6400
Semnopithecus	*entellus*	M						14533
		F						10533
Pan	*troglodytes*	M	3	840	825 – 925			49567
		F	2	680	387 – 830			40367
Symphalangus	*syndactylus*	M	1	612				11900
		F	2	564	548 – 580			10700
Propithecus	*verreauxi*	M						3475
		F						3615
Indri	*indri*	M						5830
		F						6840

[1] *n* = number of individuals with associated total length (TOTL) and head and body length (TrL) measurements in the AMNH and NMNH catalogs.

[2] Average body weights from Smith and Jungers (1997), Delson et al. (2000), and DiFiore and Campbell (2007); see those sources for sample composition and ranges.

specific regression model.) Larger-bodied Old World monkeys and apes were included in the sample as one way to account for a fossil that is absolutely larger than its closest platyrrhine relatives. Callitrichines were not included as they are much smaller and exhibit subfamily-specific postcranial allometries that differ from the patterns seen in the rest of the platyrrhines, potentially due to a dwarfing event in their evolutionary history (Ford, 1980; Ford and Corruccini, 1985) and/or their claw-like nails which change their biomechanical relationship to arboreal substrates during locomotion (Jungers, 1985).

A Microscribe 3DX digitizer was used to collect a set of *x, y, z* coordinate points that define various aspects of the long bones, including: the distal humerus; proximal ulna; complete, proximal, and distal femur; complete, proximal, and distal tibia; and the talus (Fig. 2.1; Table 2.2). These elements are all well-preserved in *Protopithecus* on at least one side of the body. So far, few 3DGM analyses involving postcrania have been published (e.g., Drapeau, 2008; Harcourt-Smith et al., 2008; Harmon, 2009). Landmark points on postcranial elements have not been standardized in the same way as the more traditional craniometric points used in other types of osteological studies. As there are few biologically homologous Type I landmarks, such as the meeting point of two sutures, on postcranial elements, sets of Type II landmarks, those that are defined by the geometry of the specimens (Bookstein, 1991), were designed specifically for this study. They are meant to capture the shape of aspects of the bones suggested to be functionally relevant in previous studies of primate postcranial morphology. Most landmarks fall on either muscle attachment sites or geometrically defined points around a curved articular surface, such as the head of the femur. Careful examination of all of the taxa in the comparative sample made sure that landmarks were present and easily repeatable across all functional and phylogenetic groups.

Figure 2.1. 3D landmarks used to calculate the centroid size of postcranial elements. Photographs are of *Protopithecus*. Left femur (left), right distal humerus (top left), left proximal ulna (top right), left tibia (middle), left talus (bottom). Scale bars = 1 cm. See Table 2.2 for landmark definitions.

Table 2.2. Anatomical landmark definitions.

Distal Humerus	Anterior	
	A1	Most lateral point
	A2	Most medial point
	A3	Most lateral point on capitulum
	A4	Most medial point on capitulum
	A5	Most superiolateral point on trochlea (excluding capitulum)
	A6	Most inferiomedial point on trochlea (excluding capitulum)
	A7	Most superior point on medial epicondyle
	A8	Most inferior point on medial epicondyle
	A9	Most superior point on lateral epicondyle
	A10	Most inferior point on lateral epicondyle
	Posterior	
	P1	Most superior point of olecranon fossa
	P2	Most inferiomedial point of olecranon fossa
	P3	Most inferiolateral point of olecranon fossa
	P4	Deepest point of olecrannon fossa
	P5	Most medial point on trochlea
	P6	Most lateral point on trochlea
	P7	Tip of the medial epicondyle
Proximal Ulna	U1	Most proximal point on the olecranon
	U2	Most medial point on the maximum constriction of the olecranon
	U3	Most lateral point on the maximum constriction of the olecranon
	U4	Most posterior point on the olecranon
	U5	Most anterio-medial point of the olecranon
	U6	Most anterio-lateral point of the olecranon
	U7	Most medial point on the wing of the proximal articular facet
	U8	Most lateral point on the wing of the proximal articular facet
	U9	Most anterior point on the proximal border of the proximal articular facet
	U10	Most disto-medial point of the proximal articular facet
	U11	Most disto-lateral point of the proximal articular facet
	U12	Deepest point in the midline of the trochlear notch
	U13	Most posterio-lateral point of the distal articular facet
	U14	Most anterior point of the distal articular facet
	U15	Most anterior point of the radial facet
	U16	Most posterior point of the radial facet
	U17	Most proximal point of the radial facet
	U18	Most distal point of the radial facet
	U19	Deepest point in the radial facet
Femur	Proximal	
	F1	Middle of fovea capitus
	F2	Most proximal point on the femoral head
	F3	Most proximal point on the facet margin around the femoral head
	F4	Most distal point of the facet margin around the femoral head
	F5	Most anterior point of the facet margin around the femoral head
	F6	Most posterior point of the facet margin around the femoral head
	F7	Maximum point of constriction on ridge running from lesser trochanter to the femoral head
	F8	Deepest point of the proximal neck
	F9	Middle of the trochenteric fossa

	F10	Tip of greater trochanter
	F11	Most lateral point of greater trochanter
	F12	Most proximoanterior point of the greater tubercle
	F13	Tip of lesser trochanter
	F14	Origin of pectineal line
	Distal	
	F15	Most medial point
	F16	Most lateral point
	F17	Most proximomedial point of the patellar articular surface
	F18	Most proximolateral point of the patellar articular surface
	F19	Most proximal point of the patellar articular surface
	F20	Most distal point of the patellar articular surface
	F21	Most distal point of the medial condyle
	F22	Most distal point of the lateral condyle
	F23	Most posterior point of the medial condyle
	F24	Most posterior point of the lateral condyle
	F25	Most proximomedial point of the posterior aspect of the medial condyle
	F26	Most proximolateral point of the posterior aspect of the lateral condyle
	F27	Most proximolateral point of the posterior aspect of the medial condyle
	F28	Most proximomedial point of the posterior aspect of the lateral condyle
	F29	Most posterio-medial point of the groove (notch)
	F30	Most posterior point of the groove (notch)
Tibia	Proximal	
	Tib1	Most anterior point on the medial tibial condyle on outer edge of articular surface
	Tib2	Most medial point on the medial tidial condyle
	Tib3	Most posterior point on the medial tibial condyle
	Tib4	Most lateral point on the medial tibial condyle
	Tib5	Most anterior point on the lateral tibial condyle
	Tib6	Most medial point on the lateral tidial condyle
	Tib7	Most posterior point on the lateral tibial condyle
	Tib8	Most lateral point on the lateral tidial condyle
	Tib9	Most anterior point on the tibial tuberosity
	Distal	
	Tib10	Most anterior point on the talar facet
	Tib11	Most medial point on the talar facet
	Tib12	Most posterior point on the talar facet
	Tib13	Midpoint of the lateral edge of the talar facet
	Tib14	Midpoint of the groove between the talar facet and the medial malleolus
	Tib15	Most anterior point of the groove between the talar facet and the medial malleolus
	Tib16	Most posterior point of the groove between the talar facet and the medial malleolus
	Tib17	Most medial point of the medial malleolus
	Tib18	Distal tip of the medial malleolus
	Tib19	Most lateral point on the fibular facet
Talus	Dorsal Surface	
	Tal1	Most distal point of the trochlear groove
	Tal2	Most distal point of contact between the medial malleolar facet and the trochlear surface
	Tal3	Most dorsal point on the medial facet margin
	Tal4	Most proximal point of contact between the medial malleolar facet and the trochlear surface
	Tal5	Most proximal point of the trochlear groove
	Tal6	Most dorsal point on the lateral facet margin

Tal7	Most dorsal point on the trochlear groove
Tal8	Most distal point on medial malleolar facet
Tal9	Most distal point on lateral malleolar facet
Tal10	Most plantar point on lateral malleolar facet
Tal11	Deepest (most medial) point on lateral malleolar facet
Tal12	Most dorsal point of the navicular facet
Tal13	Most medial point of the navicular facet
Tal14	Most lateral point of the navicular facet
Tal15	Most proximal point of contact between the lateral malleolar facet and the trochlear surface
Tal16	Most distal point of contact between the lateral malleolar facet and the trochlear surface
Tal17	Most plantar point on medial malleolar facet
Tal18	Most distal point of the navicular facet
Plantar Surface	
Tal19	Most disto-lateral point of the posterior calcaneal facet
Tal20	Lateral end of the narrowest distance across the posterior calcaneal facet
Tal21	Most proximo-lateral point of the posterior calcaneal facet
Tal22	Most proximal point of the posterior calcaneal facet
Tal23	Most proximo-medial point of the posterior calcaneal facet
Tal24	Medial end of the narrowest distance across the posterior calcaneal facet
Tal25	Most disto-medial point of the posterior calcaneal facet
Tal26	Most distal point of the posterior calcaneal facet
Tal27	Deepest (most dorsal) point of the posterior calcaneal facet
Tal28	Most proximal point of the anterior calcaneal facet
Tal29	Most medial point of the anterior calcaneal facet
Tal30	Most distal point of the anterior calcaneal facet
Tal31	Most lateral point of the anterior calcaneal facet
Tal32	Most plantar point on the navicular facet
Tal33	Most lateral point of contact between the navicular facet and the distal calcaneal facet

The independent variable used here in estimating body size by linear regression is the centroid size (the square root of the sum of squared distances of a set of landmarks from their centroid; Bookstein, 1991) of these skeletal elements. Centroid size for each element in the sample was calculated using the *morphologika²* v.2.5 software package (O'Higgins and Jones, 2006) (Table 2.3; Table 2.4). Centroid size will give a better estimate of overall joint size than simple areas calculated from 2D length and breadth measurements. It has also been shown to be highly correlated with body mass in various Old World monkeys (Frost et al., 2003), indicating its usefulness as a proxy for body size similar to the more commonly used molar length or cranial length. Overall joint size is important to capture accurately as the joint surfaces are the weight-bearing parts of the limb bones that are most closely associated with sheer "body size", more so than full bone lengths, which can vary widely under multiple selective factors in mammals (Ruff, 1990; Scott, 1990; Anyonge, 1993; Ruff, 2002). Postcranial remains in general have been shown to be useful in similar previous studies, yielding more statistically robust equations than craniodental variables (e.g., Ruff et al., 1989; Jungers, 1990; Rafferty et al., 1995; Ruff, 2002).

Three aspects of "body size" were predicted for the fossil: body weight (kg); total length (TOTL; mm), which includes the length of the tail (TAILL); and trunk length (TrL; mm), which includes the length of the skull and trunk (TOTL = TAILL + TrL; Ford and Corrucini, 1985). The two length measurements are important in this case because they can be used to calculate a tail to trunk length ratio, which can in turn be used to begin to confirm that *Protopithecus* had a prehensile tail like its extant ateline relatives. TOTL and TrL measurements were found in the AMNH and NMNH catalogs for all specimens in the comparative sample (n = 345; Table 2.1). Only about a third of those specimens had associated body weights (n = 102; Table 2.5).

Table 2.3. Species mean centroid sizes, forelimb and femur.

				Distal Humerus			**Proximal Ulna**			**Full Femur**			**Proximal Femur**			**Distal Femur**	
			n	**Average**	**Range**	***n***	**Average**	**Range**	***n***	**Average**	**Range**	***n***	**Average**	**Range**	***n***	**Average**	**Range**
Alouatta	*belzebul*	M	3	42.2	41.1-42.8	3	42.8	41.9-43.9	3	404	382-437	3	41.9	41.0-43.3	3	43.8	42.8-45.0
		F	1	39.6		1	39.8		1	400		1	42.2		1	43.2	
	caraya	M	11	42.8	33.1-47.3	11	43.0	34.7-49.5	11	399	343-426	11	43.9	37.1-48.3	11	44.1	38.5-46.9
		F	11	38.2	34.7-40.6	11	37.5	33.9-39.3	10	365	345-384	10	38.8	36.4-42.7	10	40.2	38.4-43.3
	guariba	M	0			0			0			0			0		
		F	2	37.1	36.0-38.2	2	34.4	35.0-33.8	2	340	339-342	2	37.6	36.2-39.0	2	38.2	37.9-38.5
	palliata	M	8	45.3	42.4-49.6	7	43.2	41.0-46.7	8	384	362-404	8	43.8	41.3-46.9	8	41.9	40.6-44.1
		F	2	38.8	36.5-41.2	2	38.1	35.2-41.1	2	371	345-397	2	38.0	34.9-41.1	2	39.2	37.7-40.7
	pigra	M	2	48.2	47.3-49.2	1	50.2		1	422		1	52.2		1	48.2	
		F	1	42.1		0			0			0			0		
	seniculus	M	9	46.2	39.7-50.0	9	44.1	38.7-47.5	9	414	375-452	9	44.4	41.2-47.2	9	45.3	41.3-48.7
		F	11	38.9	33.4-45.8	10	37.4	34.4-43.5	11	373	348-398	11	37.9	33.9-40.8	11	40.1	37.2-42.5
Lagothrix	*lagotricha*	M	2	44.4	43.4-45.3	2	40.3	40.1-40.6	2	428	422-434	2	47.6	46.1-49.2	2	46.5	45.9-47.1
		F	4	41.2	39.4-43.2	4	36.4	34.7-37.6	4	401	384-424	4	43.6	43.0-44.6	4	44.5	43.5-45.9
Brachyteles	*arachnoides*	M	3	50.6	46.8-52.8	3	40.4	38.4-40.7	3	510	492-524	3	53.7	52.7-55.5	3	53.0	49.2-55.1
		F	4	47.9	45.9-49.7	4	39.4	37.6-40.8	4	500	477-511	4	52.9	50.1-55.5	4	52.1	48.8-54.6
Ateles	*belzebuth*	M	1	48.8		1	41.7		1	489		1	57.4		1	58.6	
		F	1	44.5		1	37.1		1	496		1	50.1		1	52.4	
	geoffroyi	M	0			0			0			0			0		
		F	4	46.7	45.6-47.4	4	38.4	37.1-40.3	4	494	479-522	4	50.0	47.1-54.5	4	52.9	49.9-57.8
	paniscus	M	1	49.3		1	39.7		0			0			0		
		F	0			0			0			0			0		
Aotus	*azarae*	M	14	22.0	19.8-24.2	14	20.4	18.3-23.2	13	241	205-266	13	26.2	22.5-28.4	13	24.8	21.8026.4
		F	15	21.2	19.2-23.3	15	19.9	18.0-21.7	14	237	214-252	14	25.9	22.7-29.0	14	24.0	22.2-25.8
Pithecia	*monachus*	M	3	29.6	25.6-33.5	3	26.4	21.2-30.7	3	355	328-387	3	31.8	29.6-33.6	3	31.6	29.5-34.4
		F	2	31.1	30.9-31.3	2	28.1	27.3-29.0	3	337	322-362	3	31.9	31.0-33.5	3	32.6	31.1-33.6
Chiropotes	*satanus*	M	2	33.6	30.3-37.0	2	30.5	28.2-32.8	2	352	332-371	2	32.2	31.4-33.1	2	32.7	30.5-35.0
		F	0			0			0			0			0		
Cebus	*albifrons*	M	12	33.7	31.0-36.5	13	31.7	29.3-35.2	12	325	299-357	12	34.7	31.4-36.9	12	34.2	30.2-37.5
		F	14	29.7	26.5-34.8	14	27.4	25.6-31.2	14	303	271-350	14	31.2	27.8-36.8	14	31.4	28.5-37.3
	apella	M	12	34.6	33.1-37.9	12	31.5	30.0-34.1	13	327	310-350	13	35.3	32.8-37.9	13	34.0	32.0-37.3
		F	13	30.4	27.5-34.1	13	27.8	24.9-32.1	12	300	281-319	12	31.5	28.0-34.7	12	31.0	27.7-34.4
	olivaceous	M	3	33.4	33.1-33.9	3	32.9	32.5-33.2	3	352	344-358	3	38.0	37.5-38.7	3	37.4	36.9-37.9
		F	2	30.6	29.4-31.9	2	30.5	30.6-30.4	2	343	326-361	2	35.1	32.8-37.5	2	34.3	33.7-34.9
Colobus	*angolensis*	M	5	44.3	42.7-47.5	3	42.9	40.7-44.3	4	493	475-513	4	49.6	46.4-52.6	4	51.4	47.5-54.7
		F	1	40.3		1	38.6		1	454		1	47.4		1	47.8	
	guereza	M	16	45.2	40.7-48.8	8	45.1	40.1-48.9	16	489	448-532	16	51.2	46.7-54.5	16	52.4	46.9-56.7
		F	12	39.6	36.9-41.2	7	38.5	36.7-40.3	12	451	420-470	12	46.1	44.3-49.4	12	48.4	44.7-50.4
Lophocebus	*albigena*	M	6	43.5	40.9-45.7	4	43.9	40.7-47.0	6	505	469-540	6	49.8	46.4-51.8	6	49.7	47.1-52.4
		F	3	38.2	34.9-40.1	2	35.9	33.8-38.1	3	439	419-449	3	42.3	39.7-44.2	3	42.5	40.9-43.7
Macaca	*nemestrina*	M	4	52.3	48.2-55.6	4	51.1	46.5-56.4	5	521	471-566	5	58.0	52.4-63.0	5	57.2	51.4-62.5
		F	1	42.2		2	37.0	33.0-41.0	2	403	388-418	2	42.8	39.2-46.4	2	42.7	39.9-45.5
	brunnescens	M	1	47.1		1	46.0		1	437		1	53.4		1	57.9	
		F	2	39.6	37.9-41.3	2	38.0	35.7-40.3	2	386	377-395	2	49.5	46.4-52.6	2	45.8	44.9-46.7

	fascicularis	M	2	36.3	32.9-39.8	2	36.4	34.4-38.3	2	353	339-366	2	43.3	41.4-45.2	2	40.8	37.5-44.1
		F	2	30.1	28.8-31.3	2	29.2	28.9-29.4	2	317	314-319	2	34.2	33.4-35.0	2	32.8	32.5-33.0
	niger	M	0			0			0			0			0		
		F	1	35.3		1	35.9		1	362		1	42.7		1	43.4	
	thibetana	M	4	54.8	52.2-56.9	4	55.1	52.7-58.5	4	425	417-445	4	59.6	58.5-61.5	4	59.1	58.6-59.6
		F	0			0			0			0			0		
	tonkeana	M	1	51.2		1	48.3		1	431		1	59.6		1	55.2	
		F	0			0			0			0			0		
	mulatta	M	2	47.9	41.9-53.8	2	49.3	44.7-54.0	2	421	409-434	2	52.4	46.3-58.4	2	51.2	47.3-55.0
		F	0			0			0			0			0		
	sylvanus	M	1	52.4		1	49.9		1	491		1	56.7		1	56.9	
		F	1	42.8		1	41.6		0			0			0		
Nasalis	*larvatus*	M	8	54.5	52.0-57.8	8	51.0	47.2-53.4	8	598	573-630	8	62.5	59.1-65.6	8	64.1	61.1-69.1
		F	1	45.8		1	41.5		1	531		1	53.7		1	53.0	
Papio	*hamadryas*	M	11	64.2	55.4-71.9	11	65.8	57.1-70.6	11	632	597-710	11	76.9	66.2-84.3	11	72.3	67.0-77.8
		F	7	53.7	48.7-60.5	7	54.8	51.8-60.3	7	552	523-634	7	65.3	58.8-73.1	7	61.5	56.1-68.7
Presbytis	*pileatus*	M	1	43.9		1	43.9		1	484		1	51.3		1	51.1	
		F	1	42.5		1	40.7		0			0			0		
	cristatus	M	3	38.8	36.2-41.3	3	37.2	35.9-39.7	3	447	432-456	3	43.9	39.9-47.3	3	44.4	40.6-47.3
		F	3	36.0	33.7-37.8	3	35.4	33.4-37.0	3	426	389-422	3	42.1	39.1-43.7	3	42.2	38.6-44.6
	johni	M	1	45.2		1	44.2		1	565		1	54.6		1	56.2	
		F	3	40.9	39.8-42.2	3	41.4	40.3-42.7	3	502	497-508	3	47.4	45.3-50.8	3	50.2	48.4-52.7
	melalophos	M	2	38.5	37.7-39.2	2	35.7	35.0-36.4	2	471	484-458	2	43.9	43.6-44.1	2	47.1	47.0-47.2
		F	1	36.4		1	34.9		1	502		1	43.1		1	45.4	
	obscurus	M	3	39.9	35.9-43.4	2	36.8	34.1-39.4	3	430	397-451	3	43.7	40.5-45.8	3	44.7	41.5-46.4
		F	1	37.1		1	35.6		1	420		1	42.7		1	43.8	
	rubicundus	M	4	38.2	37.8-38.9	4	35.7	35.3-36.1	4	511	486-525	4	44.9	42.3-47.3	4	48.1	46.5-49.4
		F	2	36.1	35.1-37.1	2	34.1	33.0-35.2	2	500	488-513	2	42.2	41.0-43.5	2	45.1	43.3-46.7
	frontatus	M	2	36.5	35.5-37.5	2	34.8	34.4-35.1	3	484	474-494	3	42.5	41.6-43.8	3	44.5	43.1-45.4
		F	5	36.2	34.7-37.7	5	34.4	32.9-35.4	5	482	461-498	5	41.9	41.2-42.5	5	44.2	42.8-45.5
	potenziani	M	1	38.7		1	34.2		1	458		1	42.4		1	44.3	
		F	0			0			0			0			0		
Semnopithecus	*entellus*	M	1	44.1		1	46.4		1	535		1	52.7		1	54.7	
		F	0			0			0			0			0		
Pan	*troglodytes*	M	12	97.9	89.9-108	12	78.3	70.6-90.7	10	733	652-803	10	101	91.8-110	10	106	94.9-116
		F	4	89.2	84.6-92.8	5	74.9	68.9-80.2	5	728	689-767	5	94.7	89-104	5	101	94.1-107
Symphalangus	*syndactylus*	M	1	55.6		1	43.8		1	545		1	60.3		1	58.9	
		F	2	52.5	51.9-53.0	2	39.9	39.2-40.8	1	524		1	53.5		1	51.6	
Propithecus	*verreauxi*	M	4	30.4	29.4-33.3	3	24.3	23.0-25.3	3	423	412-434	3	36.8	36.2-37.2	3	37.8	37.3-38.7
		F	4	33.1	29.6-41.8	5	27.2	24.0-34.0	4	476	431-560	4	43.2	37.7-51.2	4	43.5	36.7-52.9
Indri	*indri*	M	1	38.1		1	30.9		1	585		1	48.8		1	50.8	
		F	1	41.9		1	33.8		1	629		1	51.0		1	53.2	

Table 2.4. Species mean centroid sizes, tibia and talus.

				Full Tibia			Proximal Tibia			Distal Tibia			Talus	
			n	**Average**	**Range**	***n***	**Average**	**Range**	***n***	**Average**	**Range**	***n***	**Average**	**Range**
Alouatta	*belzebul*	M	3	304	293-326	3	30.9	30.7-31.2	3	20.3	19.8-21.2	2	50.1	50.1-50.2
		F	1	294		1	30.1		1	21.8		1	48.6	
	caraya	M	10	304	258-325	10	32.2	27.3-35.5	10	20.8	17.7-22.9	8	48.9	44.1-52.7
		F	11	276	261-288	11	29.0	27.6-31.2	11	18.8	16.8-20.7	6	44.9	40.1-47.8
	guariba	M				0			0			0		
		F				2	26.0	25.5-26.4	2	17.9	17.7-18.1	2	40.2	40.1-40.4
	palliata	M	8	279	261-293	8	31.0	29.9-32.1	8	20.6	19.6-22.0	7	47.6	46.2-48.5
		F	2	267	258-277	2	29.2	27.9-30.4	2	19.2	18.5-19.9	2	42.2	40.3-44.1
	pigra	M	1	325		1	34.6		1	22.3		1	51.2	
		F	2	254	253-254	0			0			0		
	seniculus	M	7	315	296-342	7	32.0	29.2-34.8	7	20.9	19.7-21.7	4	50.5	48.9-51.7
		F	11	277	260-296	11	29.0	25.4-31.0	11	19.2	17.4-20.9	7	44.2	40.4-46.7
Lagothrix	*lagotricha*	M	2	336	334-338	2	33.3	33.2-33.4	2	22.2	22.0-22.5	2	51.0	51.0-51.1
		F	4	312	294-326	4	31.9	30.2-33.4	4	20.5	19.8-22.2	4	48.1	45.2-52.3
Brachyteles	*arachnoides*	M	3	391	379-400	3	37.6	34.0-42.4	3	25.6	24.9-26.8	2	58.1	57.3-59.0
		F	4	374	352-383	4	36.4	35.8-37.5	4	25.9	24.0-27.5	2	55.7	55.0-56.3
Ateles	*belzebuth*	M	1	398		1	40.1		1	29.7		0		
		F	1	393		1	36.6		1	27.2		1	59.4	
	geoffroyi	M	0			0			0			0		
		F	4	390	376-407	4	38.2	35.4-41.9	4	25.5	23.9-26.4	3	57.9	56.4-60.1
	paniscus	M	0			0			0			0		
		F	0			0			0			0		
Aotus	*azarae*	M	13	198	175-218	13	18.6	16.1-20.9	13	11.2	10.2-12.7	8	28.5	26.5-30.6
		F	15	197	179-215	15	18.1	16.8-19.3	15	10.8	9.1-12.7	8	27.9	24.1-30.3
Pithecia	*monachus*	M	2	279	262-297	2	24.9	23.0-26.8	2	15.0	13.9-16.2	2	34.7	36.5-32.9
		F	2	260	248-272	2	23.8	22.8-24.7	2	14.7	14.6-14.8	1	36.0	
Chiropotes	*satanus*	M	2	266	244-287	2	24.9	23.1-26.6	2	16.0	15.0-17.1	2	38.3	35.2-41.3
		F	0			0			0			0		
Cebus	*albifrons*	M	12	257	236-275	12	25.6	24.0-29.1	12	16.1	14.8-17.7	8	39.9	36.9-44.0
		F	14	241	214-271	14	23.6	21.6-28.4	14	14.8	13.2-17.0	8	38.2	34.6-44.1
	apella	M	13	253	245-277	13	26.2	24.0-28.9	13	16.2	14.7-17.4	10	41.6	39.0-43.8
		F	12	234	226-242	12	23.4	21.2-25.3	12	14.5	12.9-15.7	10	37.8	33.6-41.4
	olivaceous	M	2	282	280-283	2	26.7	26.3-27.1	2	17.2	16.7-17.6	3	40.9	39.8-41.8
		F	2	276	267-285	2	25.4	23.8-27.1	2	16.2	15.8-16.6	2	40.0	37.9-42.2
Colobus	*angolensis*	M	2	389	379-399	2	41.4	41.3-41.6	2	23.2	22.9-23.5	3	56.2	53.7-59.3
		F	1	338		1	38.7		1	22.1		1	52.9	
	guereza	M	3	390	371-415	3	41.8	36.8-46.2	3	24.2	21.4-27.0	7	56.7	52.1-63.8
		F	3	346	322-364	3	37.0	36.4-37.9	3	22.2	21.2-24.0	4	54.4	51.9-55.9
Lophocebus	*albigena*	M	3	390	381-397	3	37.6	37.0-38.0	3	22.9	22.2-23.5	2	54.6	53.7-55.5
		F	1	364		1	32.4		1	19.8		2	47.9	46.0-49.7
Macaca	*nemestrina*	M	2	418	407-428	2	43.6	42.0-45.2	2	24.5	24.1-24.9	4	58.5	56.3-60.8
		F	0			0			0			1	48.5	
	brunnescens	M	1	344		1	40.9		1	24.8		0		
		F	2	305	298-311	2	33.6	33.2-33.9	2	21.6	21.3-21.9	0		

	fascicularis	M	2	282	272-291	2	28.5	26.1-30.9	2	17.7	16.5-18.4	2	42.2	40.1-44.3
		F	1	245		1	23.1		1	14.3		1	36.1	
	niger	M	0			0			0			0		
		F	1	282		1	31.3		1	20.5		0		
	thibetana	M	1	322		1	42.6		1	24.7		4	58.8	55.6-60.3
		F	0			0			0			0		
	tonkeana	M	1	345		1	39.5		1	23.8		1	54.7	
		F	0			0			0			0		
	mulatta	M	0			0			0			1	53.5	
		F	0			0			0			0		
	sylvanus	M	0			0			0			1	59.1	
		F	0			0			0			1	52.6	
Nasalis	*larvatus*	M	6	453	448-464	6	46.2	44.5-49.6	6	28.4	27.6-29.3	7	71.2	67.4-74.3
		F	1	401		1	38.1		1	24.8		1	62.4	
Papio	*hamadryas*	M	3	494	449-541	3	55.8	52.4-58.1	3	33.4	30.5-35.1	5	73.3	68.0-77.1
		F	1	398		1	46.0		1	28.9		3	65.4	63.7-67.5
Presbytis	*pileatus*	M	1	363		1	41.8		1	24.8		0		
		F	1	326		1	36.7		1	20.6		0		
	cristatus	M	2	341	337-344	2	33.2	30.6-35.7	2	20.1	18.6-21.5	1	51.3	
		F	1	348		1	34.1		1	19.4		2	46.1	44.7-47.6
	johni	M	1	432		1	43.6		1	25.7		1	57.6	
		F	2	379	373-385	2	38.3	36.5-40.1	2	23.4	22.5-24.3	0		
	melalophos	M	1	375		1	34.5		1	21.1		2	50.9	49.0-52.7
		F	1	377		1	33.4		1	20.0		1	48.3	
	obscusus	M	1	310		1	31.8		1	18.5		2	50.5	46.2-54.8
		F	1	321		1	34.0		1	18.7		0		
	rubicundus	M	2	383	363-402	2	36.7	35.7-37.7	2	20.7	20.5-21.0	2	50.6	49.5-51.7
		F	2	372	364-381	2	33.0	32.5-33.6	2	19.1	19.1-19.2	2	41.1	36.2-46.1
	frontatus	M	0			0			0			2	48.9	47.3-50.5
		F	0			0			0			2	49.3	47.6-51.0
	potenziani	M	0			0			0			1	46.4	
		F	0			0			0			0		
Semnopithecus	*entellus*	M	0			0			0			1	57.1	
		F	0			0			0			0		
Pan	*troglodytes*	M	12	522	470-586	12	72.8	64.2-80.8	12	44.7	41.1-50.3	9	102	91.2-115
		F	5	522	494-547	5	68.2	63.8-71.4	5	42.0	40.1-43.8	5	101	97.4-106
Symphalangus	*syndactylus*	M	2	382	378-386	2	43.5	41.4-45.5	2	23.7	21.8-25.6	1	58.2	
		F	1	369		1	40.0		1	22.6		1	50.3	
Propithecus	*verreauxi*	M	3	302	300-305	3	27.4	27.3-27.6	3	16.3	15.9-16.5	3	40.2	38.0-43.9
		F	5	333	305-393	5	31.6	28.6-39.1	5	18.2	15.7-22.9	3	43.7	38.2-54.2
Indri	*indri*	M	1	420		1	37.8		1	23.3		0		
		F	1	457		1	38.1		1	22.6		1	55.3	

Table 2.5. Individuals with associated body weights.

Genus	Species	Specimen #	Body Weight (g)
Alouatta	*belzebul*	NMNH 518228M	8000
		NMNH 518226F	5000
		NMNH 518227F	5500
	caraya	AMNH 211605M	8300
		NMNH 518232M	6500
		NMNH 518236M	7300
		NMNH 518239M	7300
		NMNH 518241M	7200
		NMNH 518242M	7100
		NMNH 518230M	5000
		AMNH 211498M	9300
		AMNH 211504M	8300
		NMNH 518233F	3500
		NMNH 518237F	3400
		NMNH 518238F	4800
		NMNH 518240F	4600
		NMNH 518243F	5400
		AMNH 211497F	5200
		AMNH 211501F	4900
		NMNH 518231F	3500
	guariba	NMNH 518244M	7200
		NMNH 518247M	5300
		NMNH 518248M	4600
		NMNH 518254M	6200
		NMNH 518256M	6800
		NMNH 518251M	6200
		NMNH 518246F	4600
		NMNH 518249F	4100
		NMNH 518252F	5000
		NMNH 518253F	3700
		NMNH 518255F	4500
	palliata	NMNH 338105M	7000
		NMNH 338106M	8600
		NMNH 338107M	7700
		NMNH 338104F	6600
	seniculus	AMNH 169608M	6500
		AMNH 169618M	6500
		AMNH 169638M	6900
		AMNH 169609M	7000
		AMNH 169619M	6800
		AMNH 169634M	6900
		AMNH 169639M	5000
		AMNH 169777M	7000
		AMNH 169645M	6900
		AMNH 169641F	4000
		AMNH 169661F	5400
		AMNH 169652F	3500
		AMNH 169663F	4600
		AMNH 42307F	5000
		AMNH 42416F	7500
		AMNH 169606F	4200
		AMNH 169626F	4300
		AMNH 169624F	3800
		AMNH 169632F	4100
		AMNH 169648F	4500
		NMNH 398507F	4700
Ateles	*paniscus*	NMNH 518551M	5000
		NMNH 546249F	8000
Aotus	*azarae*	AMNH 248393M	900
		NMNH 33718M	790
		NMNH 503709M	840
		NMNH 337316M	660
		NMNH 337317F	670
		NMNH 337315F	690
Cebus	*albifrons*	AMNH 211550F	2200
	apella	AMNH 211578M	3900
Colobus	*angolensis*	NMNH 452615M	8700
		NMNH 452616M	10600
	guereza	NMNH 452619M	11400
		NMNH 452621M	7300
		NMNH 452620M	6300
		NMNH 452625M	9900
		NMNH 452629M	10200
		NMNH 452628M	9200
		NMNH 452635M	11400
		NMNH 452643M	9000
		NMNH452622M	10600
		NMNH 452641F	9000
		NMNH 452624F	7400
		NMNH 452636F	7500
		NMNH 452642F	6400
		NMNH 452634F	9600
Lophocebus	*albigena*	NMNH 452500M	8400
		NMNH 452502M	8500
		NMNH 452498F	6900
Macaca	*fascicularis*	NMNH 344989F	2300
	mulatta	NMNH 173813M	12700
	sylvanus	NMNH 476786F	9000
Nasalis	*larvatus*	NMNH 153802M	20400
Papio	*hamadryas*	NMNH 236976M	34000
		NMNH 384229M	25000
		NMNH 452509M	20000
		NMNH 384228F	18000
		NMNH 384227F	17000
Presbytis	*cristatus*	NMNH A49695M	8000
	rubicundus	NMNH 151826M	6100
	frontatus	NMNH 151825M	5600
		NMNH 151823F	5900
		NMNH 151820F	5700
		NMNH 154362F	5300
	potenziani	NMNH 121673M	7100
Pan	*troglodytes*	AMNH 174860F	41000

Male and female species mean body weights were instead compiled from the literature to produce the body weight predictive equations (Table 2.1). Using body weight, TOTL, and TrL will mitigate difficulties inherent in using weight alone as a proxy for body size, as individual body weight can be expected to vary seasonally due to food availability (e.g., Terborgh, 1983), based on female reproductive condition, and with regard to recording techniques in the field or in the lab. TOTL and TrL are not without problems, as differing allometries of the tail, skull, and trunk are also at work in different taxonomic subgroups of the sample (see below). All three values are reported to give the most comprehensive estimate possible for the overall size of the extinct animal.

As many of the taxa in the comparative sample are quite sexually dimorphic, separate data points for male and female species mean values were used to develop the predictive regression equations. For those equations predicting body weight, three different subsets of the full comparative sample were used: atelines only, platyrrhines only, and the full sample. For the length measurements, only the platyrrhine sample was used in the final analysis because it became evident in preliminary studies that different tail proportions are exhibited by platyrrhines, arboreal cercopithecoids, terrestrial cercopithecoids, and hominoids with no tails. These four groups can be distinguished on the basis of differing slopes in the full sample regression (Fig. 2.2).

All means were log-transformed using the natural logarithm. Because of the bias introduced by de-transforming the solution to each equation in order to derive the predicted body size estimates, a correction factor should be applied (Smith, 1993). Previous publications have chosen to use the Quasi-Maximum Likelihood Estimator (QMLE = exp [MSE/2] where MSE is the mean square error of the regression equation; Delson et al., 2000; Jungers et al., 2008) and

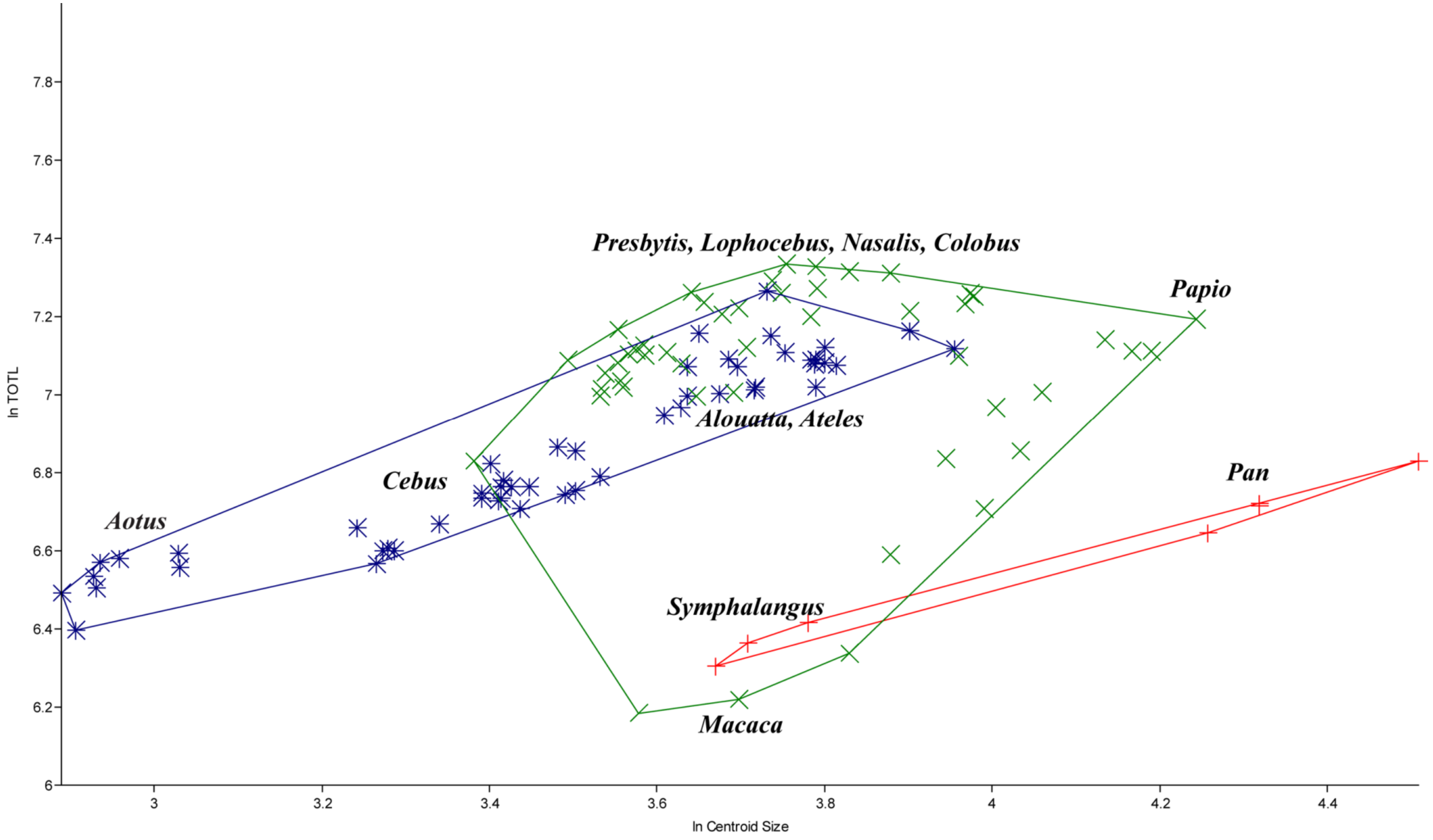

Figure 2.2. Ln centroid size of the proximal ulna plotted against ln total length.
Three distinct groups are bound by convex hulls: platyrrhines (blue), cercopithecoids (green), and hominoids (red). The cercopithecoid group is further divided into arboreal (top) and terrestrial clusters (bottom). This grouping pattern reflects different tail proportions and was seen in every element when plotted against total length.

that procedure is followed here as well. It should be noted that the QMLE has been found to overcompensate for bias (Ruff, 2003) and is only one relatively small factor to consider in evaluating regression equations (Smith, 1993). Because it is directly related to the standard error of the equation, the magnitude of the correction factor will depend on the strength of the relationship between the two variables used to produce the equation; the better the fit, the smaller the correction (Dagosto and Terranova, 1992). The QMLE, and other de-transformation bias correction factors, were developed with reference to ordinary least squares regression so they were only applied to the estimates from those equations (see below).

Univariate regression is used with each element alone (see Ruff, 2003 for discussion of why it is not necessarily helpful to use multivariate step-wise regressions with several elements combined, especially when the locomotor pattern of the fossil taxon of interest is an unknown). As the literature on the topic of body size estimation is equivocal on their appropriate usage, both ordinary least squares (OLS, Model I) and reduced major axis (RMA, Model II) regression equations were produced. OLS regression should be used in body size prediction because there is a clear dependent variable (body size) that is conditional upon an independent variable (skeletal estimator) (McArdle, 2003; Smith, 2009 and references within). However, OLS regression does not deal well with cases of extrapolation (Ricker, 1973; Conroy, 1987). RMA regression has been used previously in cases where the fossil under investigation is outside the range of body size encompassed in the comparative sample used to create the model (Jungers, 1988; Aiello, 1992; Ruff, 1998) and reporting estimates based on multiple models has been suggested as a necessary step in cases of extrapolation (Delson et al., 2000). Here, both OLS and RMA were used for each element against the smaller-bodied ateline and platyrrhine samples, and only OLS was used for the full sample which includes the larger-bodied Old World monkeys and apes.

Comparing equations derived from different reference samples and regression models to determine the “best” equation was done by calculating the standard error of the estimate (SEE) and mean prediction error (MPE) for each equation (Dagosto and Terranova, 1992; Delson et al., 2000). These are important values to consider in ranking prediction equations; just because an equation has a high R^2 does not mean the equation is actually a good predictor. This issue was discussed by Conroy (1987) who had very high R values for all equations (0.91 – 0.99), but when the regression lines were shown graphically, many points fell outside of their 95% confidence intervals. The SEE is a test of consistency or dispersion around the regression line while the MPE is a test of how accurate the equation is at predicting the size of individuals with known dimensions. The equation for calculating %SEE for log-transformed data used by Ruff (2003) is used here as well:

$$\exp(\text{SEE} + 4.6052) - 100.$$

The equation for calculating prediction error is:

$$\text{PE} = \frac{\text{actual mass} - \text{estimated mass}}{\text{estimated mass.}} \times 100$$

The MPE is then calculated for each variable as the mean of the absolute values of the prediction errors summed over all taxa (Delson et al., 2000). The MPE should give the same ranking of predictor variables as the SEE (Ruff, 2003). All individuals in the sample had associated TOTL and TrL measurements in the museum catalogs with which to calculate prediction errors. The subset of individuals that also had associated weights recorded in the museum catalogs were used to calculate MPE for the body weight estimation equations (Table 2.5).

Results

A relatively wide range of body size estimates were recovered for *Protopithecus*: 12-35 kg; 1479-1887 mm TOTL; and 613-831 mm TrL. These ranges reflect the use of different skeletal elements, reference samples, and regression models (Table 2.6; Table 2.7). The low values of these ranges are all larger than the average body weight, TOTL, and TrL for any of the modern platyrrhine taxa in the reference sample (Figs. 2.3-5). The low TOTL value of 1479 mm is outside the range of all living platyrrhine species (Fig. 2.4), but the low TrL value of 613 mm is inside the range of values for some of the larger species of *Alouatta* (Fig. 2.5).

The extreme highs and lows should most likely be disregarded as they come from skeletal elements that give very low or very high estimates in every configuration of the data. Choosing the "best" equation and "best" estimated value from among the results is a moot point, given the range of values reported here. However, the equation with the combined highest R^2 (= 0.98) and lowest %SEE (= 11.0), MPE (= 14.7), and QMLE (= 1.005) is that using the distal humerus with a platyrrhine-only reference sample; this gives an estimate of 28 kg for the TBV specimen and 24 kg for the LS specimen. Condensing all of the values reported in Tables 2.6 and 2.7 into an average, disregarding the obvious extreme outliers in estimate and confidence statistics, gives a body size of approximately 23 kg, 1675 mm TOTL, and 710 mm TrL. As an alternative to compiling an average value, a histogram of all body weight predictions shows 19, 21, and 25 kg as the most frequent estimates with a reasonable range from 17-29 kg (Fig. 2.6). These modal estimates are predicted by equations in all three permutations of the reference sample (Table 2.6). Out of all of the species in the comparative sample, the predicted values for *Protopithecus* are most comparable to those of a large male *Papio* or *Nasalis* (Figs. 2.3-5).

Table 2.6. Body weight estimates for *Protopithecus brasiliensis*.

		Ateline Reference Sample **Body Weight[1] (kg)**	**Slope**	**Intercept**	**R^2**	**%SEE**	**MPE**	**QMLE**
Distal Humerus	OLS	25, 22	2.6641	-1.2007	0.85	11.8	13.2	1.006
	RMA	28, 25	2.8962	-2.0768			14.7	
Proximal Ulna	OLS	13	1.911	1.8112	0.34	7.5	16.1	1.028
	RMA	21	3.2599	-3.167			17.9	
Full Femur	OLS	12	1.8492	-2.3129	0.65	19.4	15.9	1.016
	RMA	14	2.2921	-4.9879			19.8	
Proximal Femur	OLS	19, 19	1.9361	1.474	0.80	14.3	12.9	1.009
	RMA	21, 21	2.1628	0.60993			14.0	
Distal Femur	OLS	15	1.8552	1.761	0.63	19.9	21.9	1.016
	RMA	18	2.3307	-0.05746			24.5	
Full Tibia	OLS	11	1.279	1.5016	0.51	9.7	18.6	1.019
	RMA	14	1.7864	-1.4247			19.5	
Proximal Tibia	OLS	17	2.028	1.7882	0.68	18.6	19.3	1.015
	RMA	20	2.4667	0.25931			20.0	
Distal Tibia	OLS	12	1.4775	4.2857	0.54	22.5	19.1	1.021
	RMA	15	2.0122	2.6322			20.5	
Talus	OLS	17	2.0986	0.6514	0.65	19.9	18.9	1.017
	RMA	21	2.6052	-1.3268			22.3	
		Platyrrhine Reference Sample						
Distal Humerus	OLS	28, 24	2.8741	-2.0023	0.98	11.0	14.7	1.005
	RMA	29, 25	2.9099	-2.1322			15.1	
Proximal Ulna	OLS	18	2.8626	-1.7273	0.90	23.6	16.7	1.023
	RMA	19	3.013	-2.2609			17.1	
Full Femur	OLS	17	3.1683	-10.359	0.87	28.4	28.9	1.032
	RMA	19	3.4051	-11.761			31.0	
Proximal Femur	OLS	32, 31	2.9936	-2.5929	0.92	21.9	22.7	1.020
	RMA	35, 33	3.1282	-3.0876			22.6	
Distal Femur	OLS	21	2.8278	-1.9831	0.91	22.0	27.3	1.020
	RMA	23	2.956	-2.4544			26.5	
Full Tibia	OLS	19	3.0895	-9.0829	0.74	41.7	39.0	1.063
	RMA	23	3.5882	-11.909			41.8	
Proximal Tibia	OLS	27	3.1941	-2.3123	0.92	20.4	21.9	1.017
	RMA	29	3.3201	-2.7355			21.6	
Distal Tibia	OLS	18	2.5462	0.9449	0.90	24.3	25.4	1.024
	RMA	20	2.6864	0.53375			23.8	
Talus	OLS	27	3.2642	-3.9446	0.92	21.9	23.4	1.020
	RMA	29	3.4107	-4.4983			24.2	
		Full Reference Sample						
Distal Humerus	OLS	28, 25	2.6351	-0.9848	0.89	25.1	16.8	1.025
Proximal Ulna	OLS	18	2.6011	-0.6623	0.87	27.9	19.9	1.031
Full Femur	OLS	13	2.6665	-7.413	0.73	43.9	27.4	1.068
Proximal Femur	OLS	26, 25	2.6714	-1.3936	0.91	22.7	17.7	1.021
Distal Femur	OLS	19	2.6081	-1.1723	0.92	22.2	19.2	1.020
Full Tibia	OLS	16	2.8064	-7.4877	0.71	47.6	42.2	1.075
Proximal Tibia	OLS	19	2.6463	-0.512	0.91	24.1	28.4	1.023
Distal Tibia	OLS	21	2.6484	0.7535	0.89	26.5	21.2	1.027
Talus	OLS	23	2.9496	-2.7161	0.91	24.3	20.3	1.024

[1] For all paired estimates, the first is for the TBV specimen and the second is for the LS specimen

Table 2.7. Total length (TOTL) and trunk length (TrL) estimates for *Protopithecus brasiliensis*.

		TOTL[1] (mm)	**Slope**	**Intercept**	**R^2**	**%SEE**	**MPE**	**QMLE**	**TrL (mm)**	**Slope**	**Intercept**	**R^2**	**%SEE**	**MPE**	**QMLE**
Distal Humerus	OLS	1725, 1656	0.8379	3.8845	0.89	6.9	7.4	1.002	709, 685	0.7155	3.5163	0.70	11.4	8.1	1.006
	RMA	1781, 1705	0.88799	3.7028			7.7		775, 743	0.85775	2.9998			8.5	
Proximal Ulna	OLS	1479	0.8212	3.998	0.87	7.7	6.8	1.003	645	0.7891	3.2968	0.89	6.5	6.0	1.002
	RMA	1522	0.88255	3.7799			7.4		659	0.83594	3.1302			6.3	
Full Femur	OLS	1509	0.9373	1.3741	0.83	8.5	7.6	1.003	623	0.7545	1.6482	0.57	13.8	10.2	1.008
	RMA	1569	1.0259	0.85124			7.9		694	1.0028	0.18177			9.9	
Proximal Femur	OLS	1809, 1789	0.8948	3.627	0.87	7.5	6.3	1.003	721, 714	0.7204	3.4614	0.59	13.4	9.6	1.008
	RMA	1887, 1865	0.95888	3.3918			6.5		831, 822	0.93735	2.6653			9.4	
Distal Femur	OLS	1595	0.8368	3.8393	0.89	6.6	6.4	1.002	650	0.6714	3.6405	0.60	13.1	10.1	1.008
	RMA	1637	0.88362	3.6676			6.4		724	0.86378	2.9348			9.7	
Full Tibia	OLS	1541	0.8891	1.8947	0.66	12.7	8.8	1.007	613	0.6422	2.4845	0.35	17.8	13.0	1.014
	RMA	1700	1.096	0.726			8.6		757	1.0872	-0.029076			11.0	
Proximal Tibia	OLS	1689	0.9174	3.8366	0.87	7.6	7.6	1.003	682	0.7403	3.6241	0.59	13.4	9.8	1.008
	RMA	1756	0.98532	3.609			7.9		775	0.96319	2.8776			9.7	
Distal Tibia	OLS	1523	0.753	4.7069	0.87	7.4	6.6	1.002	624	0.5966	4.3587	0.57	13.6	10.5	1.008
	RMA	1568	0.80515	4.5543			6.7		694	0.78707	3.8016			9.9	
Talus	OLS	1670	0.9389	3.3558	0.83	8.5	7.9	1.003	708	0.829	2.974	0.63	13	9.9	1.007
	RMA	1757	1.0301	3.0117			7.8		798	1.0436	2.1639			10.0	

[1] For all paired estimates, the first is for the TBV specimen and the second is for the LS specimen.

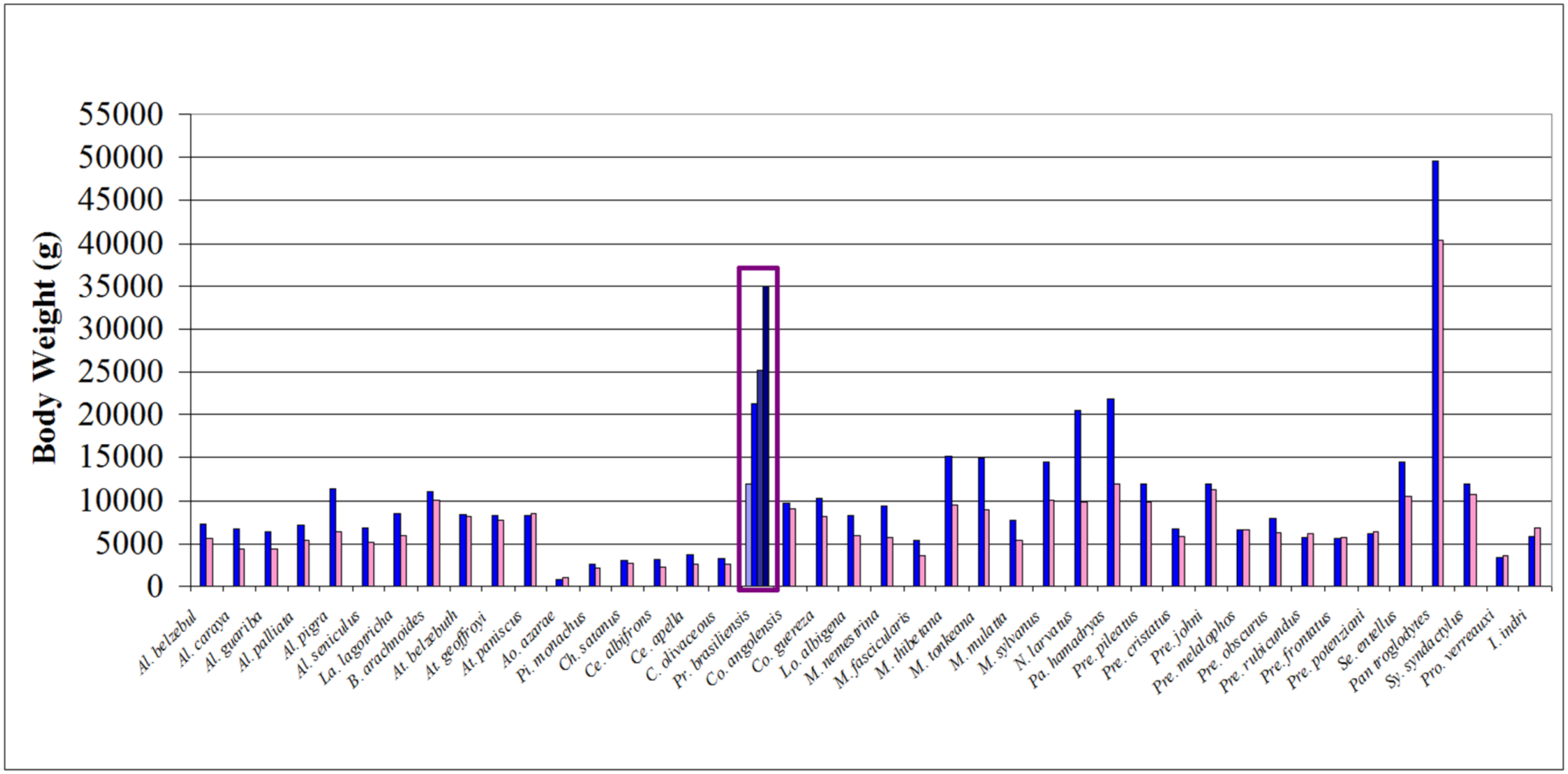

Figure 2.3. Body weight estimates for *Protopithecus* compared to the entire reference sample.
Bars for extant species are the male average and female average compiled from the literature. Bars for the fossil are the low estimate (full tibia OLS ateline sample), low average (OLS ateline sample), high average (RMA platyrrhine sample), and high estimate (TBV proximal femur RMA platyrrhine sample). The low estimate is larger than any extant platyrrhine species to its left but all estimates are in the range of the catarrhine species to its right.

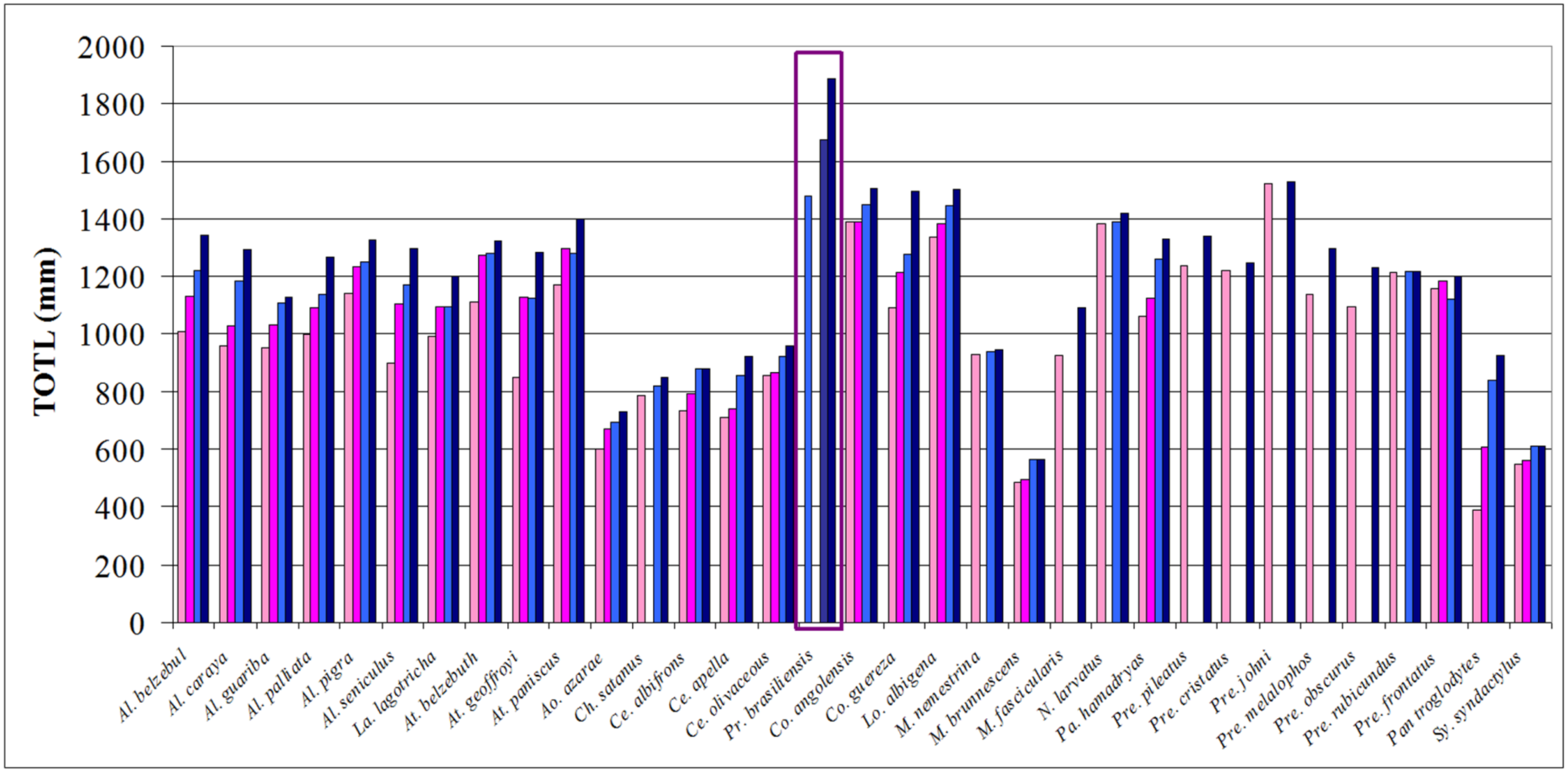

Figure 2.4. Total length (TOTL) estimates for *Protopithecus* compared to the reference sample.
Where all values were available in the museum catalogs, bars for the extant sample represent low value, female average, male average, and high value for each species. Bars for the fossil represent low estimate, average, and high estimate. As for body size, the low estimate is longer than any living platyrrhine to its left but in the range of the catarrhines to its right. However, the average length estimated for the fossil is longer than any extant primate species in the sample, perhaps reflecting its relatively long tail.

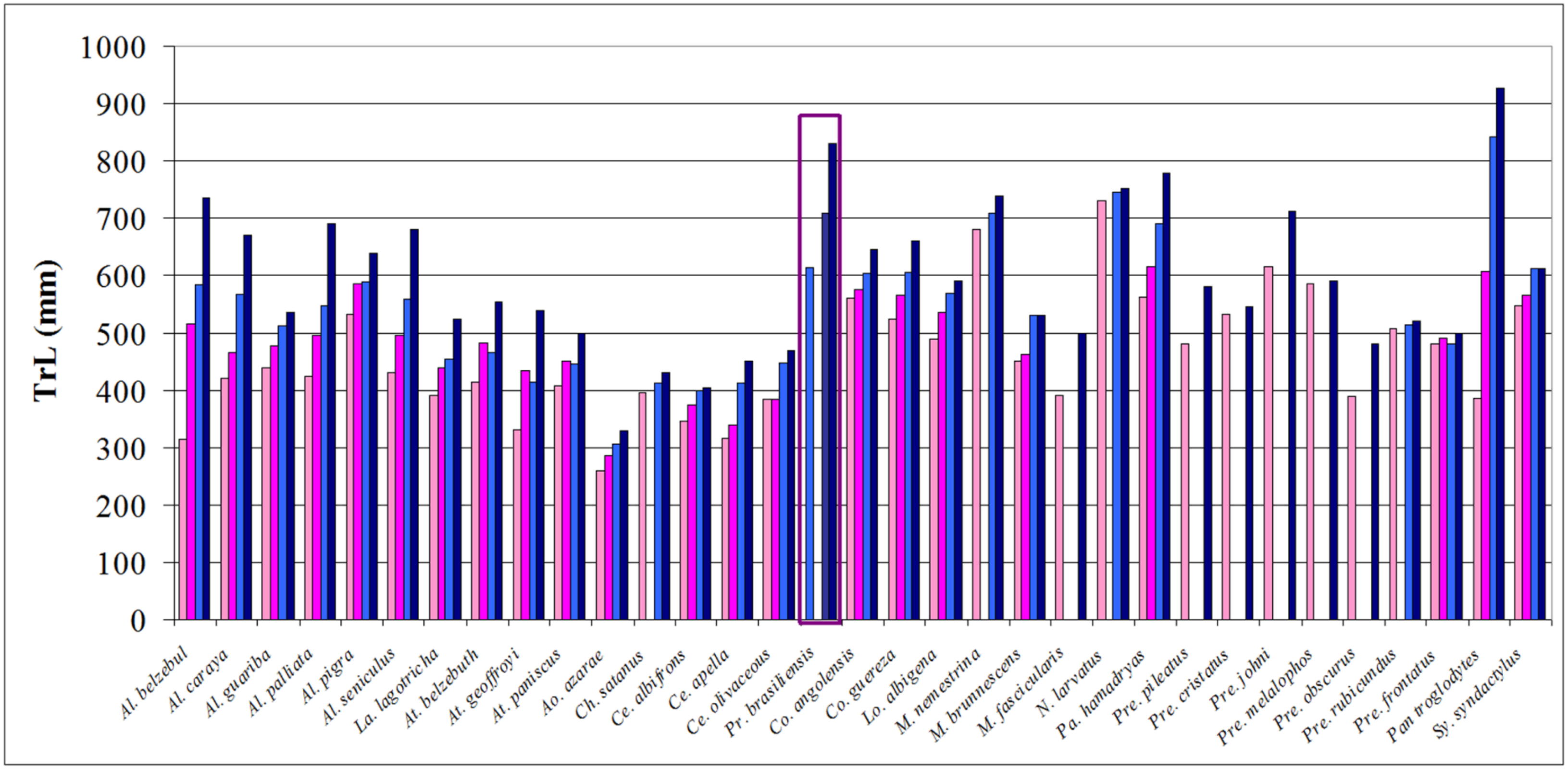

Figure 2.5. Trunk length (TrL) estimates for *Protopithecus* compared to the reference sample.
Where all values were available in the museum catalogs, bars for the extant sample represent low value, female average, male average, and high value for each species. Bars for the fossil represent low estimate, average, and high estimate. The low and average estimates for the fossil are within the range of all extant primates in the sample, due to the negative allometry of trunk length and body weight and/or the shorter trunks of species that use suspensory locomotion.

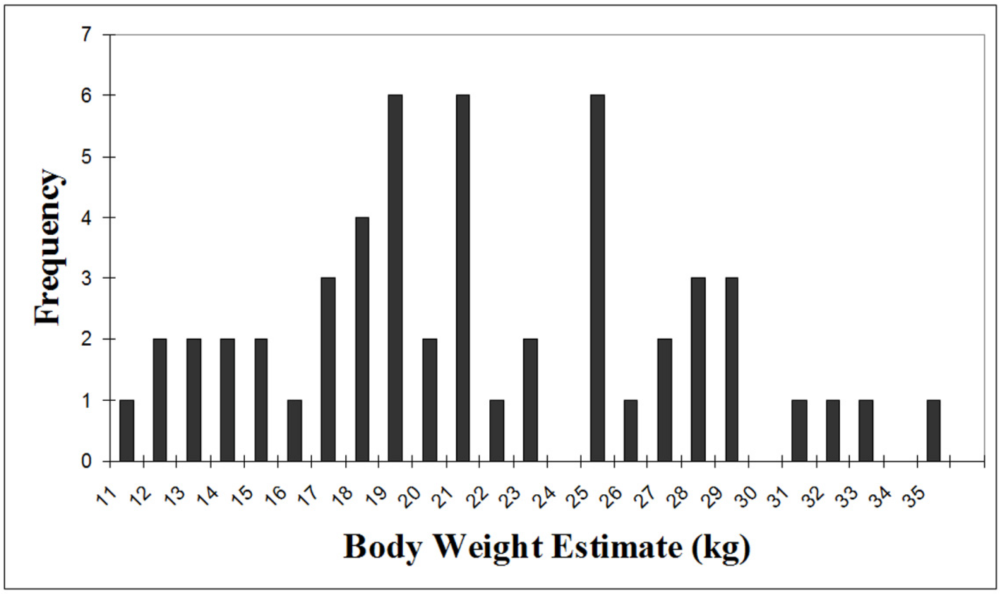

Figure 2.6. Histogram showing the frequency of each predicted estimate.
A range of 17-29 kg seems reasonable with 19, 21, and 25 kg being the most frequent predictions for *Protopithecus*. These three estimates were given by equations based on several skeletal elements in all three subsets of the reference sample.

The majority of the R^2 values are above 0.8. Most equations have %SEE values around 15-25%, with the total body length equations much lower at 6-13%; Ruff (2003) concludes that the best one can do is probably 10-15%. Similarly, the low MPE values calculated here are comparable to those of the equations considered to be among the best by Delson et al. (2000). These low values were also used to justify including both male and female means in the comparative sample and not creating separate equations for each sex. Only three of the QMLE correction factors are above the 6% value suggested by Smith (1993) to be the maximum cutoff for usable equations.

The average TOTL of about 1675 mm for *Protopithecus* is much longer than the average TOTL of any of the male Old World monkey species in the comparative sample, but the fossil's average TrL of about 710 mm is within the range of the larger males (Figs. 2.4-5). As Schultz

(1938) and many others subsequently noted in catarrhines, trunk length [defined both as "head and body length" (Ford and Corrucini, 1985) and "precaudal vertebral column length" (Majoral et al., 1997)] also scales with negative allometry with body mass across platyrrhine primates. This allometric scaling effect could partially explain the relatively long TOTL but relatively short TrL of the larger-bodied *Protopithecus*. However, the relatively short head and body length of *Protopithecus* predicted here, while potentially related to allometric effects, could also be a locomotor adaptation. A short overall vertebral column is a feature of terrestrial primates (e.g., Anapol et al., 2005), but a short lumbar region is also characteristic of suspensory primates like *Ateles* and the hylobatids (e.g., Erikson, 1963). Like various other postcranial traits, a short lumbar region has been suggested as a functional adaptation to multiple locomotor patterns (see Chapter 4); it could also be a way to resist buckling of the vertebral column during vertical climbing in large bodied species (Jungers, 1984a). The length of this specific part of the vertebral column is unknown for the incomplete fossil.

The relative proportions of two different anatomical areas, the skull and the tail (see below), could also be affecting these length measurements. Because the "head and body length" measurement used here is longer than the "skeletal trunk length" measurement discussed in various allometric studies (e.g., Jungers, 1984a), including species in the comparative sample which vary greatly in relative skull length will affect the consistency of the equations. This would be especially problematic if the end point of the length was measured by some observers from glabella and by others from prosthion, as the longer snout of *Alouatta*, *Protopithecus*, and the papionins would be skewing the results in an unequal fashion. These measurement details are not recorded in the museum catalogs.

The centroid size of the full femur and tibia, values related to overall bone length, were the worst predictors of body size of those used here; this agrees with previous work where long bone lengths were less successful than various measures of joint sizes (e.g., Ruff, 2003). Correlations related to joint surfaces at the proximal and distal end of the tibia are also not very strong. It has been suggested that the tibia is not as good as some of the other postcranial elements for body size estimation because of the variable role of the fibula in weight support (Ruff, 2003). The distal humerus of *Protopithecus*, for which there are two specimens, presents a different problem. The specimen that is part of the more recently discovered complete skeleton from Toca da Boa Vista seems to overestimate body size, perhaps because it exhibits a very large brachioradialis flange which increases the measured width and height of the joint surface (Fig. 2.7). The other distal humerus specimen, which was part of the material discovered by Lund in Lagoa Santa, is smaller and gives estimates closer to the average values for the three aspects of size. This could potentially mean that the two humeri represent a male and female of a dimorphic species, or that they belong to two different species.

The performance of some of the other predictor variables investigated here is harder to explain. For example, it is unclear why the proximal femur gives such large estimates when used with the platyrrhine sample even though those equations have comparable confidence statistics to the rest of the "better" variables. Similarly, the ulna is producing very low estimates, despite having relatively good confidence statistics. The over- and under-estimating of various joint sizes could be investigated by producing bivariate plots of joint size and long bone length, a method used by Millien and Bovy (2010) to investigate allometric relationships in fossil rodents, where the sample included small-bodied extant and much larger fossil species. This would require long bone length measurements for each individual in the comparative sample, data

Figure 2.7. *Protopithecus* distal humerus.
Note the size difference, especially in the brachioradialis flange and shaft diameter, between the specimen from Toca da Boa Vista (left) and the specimen from Lagoa Santa (right). Scale bars = 1 cm.

which has yet to be collected. The proximal femur as defined here (see Fig. 2.1) includes more than just the femoral head, the element used to produce the original catarrhine-based body size estimates for *Protopithecus* (Hartwig, 1995a; Hartwig and Cartelle, 1996). However, the results are comparable: a similarly large value of 25-26 kg is estimated here from the full sample equation. As mentioned above, it is much easier to pick out and discuss the less useful skeletal elements as opposed to determining the “best” ones to use. The distal humerus, proximal ulna, and proximal femur seem to produce more robust equations, but they still give variable estimates depending on the reference sample used.

Discussion

Explaining the large body size of *Protopithecus* is a challenge crucial to illuminating various aspects of its paleobiology. Hartwig and Cartelle (1996) suggested that the fossil's large size could be part of the general tendency of late Pleistocene mammals to increase in body mass (e.g., Martin and Klein, 1984). However, while *Protopithecus* is much larger than any extant platyrrhine, it is not large for a primate and especially unremarkable when compared to other Pleistocene South American mammals such as the ground sloths and glyptodonts. This should be taken into consideration when the temptation arises to refer to *Protopithecus* as a "giant" fossil platyrrhine, as has been done in the literature (e.g., Hartwig, 1995a). The relatively recent late Pleistocene date for the caves in which the *Protopithecus* remains were found (Auler et al., 2006) could be used to interpret *Protopithecus* as evidence for Cope's rule of phyletic size increase (Stanley, 1973) at work in the ateline lineage. However, *Protopithecus* has been suggested to represent a late-surviving holdover from an earlier Miocene "stage" in alouattin evolution (Rosenberger et al., 2009). If the fossil is a basal member of the alouattin clade, a size decrease over evolutionary time also makes sense as an explanation for the evolution of various unique aspects of extant howler monkey morphology (see Chapter 5). The size range of the entire platyrrhine radiation seems to have been broader in the past than it is today, and while it might not be immediately clear why the larger size class evolved and eventually went extinct, its relation to the living atelines can shed light on their evolutionary history.

Protopithecus and the prehensile tail: Part 1

An important part of the suspensory locomotion practiced by living ateline primates is the use of a prehensile tail which can support their entire body weight and which itself weighs as much as one of the hindlimbs (Grand, 1984). The main skeletal distinctions between prehensile and non-prehensile tails are the overall length of the tail and the robusticity of the lumbar and caudal vertebrae (Schultz, 1961; Ankel, 1972; German, 1982; Rosenberger, 1983; Lemelin, 1995; Meldrum, 1998; Organ, 2010). While the *Protopithecus* caudal vertebrae were not included in the sample analyzed here, inferences about tail length can still be made from the results of this study. Predicting the TOTL and TrL of the fossil allows the calculation of a tail to head and body length ratio, which indicates whether or not the tail is elongated relative to trunk length. The TAILL:TrL index for the fossil is 1.4 which is within the range of mean values for three of the extant prehensile-tailed ateline genera: *Alouatta* = 1.1, *Lagothrix* = 1.4, and *Ateles* = 1.7 (Table 2.8; data for *Brachyteles* was unavailable). However, this datum should not be used in isolation to "prove" the prehensility of the *Protopithecus* tail. Means of many non-prehensile-tailed species in the larger sample, such as *Lophocebus* (= 1.6) and *Presbytis* (= 1.4), are also high in the ateline range; just because a tail is elongated does not automatically mean it was prehensile.

While detailed analyses of the muscle attachment sites on the fossil caudal vertebrae and the dimensions of the sacral opening can contribute more to addressing this question (as in Ankel, 1972; Youlatos, 2003; Schmitt et al., 2005; Organ et al., 2009), *Protopithecus* is an ateline primate and since all of the other atelines have a prehensile tail, it is relatively safe to infer that the fossil also possesses this trait. The larger ecological picture also favors this interpretation. Various aspects of South American forest structure, such as the lack of lianas, may have led to the parallel evolution of a prehensile tail used during locomotion in many mammalian lineages (Emmons and Gentry 1983; Lockwood 1999). However, it would still be informative to use principles of biomechanics to model the feasibility of a 23 kg monkey supporting its entire body weight with a fully prehensile tail (e.g., Preuschoft and Demes, 1985).

Table 2.8. Tail length (TAILL) to trunk length (TrL) index.

Genus	**Species**		**TAILL:TrL**	**Genus**	**Species**		**TAIL:TrL**
Protopithecus	*brasiliensis*		1.4				
Alouatta	*belzebul*	M	1.1	*Colobus*	*angolensis*	M	1.4
		F	1.2			F	1.4
	caraya	M	1.2		*guereza*	M	1.1
		F	1.2			F	1.1
	guariba	M	1.2	*Lophocebus*	*albigena*	M	1.5
		F	1.1			F	1.6
	palliata	M	1.1	*Macaca*	*nemestrina*	M	0.3
		F	1.2		*brunnecens*	M	0.1
	pigra	M	1.1			F	0.1
		F	1.1		*fascicularis*	M	1.2
	seniculus	M	1.1			F	1.4
		F	1.2	*Nasalis*	*larvatus*	M	0.9
Lagothrix	*lagotricha*	M	1.4	*Papio*	*hamadryas*	M	0.8
		F	1.5			F	0.8
Ateles	*belzebuth*	M	1.7	*Presbytis*	*pileatus*	M	1.3
		F	1.6			F	1.6
	geoffroyi	M	1.7		*cristatus*	M	1.3
		F	1.6			F	1.3
	paniscus	M	1.9		*johni*	M	1.1
		F	1.8			F	1.5
Aotus	*azarae*	M	1.3		*melalophos*	M	0.9
		F	1.3			F	1.2
Chiropotes	*satanus*	M	1.0		*obscurus*	M	1.8
Cebus	*albifrons*	M	1.2			F	1.6
		F	1.1		*rubicundus*	M	1.4
	apella	M	1.1		*frontatus*	M	1.3
		F	1.2			F	1.4
	olivaceous	M	1.1				
		F	1.2				

Conclusions

After investigating the relationship between body size and a variety of skeletal dimensions in atelines, platyrrhines, and larger-bodied anthropoids, it can be concluded that despite reasonably strong statistical relationships between some of the anatomical elements, there is enough variation in any taxonomically appropriate, robust sample of primate species to make fossil body size prediction challenging. Even with all of the relevant numbers reported, it is very difficult to pick the “best” skeletal element or the “best” equation from those developed in this study, and for use in future predictions of body size in fossil platyrrhines and primates more generally. Of course, the nature of these limitations will change depending on the fossil or question of interest. Accordingly, it is desirable that multiple skeletal elements and equations are evaluated in producing an estimate of any aspect of body size. Additionally, since for statistical reasons there will never be a single value capable of summarizing the sample-based information on body size for an individual fossil or fossil taxon, it is desirable that mean estimates include a range of values and confidence statistics based on the particulars of the equations used. In this case, having the opportunity to empirically compare so many equations at once suggests that there are some elements that should be avoided when making predictions, such as the tibia, which was always among the worst predictors in every configuration of the data presented here.

Despite these caveats, the original interpretation of *Protopithecus* as a member of a previously unknown large-bodied size class of the platyrrhine radiation can now be supported by an independent investigation and analysis. Inferences about its paleobiology and behavior, and what that means for the evolutionary history of the living ateline primates, can now be made more confidently with this in mind. *Protopithecus* is a special case where many elements of the same individual can be used at once. Having such a complete skeleton is a priceless asset and *Protopithecus* should be used a test case for many of the methods employed by paleontologists in reconstructing aspects of fossil behavior.

CHAPTER 3

CRANIAL BASE MORPHOLOGY AND ITS POTENTIAL RELATIONSHIP TO THE HYOID IN *PROTOPITHECUS* AND *ALOUATTA*

Introduction

There are many fields of study interested in the head and neck and the functional morphology and evolution of the structures referred to by various authors as the either the aerodigestive tract (e.g., Laitman, Reidenberg, Crelin et al.) or the supralaryngeal vocal tract (e.g., Fitch, Hauser, Nishimura et al.), reflecting their anatomical or linguistic bias, respectively. Much is known about the embryological precursors and postnatal development of the laryngeal cartilages, especially in humans (Frazer, 1910; Crelin, 1976; Magriples and Laitman, 1987; Wolfson and Laitman, 1990; Isaacson and Birnholz, 1991; Tucker, 1996; Som et al., 2004; Henick, 2006; Laitman et al., 2006). Many mammals have modified the position, shape, size, or number of various components of their larynges as adaptations for specialized feeding and/or vocalization behaviors: for example, toothed whales and dolphins (Reidenberg and Laitman, 1994); bats (Sprague, 1943; Veselka et al., 2010); felids (Pocock, 1916; Weissengruber et al., 2002; Klemuk et al., 2011); ruminants (Saber and Hofmann, 1985; Frey et al., 2007); xenarthrans (Naples, 1986; Perez et al., 2010); and koalas (Charlton et al., 2011). Among primates, the two most well-known examples of taxa with modified larynges and associated structures are humans and howler monkeys.

Because *Protopithecus* has been suggested to belong to the alouattin tribe, the focus of this chapter is on testing this hypothesis by looking for shared derived traits between the fossil and extant *Alouatta*. These include aspects of the cranium and mandible that have been suggested to be related to the unique hyoid morphology seen in *Alouatta*. *Alouatta* is said to make the loudest vocalizations of any terrestrial vertebrate and has the largest, most inflated hyoid bone within the primate order. It is therefore not unreasonable to hypothesize that these traits are related, as has been suggested historically in the literature (e.g., Hershkovitz, 1949; Kelemen and Sade, 1960; Schön, 1971). While the basic anatomy of the hyoid bone, thyroid and epiglottic cartilages, and air sacs of *Alouatta* have been described by many authors (see below), inter- and intra-specific variations are not as well known and there is debate about how their morphology relates to diet, vocalizations, body size, respiration, and the functional morphology of the skull. However, this should not stop us from investigating this area of the fossil, as phenetic similarities could still be valuable in supporting or refuting the phylogenetic hypotheses of Hartwig and Cartelle (1996) concerning *Protopithecus*.

The *Protopithecus* cranium and mandible exhibit characters that are inferred to be related to the unique morphology underlying the vocalization production mechanism in *Alouatta*. These were suggested to include an extended basicranial region, airorynchous face, and a posteriorly deepening mandible (Hartwig and Cartelle, 1996; Hartwig, 2005). These structural modifications, at least in part, allow for the accommodation of the greatly enlarged hyoid bone and associated laryngeal cartilages of the howler monkeys (Biegert, 1963; Schön, 1976; Watanabe, 1982). Unfortunately, the hyoid bone itself is not preserved in the *Protopithecus* remains. It should be possible, however, to infer the presence or absence of a greatly pneumatized hyoid, and by extension howler monkey-like vocalizations and social behavior, based on basicranial dimensions. If basicranial dimensions co-vary in predictable ways with hyoid dimensions in the living howler monkeys, which have species-specific hyoid sizes and shapes (Hershkovitz, 1949), then the basicranium of the fossil can be used to reconstruct the size and shape of its hyoid.

The first to attempt relating cranial base dimensions to pharyngeal dimensions with the hopes of answering questions about vocal abilities in fossils were Laitman, Heimbuch, and Crelin in 1979. Finding a correlation between the overall cranial base shape and the bony structure of the hyoid might circumvent problems encountered by those researchers while trying to relate cranial base angles to soft tissue dimensions within the hominin lineage (e.g., Laitman et al., 1979; Laitman and Heimbuch, 1982; Lieberman and McCarthy, 1999). Two differences between humans and howlers are expected to make this line of inquiry more tenable in the monkeys: first, while hyoid size and shape varies amongst modern humans (e.g., Papadopoulos et al., 1989), the overall shape is similar throughout the fossil history of our genus (Arensburg et al., 1990; Capasso et al., 2008; Martinez et al., 2008), showing less interspecific variation than that seen in *Alouatta*. The high degree of variation in both hyoid (Hershkovitz, 1949) and cranial base shapes (Halenar, 2008) amongst species of extant *Alouatta* should make co-variation between the two anatomical areas easier to see statistically. Second, unlike in humans, the hyoid bone of *Alouatta* is always attached to the cranial base through a chain of cartilaginous, or sometimes even ossified, elements, i.e., the more common "integro-cornuate" condition (Howes, 1896). It also sits wedged between the gonial angles of the mandible. These anatomical constraints suggest the possibility that a strong relationship between hyoid, cranial base, and mandibular morphology can be established in the living and fossil taxa. Also, the three-dimensional geometric morphometric techniques for capturing overall shape used here might prove to be an advance over the original attempts to infer hyoid position in hominins, using the morphologically less sensitive cranial base angle.

It must be noted that even if parts of the basicranium and mandible are indicative of large hyoid size in the living howler monkeys, they might not be useful for accurate predictions of hyoid size for *Protopithecus* because of the fossil's much larger body size (see Chapter 2). That is, extreme *Alouatta*-like modifications of the head to accommodate an enlarged hyoid may not have been necessary in a species 2-3 times the mass of a living howler. Thus, it needs to be determined if a reconstructed hyoid of *Protopithecus* is not just large, but *en*larged relative to body mass. Even if results suggest that the hyoid was not enlarged and/or pneumatized, they will still have relevance for the evolution of howler specializations. The possession of an absolutely large subbasal space without a relatively large hyoid would provide information about the pre-adaptive pathway leading to extant *Alouatta.* It may suggest a more primitive state of the derived howler vocalization mechanism, which may have been similar to the vocal tract anatomy seen in other primates that give long calls without the use of a pneumatized hyoid.

Long call vocalizations in Alouatta

The genus *Alouatta* is one of many primates that include long calls as part of their vocal repertoire. These calls have been suggested to serve the biological roles of group spacing, conflict avoidance by means of opponent strength assessment, and resource defense in various primates and are especially important in a dense forest habitat where sight and smell may not be as useful for long distance communication (Gautier and Gautier, 1977; Robinson, 1979; Byrne, 1981; Sekulic, 1982; van Roosmalen, 1985; Schön, 1986; Whitehead, 1987; Snowdon, 1989; Chapman and Lefebvre, 1990; Boinski, 1991; Elowson et al., 1991; Clark and Wrangham, 1993; Mitani and Nishida, 1993; Chiarello, 1995; Fitch and Hauser, 1995; Hauser, 1996; Mitani and Stuht, 1998; Boinski, 2000; Milton, 2000; Wich and Nunn, 2002; Oliveira and Ades, 2004; Spehar, 2006). In howler monkeys, the long calls are given usually in the morning and in the afternoon by the adult males of the group; adult females will also sometimes participate in roaring during intergroup encounters, potentially as part of anti-infanticide behaviors (Crockett and Sekulic, 1984; Whitehead, 1989; Kitchen, 2006). These morning and afternoon peaks in calling behavior are partially a side-effect of the long resting period used by the howlers for digesting their mostly folivorous diet (Milton, 1980). Since the so-called "dawn chorus" is given in concert by all howler groups living in an area, it is generally agreed to act as a spacing mechanism, especially when home ranges overlap (Carpenter, 1934; Chivers, 1969; Baldwin and Baldwin, 1976; Sekulic, 1982; da Cunha and Byrne, 2006). In all species, howling bout duration seems to increase with increasing population density, further supporting that interpretation (Chivers, 1969; Chiarello, 1995; Cornick and Markowitz, 2002). However, many socioecological variables differ from species to species (Table 3.1), making a blanket explanation for all howling bouts difficult to articulate. As noted by Hershkovitz (1949): "Highly localized environmental conditions, such as quality and availability of food and water, are of greater significance in growth and development of these very sedentary and sluggish monkeys than in any other species of American simian" (p. 388).

The size of the social group in general, and more specifically the number of males in the group, varies from one species of *Alouatta* to another and this can also affect the amount of calling. For example, *A. palliata* on Barro Colorado Island howl less frequently than *A. seniculus* in Venezuela partially because the *A. palliata* groups already contain multiple males, making howling as a mode of long-distance opponent strength assessment less of a necessity (Sekulic and Chivers, 1986). Howling has been shown to play a role in male-male competition and female mate choice (Sekulic, 1982; Crockett and Eisenberg, 1987; Van Belle and Estrada, 2008; Kowalewski and Garber, 2010), suggesting that howling can affect reproductive success; in captive European *A. caraya*, reproductive success was positively correlated with the amount

Table 3.1. Socioecological diversity in *Alouatta*.

Taxon	Distribution[1]	Habitat Type[1]	% Leaves[2]	Body Weight (kg)[3]		Pop. Density (ind./km2)[2]	Group Size[2]	Home Range (Ha)[2]	Hyoid Size*	Emphasized Frequency (Hz)[a]	Call Duration (sec)[b]
				Males	Females						
A. belzebul	Brazil (Amazon)	Primary forest Seconday forest Flooded forest	~20 Geophagy Tree bark	7.3	5.5	-	7 (5 – 14)	25.8 (4.7 – 63.2)	Large (212, 130)	480.6	4.9
A. caraya	Brazil, Paraguay, Argentina	Primary forest Riparian forest Dry deciduous forest Broadleaf forest Semiarid caatinga	~70 Eggs	6.8	4.6	154	10 (2 – 21)	2.85 (1.7 – 5.5)	Medium (164, 116)	439.7	-
A. guariba	Brazil (Atlantic Coastal Forest)	Primary forest Secondary forest Parana pines	~75	6.2	4.5	117	7 (2 – 11)	6.0 (4.1 – 7.9)	Large (197, 122)	616.6	-
A. palliata	Mexico to Ecuador	Evergreen rainforest Cloud forest Dry lowland deciduous forest Coastal mangrove forest	~50-70	7.1	5.3	18	15 (2 – 45)	40.6 (9.9 – 108)	Small (117, 74)	413.3	3.5
A. pigra	Mexico, Belize, Guatemala	Primary and secondary semideciduous and lowland rainforest	~45	11.3	6.4	25	6 (2 – 16)	-	Medium (124, 120)	598.9	5-6
A. seniculus	Northern South America	Gallery forest Mangrove swamp Semideciduous forest Savanna Woodlands Secondary forest	~50	7.2	5.6	25	7 (2 – 16)	35.7 (3.9 – 182)	Large (220, 131)	475.7	19, 8, 120

[1] From Rowe (1996)

[2] From DiFiore and Campbell (2007)

[3] From Ford and Davis (1992)

*From Hershkovitz (1949) and pers.obs – numbers in parentheses are male and female average centroid size (see Materials and Methods).

[a] From Whitehead (1995)

[b] From Whitehead (1995) and Sekulic and Chivers (1986)

of howling done by males and heard by females (Farmer et al., 2011).

Species of *Alouatta* vary in terms of the habitats in which they live and the proportion of fruit and leaves in their diet (DiFiore and Campbell, 2007; Table 3.1), important factors if the long calls are functioning in resource and/or territory defense. The one species that unequivocally seems to roar as an active part of territorial defense is *A. guariba*, the species that inhabits the much less productive Atlantic Coastal Forest (Chiarello, 1995; da Cunha and Jalles-Filho, 2007). However, the frequency of calls actually seems to decrease during the dry season in *A. pigra* (Cornick and Markowitz, 2002), so the explanation of calls serving as an advantage for resource defense when food is scarce does not apply to all species.

Alouatta can best be described as a "semi-folivorous" taxon (see Rosenberger et al., 2011), with leaves making up as much as 75% of their diet during certain times of the year (Table 3.1). With their slow gut passage rates and specialized hindgut fermentation process (Rosenberger et al, 2011 and references therein), howlers are forced to spend much of their activity budget, up to 80% in some cases (Pavelka and Knopff, 2004), resting while they extract as much nutritional value out of their food as possible. The howler's relatively low quality diet has been suggested to be related to their combination of cautious quadrupedal locomotion, relatively small home range sizes, cohesive social groups, and reliance on howling for long distance communication as part of an "energy-minimizing" strategy (Milton, 1980; Rosenberger and Strier, 1989; Strier, 1992). However, recent behavioral studies on several species (i.e., Bravo and Sallenave, 2003; Pavelka and Knopff, 2004; Asensio et al., 2007; Agostini et al., 2010; Palma et al., 2011) find no correlation between percent leaves in the diet and either time spent resting or distance traveled. The howler groups in those studies spend 60-80% of their activity budget resting even in seasons when they are consuming mostly fruit, results that seemingly contradict a causal link between energy-minimizing and diet. Regardless of why, given the amount of time howlers spend resting, howling itself has often been suggested to serve the biological role of conflict avoidance, as physical confrontations between neighboring troops over territory boundaries or between individuals for mates would take energy that the howlers seemingly do not have to spare (Carpenter, 1934; Chivers, 1969; Baldwin and Baldwin, 1976; Milton, 1980; Whitehead, 1987; da Cunha and Byrne, 2006).

Acoustic parameters of the howler long calls, such as bandwidth and fundamental frequency, have also been shown to vary between species (Whitehead, 1995; Table 3.1). They separate the genus into two groups, one that contains *A. palliata* and one that contains all of the other species. Interestingly, *A. pigra* is in the non-*palliata* group, providing more evidence for its species-level distinction from the other Central American howlers (Smith, 1970). *A. pigra* and the other members of the non-*palliata* group vocalize continuously for much longer periods of time over a wider bandwidth and higher range of emphasized frequencies than *A. palliata* (Whitehead, 1995). Both male and female *A. palliata* also have much smaller hyoids than the species in the non-*palliata* group, which should affect the range of sounds they are able to produce (Hershkovitz, 1949; see below for further discussion). These interspecific variations in all aspects of long call behavior should have important implications for biogeography, phylogeny, and reconstructing the evolutionary history of *Alouatta*.

Unique vocal tract morphology in Alouatta: Air sacs and hyoids

Most animals that produce loud long calls do so via the help of various types of air sacs in the throat. Even other mammals that roar, like large felines, cervids, and bovids, use air sacs and not expanded hyoid bones (Saber and Hofmann, 1985; Peters and Hast, 1994;

Weissengruber et al., 2002; Frey et al., 2007). Within primates, it has long been noted that chimpanzees and gorillas have air sacs while normally humans do not, suggesting that the loss of air sacs could have played a role in the evolution of speech in modern humans, perhaps by increasing sound stability (Fitch, 2000; Nishimura, 2008; Riede et al., 2008). Their distribution across the rest of the order also provides interesting comparative information. Four types of air sacs have been designated in primates based on their tissue of origin and positioning within the vocal tract (Schön Ybarra, 1995; Hewitt et al., 2002; Frey et al., 2007; Riede et al., 2008):

1. Paired lateral air sacs that develop as outgrowths of the ventricular epithelium and sometimes merge ventrally into one large sac (*Symphalangus*, great apes, *Alouatta* species except for *palliata*, *Callicebus*, *Cebus*, *Colobus*, *Presbytis, Cercopithecus, Macaca*)
2. Paired median air sacs that originate supraglotally from a single midline opening and then balloon forward between the cricoid and thyroid cartilages (callitrichines)
3. A superomedian air sac that originates just above the glottis, splits around the stem of the epiglottic cartilage, and then expands to fill the hyoid bulla (all *Alouatta* species*, Lagothrix, Cebus, Saguinus, Aotus, Colobus* and some other Old World monkeys)
4. An infraglottal posterior air sac that passes dorsally between the cricoid cartilage and first tracheal ring and extends caudally (*Indri, Varecia, Ateles, Microcebus*).

Interestingly, the smallest species of *Hylobates*, another primate known for their loud calls, have neither air sacs nor an enlarged hyoid (Negus, 1949; Schön Ybarra, 1995; Nishimura, 2006).

The lateral air sacs have been suggested to serve a re-breathing function while the subhyoid air sacs may act along with the hyoid as resonating chambers for vocalizations (Schön, 1971; Hewitt et al., 2002; Riede et al., 2008; de Boer, 2009). *Alouatta* (except for *palliata*) has both the lateral and subhyoid air sacs and it has been noted that this gives them a "maximal adaptation to volume at a nearly total sacrifice of modulation" (Kelemen and Sade, 1960; p. 139). There is also some suggestion that the presence or absence of air sacs is related to changes in body size over evolutionary time; in many primate lineages, a decrease in body size is associated with a loss of air sacs and vice versa (Hewitt et al., 2002). This is something to keep in mind when comparing *Protopithecus* and *Alouatta*, which involves a size difference that may relate to an evolutionary decrease in body size. If so, following Hewitt et al. (2002), the presence of air sacs in the smaller-bodied *Alouatta* suggests that in this case they were not lost over evolutionary time, and therefore implying the larger-bodied *Protopithecus* possessed air sacs as well. Either way, the joint presence of air sacs and the enlarged hyoid apparatus in *Alouatta* is a measure of the selective importance of long calling in the lineage. Since the pneumatized hyoid is clearly a derived state, it is reasonable to suppose that it was preceded by a more primitive loud-sound production system, i.e., the more common air sac.

Recently, work has been done on mathematical modeling of the primate vocal tract to better understand the interactions between the air sacs and the rest of the anatomy and how those interactions affect the acoustics of the loud long calls that can be produced (de Boer, 2008; Riede et al., 2008; de Boer, 2009). Not surprisingly, the air sac acts differently whether it is surrounded by soft tissue, cartilage, or bone, but it always increases resonance (de Boer, 2009). When the air sac is contained within the rigid walls of the hyoid it is constantly kept open, meaning vocalizations must be given with an open mouth (Riede et al., 2008), and indeed *Alouatta* manipulates their lips in such a way as to maximize low-frequency sounds (Whitehead, 1995). The "boom" calls of the siamang, on the other hand, resonate through the flexible soft tissue walls of the very large ventral air sac and are given with the mouth closed (Haimoff, 1981; Riede et al., 2008). A “lumped element” model, consisting of the volume of the air sac, the thickness and stiffness of the walls that reverberate the sounds, and the dimensions of the neck that connects the air sac to the rest of the supralaryngeal vocal tract, all of which introduce resistance to the sound waves through inertance and damping, can be used with a “transmission line” model of the vocal tract to approximate the low frequencies found in *A. seniculus* and *A. guariba* calls (de Boer, 2008; de Boer, 2009). The lower resonances that the air sacs, and other things that increase the length of the vocal tract such as protrusion of the lips, help to produce, can increase the perceived body size of the caller, an advantage when calls are used to help avoid physical confrontation between males of neighboring groups (Fitch and Hauser, 1995).

The other relatively well-studied aspect of the supralaryngeal vocal tract that varies considerably across primates is the hyoid bone. The hyoid serves as an attachment point for muscles and ligaments that also serve the mandible, tongue, laryngeal cartilages, pharynx, sternum, and cranial base; hence its proposed functions involving several systems including respiration, swallowing, and vocalizations. The hyoid has embryological origins in the second and third branchial arches; the second arch also gives rise to the stylohyoid ligament and the styloid process of the temporal bone. The hyoid bone usually lies at or above the entrance to the larynx, but there are some mammals, such as whales (Reidenberg and Laitman, 1994), where it is positioned below the larynx. The hyoid apparatus consists of two basic parts: inferiorly, the unpaired basihyal and paired thyrohyal “horns” which connect the basihyal to the thyroid cartilage and, superiorly, the paired suspensory stylohyoid chains which are made up of four cartilaginous or ossified links, the ceratohyal, epihyal, stylohyal, and tympanohyal, that connect the basihyal to the temporal bone (e.g., Howes, 1896; Negus, 1949).

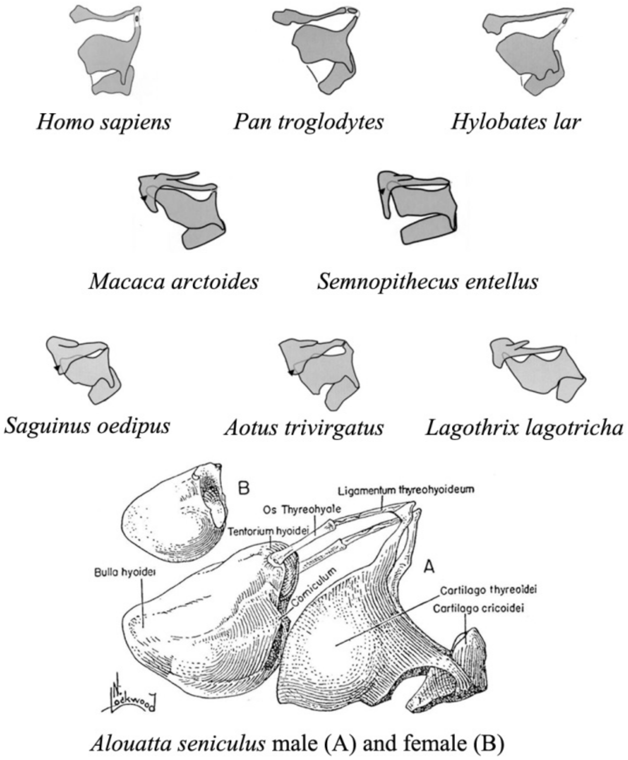

Figure 3.1. Morphology of the hyo-laryngeal complex in primates.
Line drawings based on laryngeal disections modified from Nishimura (2003), *Alouatta* from Hershkovitz (1949).

It is the size and shape of the basihyal portion that varies across primate species. Some Old World monkeys have a caudally expanded basihyal that covers the top of the thyroid cartilage (Negus, 1949; Hilloowala, 1975; Nishimura, 2003), but none are as extremely modified as that of *Alouatta* (Fig. 3.1). Howler monkeys are the only living primates that have evolved a pneumatized hyoid bone with a large, hollow balloon-like basihyal, argued to serve, along with their air sacs, as a resonating chamber (Chapman, 1929; Kelemen and Sade, 1960; Schön, 1971; Hewitt et al., 2002). As the larynx of howlers, and the other non-human primates, is positioned so high in the throat, the supralaryngeal dimensions of the pharynx are small, limiting the range of sounds that can be made (Laitman and Reidenberg, 2009). The expanded hyoid bone and air sacs poitioned above the larynx in *Alouatta* increase the volume of this space and, along with stretching out the neck and manipulations of the lips (Schön, 1986; Whitehead, 1995), make their loud long calls possible.

The size of the hyoid and the anatomical space it requires are not trivial. For example, an average endocranial volume for a mixed sex sample of sixteen *A. belzebul* individuals was 55 ml and the average hyoid volume for four males of that species was 57 ml; in two individuals, hyoid volume was approximately 140% of endocranial volume (pers. obs.). The laryngeal cartilages are also enlarged in *Alouatta*, especially the thyroid, cuneiforms, and epiglottis, which are also sometimes ossified (Kelemen and Sade, 1960; Hill, 1962). The basihyal is joined to the thyroid cartilage with a membranous attachment and the two are free to move more independently of one another in *Alouatta* than in other primates (Schön Ybarra, 1995). As mentioned above, the stylohyoid chain in *Alouatta* is of the common mammalian integro-cornuate type, connecting to the cranial base anterior to the stylomastoid foramen (Howes, 1896; Hilloowala, 1975). Not enough is known about variation in the associated hyoid musculature, and hence how the hyoid moves during howling in the different species, as only a few specimens of *A. seniculus* (Hill, 1962; Schön, 1968, 1971), *A. palliata* (Kelemen and Sade, 1960; Hilloowala, 1975), and *A. caraya* (Schön, 1971) have been dissected. The hyoid bone itself, which was originally referred to as the “throttle-bone”, was first described by Grew (1681) in his catalogue of the collections of the Royal Society: “…’tis hollow, and very hard. Exceeding thin and so half transparent…On the top furrow’d, so as to resemble a Puppies Skull” (p. 11).

While the unique morphology of the bone was mentioned by many early authors, and most often described with the howler long calls in similarly evocative language, variation in hyoid size and shape amongst the species of *Alouatta* was first systematically described by

Hershkovitz in 1949. The morphology of this region has been used as a diagnostic character for species recognition since then by Hill (1962) and many others. The development of the tentorium superiorly and the size and shape of the posterior opening of the basihyal are the most important variables for distinguishing the species from one another (Hershkovitz, 1949; Hill, 1962). Male *A. seniculus* individuals have the largest most inflated hyoid bullae with relatively small posterior openings and wide convex tentoria. *A. guariba* has a larger posterior opening with a less inflated tentorium and no cornua. The hyoid of *A. belzebul* is also in a larger size class with the largest posterior opening and a slightly concave tentorium. Of the larger species, *A. caraya* has the smallest tentorium but a very large posterior opening and a uniquely shortened anteroposterior dimension that gives the bone a "snub-nosed" appearance. The hyoid bullae of *A. palliata* are the smallest with a flared opening, extremely reduced tentorium, and broad attachment sites for the thyrohyal proximally and the stylo-hyoid ligament distally. While *A. pigra* has been considered a subspecies of *A. palliata* and shares with it a Central American distribution, the female hyoid looks more similar to that of the South American species, while the bone in the male has a very unique, almost two-dimensional appearance (Fig. 3.2).

These qualitative descriptions led Hershkovitz (1949) to divide the genus into three groups: the Seniculus group which includes *A. seniculus, A. belzebul*, and *A. guariba*; the Palliata group which includes *A. palliata* and *A. pigra*; and the Caraya group for the snub-nosed *A. caraya*. For Hershkovitz, these groups have evolutionary significance, with *A. palliata* retaining the ancestral condition and *A. seniculus*, especially the males, exhibiting the most derived hyoid shape. Interestingly, while *Alouatta* males do have larger, more inflated hyoid bullae than females of the same species, body size differences between the species do not seem to correspond to differences in hyoid size, or the length of the supralaryngeal vocal tract

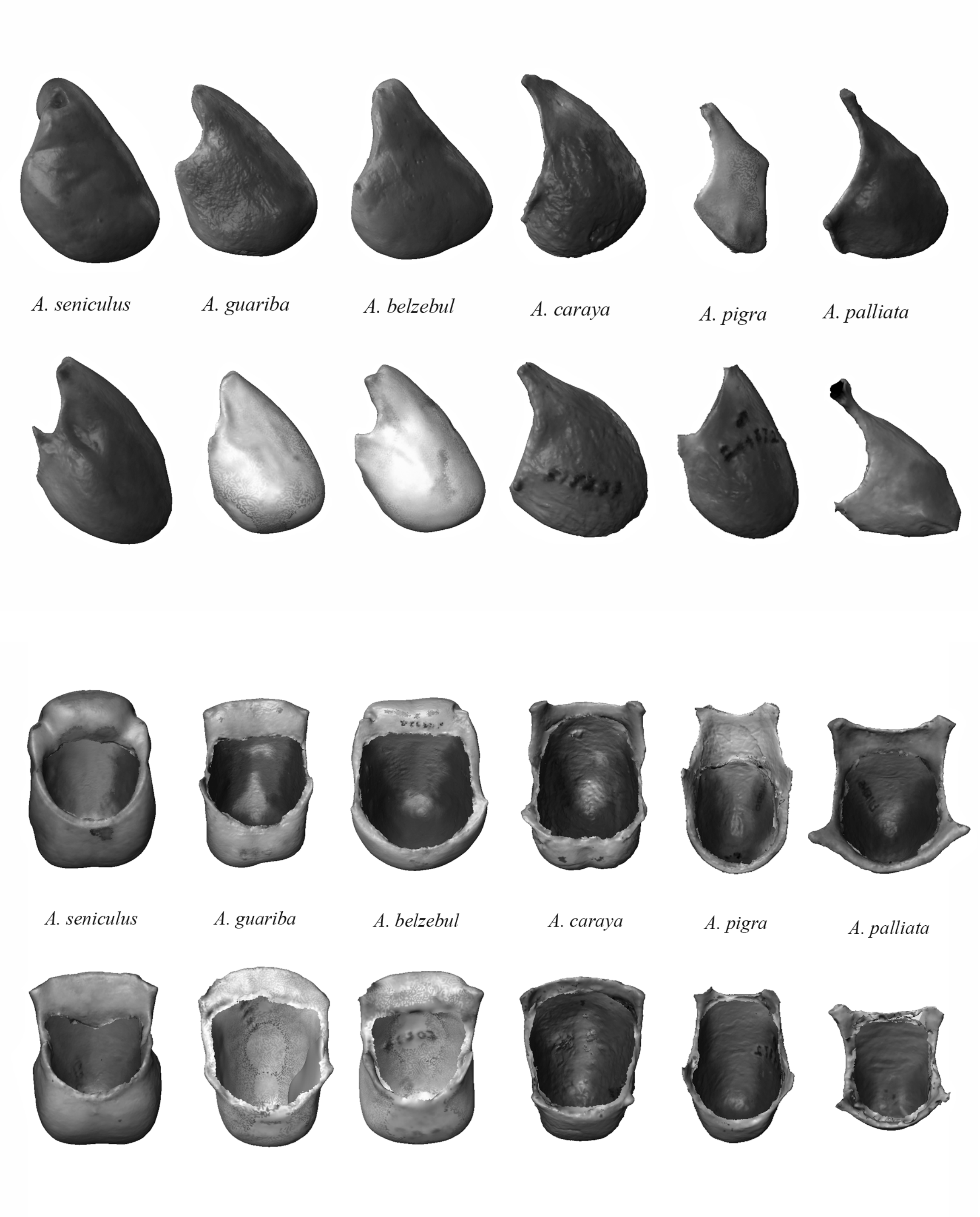

Figure 3.2. Interspecific variation in hyoid shape across *Alouatta*, lateral (top) and posterior (bottom) views. Images are .ply files created from laser surface scans of individual specimens (see Materials and Methods – ragged edges around the posterior opening of the hyoid are an artifact of the scan editing process) chosen from the hyoid sample as typical representatives of each species and scaled to similar size to emphasize shape differences. Top row in each view are males, bottom row are females (*A. pigra* female is mislabeled as a male).

(Hilloowala, 1975; Schön Ybarra, 1995). In other words, the species with the largest average body size does not have the absolutely largest hyoid volume (Table 3.1). These differences in howler monkey hyoid size and shape do, however, seem to correlate with various acoustic features of their calls: *A. palliata* has been shown to vocalize for shorter periods of time over a narrower bandwidth and higher frequency (Sekulic and Chivers, 1986; Whitehead, 1995), they have the smallest hyoids (Hershkovitz, 1949), and as mentioned above, they only have one type of air sac. The impact of this anatomical specialization on the howler skull has yet to be adequately investigated and synthesized, but various unique aspects of cranial and mandibular morphology in *Alouatta* have been suggested to be related to the large size of these vocal tract structures.

Craniomandibular morphology and the vocal tract in Alouatta and Protopithecus

Unfortunately, the *Protopithecus* mandible is incomplete so comparisons of some of the more important regions cannot be made to *Alouatta* with certainty (Fig. 3.3). For example, the posterior portion of the fossil mandible is missing so it is not immediately apparent if the gonial region is expanded as in *Alouatta*, although this was suggested by Hartwig (2005) based on the slope of the inferior border that is preserved. Like many craniomandibular traits that are uniquely exaggerated in *Alouatta*, a wide bi-gonial breadth has been explained both as functionally important for processing a mostly folivorous diet as well as an architectural consequence of the enlarged hyoid bone. Flaring of the gonial angles allows the mandible to pass lateral to the enlarged hyoid bone during maximum gape, and their expansion also provides a larger area of attachment for the masseter muscles used during chewing (see Herring, 1975; Bruner et al., 2004). The growth of the mandible during ontogeny is tied to hyoid development, as the gonial angles move further laterally and posteriorly in males than in females to make room

Figure 3.3. Comparison of *Protopithecus* (left) and *Alouatta sp.* (right) cranial morphology. Lateral view (top) and basal view (bottom). Scale bars = 1 cm.

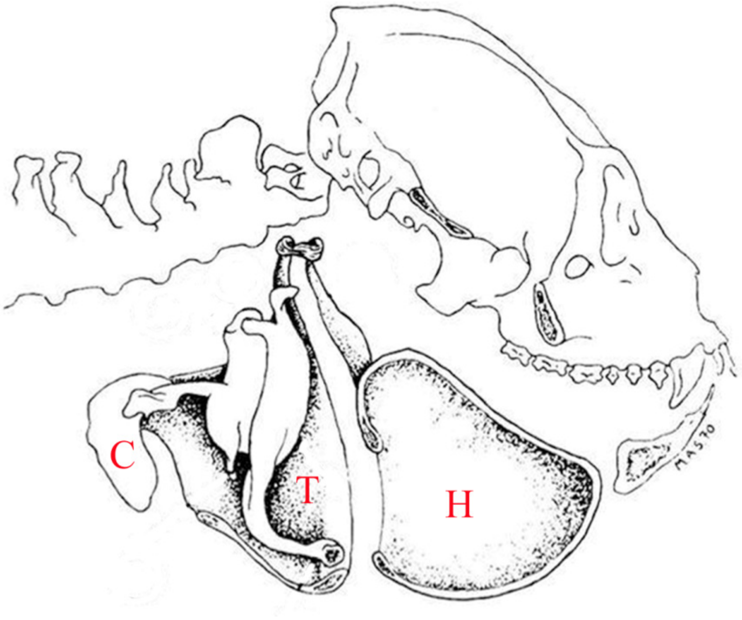

Figure 3.4. Spatial relationship between the hyo-laryngeal apparatus and the cranium in *Alouatta*. The mandible and zygomatic arch are cut away to show the hyoid (H) and thyroid (T) cartilages in cross-section, as well as the cricoid cartilage (C), aretynoid, cuneiform, and epiglottis. Drawing is of a male *A. seniculus*, modified from Schön (1971).

for the former's larger hyoid (Watanabe, 1982). The medial pterygoid muscle, which also attaches to the gonial angle, is thought to elevate and protract the mandible during howling (Schön, 1968), also suggesting that various aspects of mandibular morphology in *Alouatta* are related to the production of vocalizations.

In the cranium, the long narrow base with an airorynchous face and flat, posteriorly facing nuchal plane, traits that are also seen to some degree in *Protopithecus*, are most often argued to be associated with opening space for the enlarged hyoid (Biegert, 1963; Hartwig and Cartelle, 1996; Miller and Begun, 1998; Figs. 3.3-4). One line of evidence supporting this functional interpretation comes from the spatial relationships between the shared airorynchous face and well-developed anatomical structures used in vocal production seen in both *Alouatta* and *Pongo* (Biegert, 1963; Shea, 1985; Bruner et al., 2004). However, just as in the mandible, these same traits have been functionally linked to folivory. For example, similar functional analogies have been drawn between the large subfossil lemur *Megaladapis* and the extremely folivorous Australian koala (*Phascolarctos*) based on similar degrees of airorynchy and a vertical nuchal plane that change the orientation of the head on the neck and make it easier to crop leaves (Tattersall, 1972). Other folivorous subfossil lemurs, *Palaeopropithecus* and *Archeoindris*, share these cranial traits as well (Godfrey and Jungers, 2002). Interestingly, male koalas also give quite a loud long call during mating season and have a modified larynx (Charlton et al., 2011), further suggesting that howling, folivory, and vocal tract specializations go hand, in hand, in hand; as described above, it could be that the less caloric energy an animal receives from its main dietary resource, the more important howling becomes as a way to avoid costly physical confrontations between individuals over territory and mates. The way the vocal tract and cranium are modified would then vary from species to species based on other functional and selective pressures.

This argument goes both ways, however, as *Alouatta* and *Brachyteles* share dental adaptations to their semi-folivorous diet, but *Brachyteles* skulls look more like those of their atelin relatives and do not have an airorynchous face or posteriorly directed occipital (Rosenberger et al., 2011). Nor does *Brachyteles* have the small brain of howler monkeys, another important variable to consider when thinking about the functional morphology and architectural relationships within the *Alouatta* skull (e.g., Ross and Ravosa, 1993; Lieberman et al., 2000; Jeffery, 2003). The “spatial packing” hypothesis (Biegert, 1963; Gould, 1977; Ross and Ravosa, 1993) suggests that, in primates, basicranial flexion is not adaptive but is instead related to relative brain size; the larger the brain, the more flexed is the cranial base. For *Alouatta* then, an unflexed cranial base is to be expected based on their small brain size. The extreme nature of both of those traits, the unflexed cranial base and small brain, can be further explained by the necessity for opening of the subbasal space and the lack of nutrients from their semi-folivorous diet, respectively.

Teasing apart these potential sources of selective pressure on cranial morphology may have wide reaching implications as it has been suggested that the facial profile of the Caribbean *Paralouatta* is simply a retention of a primitive atelid cranial form and not evidence that the Cuban monkey is a close relative of both *Protopithecus* and *Alouatta* (e.g., Horovitz and MacPhee, 1999). If the link between an airorynchous face with a flat nuchal plane and a folivorous diet is robust, then this might lend support to the cranial similarities between *Protopithecus, Paralouatta*, and *Alouatta* being the result of convergent evolution instead of a strong phylogenetic relationship. However, reconciling this with the frugivorous signal given by the dentitions of *Protopithecus* and *Paralouatta* is a necessary step in this line of investigation that needs to be pursued. As in many discussions of the functional and/or adaptive value of complex morphological characters, it is likely that both vocal tract morphology and the equipment necessary to process leaves have each had influence over craniomandibular morphology in *Alouatta*. The questions that *Protopithecus* can potentially answer surround the sequence of the evolutionary modifications leading to the full-blown *Alouatta* morphological pattern (see Chapter 5).

The results of quantitative work done recently on aspects of the cranial, mandibular, and hyoid variation described here are listed in Table 3.2. Many other studies on one or two species groups, most commonly *A. seniculus* and/or *A. palliata*, also exist. However, all base their conclusions on very small sample sizes and they have different foci such as ontogenetic trajectories and/or sexual dimorphism

Table 3.2. Results of previous work on interspecific variation in *Alouatta*.

Author	**Date**	**Variable**[1]	**Groups**
Hershkovitz	1949	Hyoid	(palliata + pigra) + (caraya) + (guariba + belzebul + seniculus)
Halpern	1987	Skull/hyoid	(palliata + caraya) + (seniculus + belzebul)
Whitehead	1995	Acoustics	(palliata) + (non-palliata)
Miller and Begun[2]	1998	Cranial base angle	(palliata) + (non-palliata)
Cortes-Ortiz et al.	2003	mtDNA	(palliata + pigra) + ((seniculus + caraya) + (guariba + belzebul))
Gregorin	2006	Skull/hyoid	(palliata + caraya) + (guariba + belzebul + seniculus)
Halenar	2012	Cranial base Mandible Hyoid	(palliata + non-palliata) (males) + (females) (pigra) + (palliata + caraya) + (guariba + belzebul) + (seniculus)

[1] Any difference in results between studies using the same variable could be due to differences in sample size
[2] Abstract only – more specific grouping pattern is not detailed

(Watanabe, 1982; Cole, 1990; Ravosa and Ross, 1994; Bruner et al., 2004; Blanco and Godfrey, 2006)or extant taxonomy without the inclusion of fossils or regard for the evolutionary history of the alouattin lineage (Bonvicino et al., 1995; Miller and Begun, 1998; Gregorin, 2006). The work most relevant in the present context is Halpern (1987), an unpublished dissertation using factor analysis to investigate co-variation between the hyoid, cranium, and mandible in all species of *Alouatta*, except for *A. pigra*. Over 100 *Alouatta* crania were included in the sample, but many were juveniles and not all had associated hyoids. Results indicated that linear measurements of mandibular size and cranial length were associated with one another on the first factor as the most highly correlated aspects of shape. Hyoid length, hyoid breadth, and bicondylar breadth of the mandible were associated with each other on the second factor. This pattern suggested that there was no simple relationship between the three morphological areas, hyoid, cranium, and mandible. The size of the hyoid was not as highly correlated with basicranial dimensions as expected, and it was thus concluded that both the development of the hyoid and adaptations to folivory are important for understanding howler cranial morphology. With a more comprehensive sampling of *Alouatta* and application of powerful 3DGM methods, a more nuanced analysis will hopefully clarify some of these questions and reveal more about hyoid size and shape in *Protopithecus*.

Materials and Methods

In order to investigate the size and position of the hyo-laryngeal apparatus of *Protopithecus,* it is first necessary to examine the morphological variation amongst the six most commonly recognized living species of *Alouatta: A. belzebul, A. caraya, A. guariba, A. palliata, A. pigra,* and *A. seniculus*. A Microscribe 3DX digitizer was used to collect *x, y, z* coordinate points describing the shape of the cranial base and mandible of over 400 adult male and female *Alouatta* from the collections at the AMNH, NMNH, MN, and the Field Museum of Natural History (FMNH) in Chicago (Table 3.3; Fig. 3.5; Table 3.4). An attempt was made to include populations from as many different geographic locations as possible, as *Alouatta* is a widespread genus and morphology is expected to vary greatly over almost an entire continent. This sample includes most subspecies that some recent authors would regard as distinct species from those listed above (e.g., Bonvicino et al., 1995; Groves, 2001; Rylands et al., 2005; Gregorin, 2006; see Chapter 1). Approximately 200 males and females of *Lagothrix, Ateles,* and *Brachyteles* are also included for comparative purposes, representing the morphology of related taxa with a non-pneumatized hyoid and a much smaller range of interspecific variation (Table 3.3). The fossil sample includes the cranial base and mandible of *Protopithecus* and *Caipora*, both found in the Toca da Boa Vista caves and curated in the Museu de Ciências Naturais at the Pontificia Universidade Católica de Minas Gerais in Belo Horizonte, Brazil (MCL), as well as

Table 3.3. Extant comparative sample.

Genus	Species	Subspecies	Country	Cranial Base		Mandible		Hyoid	
				M	F	M	F	M	F
Alouatta	*belzebul*	*belzebul*	Brazil	19	21	19	20	6	7
Alouatta	*belzebul*	*discolor*	Brazil	6	6	5	5	-	-
Alouatta	*belzebul*	*nigerrima*	Brazil	10	11	10	11	-	-
			N	**35**	**38**	**34**	**36**	**6**	**7**
Alouatta	*caraya*		Brazil	13	7	11	5	7	6
			Bolivia	6	9	6	8	5	6
			Paraguay	-	1	-	1	-	-
			N	**19**	**17**	**17**	**14**	**12**	**12**
Alouatta	*guariba*	*guariba*	Brazil (NE)	11	8	4	3	3	2
Alouatta	*guariba*	*clamitans*	Brazil (SE)	16	19	5	3	4	4
			N	**27**	**27**	**9**	**6**	**7**	**6**
Alouatta	*palliata*	*mexicana*	Mexico	4	7	4	6	-	-
Alouatta	*palliata*	*palliata*	El Salvador	2	1	2	1	2	1
			Honduras	3	1	2	1	-	-
			Nicaragua	3	3	2	1	-	-
			Costa Rica	2	4	2	4	-	-
Alouatta	*palliata*	*aequatorialis*	Costa Rica	2	4	2	3	-	-
			Panama	11	11	9	10	1	-
			Colombia	2	-	2	-	-	-
			Ecuador	8	7	6	7	-	-
Alouatta	*palliata*	*coibensis*	Panama	1	2	-	2	-	-
			N	**38**	**40**	**31**	**35**	**3**	**1**
Alouatta	*pigra*		Mexico	2	5	2	5	-	-
			Guatemala	8	3	6	3	2	1
			N	**10**	**8**	**8**	**8**	**2**	**1**
Alouatta	*seniculus*		Suriname	4	2	3	2	-	-
			Ecuador	1	-	1	-	-	-
			Peru	4	4	3	4	-	-
			Bolivia	3	9	3	8	2	4
			Brazil	1	2	1	2	1	-
Alouatta	*seniculus*	*sara*	Bolivia	1	2	1	2	-	-
Alouatta	*seniculus*	*insularis*	Trinidad	9	10	8	7	-	-
Alouatta	*seniculus*	*seniculus*	Colombia	31	30	29	28	26	22
			Ecuador	1	2	1	1	-	-
			Peru	15	18	12	16	3	2
Alouatta	*seniculus*	*straminea*	Guyana	4	5	3	4	2	2
			Brazil	6	5	6	5	-	-
			N	**80**	**89**	**71**	**79**	**34**	**30**
Ateles	*belzebuth*		Venezuela	3	7	3	7	-	-
			Colombia	2	1	2	1	-	-
			Peru	3	2	3	2	-	-
			N	**8**	**10**	**8**	**10**	**0**	**0**
Ateles	*fusciceps*	*robustus*	Panama	4	5	4	5	-	-
			Colombia	4	-	4	-	-	-
			N	**8**	**5**	**8**	**5**	**0**	**0**
Ateles	*geoffroyi*	*frontatus*	Nicaragua	-	3	-	3	-	-
Ateles	*geoffroyi*	*geoffroyi*	Nicaragua	-	3	-	3	-	-
Ateles	*geoffroyi*	*panamensis*	Costa Rica	6	5	6	5	-	-
Ateles	*geoffroyi*	*vellerosus*	Mexico	9	7	9	7	-	-
			Honduras	-	2	-	2	-	-
			N	**15**	**20**	**15**	**20**	**0**	**0**
Ateles	*paniscus*	*chamek*	Peru	1	8	1	7	-	-
			Brazil	4	-	4	-	-	-
Ateles	*paniscus*	*paniscus*	Guyana	1	2	1	2	-	-
			Suriname	-	2	-	2	-	-
			Brazil	-	3	-	3	-	-
			N	**6**	**15**	**6**	**14**	**0**	**0**
Brachyteles	*arachnoides*		Brazil	**13**	**10**	**13**	**7**	**0**	**0**
Lagothrix	*flavicauda*		Peru	1	1	1	1	-	-
Lagothrix	*lagotricha*	*cana*	Peru	3	1	3	1	-	-
			Brazil	7	4	7	4	-	-
Lagothrix	*lagotricha*	*lagotricha*	Colombia	1	1	1	1	1	-
			Peru	2	5	2	5	-	-
			Brazil	3	2	3	2	-	-
Lagothrix	*lagotricha*	*lugens*	Colombia	6	3	6	3	2	-
Lagothrix	*lagotricha*	*poepeggii*	Ecuador	1	-	1	-	-	-
			Peru	10	10	10	10	-	-
			N	**34**	**27**	**34**	**27**	**3**	**0**

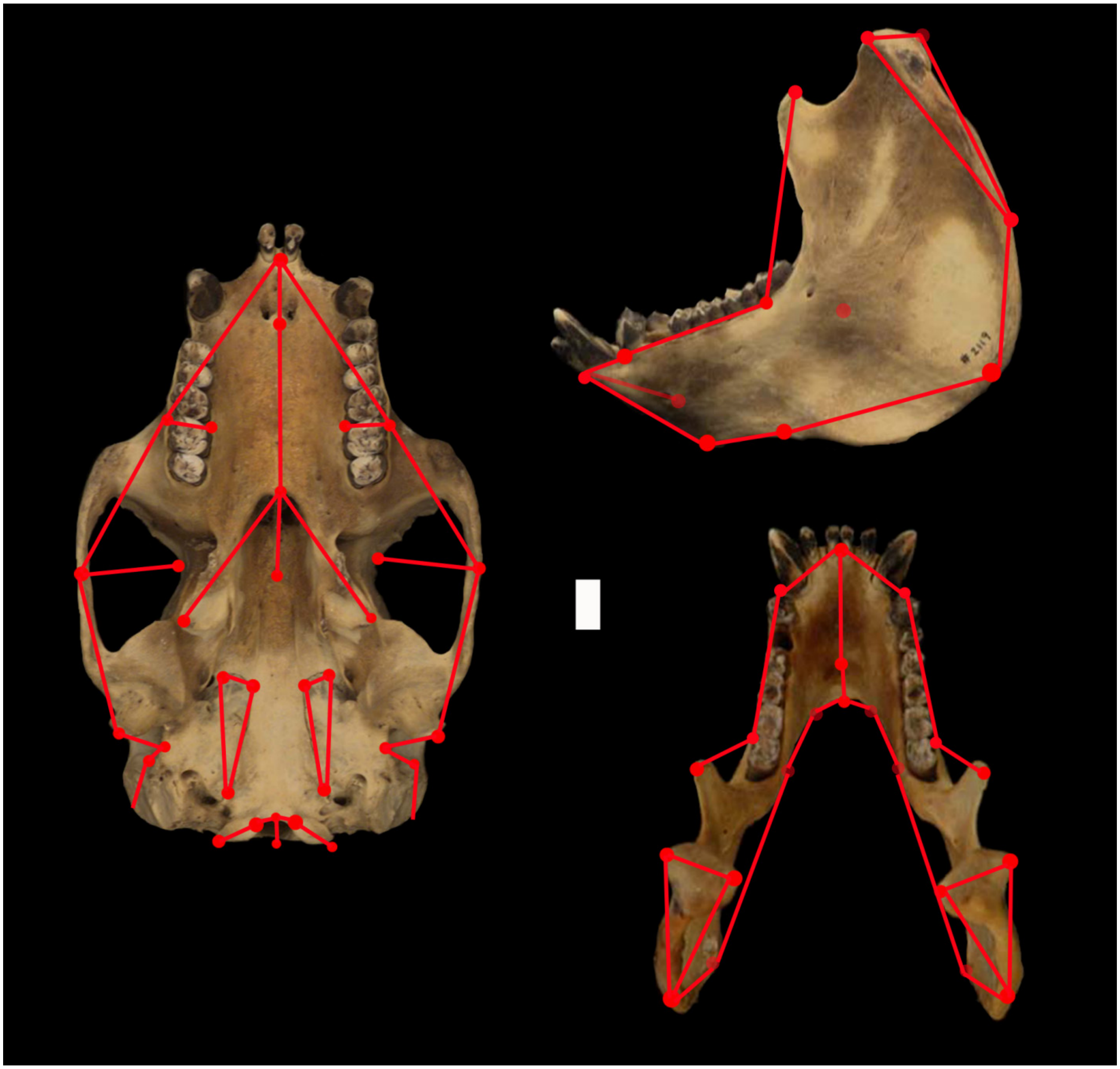

Figure 3.5. Landmarks recorded on the cranial base and mandible.
Landmarks shown in lateral view on the mandible were recorded on both sides and the mandible was positioned in such a way that all landmarks could be recorded without moving the bone. Landmarks are connected with a wireframe to make shape changes in subsequent analyses easier to visualize. See Table 3.4 for landmark definitions. Photographs are of *Alouatta caraya* (male) from the Mammalian Crania Photographic Archive. Scale bar = 1 cm.

Table 3.4. Anatomical landmark definitions.

Cranial Base

CB1[1]	Orale
CB2	Posterior incisive foramen
CB3	Alveolon
CB4	Endomolare (right)
CB5	Ectomolare (right)
CB6	Endomolare (left)
CB7	Ectomolare (left)
CB8[2]	Inferior zygomaticotemporal suture (right)
CB9[3]	Inferior zygomaticotemporal suture (left)
CB10	Most medial point in temporal fossa (right)
CB11	Most medial point in temporal fossa (left)
CB12	Inferior tip of the right lateral pterygoid
CB13	Inferior tip of the left lateral pterygoid
CB14	Hormion
CB15	Lateral point on the anterior portion of the suture outlining the petrous portion of the temporal (right)
CB16	Lateral point on the anterior portion of the suture outlining the petrous portion of the temporal (left)
CB17	Medial point on the anterior portion of the suture outlining the petrous portion of the temporal (right)
CB18	Medial point on the anterior portion of the suture outlining the petrous portion of the temporal (left)
CB19	Inferior tip of the postglenoid process (right)
CB20	Inferior tip of the postglenoid process (left)
CB21	Inferior point on the external auditory meatus (right)
CB22	Inferior point on the eam (left)
CB23	Superior point on the eam (right)
CB24	Superior point on the eam (left)
CB25	Posterior point on the suture outlining the petrous portion of the temporal (right)
CB26	Posterior point on the suture outlining the petrous portion of the temporal (left)
CB27	Basion
CB28	Opistion
CB29	Anterior point on the right occipital condyle
CB30	Anterior point on the left occipital condyle
CB31	Posterior point on the right occipital condyle
CB32	Posterior point on the left occipital condyle
CB33	Inion
CB34	Midpoint of the right half of the lambdoidal suture
CB35	Midpoint of the left half of the lambdoidal suture

Mandible

M1	Infradentale
M2	Gnathion
M3	Midpoint of the "simian shelf"
M4	Buccal C/P2 (right)
M5	Buccal C/P2 (left)
M6	Buccal M2/M3 (right)
M7	Buccal M2/M3 (left)
M8	Inferior border of the corpus below C/P2 (right)
M9	Inferior border of the corpus below C/P2 (left)
M10	Inferior border of the corpus below M2/M3 (right)
M11	Inferior border of the corpus below M2/M3 (left)
M12	Tip of the coronoid process (right)
M13	Tip of the coronoid process (left)
M14	Most lateral point on the right condyle
M15	Most medial point on the right condyle
M16	Most lateral point on the left condyle
M17	Most medial point on the left condyle
M18	Anterior point on the border of the mandibular foramen (right)
M19	Anterior point on the border of the mandibular foramen (left)
M20	Midpoint of the posterior border of the ramus (right)
M21	Midpoint of the posterior border of the ramus (left)
M22	Gonion (right)
M23	Gonion (left)

[1] Landmarks in bold are missing for *Paralouatta*
[2] Landmarks in red are missing for *Protopithecus*
[3] Landmarks in red italics are missing for *Caipora*

an AMNH cast of the *Paralouatta varonai* skull (Rivero and Arredondo, 1991). None of the fossil skulls are complete so several landmarks were left out of analyses including the full fossil sample (Table 3.4). As there is a relatively high degree of sexual dimorphism in some species, males and females were analyzed both together and separately.

Many of the landmarks are standard craniometric points that are generally considered to be the most reliable in terms of biological homology and repeatability across taxa (Type I; Bookstein, 1991). As one hypothesis being tested is the similarity of the *Protopithecus* and *Alouatta* cranial base and mandible, the landmarks were chosen to describe proposed alouattin synapomorphies: extreme airorynchy and enlargement of the palate, elongation of the midline structures of the cranial base, posterior orientation of the occipital, small size of the foramen magnum, large size of the temporal fossa and high degree of postorbital constriction, large molars, gonial angle expansion, sloping of the inferior border of the mandibular corpus, and increased width and height of the ramus. The shape of the portion of the temporal bone where the stylohyoid chain connects the hyoid with the cranial base was also included in an effort to capture this anatomical relationship. Many landmarks also fall on attachment sites for the hyoid musculature; for example, landmarks M19 and M20 on the mandibular foramen mark the posterior attachment of the mylohyoid muscle (Table 3.4). In general, if the cranial base modifications in *Alouatta* are structurally related to opening space for the hyoid, one expects that the airorynchy, elongation of the midline basicranium, and expansion of the posterior part of the mandible, all features that are captured by the landmark set, would tightly co-vary with hyoid size and shape (see below).

Over 100 undeformed *Alouatta* hyoids were laser scanned using either a portable Minolta Vivid 910 laser surface scanner or a NextEngine desktop 3D scanner. As the bony walls of many of the smaller hyoids were too thin to be "seen" properly by the lasers, the hyoid bullae were stuffed with paper towels to make the bone more opaque. The scans were edited using *Geomagic Studio* and ScanStudio HD v. 1.3.0, and a .ply file was created for each specimen (Harcourt-Smith et al., 2008). The *Landmark Editor* program (Wiley, 2006) was then used to place homologous landmark points across the superior aspect of the tentorium as well as at the four corners of the posterior opening of the basihyal. These landmarks were used as anchors for drawing automated curves that generate semi-landmarks which quantify the bulbous aspect of the anterior portion of the bone (Bookstein, 1997; Gunz et al., 2005; Fig. 3.6). This procedure captured not only the size of the hyoid, which has been approximated in previous studies by measuring its length and/or width, but also the bone's contours, which contribute to the unique shape of the hyoid in each species. Several *Lagothrix* hyoids were also scanned and landmarked, functioning as an "outgroup" (see Fig. 3.1).

The data were subjected to a generalized Procrustes analysis (GPA; Rohlf and Slice, 1990) to translate, rotate, and scale all specimens to unit centroid size using the *morphologika*^{2} v2.5 software program (O'Higgins and Jones, 2006). The curves of semi-landmarks on the hyoids were also subjected to a "sliding" protocol using a program implemented in MATLAB in order to minimize Procrustes distance between the specimens and the calculated reference specimen (Bookstein, 1997; Gunz et al., 2005). Sliding the semi-landmarks along the outline curves is an extension of the standard GPA superimposition procedure and is necessary to properly account for Type III semi-landmarks having fewer degrees of freedom than those of Type I or Type II (Adams et al., 2004). Multivariate statistics were then used to assess co-variation between aspects of basicranial, mandibular, and basihyal shape in *Alouatta*.

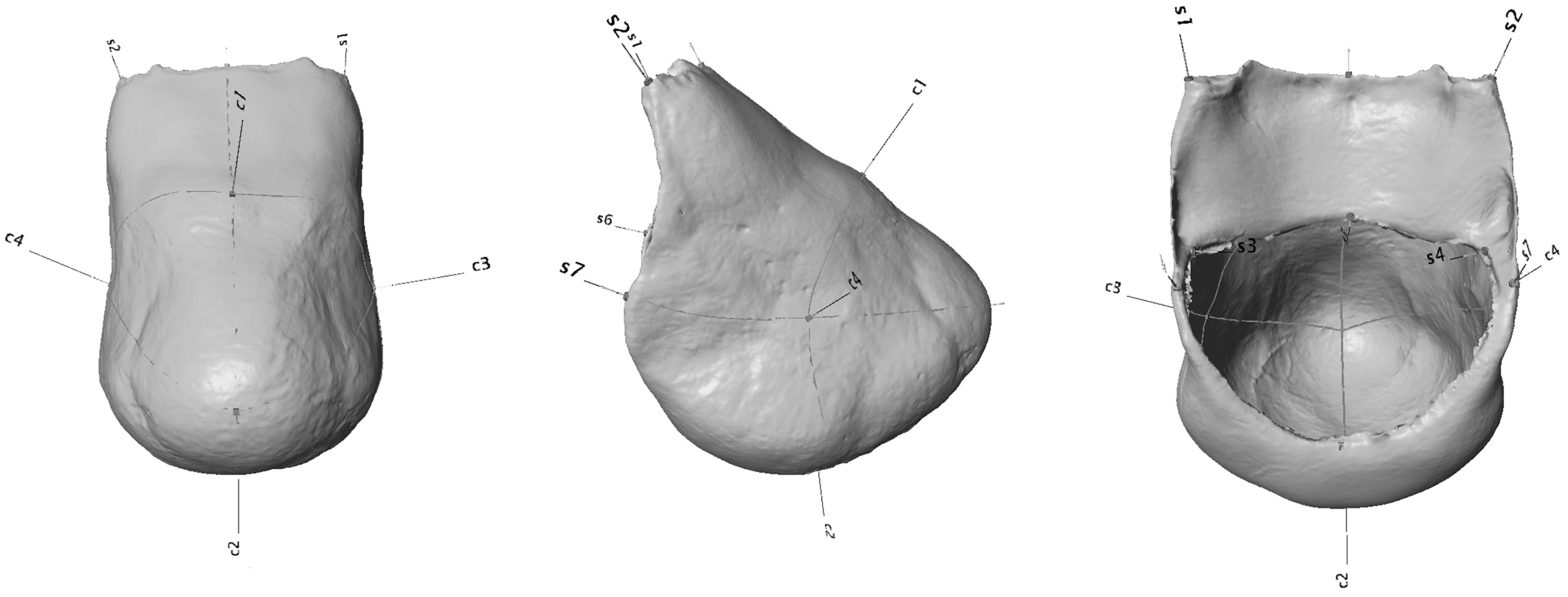

Figure 3.6. Landmarks recorded on the hyoid.
Images are from *Landmark Editor*, showing points and curves on a typical male *A. seniculus* hyoid.

Two-block partial least squares analysis (2B-PLS; Rohlf and Corti, 2000; Bookstein et al., 2003) has recently been used to assess co-variance between independent sets of data including geographic coordinates and cranial shape in both papionins and modern humans (Frost et al., 2003; Baab et al., 2010), matching laser scans of tibial-talar joint surfaces in fossil hominins (Harcourt-Smith et al., 2008), and foraging strategy and bill shape in birds (Marugan-Lobon and Buscalioni, 2006; Kulemeyer et al., 2009). Here it was used as an exploratory technique to assess levels of co-variance between the cranial base and the hyoid, the mandible and the hyoid, and the cranial base and the mandible in extant *Alouatta*. As the analysis will always find some co-variation in the two blocks of data, permutation tests were run to check for statistical significance of the results. If hyoid size and shape are very highly correlated with basicranial shape within living *Alouatta*, then the size and shape of the *Protopithecus* hyoid can be reconstructed from the relevant fossil morphology. As the hyoid bone sits between the gonial angles of the mandible in *Alouatta*, and therefore is constrained in maximum size by those bony boundaries, co-variation between the hyoid and mandible was also investigated using the same methodology.

The MorphoJ v. 1.02e software package (Klingenberg, 2011) was used to output results for the 2B-PLS analyses, in the form of both graphs and statistics such as the RV coefficient, which measures the overall strength of association between the two blocks of data (Robert and Escoufier, 1976; Klingenberg, 2009). Principal components analysis (PCA) was also used to visualize the morphological variation in the sample for the cranial base, mandible, and hyoid. The PAST 1.89 software package (Hammer et al., 2001) was used to perform and output graphical representation of the PCAs, as well as calculate minimum spanning trees, i.e., the shortest possible set of lines connecting the mean shapes for males and females of each species in the comparative sample, based on Procrustes distances between the three-dimensional shapes.

Results

Extant variation

A principal components analysis of the entire extant cranial base sample shows genus-level distinctions among the atelines as well as some species-level separation within the *Alouatta* sample (Fig. 3.7). A morphocline of sorts is formed across PC1 from the extreme airorynchy, narrow occipital, and large palate of *Alouatta* on the negative end of PC1 to the opposite configuration in *Ateles* on the positive end, with *Lagothrix* and *Brachyteles* representing intermediate morphology. PC2 separates *Alouatta* into two groups, one made up of the *A. palliata* individuals and one of the other non-*palliata* species, confirming qualitative observations discussed above. *A. palliata* has a rounder occipital and wider bi-zygomatic distance with less post-orbital constriction than the other species of *Alouatta*. These distinctions are also seen when *Alouatta* is analyzed alone, and when males and females of *Alouatta* are analyzed separately (Figs. 3.8-9). In these PCAs, *A. seniculus* seems to be the most variable species, but it is unclear whether this is because it has the widest geographic distribution or because it is represented by the largest number of individuals in the sample. *A. caraya* and *A. guariba* overlap one another, potentially reflecting their geographic proximity and their ability to hybridize (Aguiar et al., 2007; Bicca-Marques et al., 2008). However, as discussed above, *A. palliata* and *A. pigra* are always separate from each other in these analyses despite being Central American neighbors who have also been seen to hybridize (Cortes-Ortiz et al., 2007). The lack of clear separation between each of the six species is not unexpected, as their taxonomic

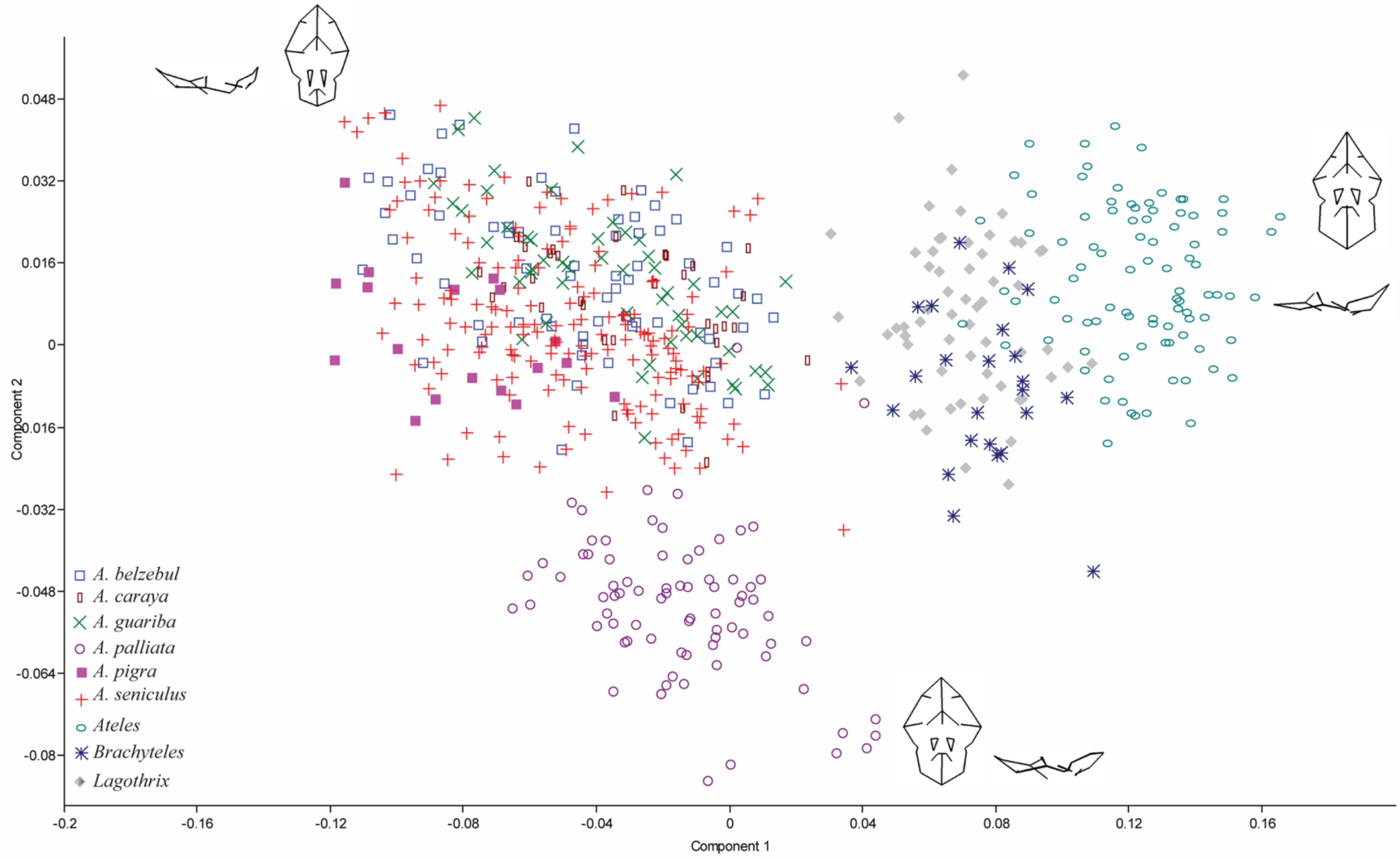

Figure 3.7. PCA results for the cranial base using the entire extant comparative sample.
As shown by the wireframes (cranial base landmarks in inferior and lateral view, with the incisors to the top and to the left, demonstrating the morphology seen in the nearest cluster of individuals – see Fig. 3.5), PC1 (51% total variance) is being driven by degree of airorynchy and relative size of the face and occipital. PC2 (6%) separates *A. palliata* from the other species based on its rounder occipital and wider bi-zygomatic breadth.

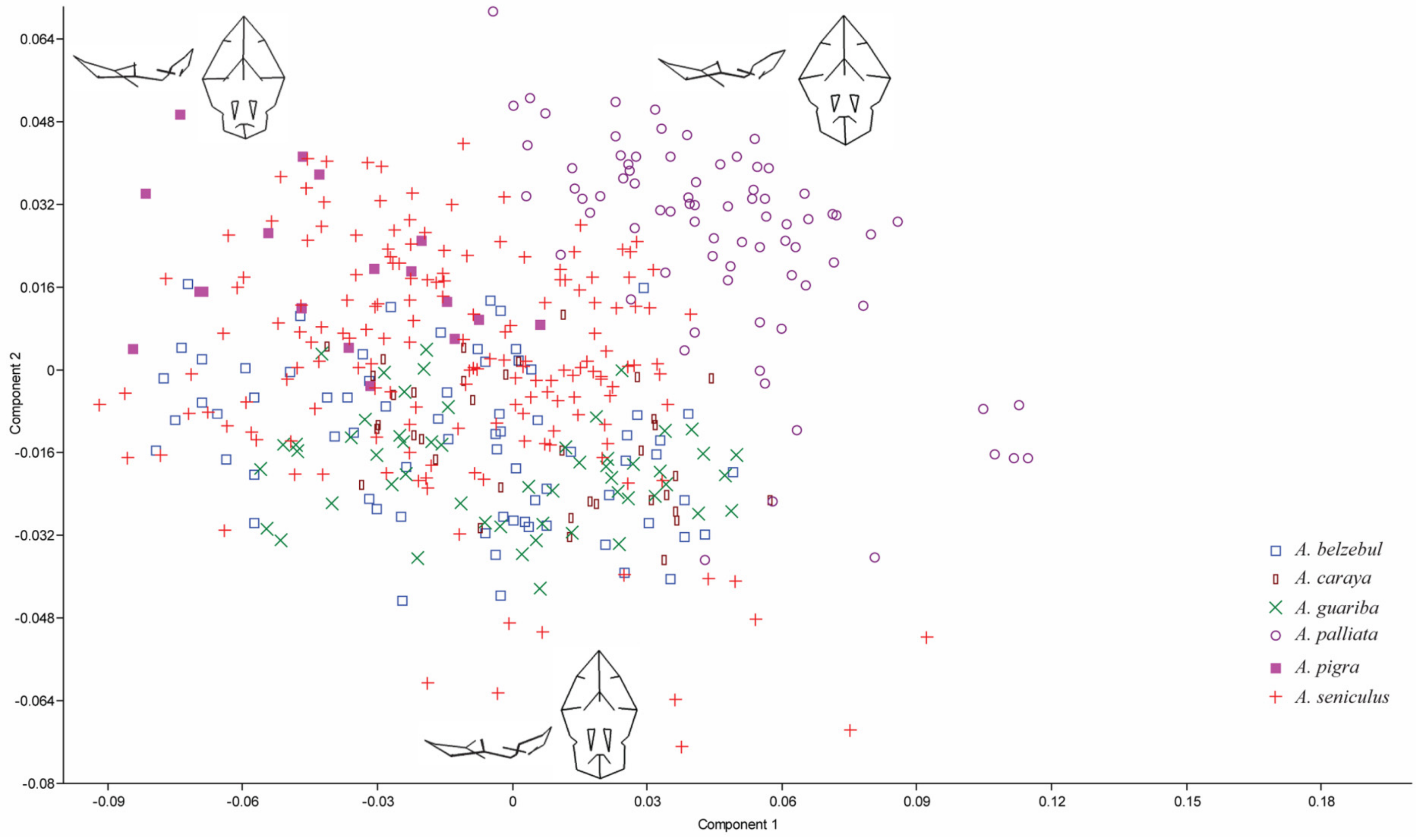

Figure 3.8. PCA results for the cranial base using the *Alouatta* sample.
PC1 (25% total variance) and PC2 (9%) separate *A. palliata* from the other species in a similar way as in Fig. 3.7. Wireframes again represent the cranial base in inferior and lateral view as they appear in the nearest cluster of individuals.

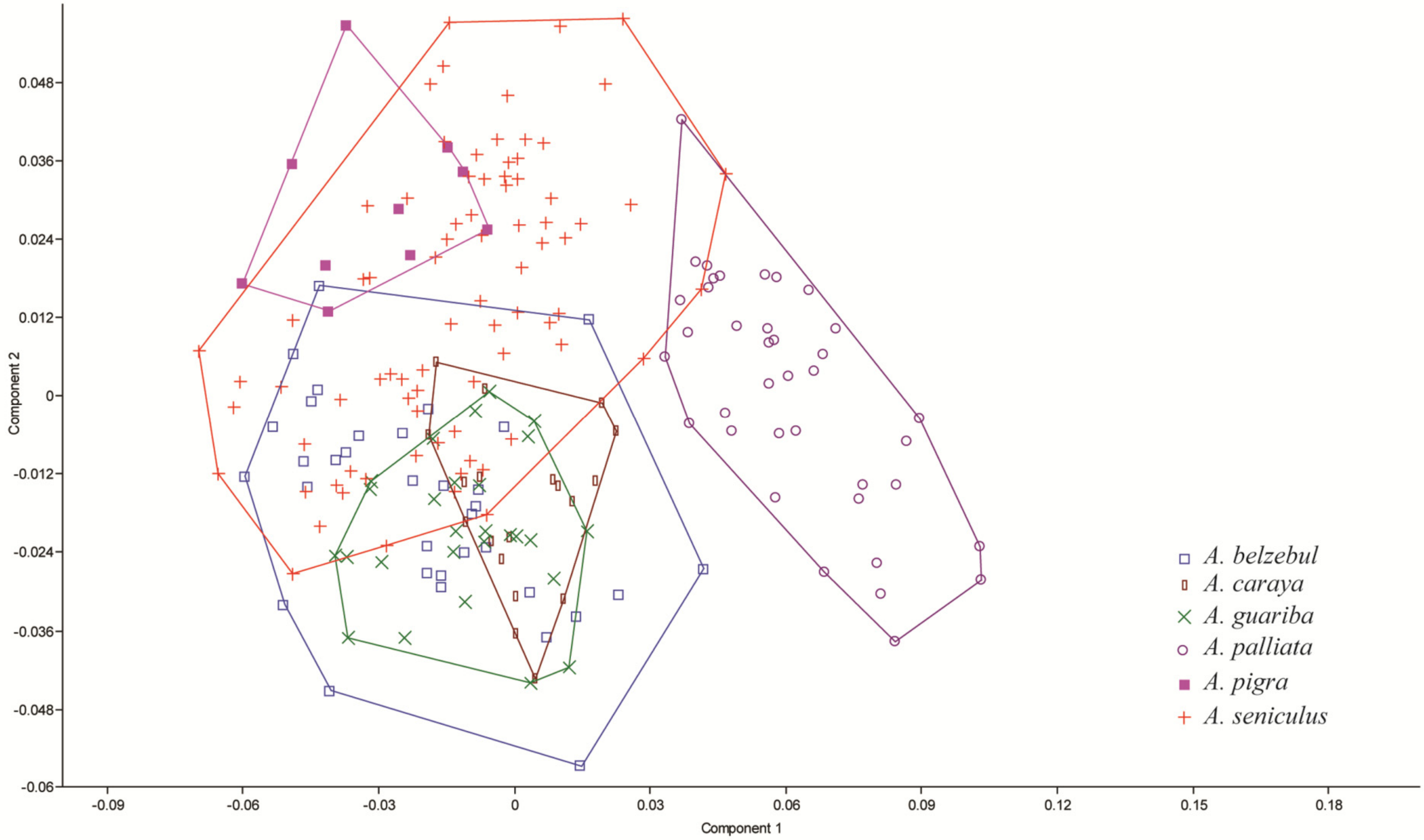

Figure 3.9. PCA results for the cranial base using the male *Alouatta* sample.
Convex hulls surround the distribution of each species. Note the clear separation between *A. pigra* and *A. palliata* and the overlap between *A. pigra* and the South American species. Also note the overlap between *A. caraya* and *A. guariba*, potentially reflecting their propensity for hybridization.

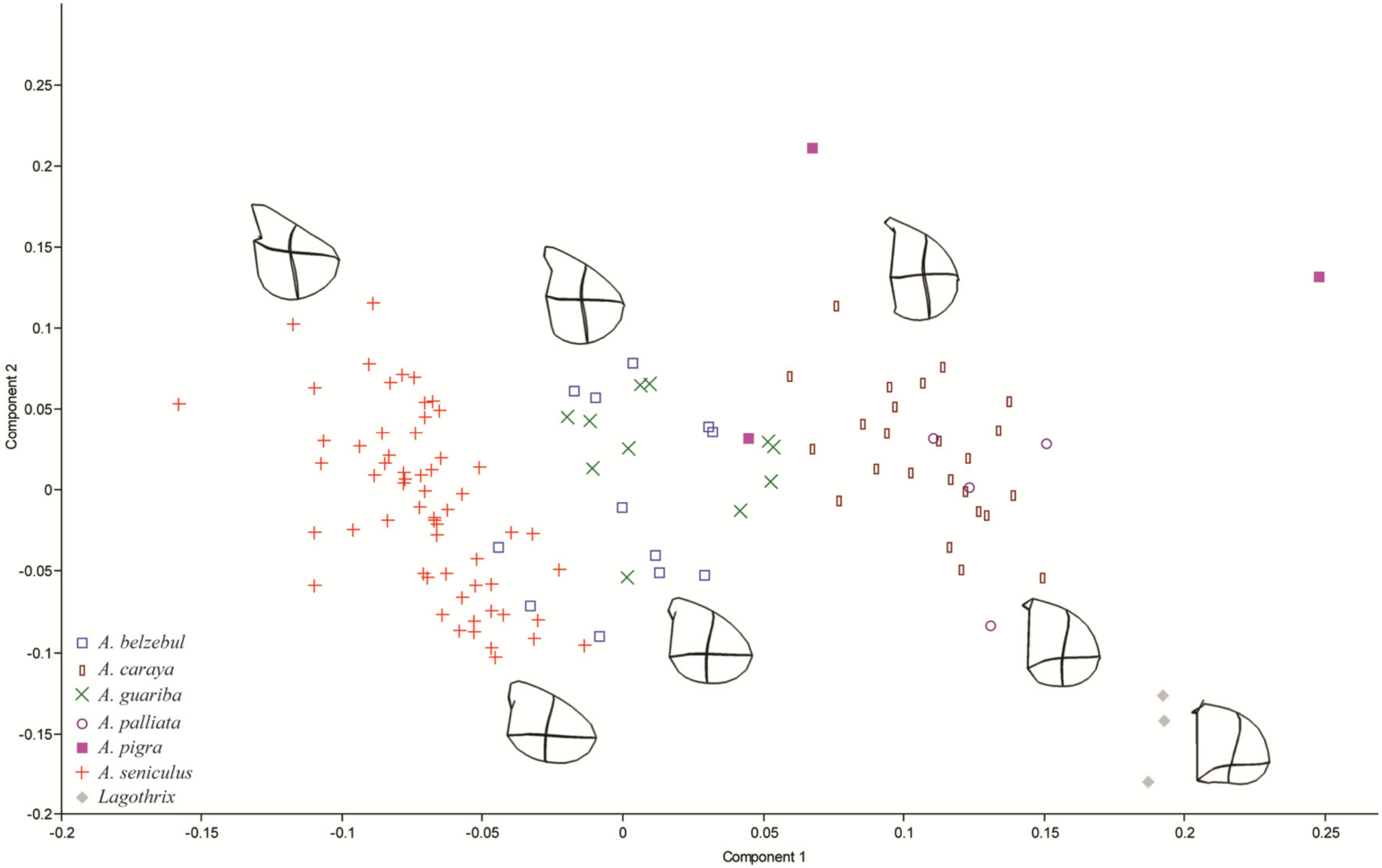

Figure 3.10. PCA results for the hyoid.
Sample includes males and females of all species of *Alouatta* and three *Lagothrix* individuals. PC1 (37% total variance) separates *A. seniculus* from the other species as the most bulbous with the smallest posterior opening while PC2 (18%) separates males, individuals towards the top of each species cluster, from females, individuals towards the bottom (see also Fig. 3.13). Wireframes show the curves on the basihyal in lateral view with the anterior portion of the bone facing to the right to more easily visualize the shape change along PC1 and the difference between males and females of each species (see Fig. 3.6).

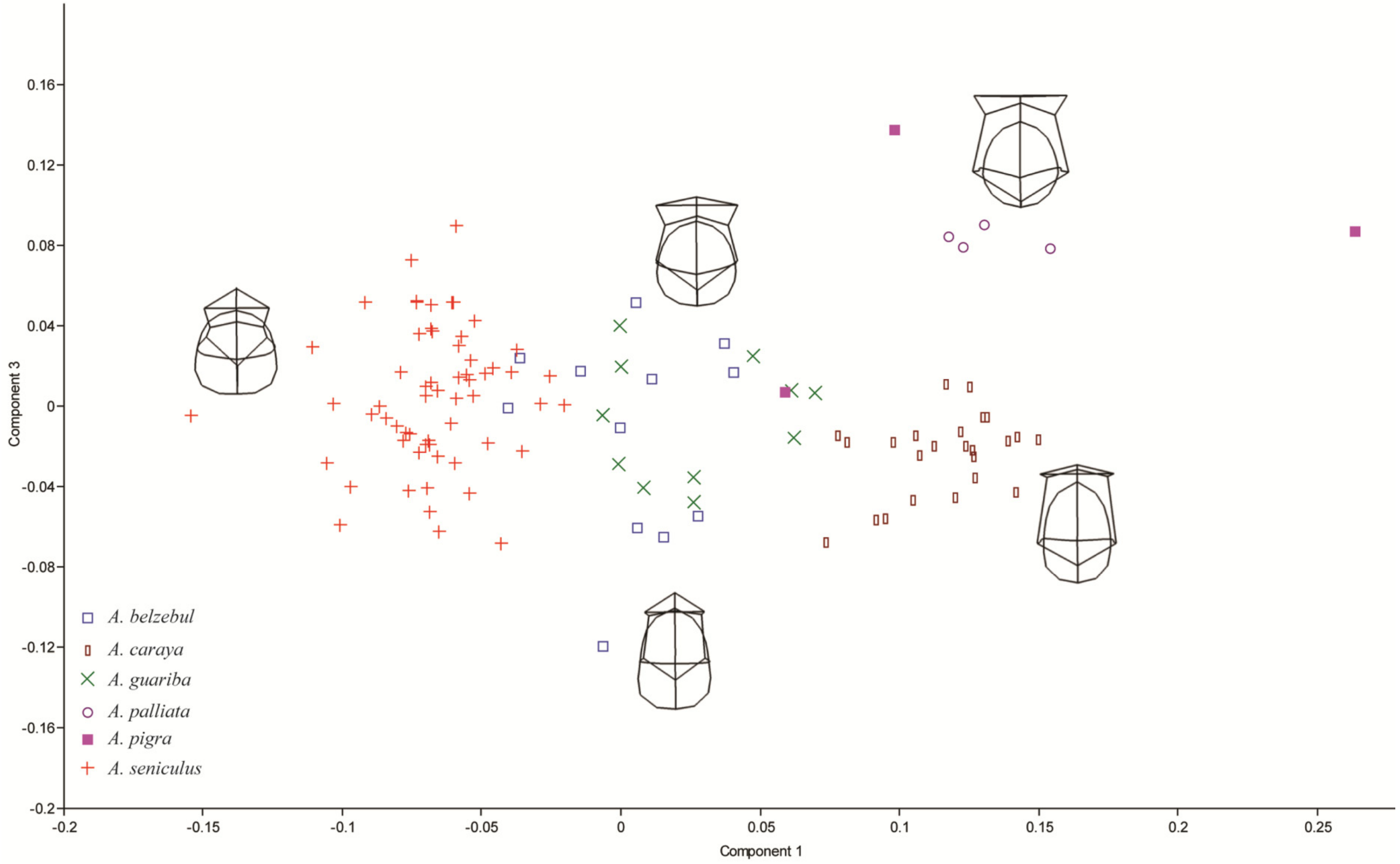

Figure 3.11. PCA results for the hyoid using the *Alouatta* sample, PC1 vs PC3.
When the *Lagothrix* individuals are excluded from the sample, PC3 (9% total variance) separates *A. palliata* from *A. caraya*. PC1 (39%) is still driven by the contours of the inferior portion of the basihyal as well as the dimensions of the posterior opening and tentorium. Wireframes show the hyoid in posterior view, again to visualize the shape differences between the species.

designations do not always reflect factors such as habitat type, diet, social group pattern, and other socioecological variables that relate to long call behavior, which may in turn influence similarities and differences in the cranial base.

Similar patterns of variation are seen when the hyoid sample is visualized (Figs. 3.10-11); the *A. palliata* and non-*palliata* groups are not as separate as expected, but this could be due to the much smaller sample size of *A. palliata* compared to the other species. These groupings do, however, generally agree with those described in previous studies of interspecific hyoid variation (Table 3.2). While having a slightly concave basihyal, the three *Lagothrix* hyoids are clearly separate from the *Alouatta* sample; *Ateles* hyoids look similar to those of *Lagothrix,* but unfortunately none could be laser scanned for this analysis. The anterior-posterior dimension of the basihyal, along with the position of the four corners surrounding the posterior opening, are the main axes of interspecific variation seen in the sample, in agreement with the qualitative descriptions given above. There is some suggestion of geographic separation within the *A. caraya* and *A. seniculus* samples; Brazilian and Bolivian *A. caraya* form relatively distinct clusters as do Colombian and non-Colombian *A. seniculus* (Fig. 3.12).

Intraspecific variation is also seen in *Alouatta* for the hyoid and the cranial base, and is especially clear in the mandible, as the larger male hyoid bone must sit within a wider male mandible (Fig. 3.13). Variation in the *Alouatta* mandible is so closely related to size that species- specific groups are not visible in the PCA results (see below). However, dimorphism indices for the cranial base and mandible, while significant, are not as high as those for the hyoid (Table 3.5). The species with the largest hyoids as measured by centroid size, *A. belzebul*, *A. seniculus*, and *A. guariba*, are also the most dimorphic. But as noted above, these are not the species with the largest body sizes nor the highest body size dimorphism indices

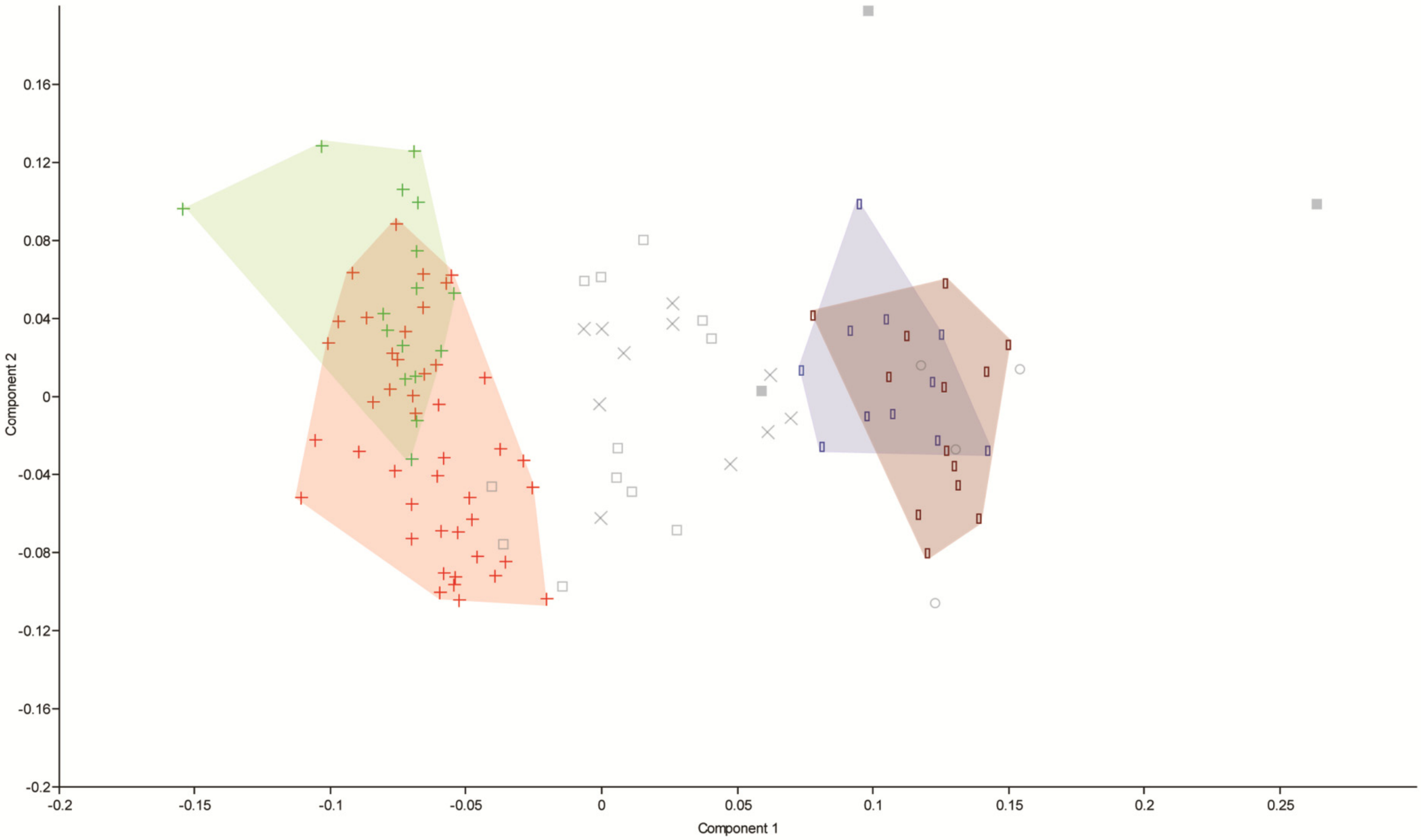

Figure 3.12. Geographic separation within the *A. seniculus* and *A. caraya* hyoid samples.
The green polygon bounds the subset of the *A. seniculus* sample not from Colombia. The *A. caraya* individuals bounded by the blue polygon are from Bolivia while those bounded in brown are from Brazil. Faded symbols indicate species as in previous figures.

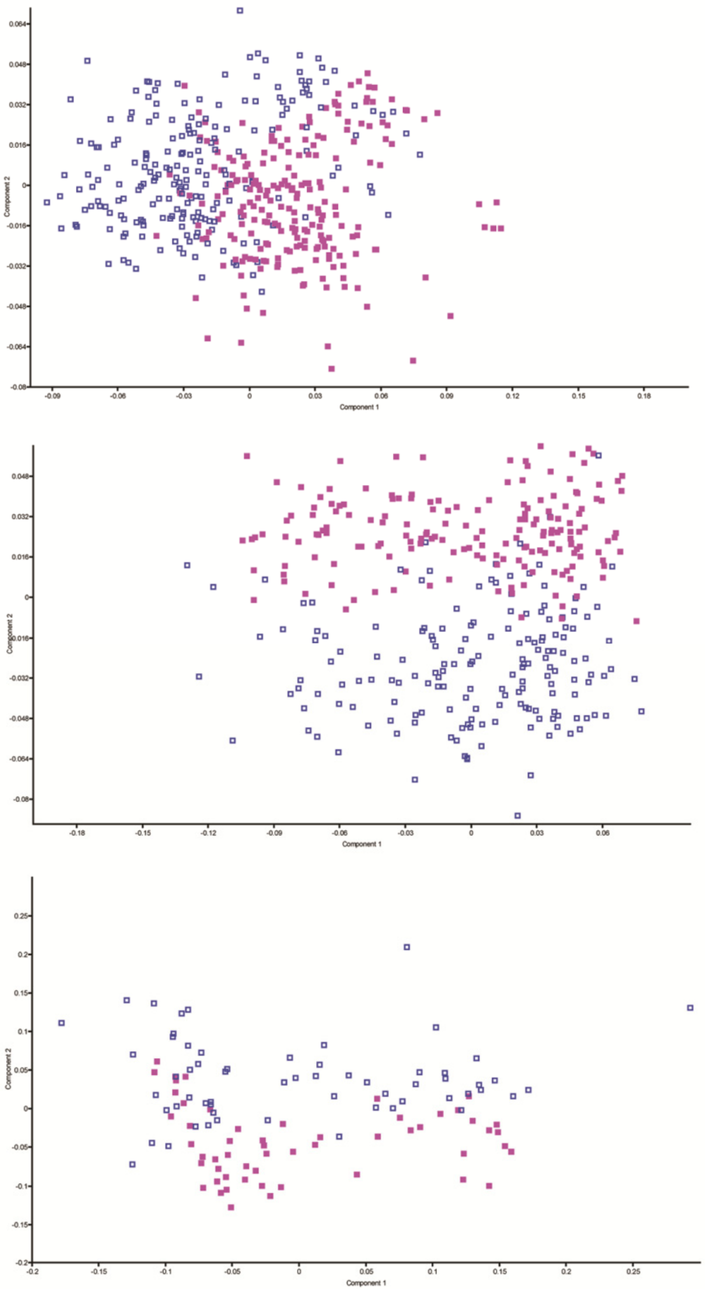

Figure 3.13. Sexual dimorphism in the *Alouatta* cranial base (top), mandible (middle), and hyoid (bottom). All three graphs are the results of PCAs with male individuals symbolized by blue squares and females by pink squares. For the cranial base, PC1 separates larger males from smaller females – regressing ln centroid size on PC1 scores gives an R^2 value of 0.6. This size distinction is even clearer for the mandible, where it is PC2 that correlates with size with an R^2 of 0.8. Graphically, the separation between males and females for the hyoid looks distinct, but the R^2 values for PC1 and PC2 are both relatively low at 0.4. This would indicate that hyoid shape differs more than hyoid size between the sexes in *Alouatta*.

Table 3.5. Sexual dimorphism in the *Alouatta* cranial base, mandible, and hyoid.

Cranial Base

	Dimorphism Index[1]	Male Centroid Size		Female Centroid Size		t_s[2]
		Average	Range	Average	Range	
A. belzebul	1.212	229	198-258	189	170-214	8.97569E-19
A. caraya	1.220	216	196-231	177	168-184	3.1858E-15
A. guariba	1.194	215	187-231	180	166-194	1.30402E-15
A. palliata	1.130	200	170-225	177	164-195	5.27008E-14
A. pigra	1.141	219	202-237	192	186-198	2.8924E-06
A. seniculus	1.181	222	186-258	188	165-220	8.76819E-34
			Mandible			
A. belzebul	1.266	219	184-241	173	155-195	9.89459E-23
A. caraya	1.197	207	185-220	173	160-212	1.38614E-08
A. guariba	1.213	205	181-225	169	161-174	6.25827E-05
A. palliata	1.157	192	160-207	166	151-177	7.61439E-16
A. pigra	1.167	210	195-223	180	173-188	1.49297E-05
A. seniculus	1.243	215	176-239	173	156-198	7.44797E-42
			Hyoid			
A. belzebul	1.631	212	177-248	130	114-145	0.001410726
A. caraya	1.414	164	150-186	116	107-127	7.9887E-10
A. guariba	1.615	197	164-213	122	119-126	1.14752E-05
A. palliata	1.581	117	115-121	74		
A. pigra	1.033	124	106-143	120		
A. seniculus	1.679	220	179-267	131	114-172	2.08292E-25

[1] Dimorphism Index = average male centroid size/average female centroid size (Ford, 1994).
[2] t_s = *t*-statistic - two-tailed, two-sample unequal variance test for equal means

(see Ford, 1994). Male hyoid centroid sizes also vary more widely from species to species than those of females. An explanation for this, as well as why there are some males on the "female side" of the clusters in Figure 3.13, could be that non-dominant but fully adult males are vocalizing less than the dominant males, and therefore have smaller musculature moving their smaller, more female-like hyoids.

These grouping patterns suggest a relatively high level of variation in cranial base and hyoid morphology that should yield robust 2B-PLS results and allow for predictions to be made about the fossil's morphology. They also show very interesting patterns in the *Alouatta*-only sample that suggest a complex relationship between morphology and behavior, with possible biogeographic implications for evolutionary relationships that should be explored in the future.

Extant co-variation

Results of the 2B-PLS analyses show that the cranial base, as defined by the landmarks recorded here, seems to have more potential predictive power than the mandible; there is less overlap between the species in terms of the possible hyoid morph on the y-axis per each cranial base morph on the x-axis (Fig. 3.14). For the mandible, the high degree of sexual dimorphism in *Alouatta* is increasing the variation within each species, making this type of one-to-one correspondence less clear (Fig. 3.15). Despite this, the correlation on the first PLS is slightly higher between the mandible and hyoid shapes (0.75, $P < 0.0001$) than between the cranial base and hyoid (0.67, $P < 0.0001$). PLS1 explains 68% of the co-variance between the cranial base and hyoid and 63% of the co-variance between the mandible and hyoid; this indicates that there are more PLS axes, and hence more shape variables, that describe meaningful co-variation between the mandible and hyoid than between the cranial base and hyoid.

The loadings of the variables on PLS1 support suggestions of a relationship between airorynchy and opening of the subbasal space; the orientation of the midline landmarks on the cranial base co-vary with the length of the hyoid, with more airorynchous individuals possessing larger more bulbous hyoids (Fig. 3.14). Co-variation on PLS1 for the mandible and hyoid also support a spatial relationship between the two bones; as the inferior border of the mandible widens outside the toothrow and increases its slope, both the mediolateral and cranio-caudal dimensions of the hyoid expand to fill the newly created space (Fig. 3.15).

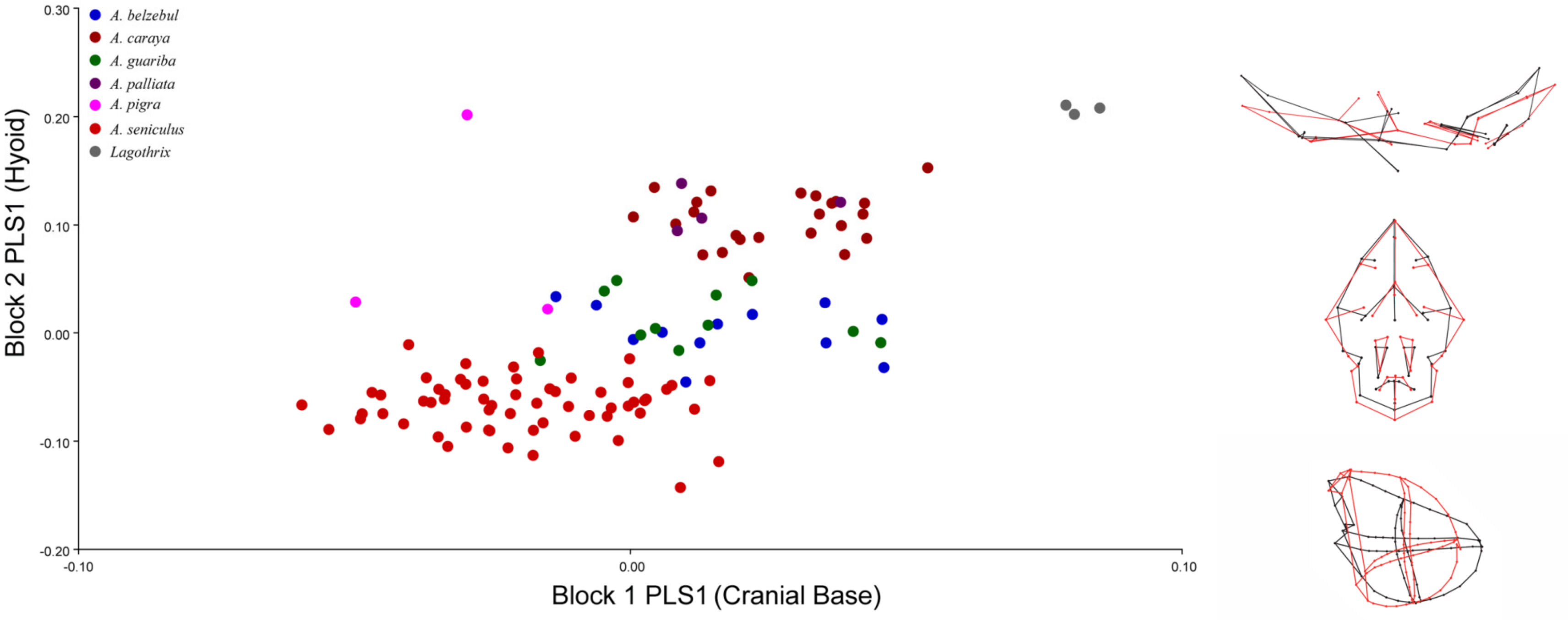

Figure 3.14. 2B-PLS results showing co-variation between the cranial base and hyoid, PLS1.
Wireframes show the shape change from the negative end of PLS1 (black) to the positive end of PLS1 (red) for the cranial base in lateral (top) and inferior (bottom) views and the hyoid in lateral view (see Figs. 3.5-6). A narrow cranial base with an airorynchous face and vertically oriented occipital are seen in individuals that also have a highly inflated, bulbous hyoid (*A. seniculus* at the bottom left) while a more flexed cranial base angle and wide bi-zygomatic breadth are found in conjunction with a shorter anteroposterior dimension of the basihyal (*Lagothrix* at the top right).

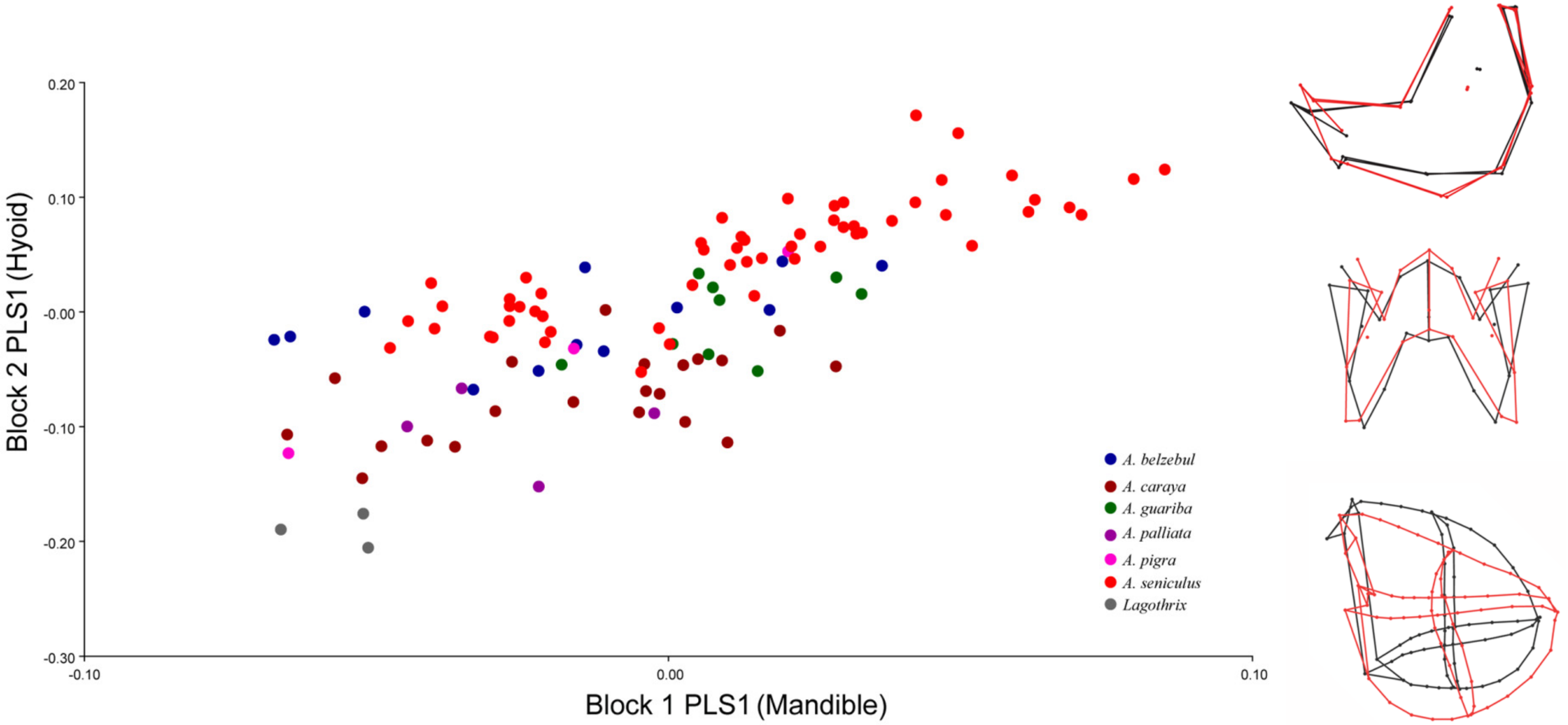

Figure 3.15. 2B-PLS results showing co-variation between the mandible and hyoid, PLS1.
Wireframes show the shape change from the negative end of PLS1 (black) to the positive end of PLS1 (red) for the mandible in lateral (top) and posterior (bottom) views and the hyoid in lateral view (see Figs. 3.5-6). A horizontal inferior border of the mandibular corpus and narrow bi-gonial width occur in individuals with a compressed cranio-caudal dimension of the hyoid (*Lagothrix* at the bottom left) while a sloping inferior border and wide bi-gonial width correspond to an expansion in all dimensions of the inferior curvature of the hyoid (*A. seniculus* at the top right). The two relatively separate clusters for each species are male individuals to the positive end of the axes and females to the negative ends.

PLS2 also explains a significant proportion of the co-variation (16-17%, $P < 0.0001$) for both the cranial base and mandible, still with relatively high, significant correlations (0.50 and 0.67, respectively, $P < 0.0001$) (Figs. 3.16-17). PLS2 reflects co-variation between the relative dimensions of the occipital to the palate and the size of the tentorium and posterior opening of the hyoid; individuals with a larger palate and smaller occipital have hyoids with a very large posterior opening and almost flat basiyhal (Fig. 3.16). The functional relationship between those aspects of the morphology is unclear. For the mandible as well, PLS2 is related to dimensions of the posterior opening and the expansion of the anterior portion of the hyoid. In the mandible, these hyoid dimensions co-vary with the anteroposterior length of the ramus and the relative position of the gonial angle; flaring gonial angles attached to a long ramus are found together with large posterior openings and more of a snub-nose look (Fig. 3.17).

The low RV coefficients for the cranial base/hyoid and mandible/hyoid analyses, 0.28 and 0.33 respectively, suggest that while correlations on pairs of PLS axes may have been relatively high, overall, the bones are not tightly integrated. There could be smaller modules within each bone that co-vary more closely with one another (Klingenberg, 2009); for example, the posterior portion of the mandible behind the M3 could have a closer relationship to the hyoid that it surrounds than the anterior portion of the bone. The highest correlations found in previous studies of co-variation amongst these bones were between their overall lengths and breadths, but smaller components like bi-gonial width, occipital width, and ramus height also had relatively high correlations with hyoid dimensions (Watanabe, 1982; Halpern, 1987). The low RV coefficients seen here leave room for other variables besides vocal tract morphology, like adaptations for processing a particular diet and/or relative brain size, to be influencing both cranial base and mandible morphology in this sample.

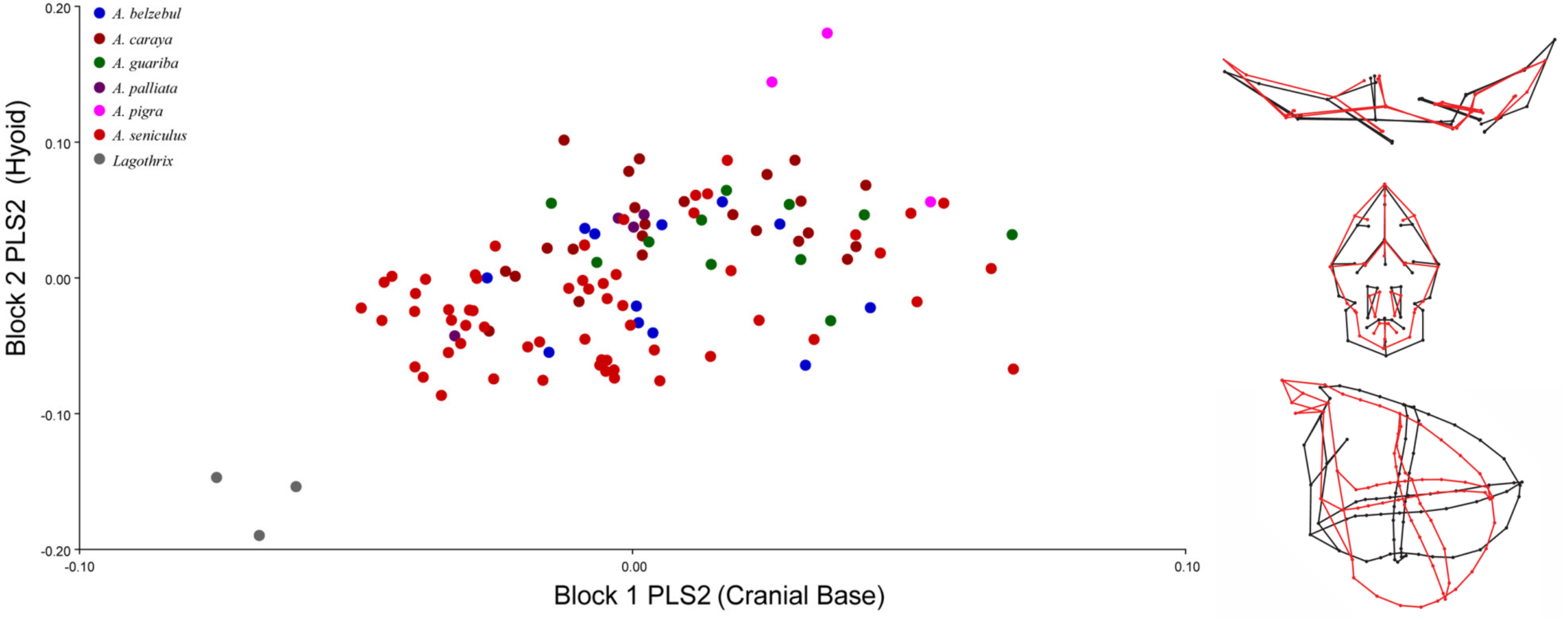

Figure 3.16. 2B-PLS results showing co-variation between the cranial base and hyoid, PLS2.
Wireframes show the shape change from the negative end of PLS2 (black) to the positive end of PLS2 (red) for the cranial base in lateral (top) and inferior (bottom) views and the hyoid in lateral view. A larger, rounder occipital region and relatively anteroposteriorly elongated hyoid are found in taxa towards the bottom left of the cluster while a wider palate, narrow occipital, and more flexed cranial base angle are found in taxa like *A. pigra* on the top right that have a much flatter hyoid with a very large posterior opening.

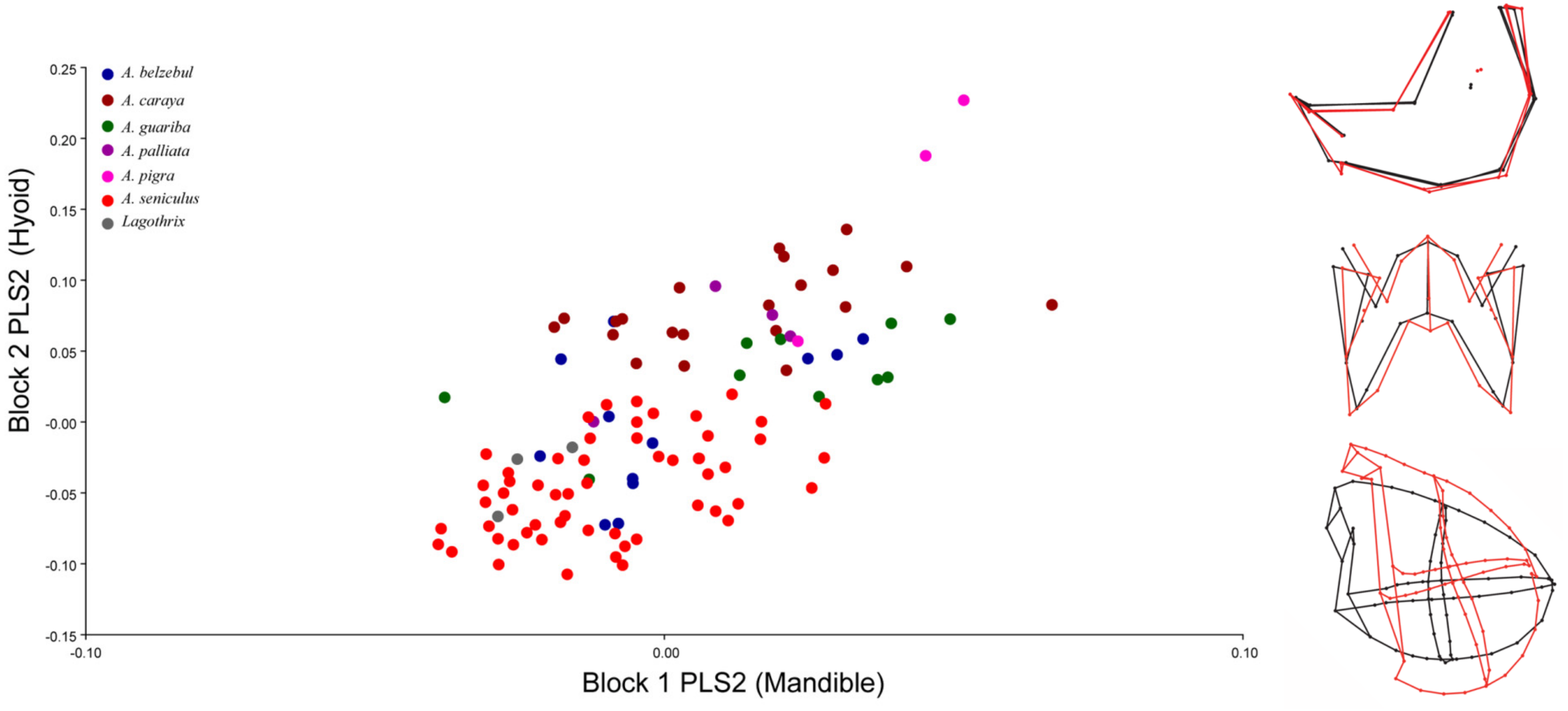

Figure 3.17. 2B-PLS results showing co-variation between the mandible and hyoid, PLS2.
Wireframes show the shape change from the negative end of PLS2 (black) to the positive end of PLS2 (red) for the mandible in lateral (top) and posterior (bottom) views and the hyoid in lateral view. The shape change in the hyoid is much more drastic with the unique form of the *A. pigra* male hyoid separating itself out on the positive end of the axis. The gonial angles of the mandible expand slightly in this taxon along with lengthening of the ramus.

Fossil affinities

When the fossil skulls are added to the extant sample, the *Protopithecus* cranial base does not fall within the *Alouatta* cluster (Fig. 3.18). While *Caipora* does fall within the 95% confidence ellipse surrounding the *Ateles* specimens, it is not nestled among them as would be expected based on its original description as simply a large spider monkey (Cartelle and Hartwig, 1996). Both Brazilian fossils fall well within the 95% confidence ellipses of the *Lagothrix* and *Brachyteles* samples (Fig. 3.19). Positioning along PC2 suggests they are closer in shape to *Lagothrix*; warping the shapes along this axis shows that *Protopithecus* in particular shares incipient airorynchy and occipital flattening with the woolly monkeys. This is especially clear when *Alouatta* is excluded from the analysis (Fig. 3.20). The fossils do not share the wider molars and palate of *Brachyteles*, a shape difference that could be related to differences in diet (Rosenberger et al., 2011; Rosenberger et al., in press). Interestingly, *Paralouatta* does fall well within the *Alouatta* cluster, based on similar degree of cranial base flattening and elongation and nuchal plane reduction and posterior orientation (Fig. 3.21). This suggests that those two genera at least do share features of the cranium suggested to be derived for alouattins (see Table 1.3).

Based on canine size and strength of the temporal lines, the *Protopithecus* skull has been suggested to belong to a male individual (Hartwig and Cartelle, 1996); males and females were analyzed separately, and in both cases *Protopithecus* still falls within the *Lagothrix* group (Figs. 3.22-23). When the male and female means are overlaid with minimum spanning trees connecting the most similar shapes, for both sexes *Protopithecus* and *Lagothrix* are connected, albeit with a relatively long branch most likely reflecting the larger size of the fossil skull (Figs. 3.22-23). As mentioned above, all three fossil skulls are incomplete and therefore are being

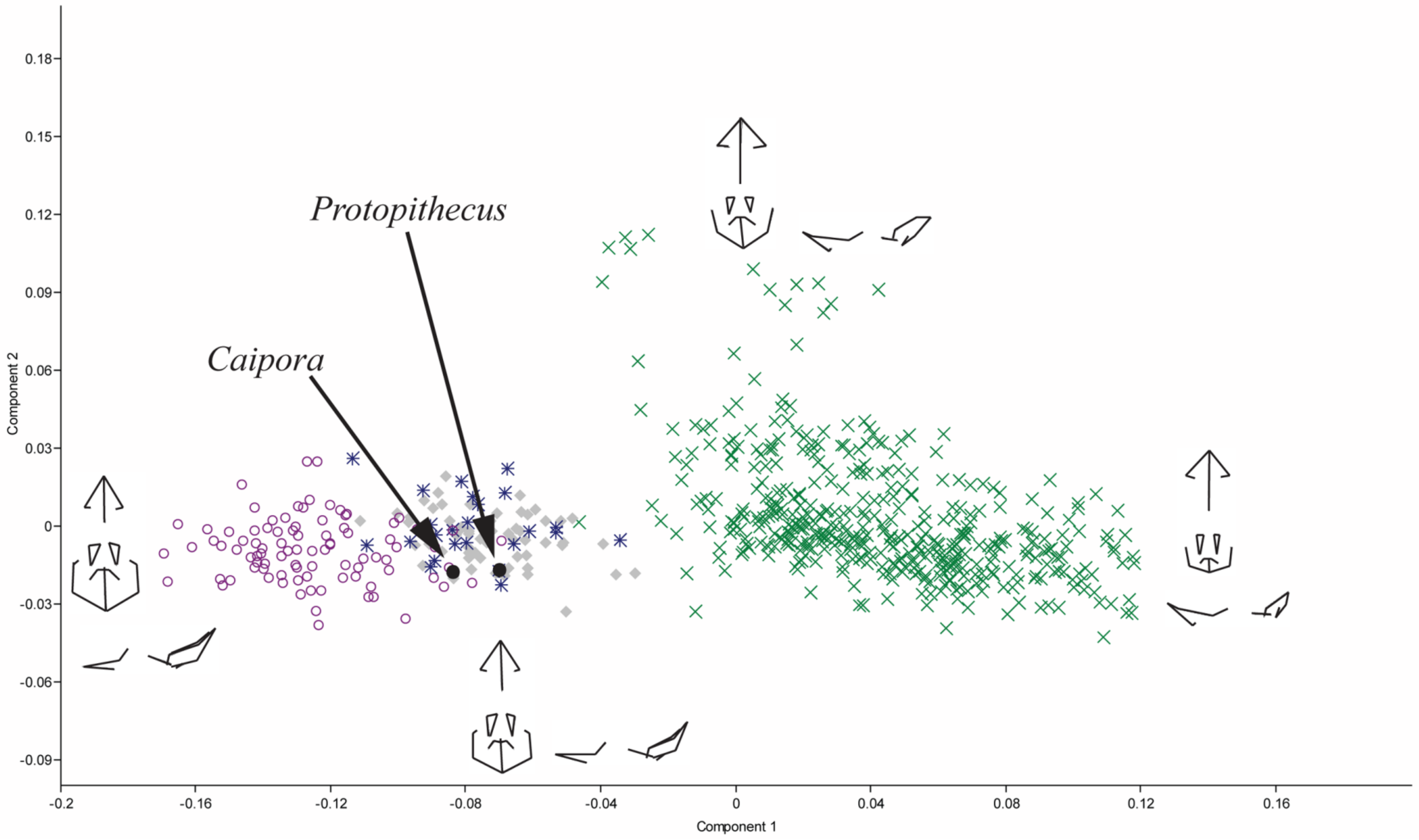

Figure 3.18. PCA results for the cranial base using the entire comparative sample plus the Brazilian fossils. Purple circles = *Ateles*, Blue asterisks = *Brachyteles*, Grey diamonds = *Lagothrix*, Green x's = *Alouatta*. Note the position of the fossils outside of the *Alouatta* cluster. Wireframes are the cranial base in inferior and lateral view, showing similar genus level shape change as previous analyses except without the landmarks that are not preserved on the fossil specimens (see Table 3.4).

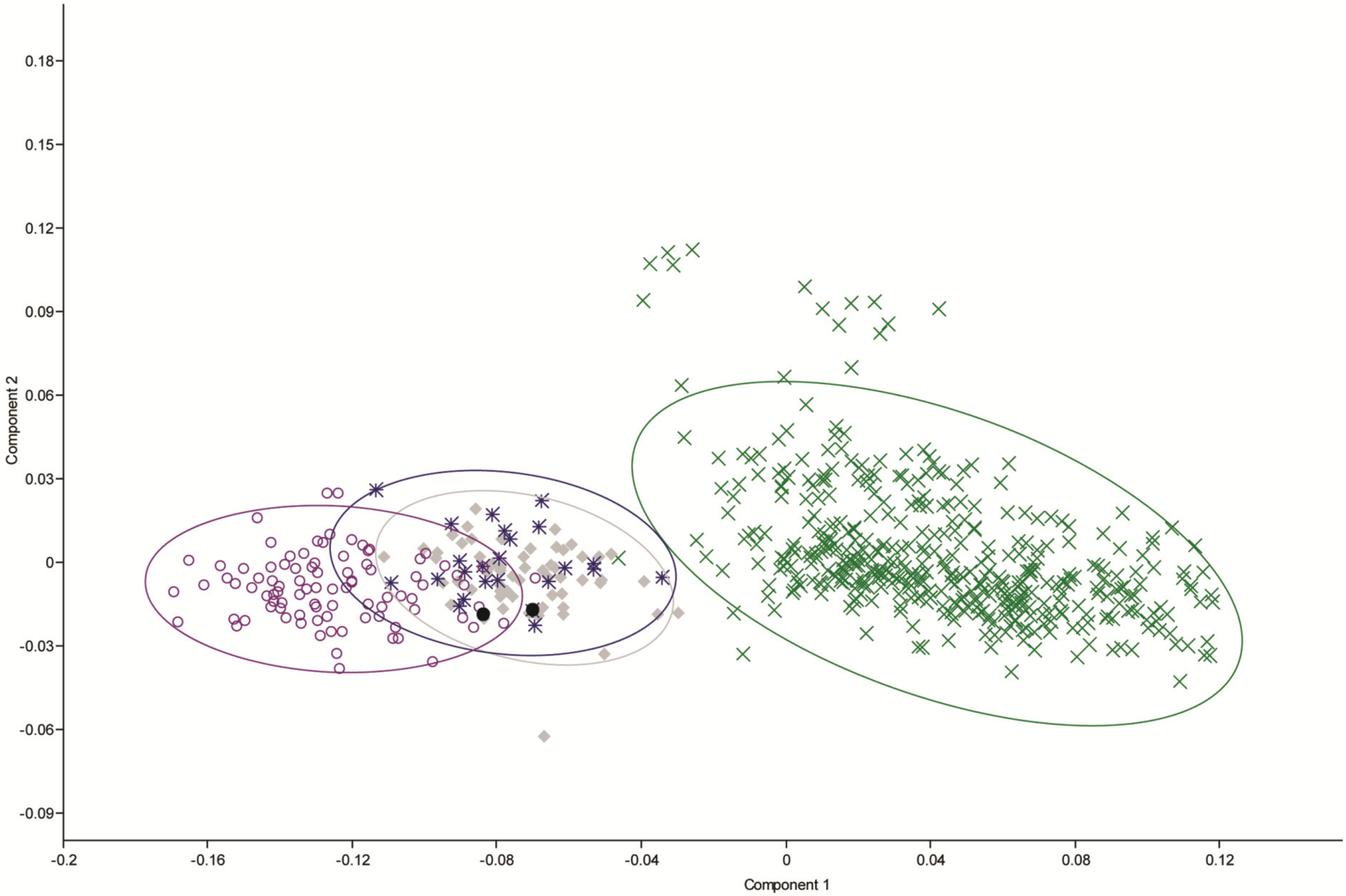

Figure 3.19. PCA results for the cranial base using the extant and fossil sample, 95% confidence ellipses.
As in Fig. 3.18, *Caipora* is on the left and *Protopithecus* is on the right. *Caipora* is within the confidence ellipse for the *Ateles* cluster as would be expected, but it is on the edge and is also encompassed by both the *Lagothrix* and *Brachyteles* boundaries. *Protopithecus* is within the almost completely overlapping distributions of both *Lagothrix* and *Brachyteles*.

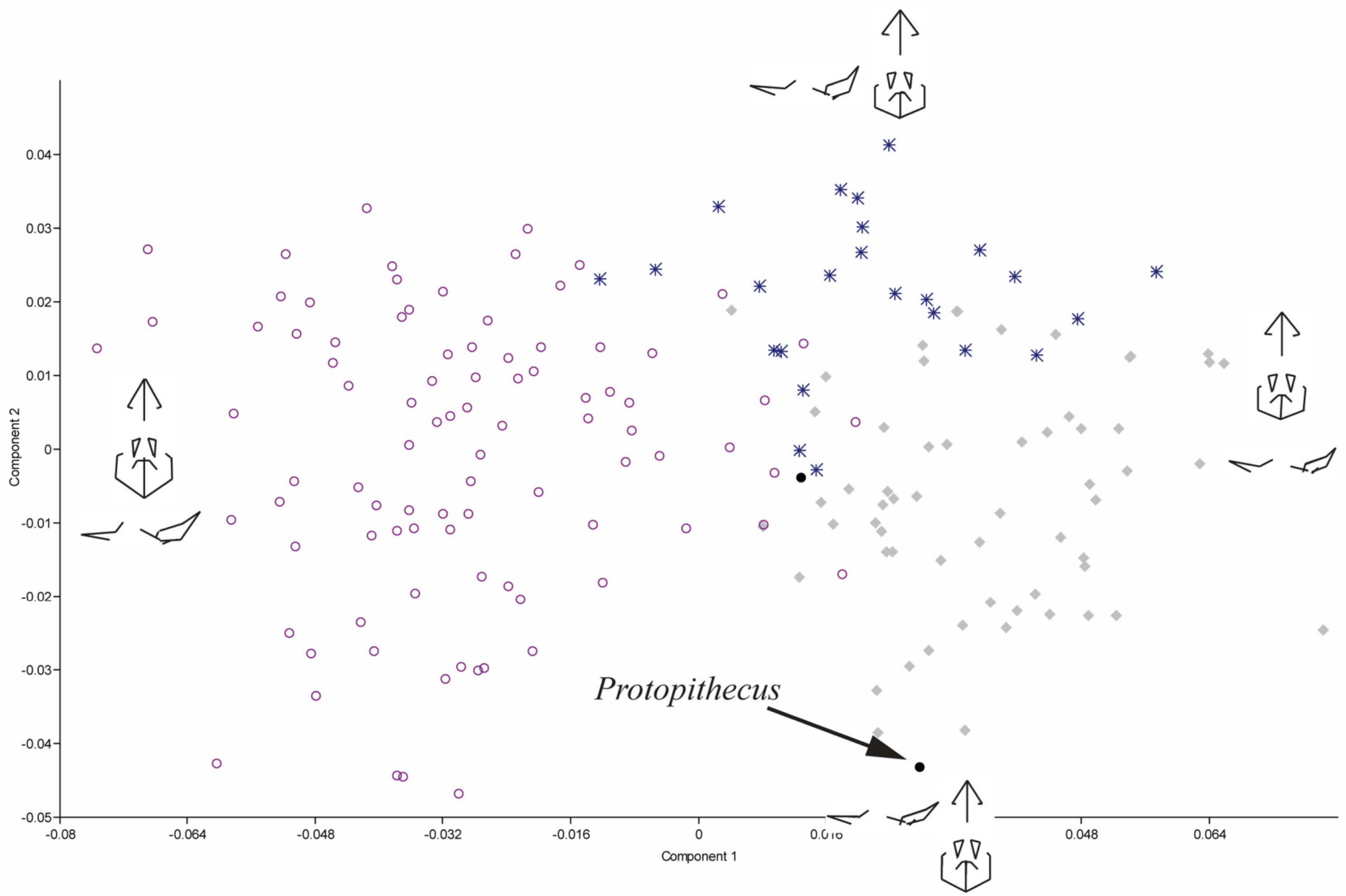

Figure 3.20. PCA results for cranial base using the extant atelin sample plus the Brazilian fossils.
Purple circles = *Ateles*, Blue asterisks = *Brachyteles*, Grey diamonds = *Lagothrix*. Wireframes are the same as Figs. 3.18-19 and show the narrower palate and upper molars that the fossils share with *Lagothrix* as opposed to *Brachyteles*.

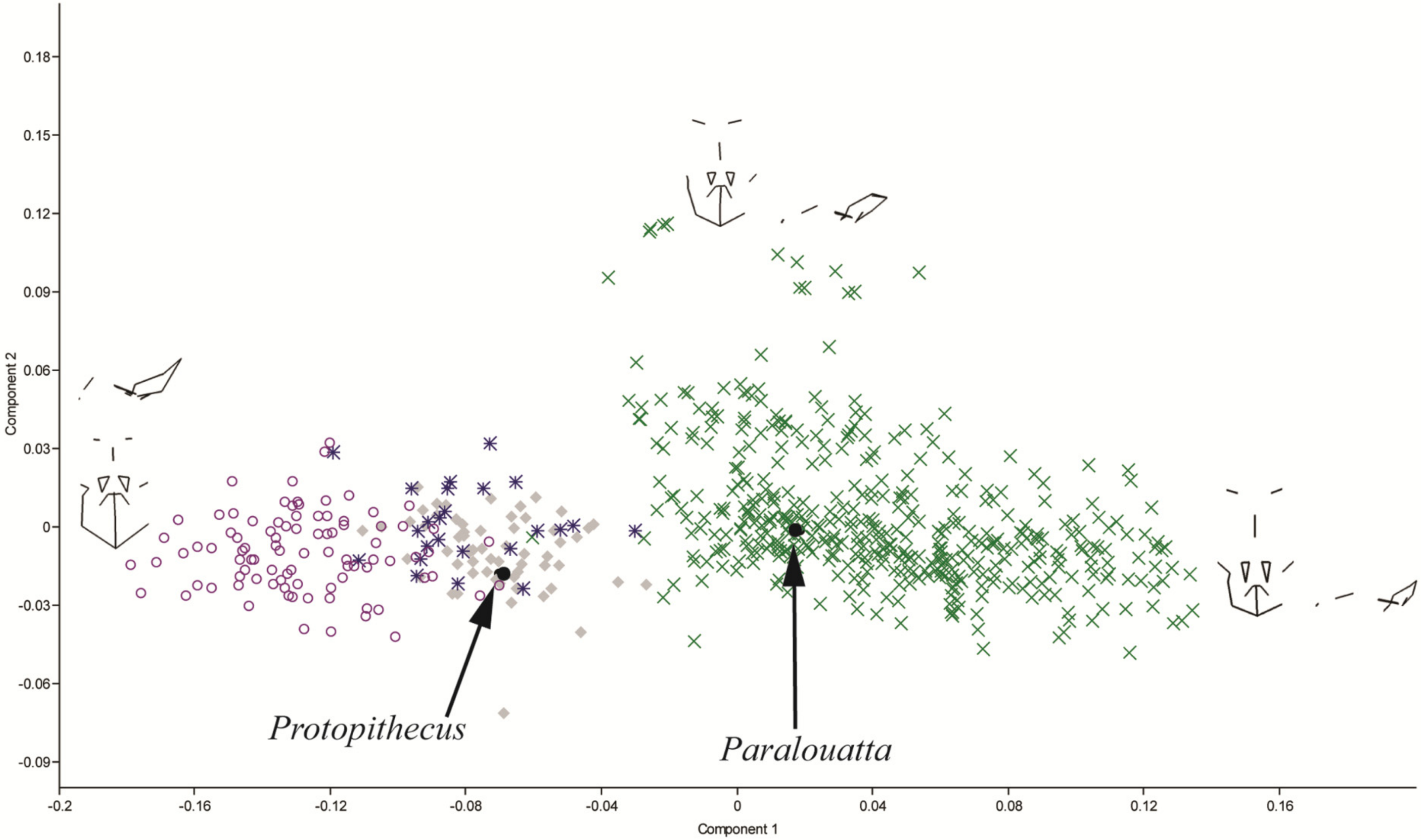

Figure 3.21. PCA results for the cranial base using the extant sample, *Protopithecus*, and *Paralouatta*.
Purple circles = *Ateles*, Blue asterisks = *Brachyteles*, Grey diamonds = *Lagothrix*, Green x's = *Alouatta* (outliers to the positive end of PC2 are *A. palliata*). Wireframes show the cranial base in inferior and lateral view as in previous figures, but with reduced landmarks due to the preservation of *Paralouatta* (see Table 3.4). PC1 (54% total variance) reflects the changes from narrow molars, a wide occipital, and flexed cranial base angle in *Ateles* to the wider molars, narrow occipital, and unflexed cranial base of *Alouatta*, traits that are seen also in *Paralouatta* but to a lesser degree in *Protopithecus*.

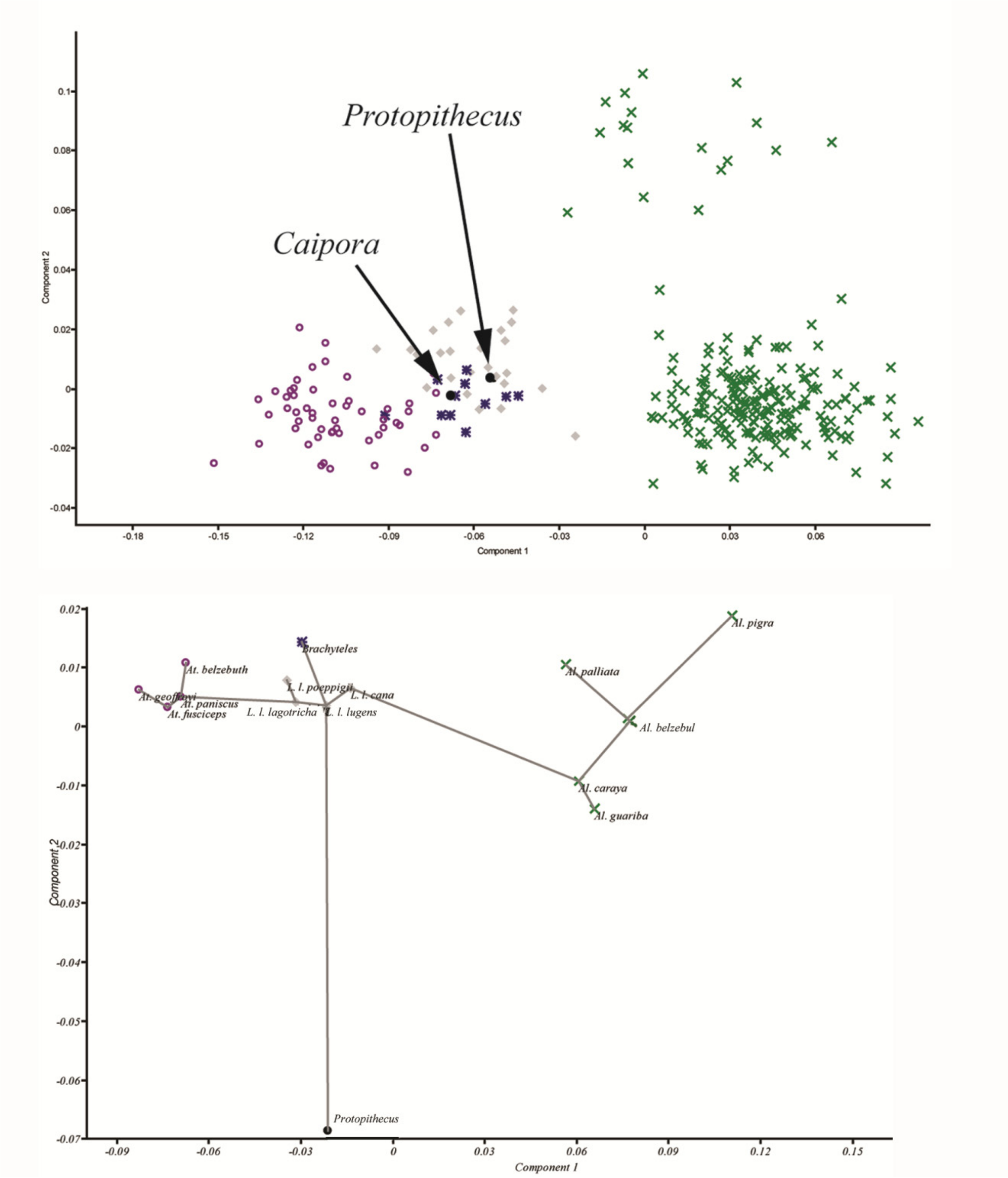

Figure 3.22. PCA results for the cranial base using female individuals (top) and species means (bottom). Despite both being interpreted as males, the fossils fall well within the female *Lagothrix* and *Brachyteles* clusters. However, the minimum spanning tree shown on the bottom indicates that the Procrustes distance between *Protopithecus* and the female *Lagothrix* means is slightly longer than it is for the male means in Fig. 3.23.

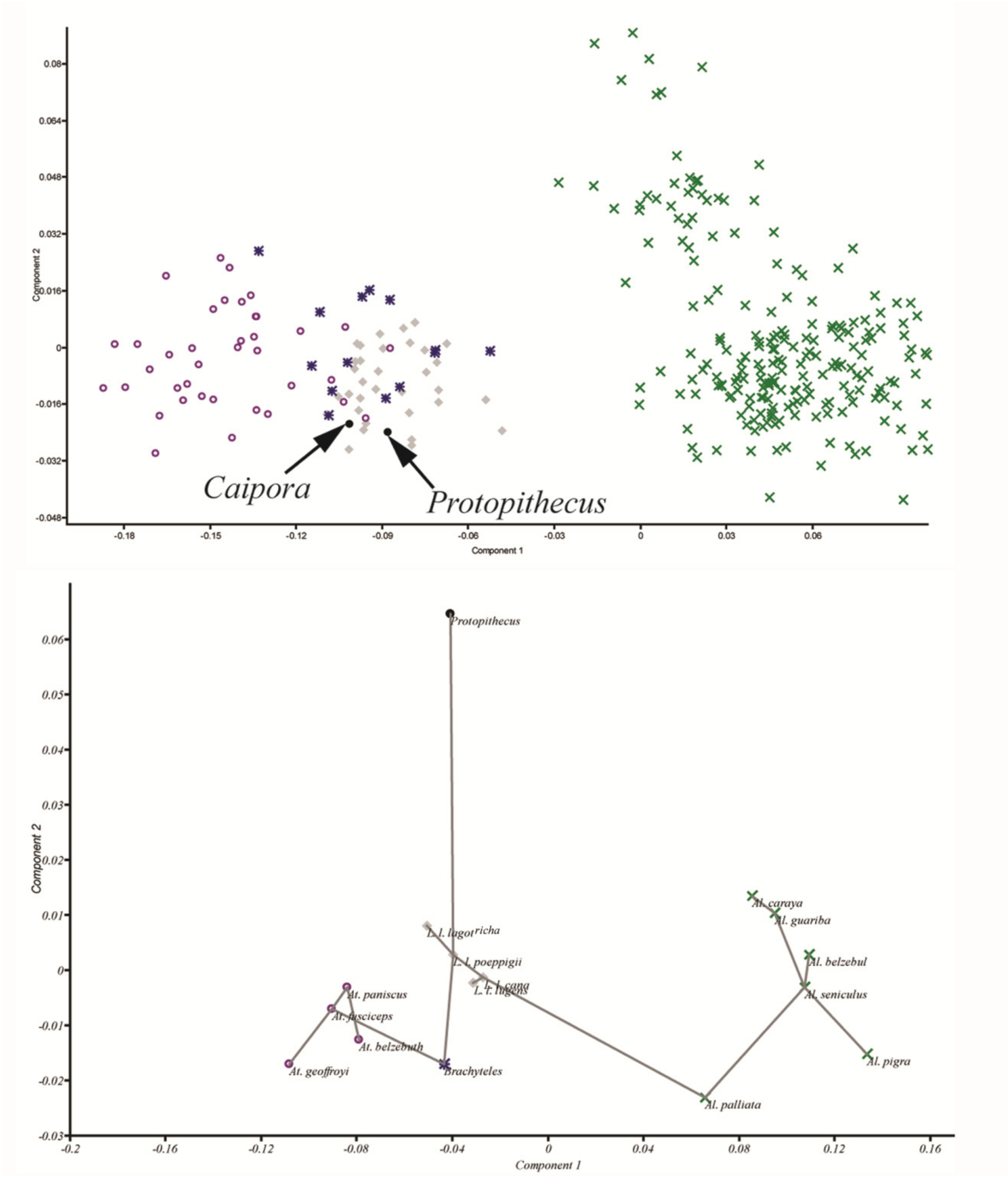

Figure 3.23. PCA results for the cranial base using male individuals (top) and species means (bottom).

compared to the extant sample using a reduced landmark set (Table 3.4). This, however, is most likely not the explanation for the unexpected positioning of *Protopithecus* and *Caipora*, as the rest of the specimens fall into the same pattern with the same shape changes along each principal components axis that was seen when the full landmark set was used to explore the extant sample.

A potential explanation does, however, rest in the composite nature of the "cranial base" as defined by the landmarks used here. Recent studies of integration and modularity in the primate skull suggest that there are at least three separate modules comprising the face, cranial base, and brain case (Lieberman et al., 2000; Marroig et al., 2004; Mitteroecker and Bookstein, 2008; Bastir and Rosas, 2009). Landmarks on the upper dentition and palate, basisphenoid, zygomatic arches, and occipital are all combined in the full landmark set despite the fact that many of these anatomical areas arise from very different embryological precursors and hence are under separate genetic, and potentially evolutionary, control (Marroig and Cheverud, 2001; Mitteroecker and Bookstein, 2008; Bastir and Rosas, 2009). In atelines, there is some evidence, albeit based on very small sample sizes, that the face and brain case are more tightly integrated than in other primates, and it is the interaction of those two regions, manifested in presence or absence of airorynchy, that is more important than localized anatomical differences within each module (Bruner et al., 2004). However, modularity could be more important in the alouattins as qualitative observation and previous quantitative studies (Cooke et al., 2007; Rosenberger et al., in press) suggest that it is mostly in the posterior portion of the skull, i.e., the small brain, strong temporal lines, and rugose posteriorly facing occipital bone, that *Protopithecus* is most similar to *Alouatta*.

Preliminary support for these findings is found when PCAs are run using only the landmarks describing the size and orientation of the occipital bone (#27-35; see Table 3.4 and

Fig. 3.5). The fossil now falls within the 95% confidence ellipse surrounding the *Alouatta* specimens (Fig. 3.24). It is the less airorynchous face and more flexed cranial base of the fossil that drives its link to the atelins in the previous PCAs; in fact, when only the landmarks on the upper dentition, palate, and temporal fossa are used (#1-11), *Protopithecus* falls closest to *Ateles* and there is separation between the more frugivorous taxa and the semi-folivorous *Brachyteles* and *Alouatta* (Fig. 3.25). This suggests that the anterior portion of the skull, in particular the size of the teeth and the temporal fossa, is more closely connected to dietary adaptations while the reorientation of the posterior portion could be more directly related to how the skull is articulated on the vertebral column. As shown in the plots above, the *Protopithecus* cranial base as a whole is not extremely elongated as is the case in *Alouatta*. The opening of the airway in the fossil, if the hyoid was enlarged, could have instead been maintained by the reorientation of the head on the neck, so that the cervical vertebrae and various soft tissue structures in the area were not impinging on the hyolaryngeal apparatus. However, the overlap of the four genera in Figure 3.24 should not be ignored. The similarities in the shape of the occipital region as defined by these landmarks could also indicate that a slightly expanded and posteriorly oriented nuchal plane is shared by atelines as a group, and therefore could be primitive. Further investigation of this morphology in other related platyrrhines would be necessary to test this hypothesis.

In the PCA results for the mandible, there is more overlap between *Ateles*, *Lagothrix,* and *Brachyteles* than was seen for the cranial base, but the shape changes from one genus to the next are clear, especially regarding bi-gonial width and the angulation of the inferior border of the bone (Fig. 3.26). These differences are still seen amongst the extant taxa when only the anterior portion preserved in the fossil is included for analysis (Fig. 3.27), suggesting that the unique positioning of the *Protopithecus* mandible is again not due to the reduced landmark set. It also

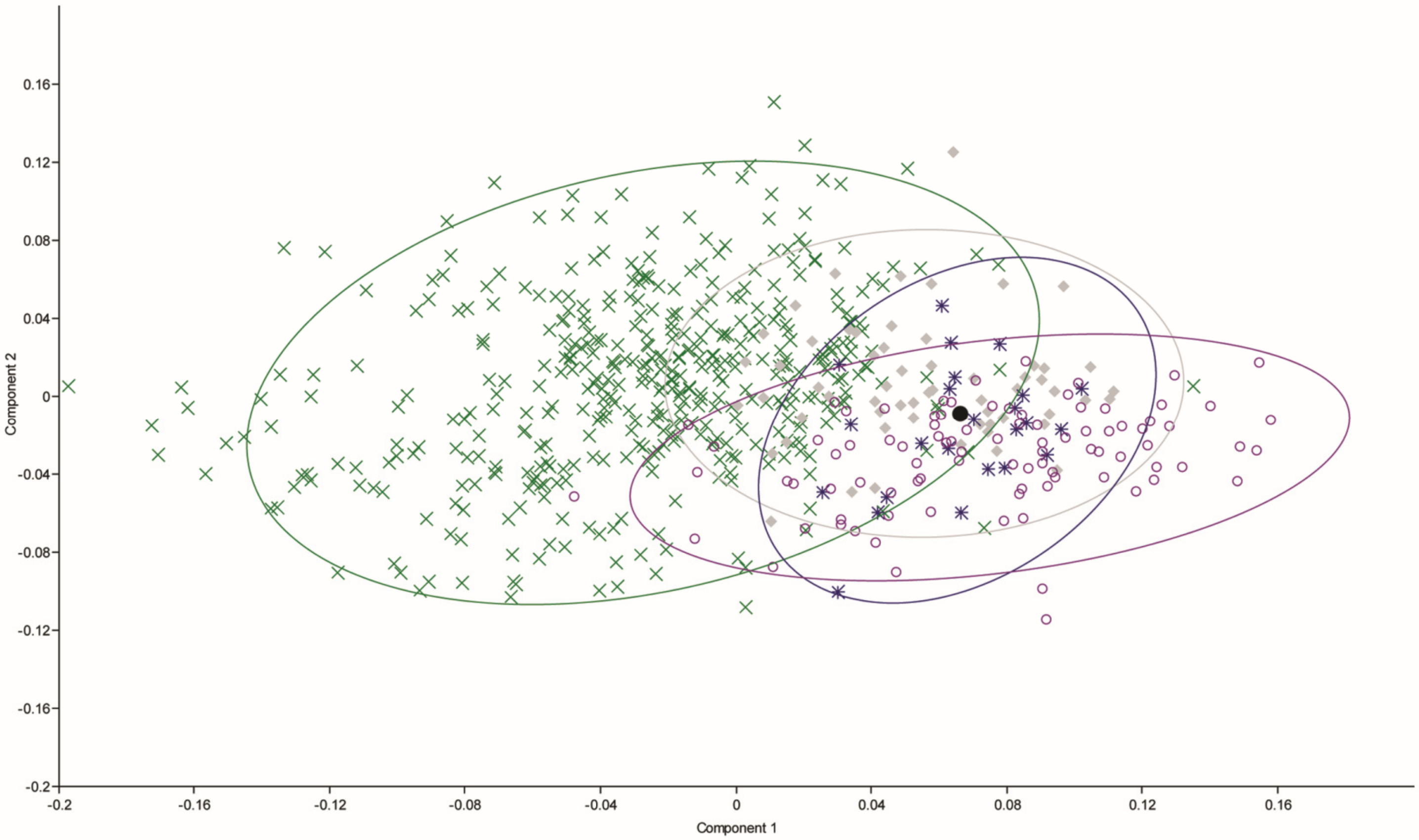

Figure 3.24. PCA results for the occipital landmarks only, 95% confidence intervals.
Purple circles = *Ateles*, Blue asterisks = *Brachyteles*, Grey diamonds = *Lagothrix*, Green x's = *Alouatta*. PC1 (33% total variance) is being driven by the length of the occipital condyles and the position of inion, representing the posteriorly directed nuchal plane and foramen magnum of *Alouatta* on the left and the more inferiorly oriented foramen magnum of *Ateles* on the right. PC2 (17%) is more directly related to position of the lateral points on the lambdoidal suture, creating a more square occipital in the *Alouatta* towards the positive end of the axis and a rounder profile in the individuals towards the negative end, most of which are *A. palliata*. For the first time, *Protopithecus* (black dot) is within the *Alouatta* distribution due to its large flattened occipital and more posteriorly oriented foramen magnum. However, the high degree of overlap between the four genera could also indicate that this configuration of the occipital and foramen magnum is primitive for the atelines.

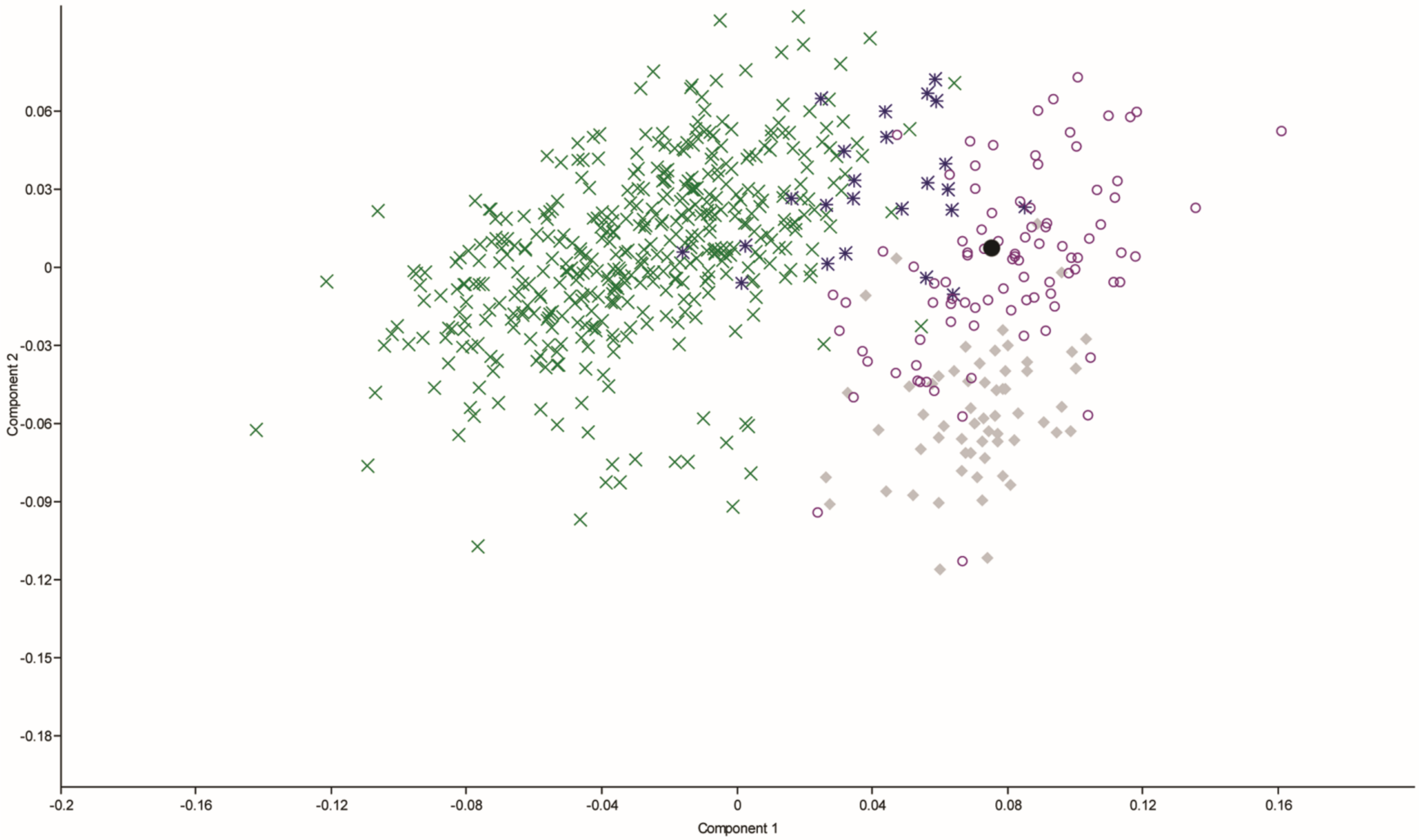

Figure 3.25. PCA results for the anterior cranial base landmarks only.
Purple circles = *Ateles*, Blue asterisks = *Brachyteles*, Grey diamonds = *Lagothrix*, Green x's = *Alouatta*. PC1 (36% total variance) separates the folivorous taxa on the left with an angled palate, wide molars, and extreme postorbital constriction from the more frugivorous taxa on the right with a flat palate, narrow molars, and wider postorbital distance. PC2 (16%) is being driven by the length of the palate and the zygomatic arches; individuals towards the positive end of the axis have a long palate and short zygomatics while individuals towards the negative end have a short palate and longer zygomatics. *Protopithecus* (black dot) has a relatively large face, but it is not as airorynchous and postorbitally constricted as *Alouatta* and its teeth are more similar in size to the more frugivorous atelines.

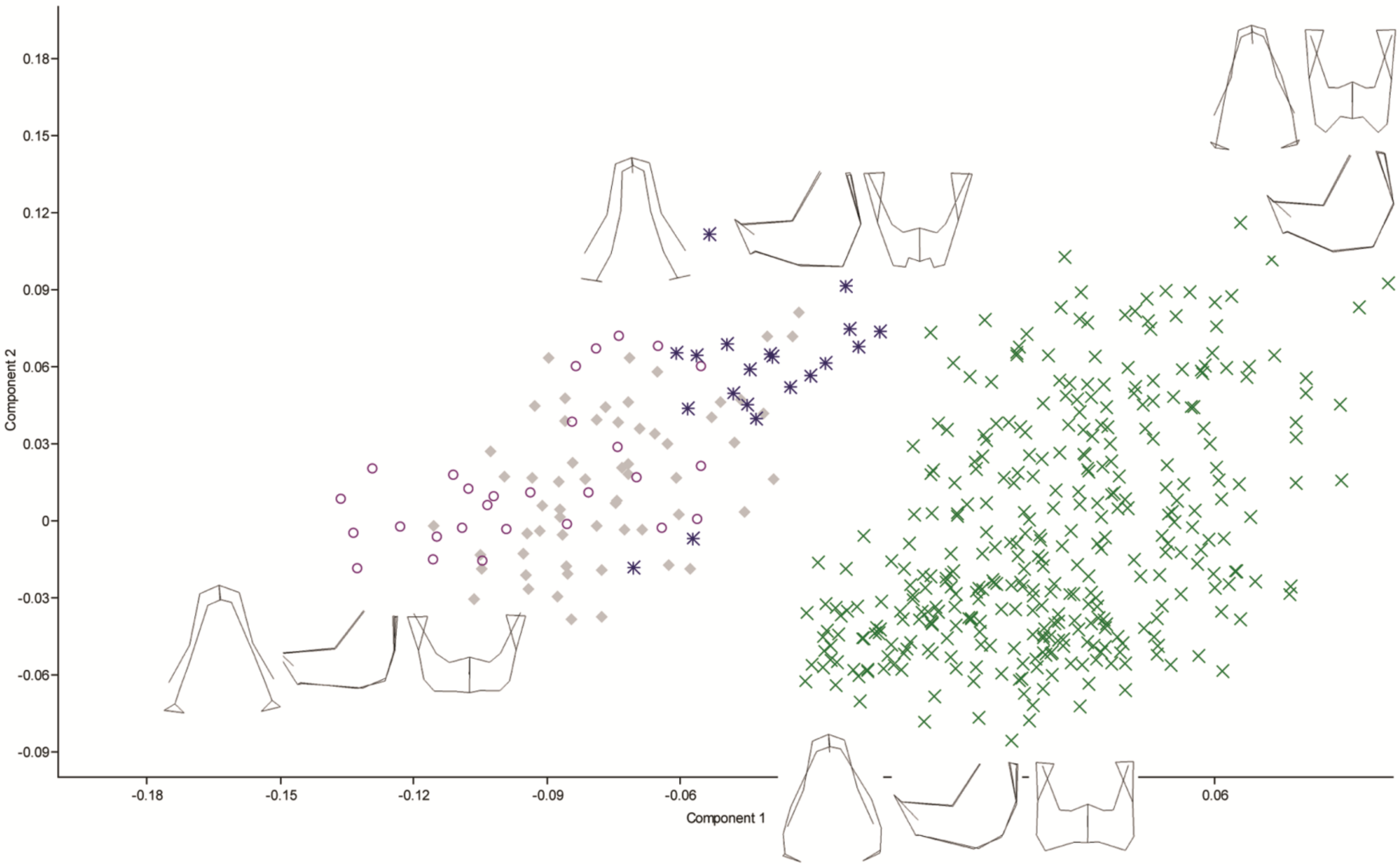

Figure 3.26. PCA results for the mandible using the entire extant comparative sample.
Purple circles = *Ateles*, Blue asterisks = *Brachyteles*, Grey diamonds = *Lagothrix*, Green x's = *Alouatta*. Wireframes represent the full landmark set recorded on the mandible in superior, lateral, and posterior view, representing the morphology seen in the individuals at the diagonal extremes of each cluster (see Fig. 3.4 for reference). This distribution is partly based on size, with the smaller mandibles of *Ateles* on the left and larger male *Alouatta* to the far right; when ln centroid size is regressed on PC1 scores, $R^2 = 0.6$. PC1 (26% total variance) shows a similar morphocline as in the cranial base, but there is more overlap between the non-*Alouatta* taxa which share a horizontal inferior border of the mandibular corpus and a coronoid process that sits above the level of the condyle. PC2 (20%) is driven by movement of the gonial angles, which are farther apart and more expansive towards the negative end of the axis.

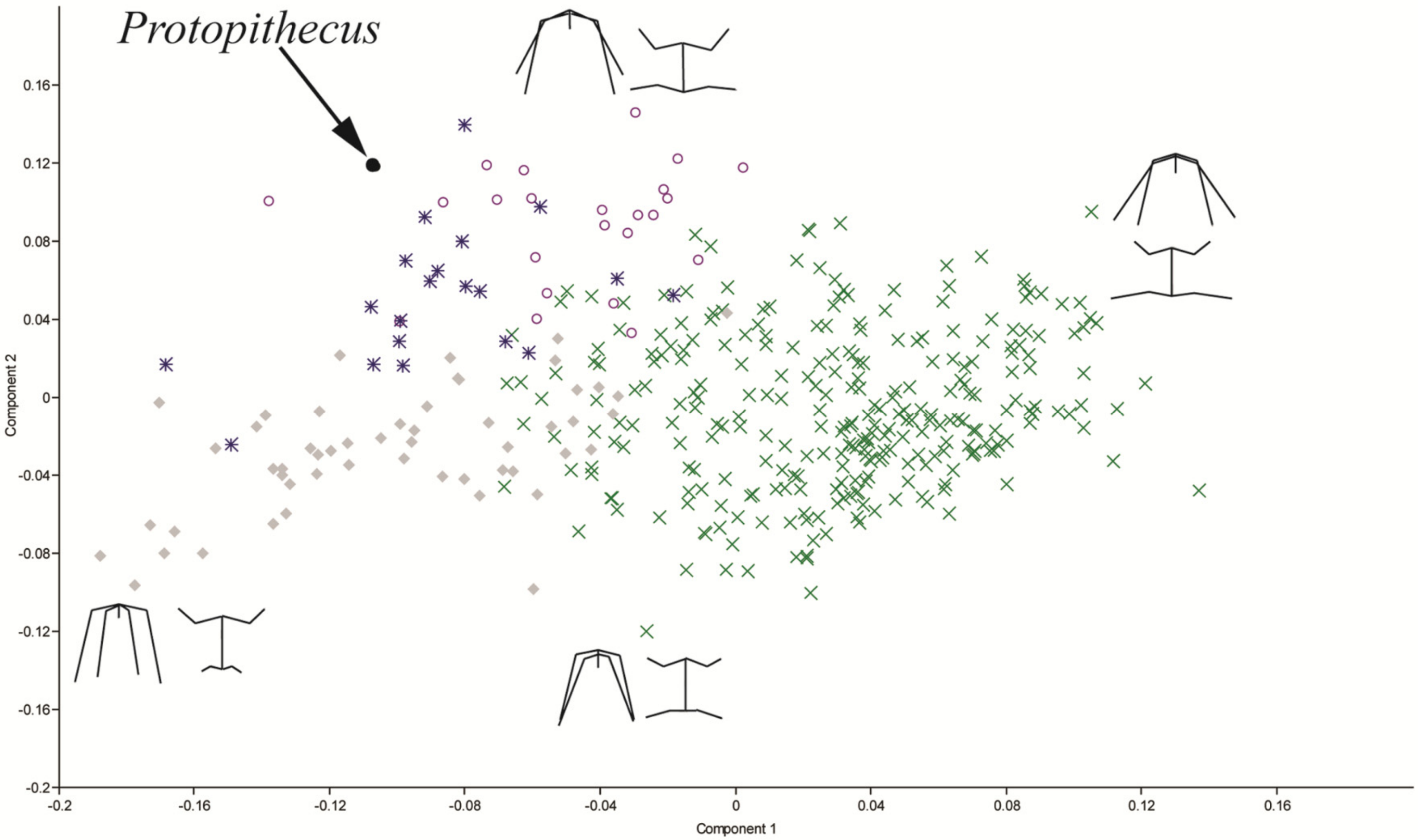

Figure 3.27. PCA results for the mandible using the extant sample and *Protopithecus*.
Purple circles = *Ateles*, Blue asterisks = *Brachyteles*, Grey diamonds = *Lagothrix*, Green x's = *Alouatta*. Wireframes are the anterior portion of the mandible only in superior and posterior views (see Table 3.4 for landmarks missing in *Protopithecus*). There is less separation amongst the extant species than seen in Fig. 3.26 because the gonial angle landmarks that were driving much of that distribution are not preserved in the fossil. However, the overall pattern is the same and bi-gonial width is indirectly represented here in the widening of the anterior portion of the inferior border of the mandibular corpus seen along PC1 (33% total variance). The *Protopithecus* mandible shares a wide incisor row and more parabolic dentition with the more frugivorous extant taxa.

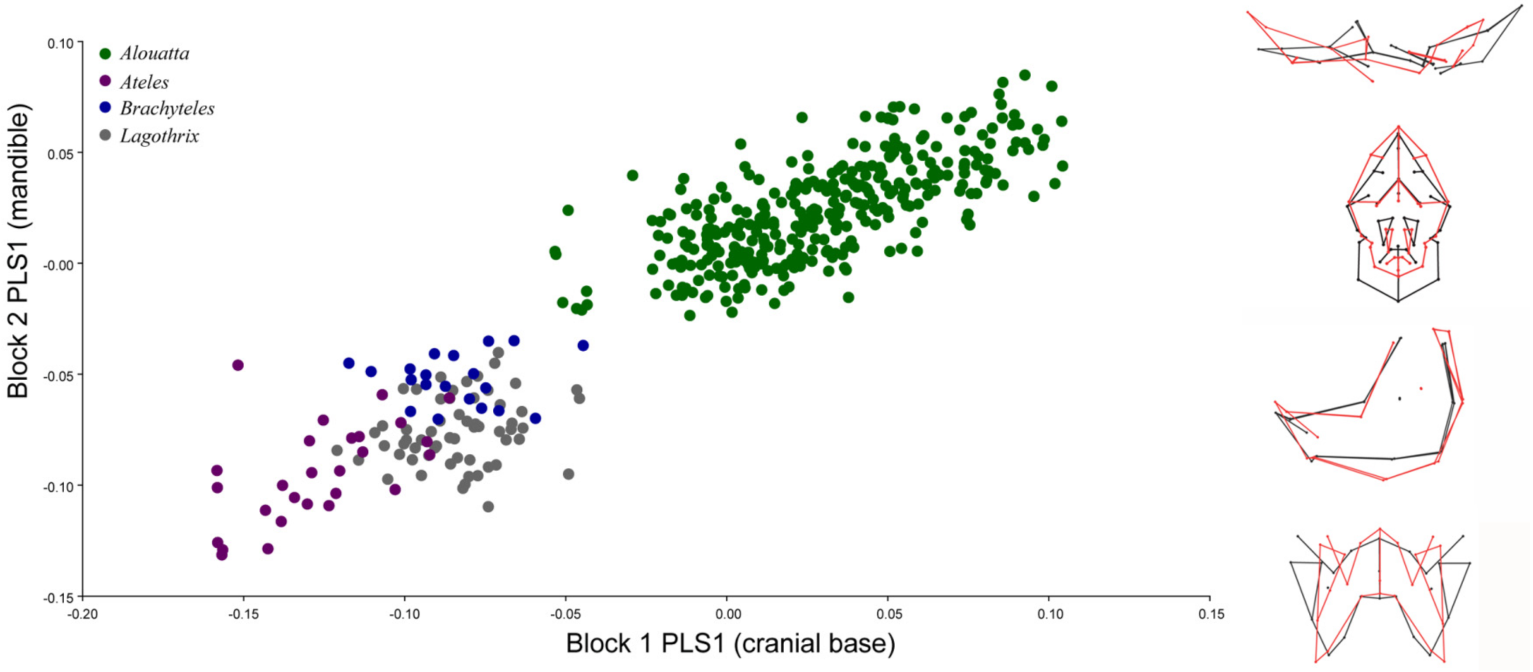

Figure 3.28. 2B-PLS results showing co-variation between the cranial base and mandible.
Wireframes show the shape change from the negative end of PLS1 (black) to the positive end of PLS1 (red) for the cranial base in lateral (top) and inferior (bottom) views and the mandible in lateral (top) and posterior (bottom) views. A large airorynchous face and small occipital are found together in *Alouatta* with a sloping inferior border and expanded gonial angles of the mandible while *Ateles* exhibits the opposite of this combination of traits.

suggests, contrary to original interpretations (e.g., Hartwig, 2005), that the *Protopithecus* mandible would not have had the extremely expanded ramus and gonial angles that are seen in *Alouatta*. This is corroborated by the results of the 2B-PLS analysis of the co-variation between the cranial base and mandible (Fig. 3.28). There is a very high correlation of 0.92 ($P < 0.0001$) between those two anatomical areas amongst the atelines on PLS1, which explains 93% of the co-variation. It is clear from the plot shown in Figure 3.28 that a genus-specific cranial base shape "goes with" a genus-specific mandible shape; a very airorynchous face with a small occipital region pairs with very wide mandibles with extremely sloped inferior borders and vice versa. As the *Protopithecus* cranial base is more similar to that of *Lagothrix* as opposed to *Alouatta*, the high correlation between the two bones suggests that the missing posterior portion of the fossil mandible also would have been non-*Alouatta*-like in shape. There seems to be a morphocline of mandibular morphology as there was for the cranial base, with *Brachyteles* and *Lagothrix* exhibiting intermediate levels of the deepening of the corpus and flaring of the gonial angles. In agreement with the cranial base results presented above, it should be noted that the anterior portion of the mandible preserved in *Protopithecus* seems to contain more information that may be related to diet rather than to vocal tract morphology. The width of the incisor row in particular places the *Protopithecus* mandible in an expected position with the more frugivorous taxa in the mandible PCA plot.

Discussion

The results presented here suggest that *Protopithecus* did not have an enlarged *Alouatta*-like hyoid apparatus. However, because the *Protopithecus* cranial base, and to some extent its mandible, looks like that of *Lagothrix*, it does not follow that its hyoid would have looked and functioned like that of the extant woolly monkey. The correlations between the cranial base and hyoid, and mandible and hyoid, on each PLS axis are relatively high, but not high enough to make exacting predictions about fossil hyoid shape. Multiple PLS axes explain relatively large portions of the co-variation between the shapes, suggesting a complex relationship between these anatomical areas. These results agree with the unexpectedly low overall co-variation found by Halpern (1987), which led to the conclusion that "hyoid size varies more independently of skull morphology than previously thought" (p. 2). An explanation is cited from Hershkovitz who describes the growth of the hyoid in male *Alouatta* continuing with use into adulthood, an observation supported by others (Ravosa and Ross, 1994; Jones et al., 2000) who found that male *A. palliata* cranial growth continues after reaching dental maturity. Differing growth trajectories amongst the anatomical regions and between the sexes and species are more variables to add to the list of diet, vocal tract morphology, and brain size as potential influences on cranial base morphology in *Alouatta*.

Within the atelines, there are two types of hyoids, *Alouatta* and non-*Alouatta*, with no intermediate form. This is unlike the situation for the cranial base and mandible where there does seem to be a cline from *Ateles* to *Alouatta*, with *Lagothrix* in an intermediate position. This is consistent with previous suggestions that the generalized cranial morphology of *Lagothrix* could be used as a model for the ateline last common ancestor (e.g., Rosenberger and Strier, 1989). *Protopithecus* belongs to the non-*Alouatta* group in all three cases. However, only the cranial base and mandible were examined here as the morphological areas most likely to be linked to hyoid size and shape. Other aspects of the *Protopithecus* skull that have been suggested to show similarities to the *Alouatta* condition should not be ignored as phylogenetic indicators and possible markers of continuity in behavior. For example, the small size of the brain and the foramen magnum (Cooke et al., 2007; Rosenberger et al., in press) as well as the strong temporal lines and postorbital constriction, are more similar to *Alouatta* than any of the atelins. While some of these traits are perhaps not seen as traditionally strong phylogenetic indicators, using this narrow taxonomic view, i.e., just looking at the polarities within the ateline subfamily, they align the fossil with alouattins as opposed to the atelins.

There are several possible explanations for why the anterior portion of the *Protopithecus* cranial base does not look like *Alouatta* while other parts of the skull do, at least from qualitative observation. As mentioned in the introduction to this chapter, the large body size of *Protopithecus* could certainly be having an effect on these results. In theory, at 20-23 kg, the subbasal space could have been large enough to support a relatively expanded hyoid bone without requiring further *Alouatta*-like changes in cranial base angle or mandibular morphology. The large, rugose, and somewhat posteriorly directed occipital bone of *Protopithecus* also suggests that the animal would have carried its head in a resting position uniquely similar to *Alouatta*, i.e., stretched out in front of its neck. This could have helped to open the subbasal space without affecting the cranial base angle or airorynchous condition of the face, aspects of the fossil morphology that these results suggest do not closely resemble *Alouatta*. At such a large body size, the hyoid bone of *Protopithecus* would have been absolutely large; the reorientation of the head on the neck, indicated by the results for the occipital landmarks, suggests a further increase in space for an at least somewhat expanded hyoid. This could be the evidence referred to at the beginning of the chapter suggesting that the hyoid was not just large, but *en*larged. Based on the results presented here, there is no way to estimate how expanded or hollowed out the basihyal of *Protopithecus* was. But if such a large animal needed to modify the articulation between its cranium and vertebral column by changing the orientation of the nuchal plane and foramen magnum, one can accept as a working hypothesis that the hyoid apparatus and vocal behaviors of *Protopithecus* may have already begun the transition towards the extremely derived *Alouatta* condition that we see today.

Alternatively, the size of the cranial base could be producing an allometric effect that is swamping out any derived characters that are qualitatively present. The fact that the large-bodied *Caipora* is also clustering with an unexpected group of extant specimens would support this hypothesis. However, size does not seem to be driving the scatter in the cranial base PCA results. All R^2 values for regressions of the PC scores on ln centroid size of the individual specimens are less than 0.6 and both *Protopithecus* and *Caipora* fall within clusters of the smaller extant taxa, not in their own separate large-bodied group. Also, *Lagothrix*, the genus that the large fossil basicrania are most similar to, is not the largest of the living species, further suggesting that size is not affecting the scatter in the PCAs. Without a more detailed allometric analysis, the large body size of the fossil must be seen as a confounding variable when attempting to interpret the phenetic results presented here with regard to their functional or phylogenetic significance.

The cranial base is related to many other functional complexes besides the supralaryngeal vocal tract and such an intricate anatomical area may not be functionally equivalent in the fossil and extant taxa. The larger body size and more frugivorous, non-folivorous, diet of *Protopithecus* would influence many areas of its biology and behavior when contrasted with *Alouatta*. Evolutionarily speaking, these results can be reconciled if *Protopithecus* is interpreted as a relatively primitive member of the alouattin tribe. It is certainly more primitive than the Cuban *Paralouatta*, for example, which does share presumed derived cranial base similarities with extant *Alouatta*. However, the similarities shown here between *Protopithecus* and

Lagothrix in many aspects of the cranial base, as well as the intermediate morphological and phylogenetic position of *Lagothrix* among the atelines, leaves open the possibility that *Protopithecus* could intead represent the ancestral ateline condition (see Chapter 5).

CHAPTER 4

POSTCRANIAL MORPHOLOGY AND LOCOMOTOR REPERTOIRE

Introduction

Positional behavior

Howler monkeys howl holding their heads in a stereotypical position, with their necks outstretched in front of their body (Baldwin and Baldwin, 1976; Schön Ybarra and Schön, 1987; Whitehead, 1989). It has been proposed that this serves to move the hyoid forward, increasing its resonating power (Schön, 1986; Whitehead, 1995). Hartwig et al. (1996) have suggested that this head posture during howling bouts is also connected with body carriage and positional behavior during other activities. Along with the head, the upper body of the howler monkey also takes on a stereotypical posture during howling bouts, with hands placed shoulder-width apart and elbows flexed and flared outwards. Unique aspects of the *Alouatta* postcranial skeleton (i.e., limb proportions, elbow joint morphology, shoulder morphology, and the shape of the rib cage) could potentially be primarily related to this postural behavior, and hence sound production, instead of being driven by selection for their slower, more deliberate form of quadrupedal locomotion (Hartwig et al., 1996).

Schön (1976) also suggested that there is a functional link between the howler's well-developed nuchal musculature posteriorly, the enlarged hyoid and relevant musculature anteriorly, and their inability to move as acrobatically as the rest of their ateline relatives. Specifically, the well-developed atlantoscapularis posterior and supraspinatus muscles in the howler monkey have both been associated with the rearrangement of the scapula and nuchal region to accommodate the enlarged hyoid bone (Schön, 1968; Youlatos, 2000). The posteriorly directed nuchal plane, and hence foramen magnum and occipital condyles, reorients the head on the neck to open the subbasal space, but also would not allow the howler to look straight ahead if it were to hang by its forelimbs (Schön Ybarra, 1984; for image of spatial relationships described here see Fig. 3.4). Another area of the postcranial skeleton which has been suggested to be unique in *Alouatta* due to the spatial requirements of the enlarged hyoid (and thyroid cartilage) is the sternum. In *Alouatta*, the manubrium is bifurcated, a condition suggested to both make room for the cartilages themselves and to provide flexibility in the lowest regions of the throat for stretching out the neck during howling (Gadow 1891; Hill, 1962; Grand, 1967; Klima, 1972).

Unfortunately, the *Protopithecus* sternum is not preserved and the scapula and proximal humerus of the fossil are too fragmentary to make any firm conclusions about their affinity to those same elements in *Alouatta* (see below). As was concluded in the previous chapter, the cranial base of *Protopithecus* is not as derived towards maximizing subbasal space as is that of extant *Alouatta*. However, the occipital region of the fossil is expanded and rugose as it is in howler monkeys, suggesting that *Protopithecus* also would have had well-developed neck musculature capable of holding up and stretching out its large head during howling bouts. Following from Schön's hypothesis, one might also conclude then that the reorientation of the head on the neck suggested by results in Chapter 3 would not have allowed *Protopithecus* to be as suspensory as some of its extant ateline relatives. Inferring postural and locomotor behavior from cranial morphology is less desirable, but in this unique case could be possible as head carriage is related to the way the rest of the body can move. (The size and shape of the semi-circular canals of the inner ear have been shown to correlate with primate locomotor patterns (e.g., Spoor et al., 2007), but the *Protopithecus* skull has not been CT scanned to allow for the visualization and measurement of this anatomical area). However, as is traditional, it will be left to the postcranial skeleton to yield information about the *Protopithecus* locomotor repertoire.

Locomotor behavior and substrate use

Locomotor behavior is one facet of *Protopithecus* paleobiology that has remained enigmatic. The original suggestion of ateline-like suspensory locomotion, which was based mostly on limb proportions (Hartwig and Cartelle, 1996), has been challenged by another hypothesis pointing to the large body size of *Protopithecus* as evidence for a "high degree" of terrestrial behavior (Heymann, 1998). More recently, several quantitative traits in the *Protopithecus* forelimb and vertebrae have been shown to group it with other "brachiating" prehensile-tailed primates (Jones, 2008), but due to the fragmentary nature of the fossil joint surfaces used to calculate some of the key indices, these results should be viewed with caution (see Chapter 1). Different methodology will be used here in an attempt to test the various hypotheses that have been proposed so far for the locomotor repertoire of *Protopithecus*. Detailed qualitative descriptions of the relevant fossil material will be given first. Then three-dimensional geometric morphometric techniques are used to capture the shape of the most well-preserved joint surfaces (see Table 1.1) and quantify aspects of their morphology that vary in predictable ways with locomotor patterns in extant primate taxa. Principal components analyses are used to visualize the major axes of shape variation within the sample. The species, or group of species, to which the fossil is most similar is used as an analog for reconstructing its locomotor repertoire.

Description of fossil material

Table 4.1 was constructed as an aid in comparing the *Protopithecus* forelimb and hindlimb with postcranial morphology described as variable amongst taxa of different locomotor patterns. The qualitative data compiled here present a muddled picture with few truly diagnostic

Table 4.1. Postcranial morphology and locomotor patterns in extant primates.[1]

	ARBOREAL QUADRUPEDALISM	SUSPENSORY	CLIMBING	CLINGING AND LEAPING	TERRESTRIAL QUADRUPEDALISM
PROXIMAL HUMERUS					
Head	oval, posteriorly directed	large, round, medially directed	oval, posteriorly directed		oval, posteriorly directed
Tubercles	equal to level of the head	**below level of the head**[2]	**below the head**, greater faces anterolaterally	**below the head**	project proximally above head
Bicipital Groove	broad, shallow	**narrow, deep**	broad, shallow		broad
Deltoid Tuberosity	broad, v-shaped, **quarter of the way down the shaft**	at least halfway down the shaft			**quarter to a third of the way down the shaft**
Humeral Shaft	short, bowed slightly outward in anterior view	long, **straight**, slender	high degree of torsion		strong medial curvature
DISTAL HUMERUS					
Medial Epicondyle		**large, medially directed**	**large, medially directed**	**medially directed**	posteriorly directed
Capitulum	**broad, distolaterally expansive**	spherical, posteriorly extensive	spherical, "unrolled"	inflated, **capitular tail**	flattened distally
Trochlea	**wide, conical**, prominent edges	**broad**, cylindrical, low edges	**broad**, cylindrical	narrow, cylindrical	narrow, strong posteriomedial edge
Zona Conoidea	**flat**	recessed, gutteral		recessed	
Brachioradialis Flange		intermediate	**enlarged**	**enlarged**	
Olecranon Fossa	**intermediate**	shallow	**intermediate**	deep	deep, lateral wall articular surface
PROXIMAL ULNA					
Olecranon Process	**intermediate**	short	**intermediate**	relatively long	long and retroflexed
Trochlear Notch	**wide, shallow**	**wide, shallow**	narrow, long		narrow, lateral articular facets
Coronoid Process	**intermediate**	not projecting	**intermediate**		high
Radial Facet	flat, **faces anterolaterally**	faces laterally	**large, shallow, faces anterolaterally**		outset, subdivided
HAND					
Thumb		vestigial			
Phalanges	**long**	**long, curved**	**long**, slender, **curved**	**long**	short

Table 4.1 Continued

PROXIMAL FEMUR					
Femoral Head		**large, globular**	**globular,** articular surface extends onto neck	Cylindrical, expansion onto neck	
Femoral Neck		long, extends proximally	extends proximally	**thick, short,** perpendicular to shaft	
Greater Trochanter	narrow and tall	**below femoral head**	**below femoral head,** large trochanteric fossa	broad, overhangs shaft anteriorly	
Lesser Trochanter		small	**large and flattened**	**large, proximally positioned**	
DISTAL FEMUR					
Patellar Groove	**shallow and wide**	**shallow and wide**	deep, **wide, asymmetrical**	deep, narrow	
Condyles		**medial projects more inferiorly**		posteriorly facing, symmetrical	
PROXIMAL TIBIA	oriented slightly posteriorly, articular surfaces asymmetrical		**overhangs the femoral shaft posteriorly**	large, convex lateral articular surface	
DISTAL TIBIA					
Talar Articular Surface				proximally extended, concave, prominent midline break	
Medial Malleolus				deep	anterior portion is hooked
TALUS					
Trochlea	**moderate medial rim angulation**	**low, rounded lateral rim**	**low, broad,** extreme medial rim angulation	parallel-sided, deep groove, sharp lateral rim	asymmetrical, high lateral rim
Talar Head	**mediolaterally broad, no torsion**		dorsoventrally compressed, plantarflexed	tibial stop	high degree of torsion
Talar Neck	**moderate angulation**		strong medial angle, short	long and straight	

[1] Compiled from Erikson (1963), Ciochon and Corruccini (1975), Schön Ybarra and Schön (1987), Gebo (1989), Gebo (1993), Larson (1993), Meldrum (1993), Rose (1993), Fleagle and Simons (1995), MacPhee and Meldrum (2006), Jones (2008), pers. obs.

[2] Those in bold describe the relevant morphology in *Protopithecus*.

characters, as the same features appear under different types of locomotion and characters found in *Protopithecus* fall under several different behavioral categories. In particular, climbing and suspensory locomotion share several characters of the hip and knee (Fleagle et al., 1981; Lockwood, 1999). These are the two locomotor categories most often listed for the atelines (e.g., Erikson, 1963; Schön Ybarra, 1984; Gebo, 1992; Youlatos, 2002; Cant et al., 2003); *Ateles* uses forelimb suspension most frequently and *Alouatta* is more of a climber using hindlimb suspension during foraging. Not being able to ally the fossil with one or the other of these very different animals would be unfortunate. Luckily, the quantitative data presented below are less equivocal.

Forelimb morphology

Unfortunately, the scapula of *Protopithecus* is very fragmentary and does not preserve morphology that would lead to functional interpretation, such as the shape of the glenoid fossa or the shape and orientation of the blade. Similarly, the proximal humerus, especially parts of the head that would make clear its size, shape, and orientation, is only present on the right side and is not well preserved (Fig. 4.1). However, the bicipital groove and size of the tubercles can be seen. The groove is relatively narrow and deep and the tubercles sit below the level of the head, a configuration that is seen in suspensory primates (e.g., Larson, 1993), and suggested to be advantageous for the function of the supraspinatus and biceps brachii in protraction and elevation of the arm and flexion of the forearm during this type of locomotion (Ashton and Oxnard, 1963; Schön, 1968; Jungers and Stern, 1981; Larson and Stern, 1986). The shaft of the humerus is straight and relatively long, but is also quite robust as would be expected in an animal of its body size. The relatively prominent deltoid tuberosity is positioned more proximally on the shaft,

Figure 4.1. Humerus of *Protopithecus*.
Note the narrow, deep bicipital groove and low tubercles on the proximal end and the large brachioradialis flange on the distal end of the Toca da Boa Vista specimen (left). The specimen from Lagoa Santa (right) is smaller and lacks the protruding brachioradialis flange, but otherwise is similar in joint morphology to the TBV specimen. Scale bar = 1 cm.

more like a generalized arboreal quadruped than a more suspensory animal (e.g., Larson, 1993).

Distally, the specimens from Lagoa Santa (LS) and Toca da Boa Vista (TBV) differ from one another in their size and robusticity (Fig. 4.1); this is especially apparent in the width of the joint and the prominent brachioradialis flange on the lateral side of the TBV specimen. The latter is one of the features pointed out by Hartwig and Cartelle (1996) that suggest an emphasis on forelimb flexion during climbing as an important part of the locomotor repertoire for this specimen. Other fossil primates that have a well-developed brachioradialis flange, such as *Adapis, Notharctus, Apidium*, and *Aegyptopithecus*, have also been suggested to emphasize climbing in their locomotor repertoire (e.g., Dagosto, 1993; Gebo, 1993; Fleagle and Simons, 1995). However, it is unclear whether the size of the flange correlates with the size and power of the brachioradialis muscle and whether the size and power of the muscle correlates with a singular locomotor pattern. Extant anthropoids such as *Cebus, Papio, Pan,* and *Pongo* also have a brachioradialis flange, but none are as prominent as that seen in the TBV *Protopithecus*, which is more similar to the large, flattened condition of many strepsirhines. Those anthropoids listed above also utilize a variety of locomotor behaviors, not all of which include climbing of the type suggested for *Protopithecus*. Orangutans, gibbons, and siamangs have all been shown to have powerful brachioradialis muscles for flexing their elbows not during climbing, but during suspensory locomotion (e.g., Michilsens et al., 2009; Oishi et al., 2009; Michilsens et al., 2010). Suspensory atelines also rely on elbow flexion to raise their center of gravity before the swing phase of their gait (Turnquist et al., 1999). Movements during suspensory locomotion and climbing both necessitate flexion at the elbow as they work against gravity, so it is no surprise that both lead to similar skeletal adaptations (e.g., Fleagle et al., 1981). Further biomechanical analyses of forearm muscle recruitment during climbing and suspensory locomotion in a wider array of non-hominoid taxa is necessary.

Non-locomotor interpretations of the size of the brachioradialis flange of the TBV *Protopithecus* can also be entertained. As mentioned above, extant *Alouatta* also keep their elbows flexed while howling, and the inferred development of this musculature in the large-bodied *Protopithecus* could also have been used in a similar positional behavior; however, it should be noted that the brachioradialis flange and associated flexor musculature are not any larger in extant *Alouatta* than the other atelines (e.g., Schön, 1968). The LS specimen is similar in shape to the larger TBV specimen suggesting that its smaller size could indicate a relatively high level of sexual dimorphism for *Protopithecus*; other atelines, especially *Alouatta*, are also sexually dimorphic in body weight, canine size, and hyoid size (e.g., Ford, 1994; see Chapter 3). However, in other taxa that have well-developed brachioradialis flanges, like strepsirhines, its size is not a sexually dimorphic character (Boyer, pers. comm.). These two humeri need to be studied in more detail to confirm their taxonomic identity and to better understand the functional implications of their morphology.

Other aspects of the joint surfaces on the two distal humeri are more similar. For example, the medial epicondyle on both specimens is large and projects medially as in arboreal quadrupedal primates; it is not retroflexed as in terrestrial Old World monkeys. Neither do the fossils exhibit the extreme distal projection of the medial edge of the trochlea like those in terrestrial primates (e.g., Rose, 1988, 1993). *Protopithecus* also does not have an entepicondylar foramen, a feature that has been lost in atelines but is frequently seen in other platyrrhines such as *Cebus*, *Aotus*, and *Pithecia* (e.g., Gebo, 1993). In many taxa, it is found in combination with the expanded brachioradialis flange, suggesting that the presence of just the flange in *Protopithecus* without the foramen is autapomorphic.

The radius of *Protopithecus* is not complete (Fig. 4.2); only the proximal end is present and the head is heavily worn. Without the entire shaft, it is hard to judge important characteristics of the radial head and tuberosity related to their orientation. The radial tuberosity itself, however, is relatively large and situated more distally on a long radial neck, increasing the length of the lever arm for the biceps into a range seen in more suspensory atelines (Jones, 2008). The head seems to be oval in shape, despite the incomplete circumference. A more circular radial head would be characteristic of a suspensory primate that tends to rotate its forearm at the elbow more frequently (Rose, 1993).

Figure 4.2. Partial proximal radius of *Protopithecus*. Scale bar = 1 cm.

Figure 4.3. Proximal ulna of *Protopithecus*.
Left ulna in anterior (left) and lateral view (right). Note the relatively reduced and straight olecranon process, the inset radial notch, and the relative overall width of the trochlear notch. Scale bar = 1 cm.

Like the distal humerus, the proximal ulna also does not have any of the classical features indicative of terrestrial locomotion in Old World monkeys (Fig. 4.3). More like an arboreal climber that uses more pronation/supination at the elbow, the radial facet is inset against the shaft of the bone and faces anterolaterally as opposed to the outset condition seen in a terrestrial primate that is built for elbow stability (e.g., Gebo, 1993; Rose, 1993). The olecranon process is not retroflexed; the superior border is angled slightly posteriorly but the whole process is relatively reduced and oriented proximally, much like in *Ateles*. However, other aspects of the joint surface are not similar to the *Ateles* condition. For example, the distal facet of the trochlear notch is much smaller and less convex. Also, the coronoid process is slightly more projecting and oriented at a shallower angle. As in the humerus, the ulna exhibits a combination of traits usually seen only in either suspensory taxa like the atelins or taxa that are more generalized

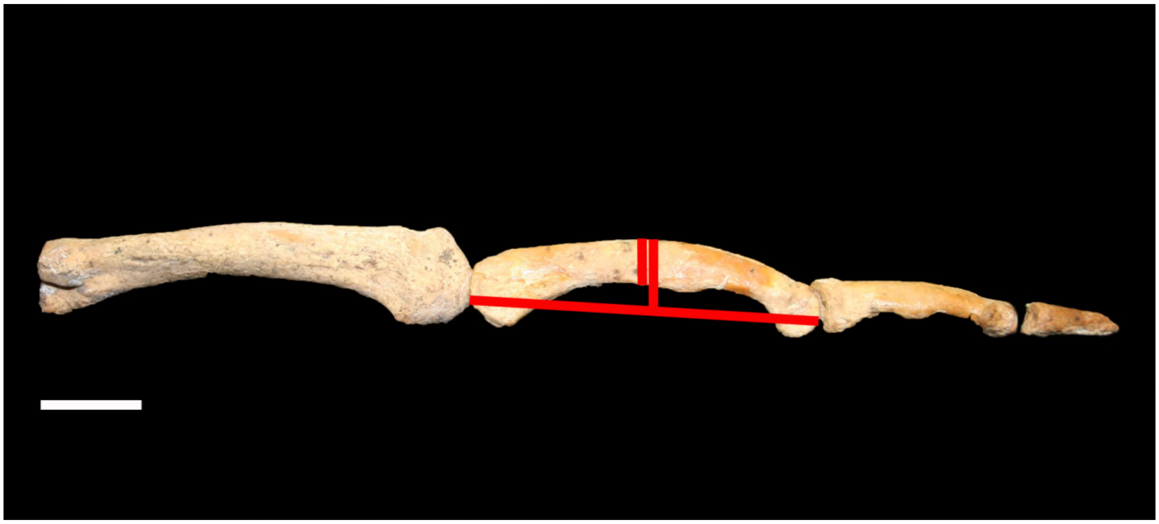

Figure 4.4. Composite ray of *Protopithecus*.
Lines on the proximal phalanx show the dimensions necessary for calculating the included angle of curvature, which on this specimen was approximately 60º. Scale bar = 1 cm.

arboreal climbers like *Alouatta*.

At the distal end of the primate forelimb, degree of phalangeal curvature is also strongly correlated with substrate preference: arboreal taxa show much more curved phalanges than terrestrial taxa due to their greater reliance on grasping branches (Susman et al., 1984; Hamrick et al., 1995; Jungers et al., 1997). Qualitative inspection of the *Protopithecus* phalanges suggests that they are curved as in arboreal primates (Fig. 4.4). In fact, the included angle of curvature (Stern et al., 1995) for one proximal phalanx of *Protopithecus* is approximately 60º (pers. obs.); this is in the high end of the range of values reported for *Ateles* and *Hylobates* but below the range of *Pongo* (Jungers et al., 1997). The phalanges also have relatively strong and distally placed flexor sheath ridges, indicating strong grasping abilities (Almecija et al., 2007; Almecija et al., 2009). Unfortunately, it is unclear whether the phalanges in the sample are from the hands or the feet. Also, there are no relevant metacarpals preserved to determine whether

Protopithecus had a vestigial pollex, a hallmark of both *Ateles* and *Brachyteles* (Biegert, 1963; Erikson, 1963; Jouffroy et al., 1991; Tague, 1997).

Axial skeleton and hindlimb morphology

The hindlimb of the atelines has been modified in unique ways due to their use of the prehensile tail (Ciochon and Corruccini, 1975). As discussed in Chapter 2, the empirical evidence is unclear on whether or not *Protopithecus* had a prehensile tail and therefore to what extent the tail might have been used in both locomotor behavior and postures involved in foraging (also see Discussion below). In living primates, the main skeletal distinctions between prehensile and non-prehensile tails are the overall length of the tail and the robusticity of the lumbar and caudal vertebrae (e.g., Ankel, 1972; German, 1982; Rosenberger, 1983; Lemelin, 1995; Organ, 2010). Within platyrrhines, there are more specific anatomical differences between the lumbar vertebrae of atelines and especially those of *Cebus*, whose tails do have grasping ability but function in a "semi-prehensile" fashion (e.g., Rosenberger, 1983). These differences are due in part to the increased bending loads incurred on the spine during the suspensory positional behaviors that the atelines engage in more frequently (Johnson and Shapiro, 1998).

The vertebrae themselves were not quantitatively investigated here, although several thoracic, lumbar, and caudal vertebrae are relatively well-preserved (Fig. 4.5). Jones (2008) includes indices of caudal robusticity and caudal transverse process width for *Protopithecus* that align the fossil with "brachiating" prehensile-tailed taxa, specifically *Lagothrix* and *Ateles*; these values are also relatively high in taxa that practice hindlimb suspension and tail support such as *Cebus*, *Cacajao*, and *Chiropotes* (e.g., Fleagle and Meldrum, 1988; Gebo, 1992; Johnson and Shapiro, 1998). Qualitatively, the *Protopithecus* lumbar vertebrae have long straight spinous

Figure 4.5. Assorted vertebrae of *Protopithecus*.
Top row are the preserved caudal vertebrae, arranged in descending size order but not meant to represent the complete tail. Bottom left are the most complete thoracic and lumbar vertebrae in inferior view. Bottom right is one of the best preserved thoracic vertebrae in lateral (top), posterior (middle), and inferior (bottom) views. Scale bar = 1 cm.

processes that are more similar to *Ateles* than *Alouatta* (pers. obs.; see Shapiro, 1993). While their spinous processes are different in shape and orientation, transverse processes on the lumbar vertebrae are more similar in the two extant genera, being oriented perpendicularly and articulating at or near the body/pedicle junction (Johnson and Shapiro, 1998). Given the differences in locomotor repertoire between *Ateles* and *Alouatta* and the existence of the (potentially) suspensory *Protopithecus*, it is possible that this similarity in transverse process morphology reflects a primitive retention in *Alouatta* from a more suspensory ancestor (Johnson and Shapiro, 1998; also see Chapter 5). There are two *Protopithecus* vertebrae that have complete transverse processes preserved: one is a thoracic vertebra (bottom right in Fig. 4.5) and the other appears to be the diaphragmatic vertebrae (top row left in Fig. 4.5), not a true lumbar, so no conclusive comparison to the living taxa can be made. Measurements of the internal structure of the caudal vertebrae indicating bending strength (e.g., Organ, 2010) would be very useful for further investigating the functional morphology of the *Protopithecus* tail.

While many single vertebrae are preserved, the vertebral column of the fossil is far from complete, and therefore the lengths of each part of the column cannot be reconstructed. This does simplify things, however, as the functional explanation for the relative lengths of the thoracic, lumbar, and caudal regions of the vertebral column are still debated. For example, despite different uses of the prehensile tail in the four ateline genera, the *Ateles* and *Alouatta* vertebral columns are assumed to be subject to similar bending stresses during various forms of suspensory behavior, and this manifests itself in a similar shortening of the lumbar region (Johnson and Shapiro, 1998). However, it has also been suggested that a shortened lumbar region would be adaptive for resisting the buckling of the vertebral column during vertical climbing by a large-bodied individual (Jungers, 1984b).

When atelines suspend their body below branches by two or more limbs plus the tail, the back bends considerably and lordosis in their shortened lumbar region is permitted by a reduction in iliac height that frees the verterbrae from being trapped between the iliac blades (Lovejoy and McCollum, 2010; Machniki et al., 2011). The ischium also is shorter in the atelines than in other primates that lack a prehensile tail (Steudel, 1981). No quantitative data were collected to specifically address these anatomical relationships here, although the right innominate of *Protopithecus* is almost complete (Fig. 4.6). Hartwig and Cartelle (1996) point out the large, deeply concave iliac fossa for the attachment of the gluteus medius muscle, which they suggest was used for hindlimb extension during climbing. However, several other functional interpretations for this muscle in atelines can be found in the biomechanical literature. For example, Grand (1968) lists the gluteus medius as a primary abductor of the hip while Stern

Figure 4.6. Partial right innominate of *Protopithecus*, lateral view. Scale bar = 1 cm.

(1971) proposes its function as a medial rotator and hip stabilizer, which he notes could be useful in many forms of locomotion used by platyrrhines including leaping and hindlimb suspension, as well as climbing. Perhaps the most radical hypothesis comes from Schön (1968), who suggests that the gluteus medius in *Alouatta* functions as a trunk stabilizer while sitting or squatting to counteract the effect of the enlarged hyoid that would otherwise tilt the upper body forward. These were all studies based on dissections; a recent study using electromyography to investigate the function of the gluteal muscles in a variety of primates, including *Ateles* (Larson and Stern, 2009), also concludes that the gluteus medius functions as a medial rotator and supports earlier suggestions that it is only an extensor in taxa with a greater trochanter that reaches above the femoral head (e.g., Stern and Susman, 1981). As discussed below, the *Protopithecus* femur does not show this morphology, although climbing could still have been an important part of the fossil locomotor repertoire.

In the hindlimb itself, the femur of *Protopithecus* is represented by two individuals: the LS left proximal femur fragment and the TBV full bones. The joint surfaces are all very well-preserved, although the lesser trochanter of the right TBV femur is abraded. As described for the humerus, the differences between the specimens seem to be mostly due to the larger size and greater robusticity of the TBV individual (Fig. 4.7). The LS specimen is broken about two thirds of the way down the shaft, but the difference in shaft diameter between the two individuals is still particularly obvious. Femoral midshaft width of the TBV specimen is 20.4 mm (pers. obs.) while the same measurement for the LS specimen is 18.65 mm (Hartwig, 1995a); this difference of 1.75 mm between the two *Protopithecus* specimens is larger than the size difference between any of the atelin genera measured by Hartwig. As in the humerus, one explanation for these differences could be a relatively high degree of sexual dimorphism in *Protopithecus*.

This size difference is also visible in various muscle attachment sites; as noted by Hartwig and Cartelle (1996), one of the unique features of the TBV proximal femur is an enlarged gluteal tuberosity for the attachment of the gluteus superficialis muscle (Fig. 4.7). *Alouatta* has the most well-developed gluteus superficialis of the atelines (Stern, 1971), and some males do seem to have an enlarged gluteal tuberosity relative to the other taxa (pers. obs.; see Fig. 6 in Ciochon and Corruccini, 1975), but more detailed investigation on a larger sample is necessary to reliably tie the size of the tuberosity to either body size or muscle mass. Regardless, the gluteus superficialis and tensor fasciae femoris of the atelines have been described as forming a muscle mass in the hip that is hypothesized to extend and rotate the hip during "antipronograde" behaviors such as climbing and hindlimb suspension

Figure 4.7. Femur of *Protopithecus*.
Toca da Boa Vista is on the left and Lagoa Santa is on the right. Note the large gluteal tuberosity on the TBV specimen which is absent on the proximal femur from LS. Also note the difference in shaft robusticity between the two specimens. Scale bar = 1 cm.

(e.g., Stern, 1971; Stern and Oxnard, 1973; Stern and Susman, 1981). Both behaviors are used frequently by *Alouatta*, with hindlimb suspension, particularly during feeding, seen even more frequently than the forelimb suspension characteristic of *Ateles* (Mendel, 1976; Schön Ybarra, 1984; Cant, 1986; Schön Ybarra and Schön, 1987; Gebo, 1992; Bergeson, 1998). The large, proximally positioned attachment sites for these muscles on the TBV *Protopithecus* femur may suggest that the fossil was using this *Alouatta*-like positional behavior as well.

Other aspects of the proximal femur also indicate non-*Ateles*-like behavior. The large, proximally placed lesser trochanter of *Protopithecus* provides attachment for the iliopsoas muscles, powerful hip and thigh flexors hypothesized to be used during climbing (Schön, 1968; Ciochon and Corruccini, 1975; Anemone, 1993; Meldrum, 1993). The lesser trochanter seems to be larger in the smaller LS individual as it projects further medially in anterior view, but in the TBV individual it is longer in the proximodistal dimension (Fig. 4.7). The greater trochanter sits below the relatively large and globular femoral head and is open posteriorly with a relatively deep trochanteric fossa widely spaced from the head and neck, similar to the configuration seen in *Brachyteles*. The femoral neck appears to be short and robust, the condition normally seen in leaping primates (Ciochon and Corruccini, 1975), but this is most likely related to body size as *Protopithecus* is much larger than any leaping platyrrhine. While the shape of the proximal femur from Lagoa Santa looks very similar to that of *Brachyteles*, the morphology of the TBV specimen that suggests well-developed musculature used during both climbing and hindlimb suspension are parts of the postcranial skeleton that provide the strongest functional link between *Protopithecus* and *Alouatta*.

The distal femur is similar to the condition seen in suspensory atelines, with a shallow patellar groove between relatively wide-set and uneven condyles, with the medial one projecting further inferiorly (Ciochon and Corruccini, 1975). As would be expected for articulation with that distal femur, the medial articular surface of the tibial plateau is larger than the lateral one (Fig. 4.8); slightly asymmetrical tibial condyles are typical of arboreal quadrupeds who maintain abducted thighs during locomotion (Grand, 1968; Gebo, 1993). The articular surfaces of the *Protopithecus* proximal tibia are divergent from one another, with a wider distance across the anterior portion of the bone than the posterior. They are not posteriorly facing, as is seen in primates that are well-adapted for leaping (Anemone, 1993), but they do overhang the shaft posteriorly as in climbing primates like *Alouatta* (Schön Ybarra and Schön, 1987). The tibial tuberosity is long, wide, and rugose, indicating a large area of insertion for the quadriceps femoris muscle via the patellar tendon. The shaft of the tibia is relatively narrow and slightly bowed medially. The medial malleolus is quite robust, projects relatively far distally, and is not rotated or hooked. The groove for the tendons of the tibialis posterior and flexor digitorum longus muscles is relatively deep and wide. On the lateral side, the fibular facet is large and slightly concave, but shows no indication of an extensive syndesmosis between the tibia and fibula as is seen in leaping primates. (The fibula is not preserved in the *Protopithecus* sample.) The articular surface for the talus is angled mediolaterally and is broad anteroposteriorly with no extension onto the anterior surface of the shaft which would create a “tibial stop”, again a trait seen in extant primates adapted for leaping (Gebo, 1993; Meldrum, 1993).

The ankle is one of the parts of the postcranial skeleton in atelines that converges on apes as a reflection of their shared use of climbing (Erikson, 1963). The talus, however, is an exception, being uniquely flattened in atelines (Gebo, 1989). They, as well as taxa like *Chiropotes*, also have a bulbous talar head with a dorsolateral extension of the articular surface, which has been suggested to provide increased mobility and supination during hindlimb

Figure 4.8. Tibia of *Protopithecus*.
Left tibia in anterior view (left), proximal end in superior view (top), and distal end in inferior view (bottom). Scale bar = 1 cm.

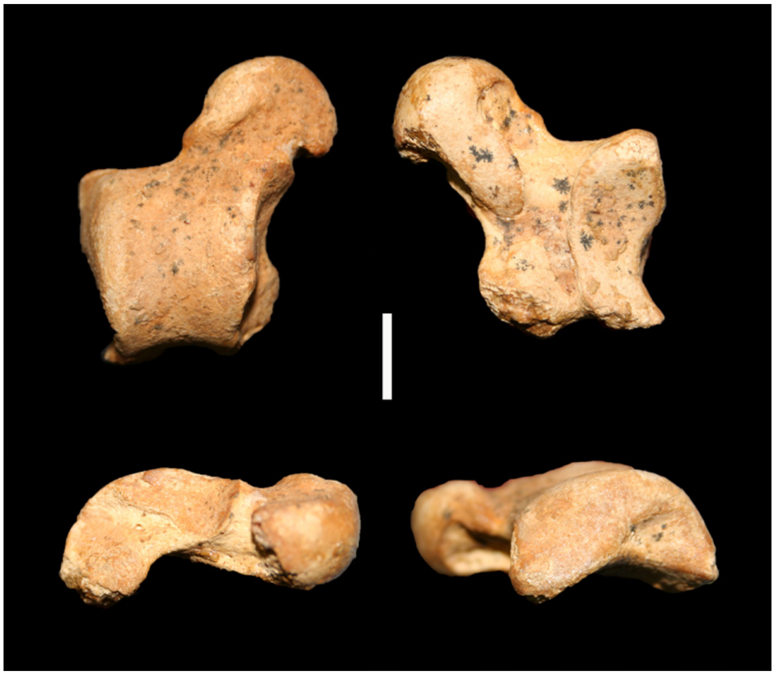

Figure 4.9. Talus of *Protopithecus*.
Left talus in superior (top left), inferior (top right), medial (bottom left), and lateral (bottom right) views. Scale bar = 1 cm.

suspension (Fleagle and Meldrum, 1988; Meldrum, 1993; Lockwood, 1999). *Protopithecus* does not exhibit this torsion of the talar head, but the articular surface is broad and sits on a relatively short neck like that seen in *Ateles* and the suspensory atelines (Fig. 4.9). The trochlea is parallel-sided, and the anterior portion is slightly wider than the posterior portion, with a relatively shallow groove running down the center. The concave medial malleolar facet and flat lateral facet indicate mobility at the ankle, potentially for inverting the foot to grasp branches (Gebo, 1993). Both facets on the plantar surface are long and narrow and the posterior calcaneal facet is only slightly concave. As mentioned above, the *Protopithecus* phalanges are curved as in arboreal taxa, but it is unclear whether they are from the hands or the feet.

While some single aspects of the joints might appear similar to non-platyrrhine taxa, there is no suite of characters seen in the *Protopithecus* forelimb or hindlimb that would suggest extreme locomotor specializations like those seen in leaping or slow climbing strepsirhines or terrestrial Old World monkeys. The *Protopithecus* postcranial skeleton combines traits possessed by extant primates that practice below-branch forelimb and hindlimb suspension as well as arboreal climbing. The qualitative aspects of the *Protopithecus* skeleton described above will be quantified using landmark-based three-dimensional geometric morphometric (3DGM) techniques in an attempt to make a more detailed comparison to a variety of extant primates.

Materials and Methods

A comparative sample of living primates was used consisting of adult male and female wild-shot individuals from collections at the AMNH, NMNH, FMNH, and the MN (Table 4.2). This set of taxa was chosen to represent a diverse array of body sizes, locomotor patterns, and phylogenetic affinities, extending the comparative framework used in previous studies of the *Protopithecus* postcranial remains. The fossil material includes: the *Protopithecus* distal humerus and proximal femur discovered in the Lagoa Santa caves which are now housed in the Universitets Zoologisk Museum in Copenhagen, Denmark (UZM); the *Protopithecus* skeleton from Toca da Boa Vista, curated in the Museu de Ciências Naturais at the Pontificia Universidade Católica de Minas Gerais in Belo Horizonte, Brazil (MCL); the skeleton of *Caipora bambuirom*, also from TBV (Cartelle and Hartwig, 1996); and several subfossil lemur specimens curated in the AMNH (*Archaeolemur sp.*: AMNH30042-B-10; *Paleopropithecus ingens*: AMNH30042-B-1, 30042-A-3, 30042-A-5; *Megaladapis edwardsi*: AMNH30042-A-1; plus several uncatalogued specimens assigned to those genera). It should be noted that the

Table 4.2. Extant comparative sample[1].

	Male Body Weight[2] (kg)		**Locomotor Repertoire[3]**	**Distal Humerus**		**Proximal Ulna**		**Femur**		**Tibia**		**Talus**	
	Average	Range		Male	Female	Male	Female	Male	Female	Male	Female	Male	Female
Propithecus	4.8	2.8 – 6.5	VCL	4	4	4	4	3	4	3	5	3	3
Indri	6.7	6.5 – 6.9	VCL	1	1	1	1	1	1	1	1		1
Archaeolemur		14 – 24	AQ, terrestrial, climbing			1							
Megaladapis		38 – 75	arboreal climbing and clinging	3		3				2			
Palaeopropithecus		45 – 52	upside-down below branch suspension	2		4							
Aotus	0.9	0.7 – 1.2	AQ, leaping	14	15	14	15	13	14	13	15	8	8
Pithecia	2.4	1.4 – 3.1	AQ, leaping	8	8	8	3	8	4	7	3	7	2
Chiropotes	3.2	2.9 – 3.5	AQ, leaping	4	1	4	1	4	1	4		4	1
Cebus	3.0	1.3 – 4.8	AQ	28	28	29	28	28	28	27	28	21	20
Alouatta	7.2	4.0 – 12.5	AQ, climbing, PHT	33	28	32	26	32	26	28	27	22	18
Lagothrix	8.5	7.1 – 10.2	AQ, climbing, PHT	6	6	6	6	6	6	6	6	6	6
Ateles	8.3	5.5 – 9.8	AQ, suspensory, PHT	9	12	9	12	8	12	7	12	5	11
Brachyteles	11.0	9.2 – 13.8	AQ, suspensory, PHT	4	3	4	3	4	3	4	3	2	2
Protopithecus		**20 - 25**	**?**	**2**		**1**		**2**		**1**		**1**	
Caipora		20.5	?	1		1		1				1	
Presbytis	7.5	5.5 – 12	AQ, leaping	19	16	17	16	19	15	8	8	12	7
Lophocebus	8.0	7.8 – 8.2	AQ	6	3	4	2	6	3	3	1	2	2
Macaca	10.5	5.4 – 18.3	AQ, terrestrial	15	7	15	8	16	7	7	4	13	3
Colobus	10.8	9.6 – 13.5	AQ, leaping	21	13	11	8	20	13	5	4	10	5
Nasalis	20.0		AQ, leaping, swimming	8	1	8	1	8	1	6	1	7	1
Papio	23.5	16.0 – 31.0	AQ, climbing, terrestrial	11	7	11	7	11	7	3	1	5	3
Symphalangus	12.0		brachiation, climbing	2	1	2	1	1	1	2	1	1	1
Pan	46.0	39.0 – 59.7	AQ, suspensory, terrestrial	10	6	11	6	10	5	12	5	9	5

[1] Data from Rosenberger and Strier (1989), Cartelle and Hartwig (1996), Fleagle (1999), Jungers et al (2002), DiFiore and Campbell (2007), Halenar (this volume).

[2] Only male body weights are listed for comparative purposes as both TBV *Protopithecus* and *Caipora* have been suggested to be males.

[3] VCL = vertical clinging and leaping, AQ = arboreal quadrupedalism, PHT = prehensile tail.

Caipora skeleton is of a subadult individual. The epiphyses of the distal humerus and proximal ulna are fully fused, however, the hindlimb epiphyses are not as well preserved. For example, the right distal femur is plastered back into place while the left epiphysis is missing altogether. For similar reasons, the tibia of *Caipora* was not available for measurement with this protocol.

A Microscribe 3DX digitizer was used to collect the three-dimensional coordinates (*x, y, z*) of a set of landmarks designed to capture the shapes that are expected to vary among living taxa of differing locomotor profiles (Fig. 4.10; Table 4.3). Data were collected on the distal humerus, proximal ulna, proximal and distal femur, proximal and distal tibia, and the talus; these elements are well preserved in *Protopithecus* on at least one side of the body. As there are few biologically homologous Type I landmarks, such as the meeting point of two sutures, on postcranial elements, sets of Type II landmarks, those that are defined by the geometry of the specimens (Bookstein, 1991), were designed specifically for this study. They are meant to capture the shape of aspects of the bones suggested to be functionally relevant in previous studies of primate postcranial morphology. Most landmarks fall on either muscle attachment sites or a geometrically defined point around a curved articular surface, such as the head of the femur. Careful examination of all of the taxa in the comparative sample made sure that landmarks were present and easily repeatable across all functional and phylogenetic groups. The wireframes included on Figure 4.10 should make the landmark choices clear as they are connected to make a picture of the shape of the articular surfaces of of the joint. During data collection, the humerus, ulna, femur, and tibia were positioned in such a way so that landmarks on all sides of the bone could be digitized without changing their orientation. The landmarks on the dorsal side of the talus were collected first and then the bone was flipped over so the landmarks on the plantar side could be collected. Four reference landmarks were recorded in

Figure 4.10. 3D landmark points captured on each element.
Landmarks are shown on the TBV *Protopithecus* and are connected as a reference for the wireframes in the following PCA figures. See Table 4.3 for landmark definitions. Scale bars = 1 cm.

Table 4.3. Anatomical landmark definitions.

Distal Humerus[1]	
Anterior	
A1	Most lateral point
A2	Most medial point
A3	Most lateral point on the capitulum
A4	Most medial point on the capitulum
A5	Most superiolateral point on the trochlea (excluding the capitulum)
A6	Most inferiomedial point on the trochlea (excluding the capitulum)
A7	Most superior point on the medial epicondyle
A8	Most inferior point on the medial epicondyle
A9	Most superior point on the lateral epicondyle
A10	Most inferior point on the lateral epicondyle
Posterior	
P1	Most superior point on the olecranon fossa
P2	Most inferiomedial point of the olecranon fossa
P3	Most inferiolateral point of the olecranon fossa
P4	Deepest point of the olecranon fossa
P5	Most medial point on the trochlea
P6	Most lateral point on the trochlea
P7	Tip of the medial epicondyle
Proximal Ulna	
U1	Most proximal point on the olecranon process
U2	Most medial point on the maximum constriction of the olecranon process
U3	Most lateral point on the maximum constriction of the olecranon process
U4	Most posterior point on the olecranon process
U5	Most anteriomedial point on the olecranon process
U6	Most aneriolateral point on the olecranon process
U7	Most medial point on the “wing” of the proximal articular facet
U8	Most lateral point on the “wing” of the proximal articular facet
U9	Most anterior point on the proximal border of the proximal articular facet
U10	Most distomedial point of the proximal articular facet
U11	Most distolateral point of the proximal articular facet
U12	Deepest point in the midline of the trochlear notch
U13	Most posteriomedial point of the distal articular facet
U14	Most anterior point of the distal articular facet
U15	Most anterior point of the radial facet
U16	Most posterior point of the radial facet
U17	Most proximal point of the radial facet
U18	Most distal point of the radial facet
U19	Deepest point in the radial facet
Femur	
Proximal	
F1	Middle of fovea capitus
F2	Most proximal point on the femoral head
F3	Most proximal point on the facet margin around the femoral head
F4	Most distal point of the facet margin around the femoral head
F5	Most anterior point of the facet margin around the femoral head
F6	Most posterior point of the facet margin around the femoral head
F7	Maximum point of constriction on ridge running from lesser trochanter to the femoral head
F8	Deepest point of the proximal neck
F9	Middle of the trochenteric fossa
F10	Tip of greater trochanter
F11	Most lateral point of greater trochanter
F12	Most proximoanterior point of the greater tubercle
F13	Tip of lesser trochanter
F14	Origin of pectineal line
Distal	
F15	Most medial point
F16	Most lateral point
F17	Most proximomedial point of the patellar articular surface
F18	Most proximolateral point of the patellar articular surface
F19	Most proximal point of the patellar articular surface
F20	Most distal point of the patellar articular surface
F21	Most distal point of the medial condyle
F22	Most distal point of the lateral condyle
F23	Most posterior point of the medial condyle
F24	Most posterior point of the lateral condyle
F25	Most proximomedial point of the posterior aspect of the medial condyle

F26	Most proximolateral point of the posterior aspect of the lateral condyle
F27	Most proximolateral point of the posterior aspect of the medial condyle
F28	Most proximomedial point of the posterior aspect of the lateral condyle
F29	Most posterio-medial point of the groove (notch)
F30	Most posterior point of the groove (notch)
Tibia	
Proximal	
Tib1	Most anterior point on the medial tibial condyle on the outer edge of the articular surface
Tib2	Most medial point on the medial tidial condyle
Tib3	Most posterior point on the medial tibial condyle
Tib4	Most lateral point on the medial tibial condyle
Tib5	Most anterior point on the lateral tibial condyle
Tib6	Most medial point on the lateral tidial condyle
Tib7	Most posterior point on the lateral tibial condyle
Tib8	Most lateral point on the lateral tidial condyle
Tib9	Most anterior point on the tibial tuberosity
Distal	
Tib10	Most anterior point on the talar facet
Tib11	Most medial point on the talar facet
Tib12	Most posterior point on the talar facet
Tib13	Midpoint of the lateral edge of the talar facet
Tib14	Midpoint of the groove between the talar facet and the medial malleolus
Tib15	Most anterior point of the groove between the talar facet and the medial malleolus
Tib16	Most posterior point of the groove between the talar facet and the medial malleolus
Tib17	Most medial point of the medial malleolus
Tib18	Distal tip of the medial malleolus
Tib19	Most lateral point on the fibular facet
Talus	
Dorsal Surface	
Tal1	Most distal point of the trochlear groove
Tal2	Most distal point of contact between the medial malleolar facet and the trochlear surface
Tal3	Most dorsal point on the medial facet margin
Tal4	Most proximal point of contact between the medial malleolar facet and the trochlear surface
Tal5	Most proximal point of the trochlear groove
Tal6	Most dorsal point on the lateral facet margin
Tal7	Most dorsal point on the trochlear groove
Tal8	Most distal point on medial malleolar facet
Tal9	Most distal point on lateral malleolar facet
Tal10	Most plantar point on lateral malleolar facet
Tal11	Deepest (most medial) point on lateral malleolar facet
Tal12	Most dorsal point of the navicular facet
Tal13	Most medial point of the navicular facet
Tal14	Most lateral point of the navicular facet
Tal15	Most proximal point of contact between the lateral malleolar facet and the trochlear surface
Tal16	Most distal point of contact between the lateral malleolar facet and the trochlear surface
Tal17	Most plantar point on medial malleolar facet
Tal18	Most distal point of the navicular facet
Plantar Surface	
Tal19	Most disto-lateral point of the posterior calcaneal facet
Tal20	Lateral end of the narrowest distance across the posterior calcaneal facet
Tal21	Most proximo-lateral point of the posterior calcaneal facet
Tal22	Most proximal point of the posterior calcaneal facet
Tal23	Most proximo-medial point of the posterior calcaneal facet
Tal24	Medial end of the narrowest distance across the posterior calcaneal facet
Tal25	Most disto-medial point of the posterior calcaneal facet
Tal26	Most distal point of the posterior calcaneal facet
Tal27	Deepest (most dorsal) point of the posterior calcaneal facet
Tal28	Most proximal point of the anterior calcaneal facet
Tal29	Most medial point of the anterior calcaneal facet
Tal30	Most distal point of the anterior calcaneal facet
Tal31	Most lateral point of the anterior calcaneal facet
Tal32	Most plantar point on the navicular facet
Tal33	Most lateral point of contact between the navicular facet and the distal calcaneal facet

[1] All bones were mounted so that landmarks on all surfaces could be digitized without changing the orientation of the specimen, except for the talus. The dorsal and plantar landmarks on each talus were recorded separately and then “dvlr-ed” back together.

both orientations so that the complete set could be combined using the DVLR (dorsal-ventral landmark registration) program (v. 0.4.12; Raaum 2006).

So far, few 3DGM analyses involving postcrania have been published (e.g., Drapeau, 2008; Harcourt-Smith et al., 2008; Harmon, 2009) and none of them are focused on platyrrhines. Three-dimensional geometric morphometric techniques, especially generalized Procrustes analysis (GPA; O'Higgins and Jones, 1998), are expected to be of particular help in answering questions about the large-bodied *Protopithecus* because it is a size-independent method that scales specimens to unit centroid size as a way of normalizing body mass differences within a sample. Principal components analyses (PCA) were employed to visualize the morphological variation within the sample for each skeletal element based on the results of a GPA, using the program *morphologika²* v2.5 (O'Higgins and Jones, 2006). Clouds of points representing groups of taxa with similar locomotor behaviors were thus produced and the locomotor behavior of the fossil was inferred based on its position with respect to the comparative sample. For example, if *Protopithecus* were to fall in the middle of a cloud of acrobatic suspensory atelines, this would support the hypothesis that it was using acrobatic suspensory locomotion.

This method was chosen over discriminant function analysis, which was used previously in a quantitative analysis involving *Protopithecus* (Jones, 2008), because it does not require the user to specify a particular locomotor category for each specimen in the comparative sample. Living primates use a variety of locomotor behaviors that leave their mark on the postcranial skeleton and reducing complex behavioral patterns, as well as taxa, to a single categorical definition may be less valuable in this context. *Protopithecus* is known to exhibit a new mosaic of morphological features and it is also far outside the body size range of all other modern platyrrhines, an important consideration for many reasons including the influence of body size on positional behavior (see Chapter 2). Including a fossil in a PCA instead of a DFA lets the fossil speak for itself with regard to its similarities to extant taxa.

Principal components analyses were run on several different iterations of the sample for each element; one including the entire comparative sample, one including only the platyrrhine taxa, and one on the male species mean landmark configuration for those platyrrhines. The male species mean PCA was then overlaid with a minimum spanning tree to connect the shapes nearest to one another based on Procrustes distance. Both the mean landmark configurations and the minimum spanning trees were calculated using the PAST software package (Hammer et al., 2001). As the comparative sample spans a relatively wide range of body sizes, for each PCA the first two principal component axes scores were regressed against ln centroid size of the specimens to test for correlation with body size. While the size of an animal is certainly related to how it can move through its habitat and is therefore relevant to the variation in the sample, it is not desirable for size alone to be driving the grouping patterns on the axes that represent the majority of that variation.

Results

Before discussing the position of *Protopithecus* within the PCA scatter obtained for each skeletal element, it should be noted that some of that scatter is reflecting the phylogenetic groups in the comparative sample as much as it is locomotor groups. Methods developed for incorporating phylogeny into comparative studies, such as independent contrasts (e.g., Nunn and Barton, 2001), were not used here but this should not prohibit meaningful conclusions to be drawn from these analyses. For anthropoids in general, and the platyrrhines in particular, phylogenetic groups are at least partly distinguished by locomotor patterns (e.g., Gebo, 1989;

Rosenberger, 1992). Generally speaking, atelines are large-bodied and suspensory/climbers, pithecines are medium-sized and leaper/climbers, and cebines are small and more generalized arboreal quadrupeds with some leaping abilities. New World monkeys have been described as a morphocline (Ciochon and Corruccini, 1975) and as a "nicely graded series of locomotor types" (Erikson, 1963). So it should be no surprise that most of the grouping patterns in the following PCAs put related taxa together, based both on phylogeny and locomotor pattern. As will be described, the morphology that changes from one position to another along the PC axes is functionally relevant.

A PCA of the entire primate-wide sample for the distal humerus results in a clear separation of New World monkeys, Old World monkeys, hominoids, and strepsirhines (Fig. 4.11). The Old World monkeys are arranged across PC1 from more arboreal taxa like *Colobus* on the left to the more terrestrial baboons on the right, with the variable macaques spanning both groups. In both the full sample and platyrrhine-only analyses (Figs. 4.11-12), the suspensory atelins form their own group separate from the more generalized arboreal taxa (*Alouatta* and *Cebus*) and those that add more leaping to their repertoire (*Aotus*, *Pithecia*, and *Chiropotes*). The three fossils, both *Protopithecus* individuals and *Caipora*, are consistently part of this atelin cluster due to their mediolaterally wide distal humerus and large medially projecting medial epicondyle. In the full sample PCA, the TBV humerus is situated closer to the strepsirhine cluster on PC2 due to the enlarged brachioradialis flange that it shares with some vertical clinging and leaping members of that group (Fig. 4.11). When a minimum spanning tree is calculated to connect the three-dimensional shapes representing the male mean landmark configuration for each species of platyrrhine in the sample, both *Protopithecus* specimens are nearest to *Ateles fusciceps* while *Caipora* is nearest to *Brachyteles* (Fig. 4.13). The two

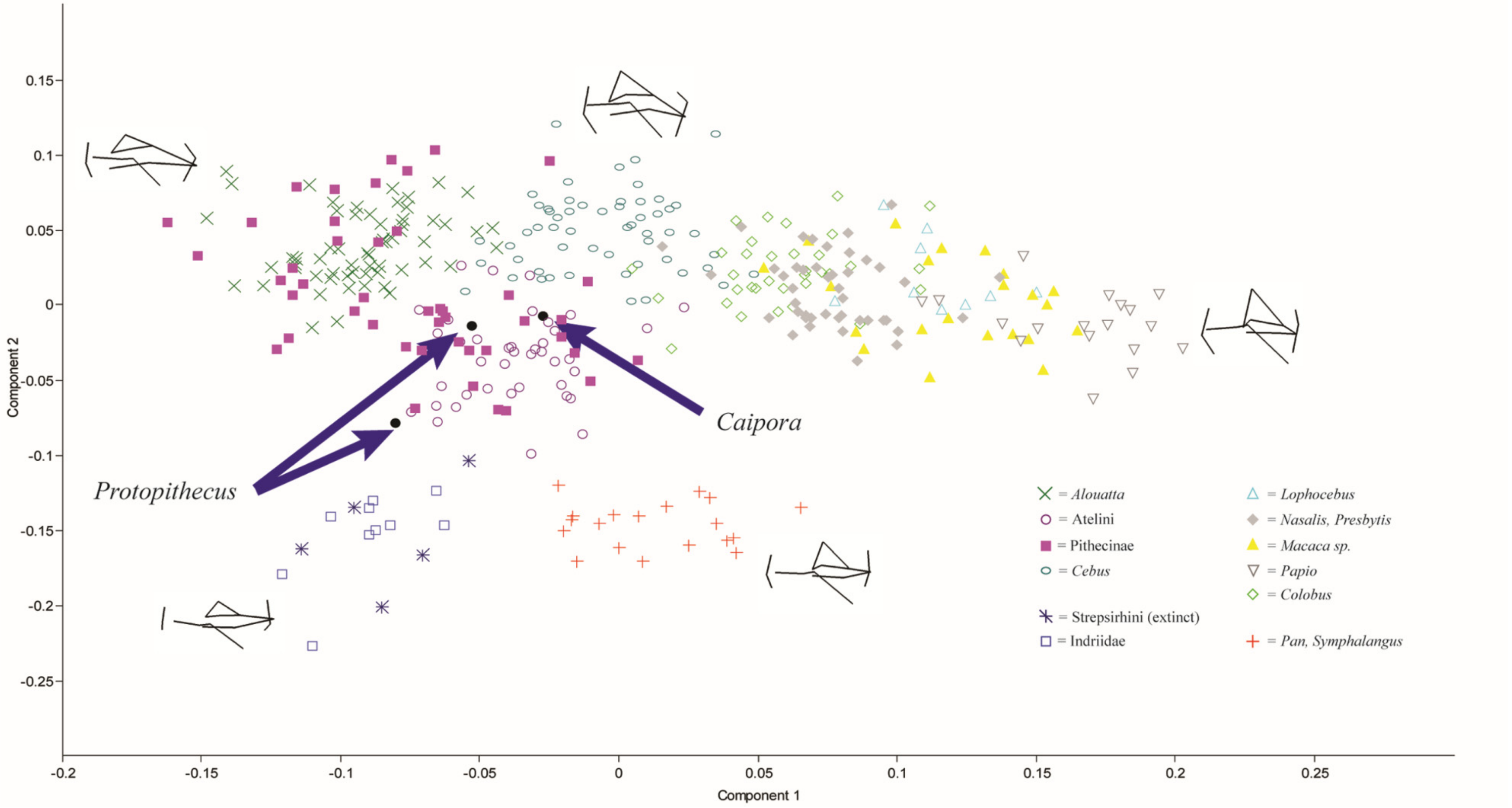

Figure 4.11. PCA results for the distal humerus using the entire comparative sample.
The taxa are arrayed across PC1 (25% total variance) based on the width of the joint, which is affected by the length and orientation of the medial epicondyle and height and depth of olecranon fossa. PC2 (14%) shows the variation based on the height of the epicondyles. The wireframes show the morphology of the individuals in the nearest cluster of a right humerus in anterior view (see Fig. 4.10 for reference). Bottom left *Protopithecus* = TBV, Top right = LS.

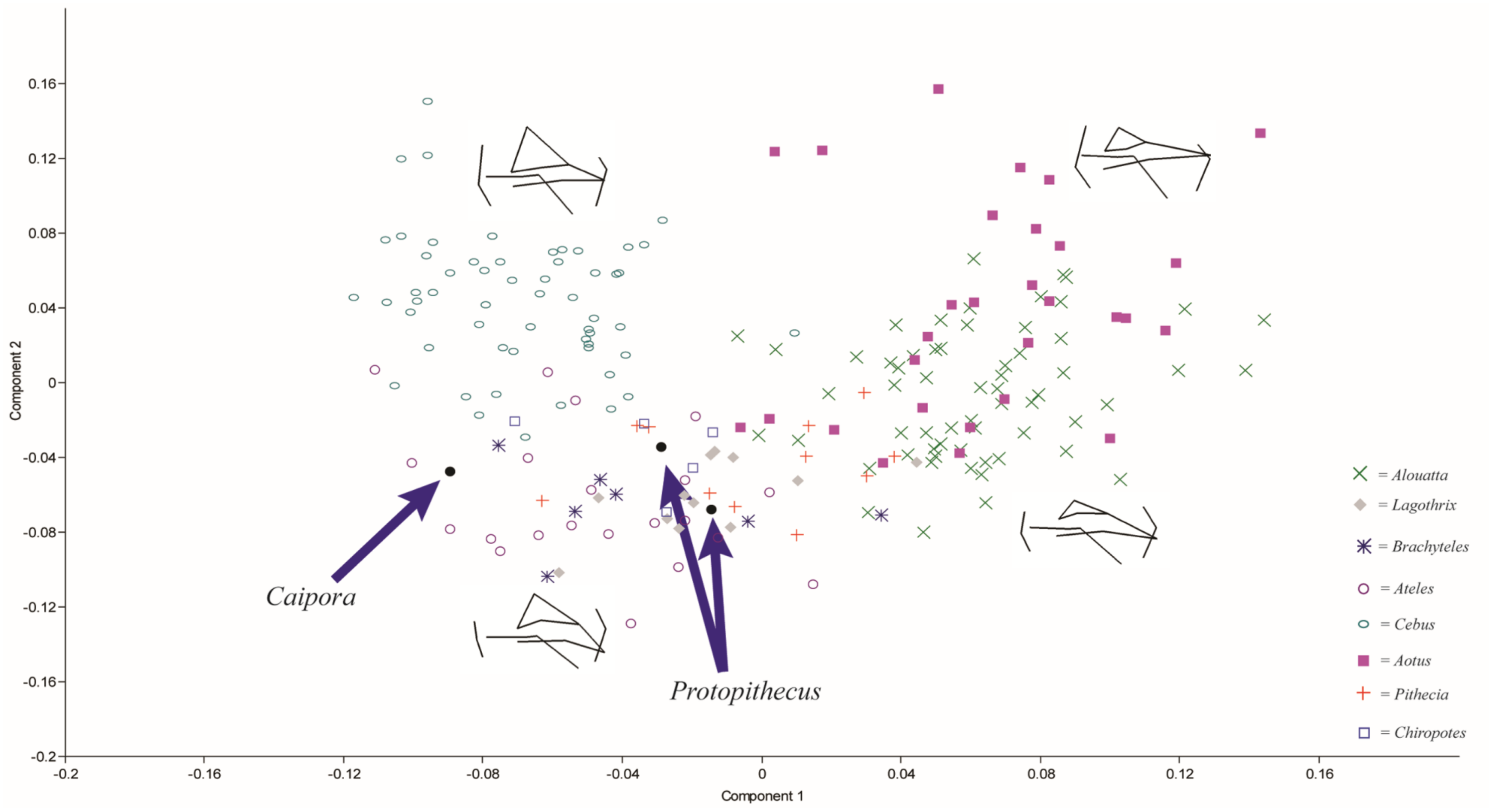

Figure 4.12. PCA results for the distal humerus using the platyrrhine taxa only.
PC1 (21% total variance) is being driven by the height of the olecranon fossa and the length of the medial epicondyle. PC2 (15%) shows the variation in the height of lateral epicondyle and the orientation of medial epicondyle. The wireframes represent the morphology of the individuals in the nearest cluster of a right humerus in anterior view (see Fig. 4.10 for reference). Top left *Protopithecus* = LS, bottom right = TBV.

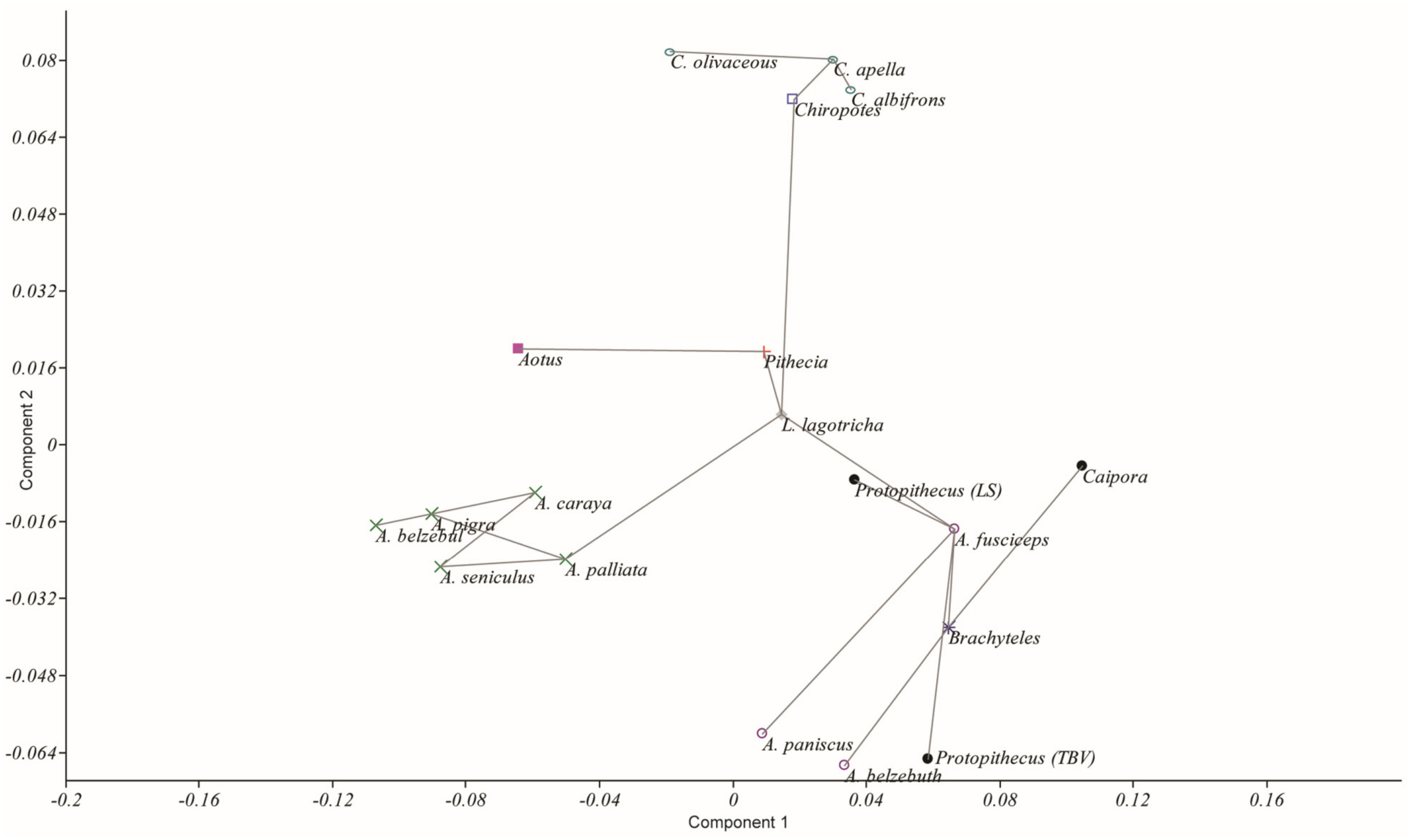

Figure 4.13. PCA results for the average male distal humerus shape using all platyrrhine species.
A minimum spanning tree connects the shapes with the shortest Procrustes distance between them. Both *Protopithecus* specimens are connected to *Ateles*, while not being connected to each other, emphasizing the differences between the two fossil specimens as described in the text.

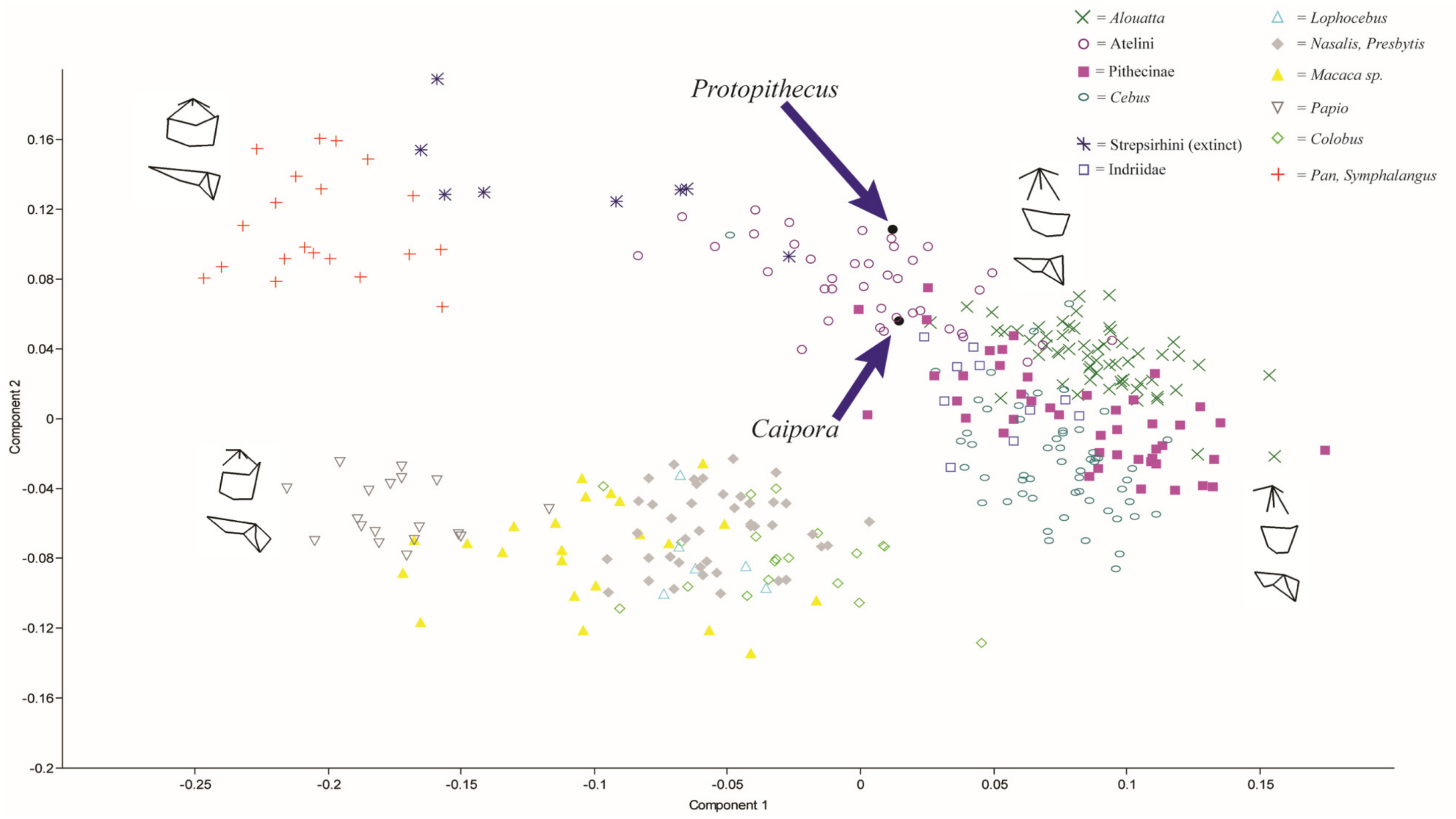

Figure 4.14. PCA results for the proximal ulna using the entire comparative sample.
PC1 (29% total variance) represents the variation in the height of the olecranon process and the width of the distal facet of the trochlear notch. Variation along PC2 (13%) is driven by the orientation of the proximal portion of the trochlear notch and the radial facet. The wireframes represent the shape of a left ulna in anterior view for the individuals in the nearest cluster (see Fig. 4.10).

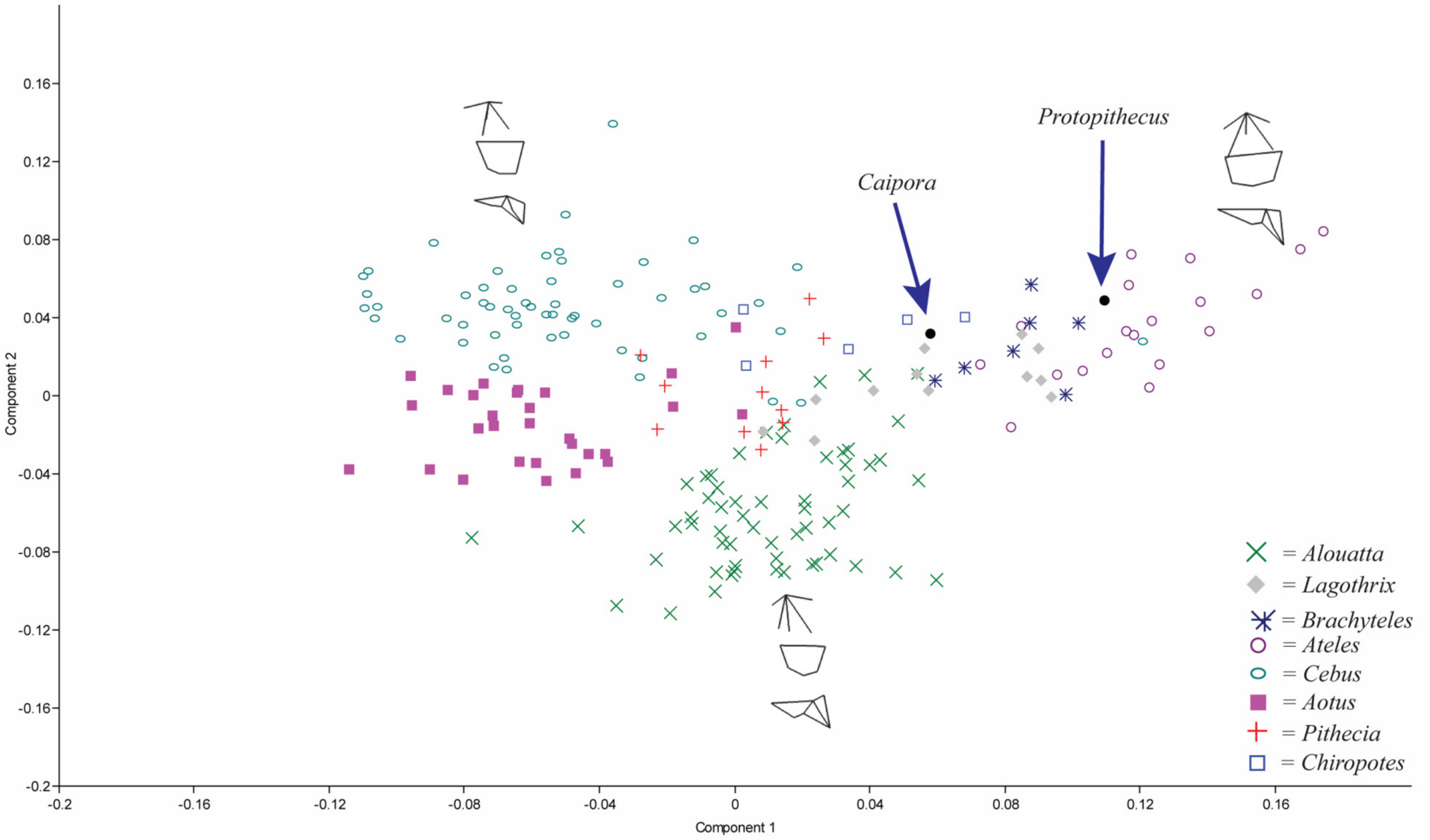

Figure 4.15. PCA results for the proximal ulna using the platyrrhine taxa only.
Morphological variation along PC1 (20% total variance) is driven by the length and orientation of the distal facet of the trochlear notch. PC2 (12%) is driven by the height of the olecranon process and the overall width of the trochlear notch. The wireframes represent the shape of the left ulna in anterior view for the individuals in the nearest cluster (see Fig. 4.10).

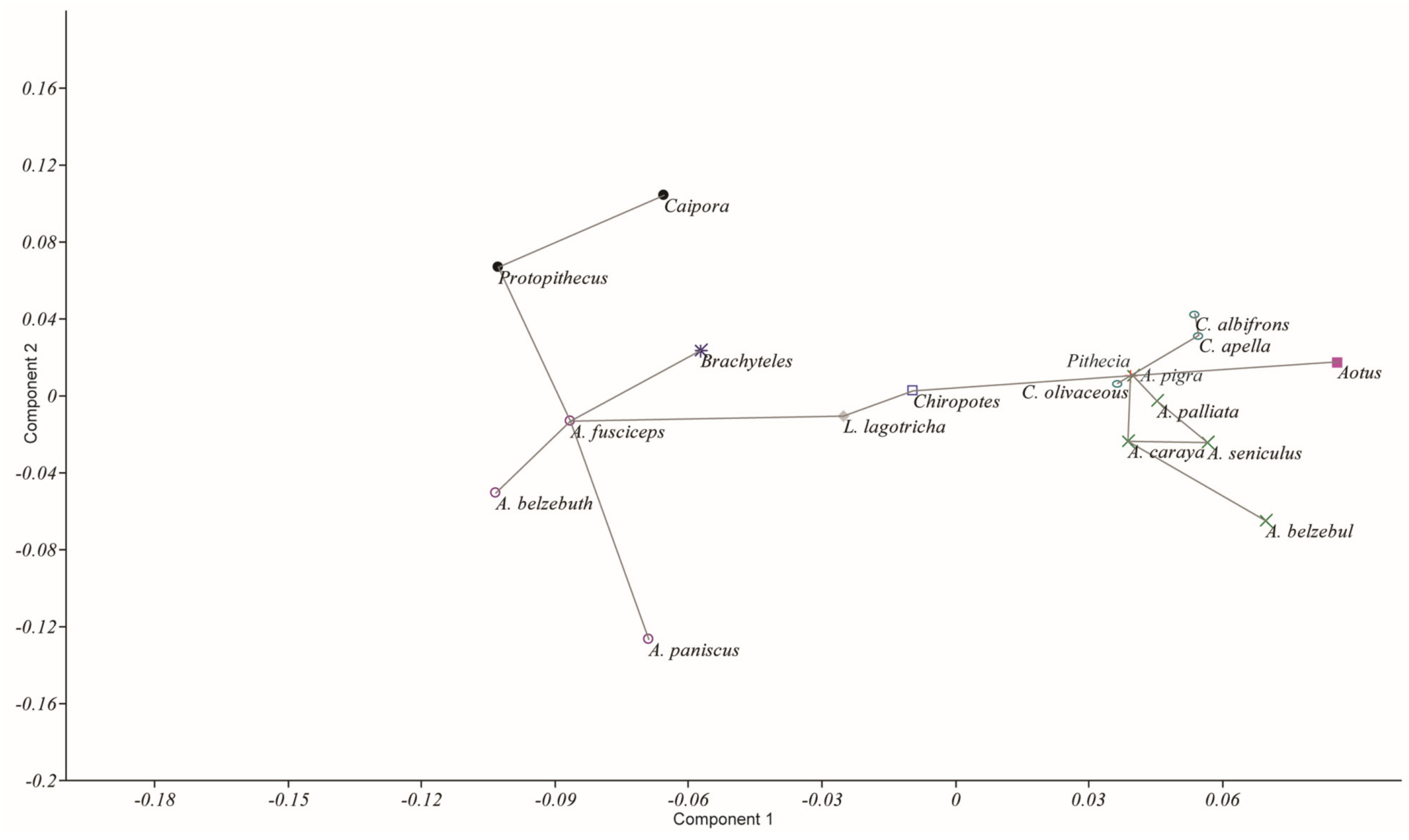

Figure 4.16. PCA results for the average male proximal ulna shape using all platyrrhine species. A minimum spanning tree connects the shapes with the shortest Procrustes distance between them. *Protopithecus* is linked with *Caipora*, most likely due to the larger body size of the two fossils, as well as with *Ateles* as in the results for the distal humerus.

Protopithecus individuals are not linked to each other, emphasizing the differences between the two specimens noted in the qualitative description above.

The full sample PCA for the proximal ulna produces clustering of New World monkeys, Old World monkeys, and hominoids similar to that seen for the distal humerus (Fig. 4.14). The strepsirhine group is different in this case, as the subfossil lemurs are separate from their extant relatives, *Propithecus* and *Indri*; the larger size of the subfossils and their extremely reduced olecranon process make them more similar to the living hominoids in the sample. When the platyrrhines are analyzed separately, the distinctions between the various taxa are clearer for the proximal ulna than they were for the distal humerus (Fig. 4.15). Again, *Protopithecus* and *Caipora* group with the more suspensory atelins, not with the less agile *Alouatta*, due to their shorter olecranon process and wider, more anteriorly-facing trochlear notch. A minimum spanning tree produces the same results as for the distal humerus, linking *Protopithecus* with *A. fusciceps* as the extant taxon sharing the most similar joint surface morphology (Fig. 4.16). For neither forelimb element is the much larger size of the fossils driving any of the grouping patterns on either PC1 or PC2. When ln centroid size of each individual in the sample is regressed against its PC score, R^2 values are all less than 0.5.

As in the qualitative descriptions above, the hindlimb of *Protopithecus* is the only part of the postcranial skeleton that shows similarities to either *Alouatta* or any Old World primate. The full femur and full tibia were not as useful for separating taxa in the comparative sample based on locomotor pattern. When both ends of the femur are analyzed at once, the main axis of variation in the PCA results is the size of the proximal and distal joint surfaces; despite a very low R^2 value of 0.08, warping along PC1 very clearly shows the difference between the smaller taxa on the right and the larger on the left (Fig. 4.17). Although in this case, size is closely related to locomotor pattern; a narrow distal femur is seen in leaping taxa while a wide patellar groove is seen in climbers, with a similar relationship surrounding the femoral head (suspensory taxa have a large globular head while leapers have a smaller more oval head; Anemone 1993). This whole bone analysis is the only one in which the two fossils are distinct from the rest of the platyrrhine taxa due to their much larger body size (Figs. 4.17-18). For the tibia also, the large size of the element in *Protopithecus* could be an explanation for its position on PC1 near clusters of *Macaca* and *Symphalangus* (Fig. 4.19). However, the fossil tibia is also close to a cluster of *Alouatta*, and when the sample is reduced to include only the platyrrhine taxa, size becomes less of a factor and a more expected result is obtained linking the fossil tibia with the suspensory atelines (Fig. 4.20).

The proximal femur presents a slightly different situation than was seen for the distal humerus. The two individuals of *Protopithecus* represented in the sample, the larger one from Toca da Boa Vista and the smaller one from Lagoa Santa, are quite different in size but not as different in morphology. Unlike the distal humerus, the minimum spanning tree links the two *Protopithecus* individuals with each other, albeit with quite a long distance between them (Fig. 4.21). Only the smaller Lagoa Santa specimen is nearest to an extant species, in this case *Lagothrix*. When the *Protopithecus* proximal femur is analyzed with the full comparative sample, PCA results group the fossils with several taxa including the strepsirhines, suspensory atelines, and *Pan* (Fig. 4.22). All of these taxa have low and laterally oriented greater trochanters as well as a rounder more robust femoral head. These results must be viewed cautiously, however, as they might be influenced by data collection artifacts relating to the order in which the specimens were microscribed. Unfortunately, a similar problem persists when the comparative sample is reduced to the platyrrhine taxa only; when PC1 and PC2 are plotted

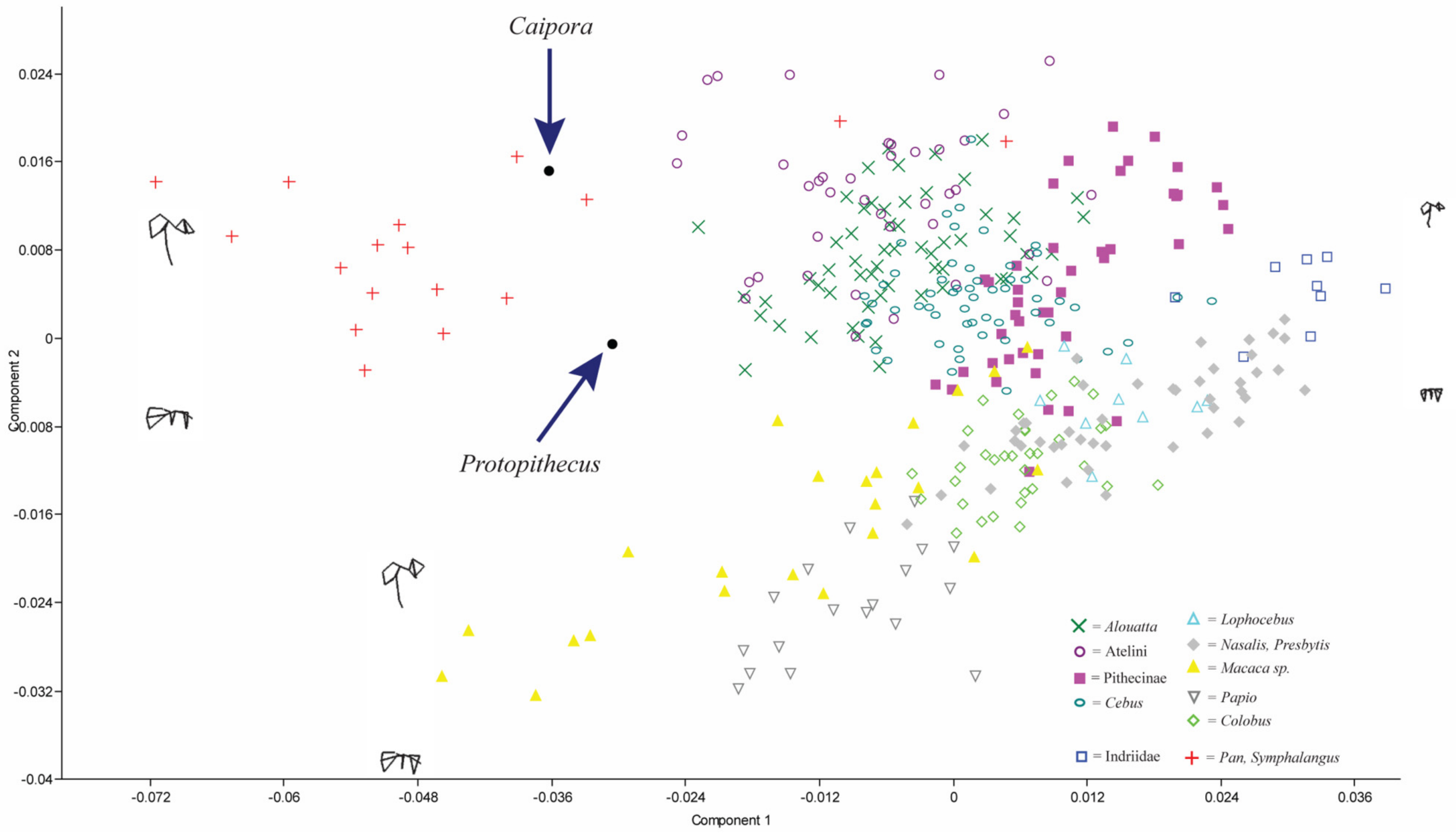

Figure 4.17. PCA results for the complete femur using the entire comparative sample.
PC1 (32% total variance) groups taxa based on the size of their joint surfaces, especially the femoral head and width of the condyles, which are largest in the chimpanzees to the negative end and smallest in *Propithecus* and *Indri* to the positive end. PC2 (15%) reflects the position of the greater trochanter in relation to the femoral head; more terrestrial taxa with a higher greater trochanter are to the negative end and suspensory taxa with the greater trochanter below the femoral head are to the positive end. Wireframes represent a left femur in anterior view (see Fig. 4.10).

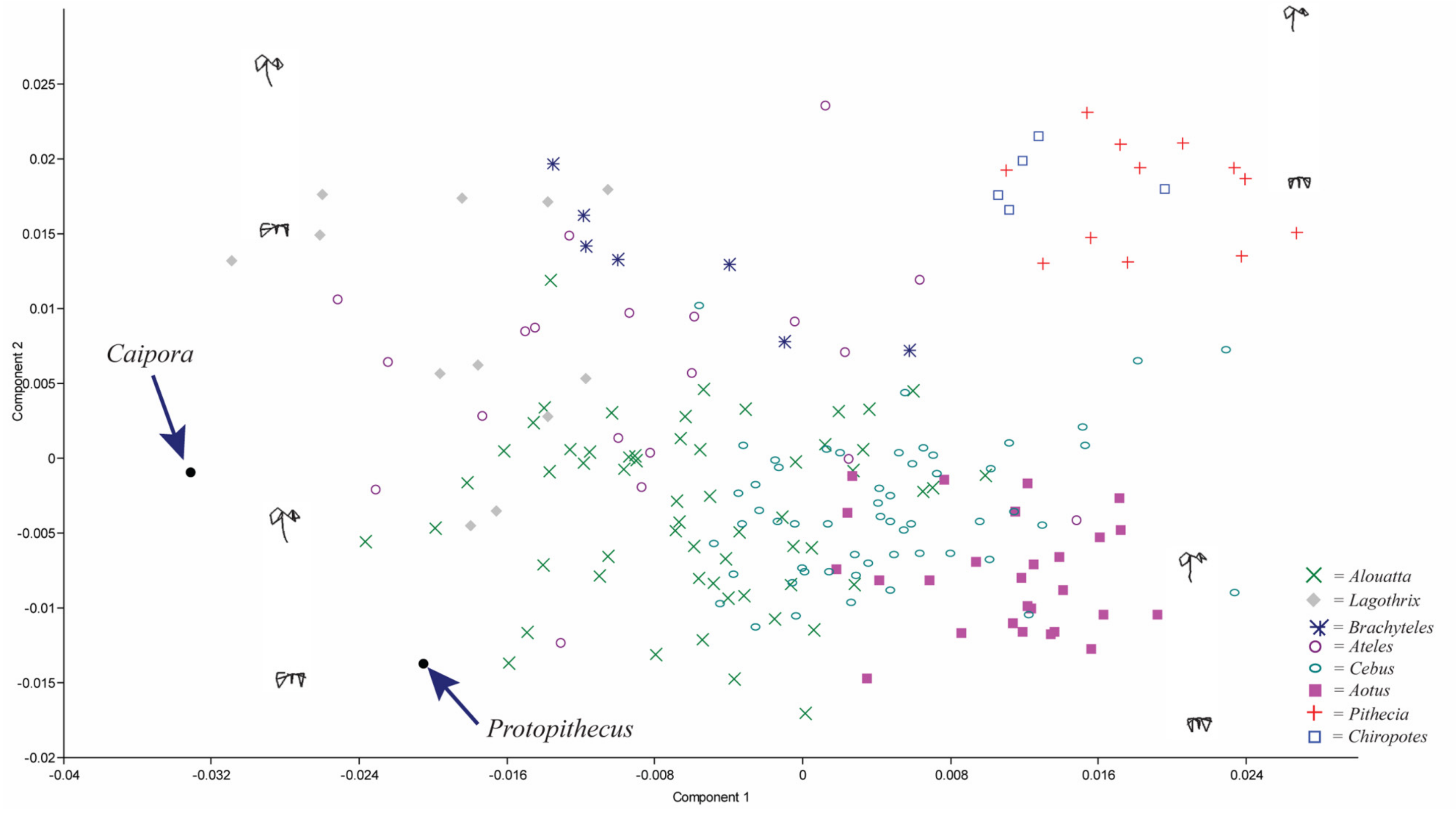

Figure 4.18. PCA results for the complete femur using the platyrrhine taxa only.
PC1 (22% total variance) is still sorting the taxa based on size; this is the only analysis where the fossils are separated from the living species, although *Caipora's* position here and in the distal femur analysis (Figs. 4.26-28) could also be due to the plaster surrounding the distal epiphysis. $R^2 = 0.3$ for the regression of PC1 scores on ln centroid size. Wireframes represent a left femur in anterior view (see Fig. 4.10)

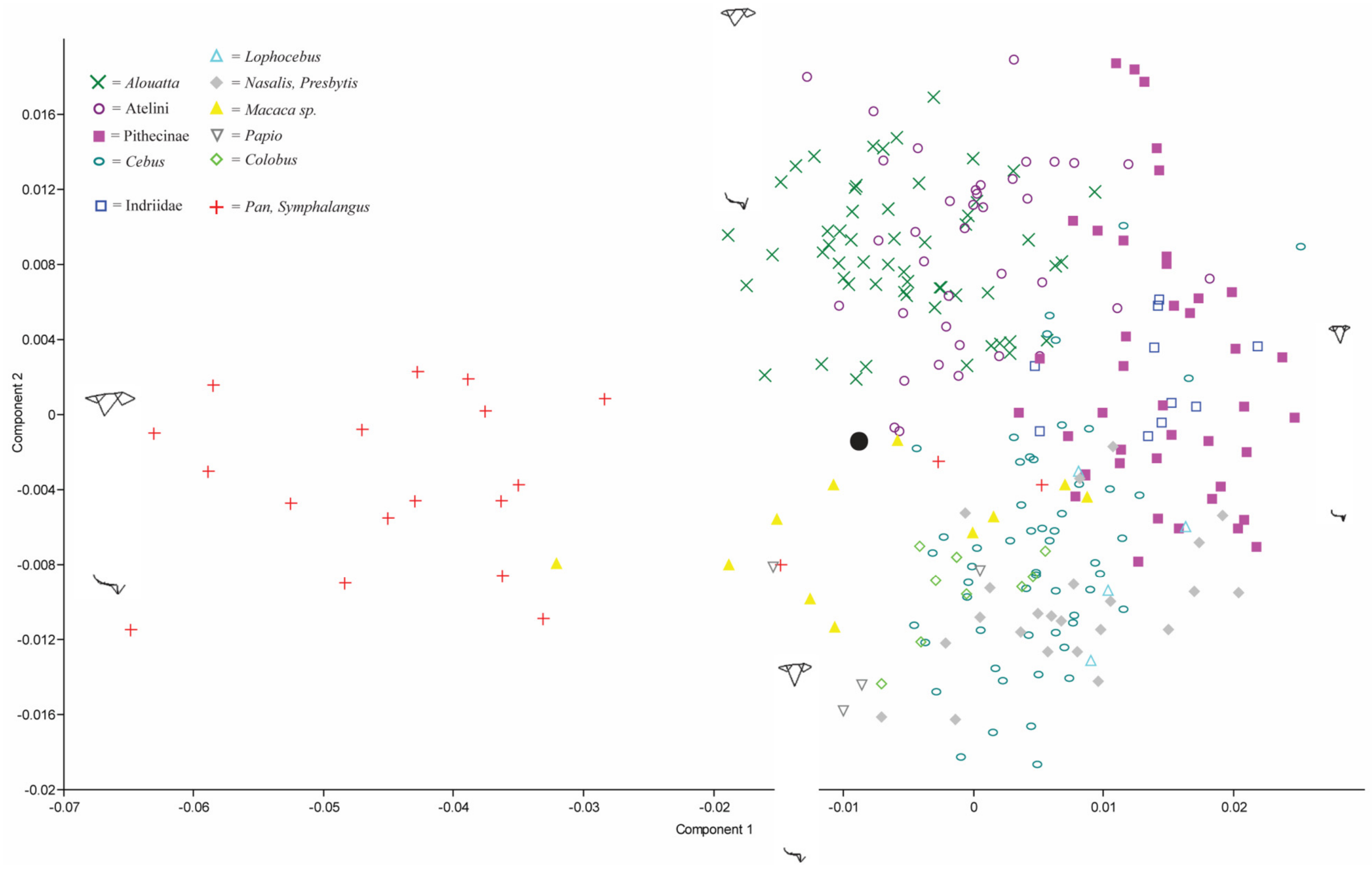

Figure 4.19. PCA results for the complete tibia using the entire comparative sample.
PC1 (35% total variance) is being driven by the size of the tibial plateau. PC2 (12%) reflects the orientation of the tibial tuberosity and medial malleolus. Wireframes represent a right tibia in anterior view.

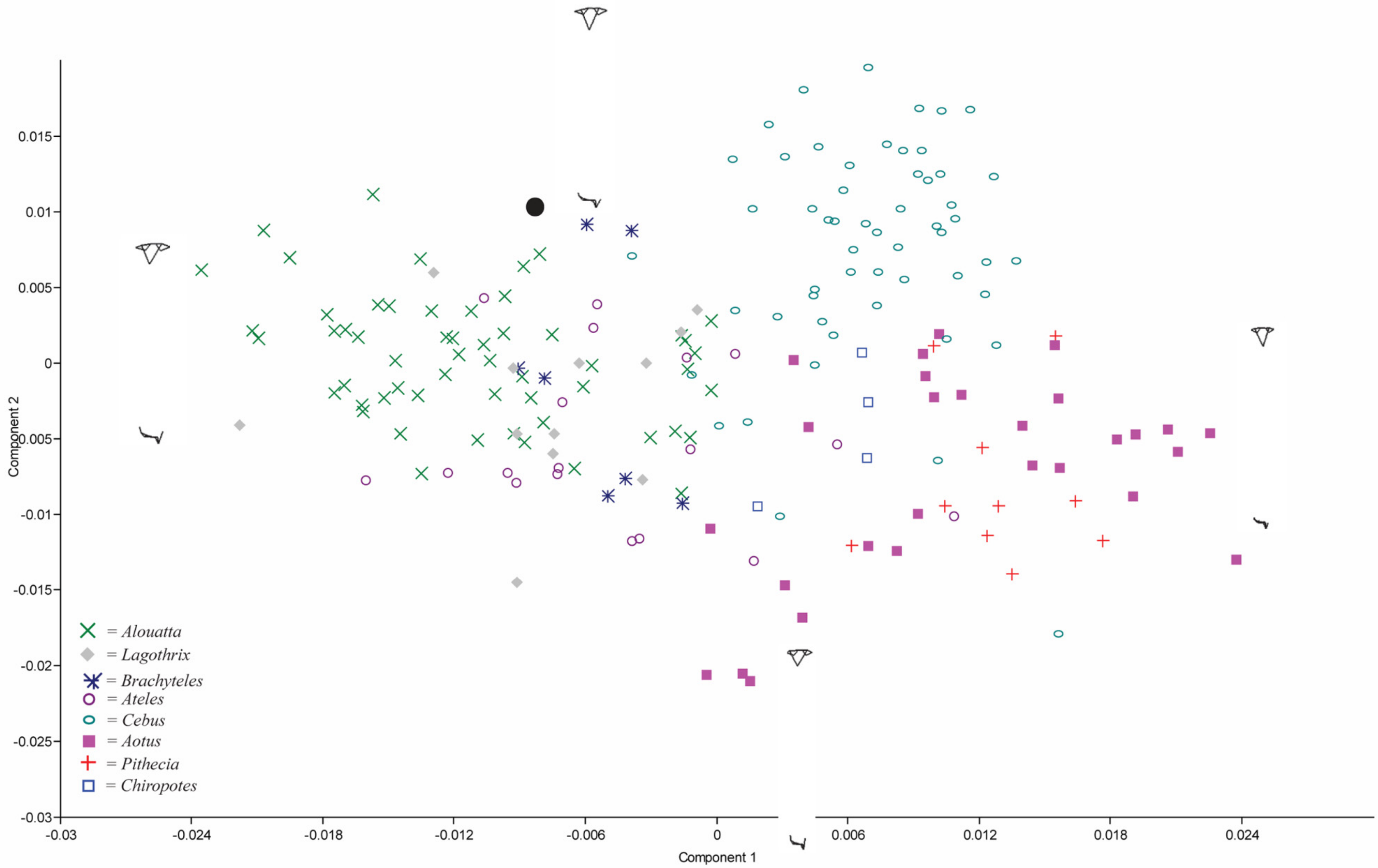

Figure 4.20. PCA results for the complete tibia using the platyrrhine taxa only.
This is one of the few times *Protopithecus* falls close to *Alouatta* as they share similar positioning of the tibial tuberosity and relative size of the articular surfaces on the tibial plateau. However, these are not the most reliable indicators of locomotor behavior as many taxa share this morphology (see Figs. 4.29-30). Wireframes represent a right tibia in anterior view.

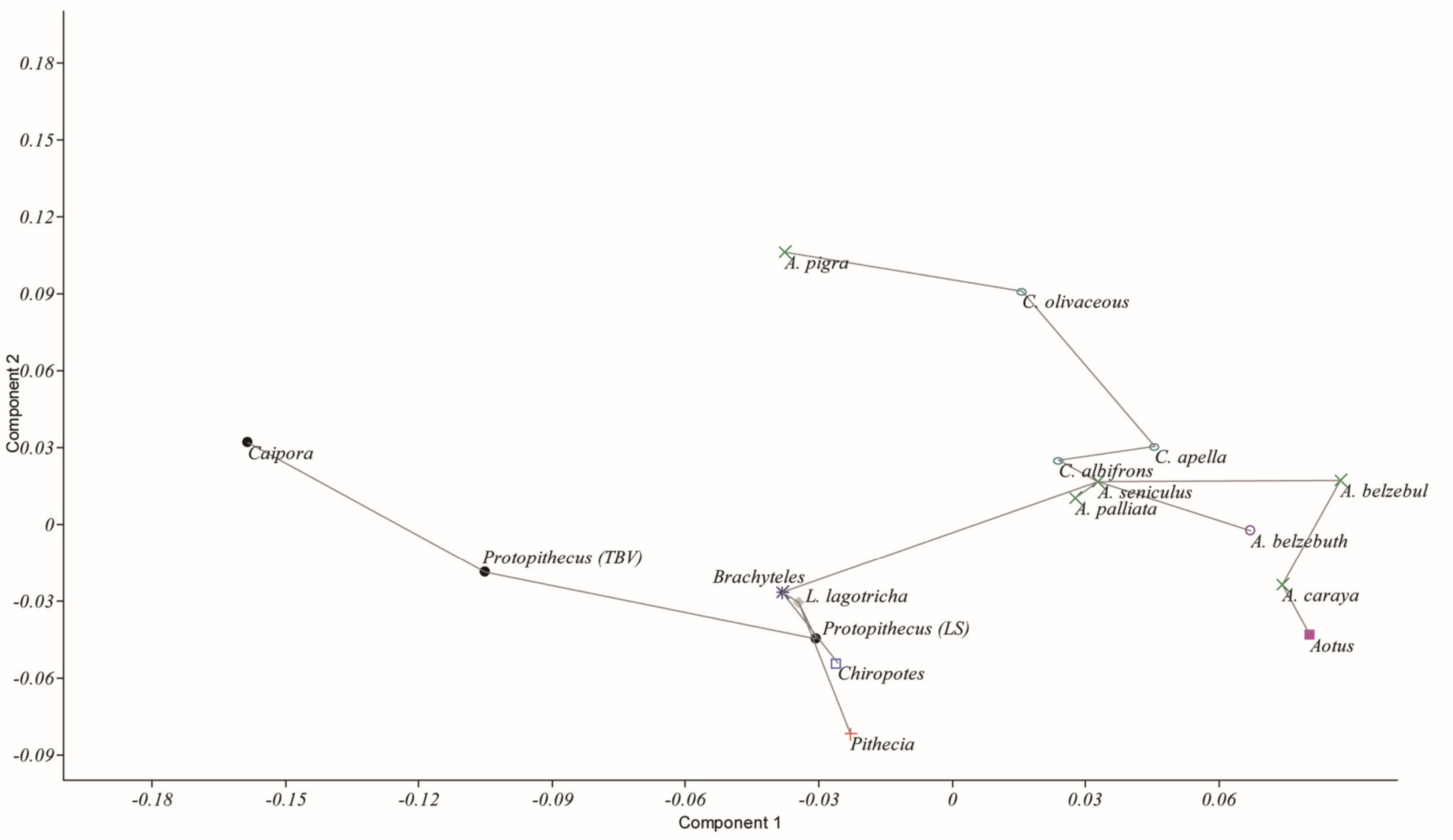

Figure 4.21. PCA results for the average male proximal femur shape using all platyrrhine species.
A minimum spanning tree connects the shapes with the shortest Procrustes distance between them. In this case, that includes the two *Protopithecus* specimens, although the distance between them is relatively long. The smaller LS specimen is nearest to *Lagothrix*.

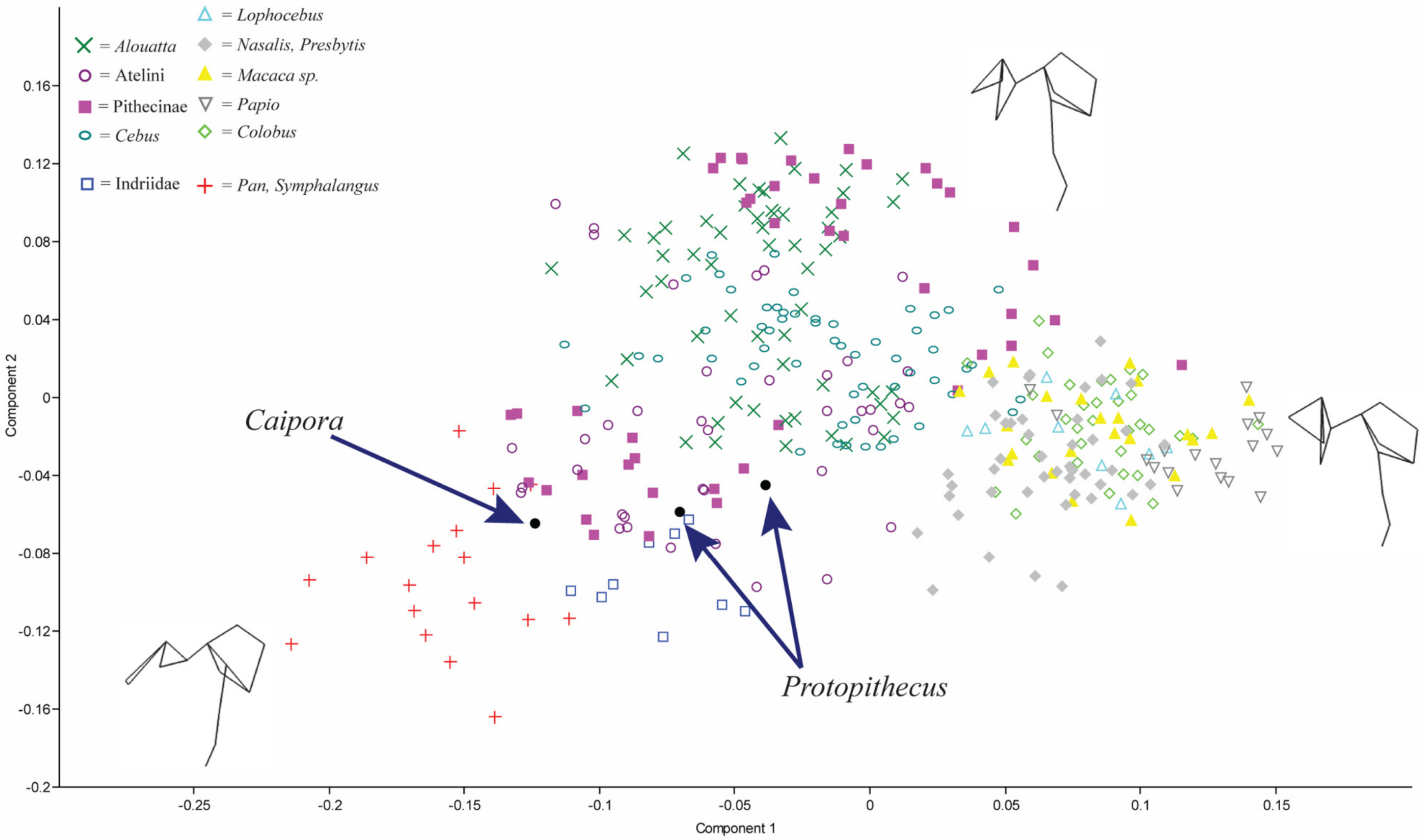

Figure 4.22. PCA results for the proximal femur using the entire comparative sample. PC1 (27% total variance) is being driven by the height and orientation of the greater trochanter, which is lower than the large, rounded head in chimpanzees and sits above the smaller, more compressed head in terrestrial Old World monkeys. Grouping on PC2 (15%) is influenced by the size and orientation of the lesser trochanter. The fossils, however, cluster with a group of species including *Pithecia, Chiropotes, Pan, Propithecus*, and *Indri* which, like the fossils, were all added to the sample towards the end of data collection. Wireframes represent a left femur in posterior view (see Fig. 4.10). Left *Protopithecus* = TBV, right = LS.

against each other, several of the genera appear to be forming separate clusters based on the museum the specimens were from instead of their morphology (Fig. 4.23).

The particular landmark set chosen for the proximal femur may not have been the most reliable one for consistent data collection. For example, landmark F9, “middle of the trochanteric fossa”, could be located very differently depending on both the amount of soft tissue still on the bone as well as the size of the element, as the tip of the Microscribe is sometimes wider than the opening of the fossa. When the more suspect landmarks (F7 and F9, i.e., those whose placement varied the most from one specimen to another when warping along the PC axes) are removed from the analysis, plotting PC1 against PC3 generates a picture more similar to the other elements of the skeleton (Fig. 4.24). Here *Protopithecus*, with its robust femoral neck and medium-sized lesser trochanter, falls closer to the suspensory atelines. Removing these two landmarks also changes the links of the minimum spanning tree; now none of the fossils in the sample are connected to each other, but *Protopithecus* is still most similar to *Brachyteles* and *Lagothrix* as in other elements (Fig. 4.25).

The results for the distal femur are more robust. Clusters of taxa seen in the PCAs are clearly based on morphological variation instead of being influenced by the specimens’ museum of origin (Figs. 4.26-27). There is overlap between the more suspensory atelines and *Alouatta* (and *Pan*, as has been noted by many authors, e.g., Erikson 1963), but the fossil is more similar to *Alouatta* with its relatively short and wide patellar groove and more asymmetrical condyles. In the minimum spanning tree, *Protopithecus* is nearest to *Alouatta palliata* as opposed to the other *Alouatta* species (Fig. 4.28), but it would be unwise to infer that this has to do with a *palliata*-specific locomotor behavior. According to some behavioral studies, *A. palliata* and *A. pigra* climb less frequently (9% (Mendel, 1976) and 4% (Cant, 1986), respectively) than other

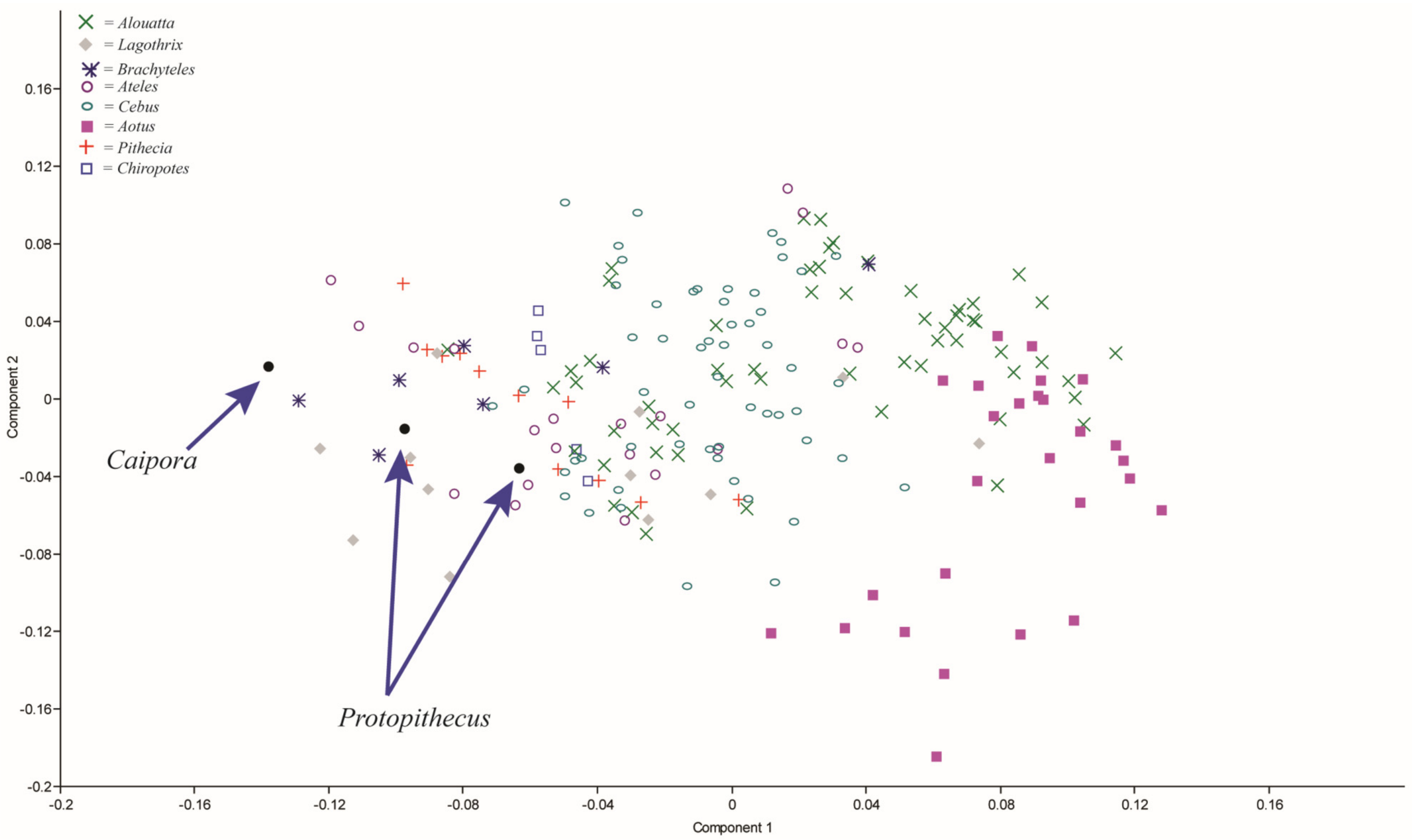

Figure 4.23. PCA results for the proximal femur using the platyrrhine taxa only.
In this analysis, PC axes are driven more by artifacts of data collection than by morphology, so wireframes are not shown. The negative ends of PC1 (27% total variance) and PC2 (15%) include specimens that were measured last and the positive ends include the specimens that were measured first from the AMNH. Specimens from the NMNH that were measured in the middle of the data collection period fall in the middle. This mostly likely explains the two separate clusters of *Aotus*, *Alouatta*, and *Cebus*. Left *Protopithecus* = TBV, right = LS.

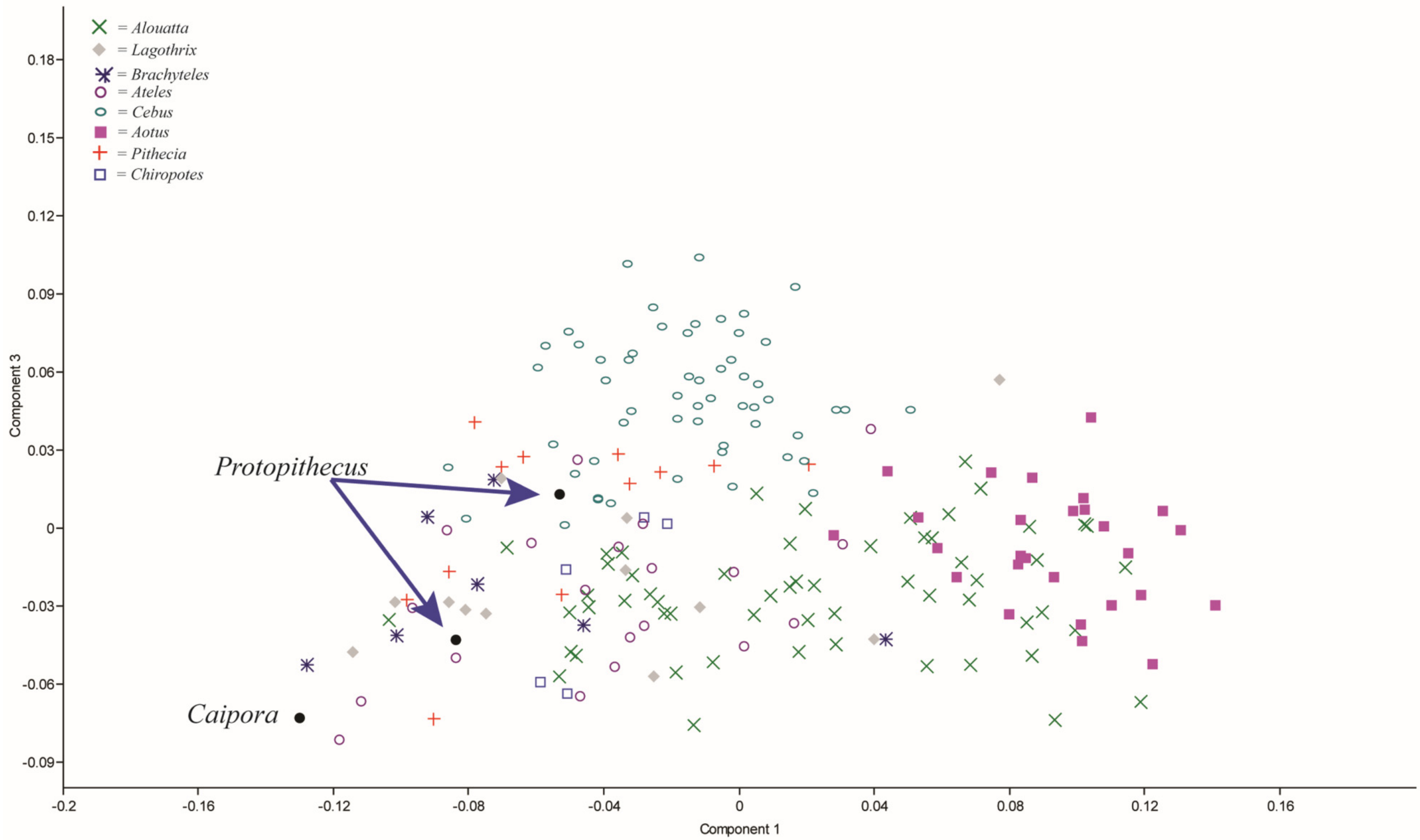

Figure 4.24. PCA results for reduced landmarks of the proximal femur using the platyrrhine taxa only, PC1 vs PC3. Taking out landmarks F7 and F9 and displaying PC1 and PC3 in order to remove as much non-morphological variation as possible, results in a position for *Protopithecus* and *Caipora* similar to the other skeletal elements with mostly suspensory atelines as their nearest neighbors. Bottom left *Protopithecus* = TBV, top right = LS.

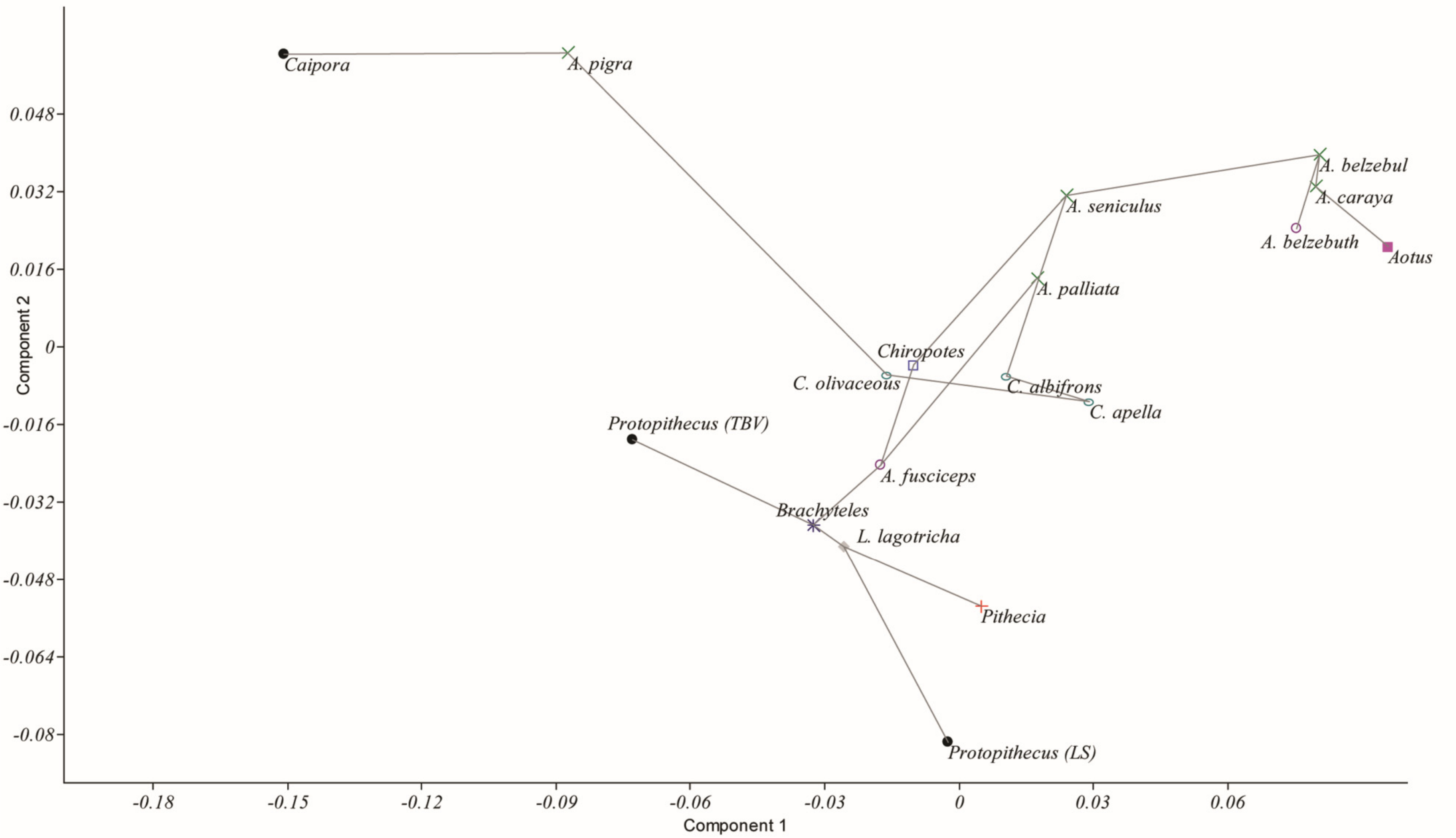

Figure 4.25. PCA results for reduced landmarks of the average male proximal femur shape using all platyrrhine species. Removing landmarks F7 and F9 from the analysis also changes the links in the minimum spanning tree. Now the two *Protopithecus* individuals are not closest to one another and each is linked to a different extant taxon, *Brachyteles* for the TBV specimen and *Lagothrix* for the LS specimen.

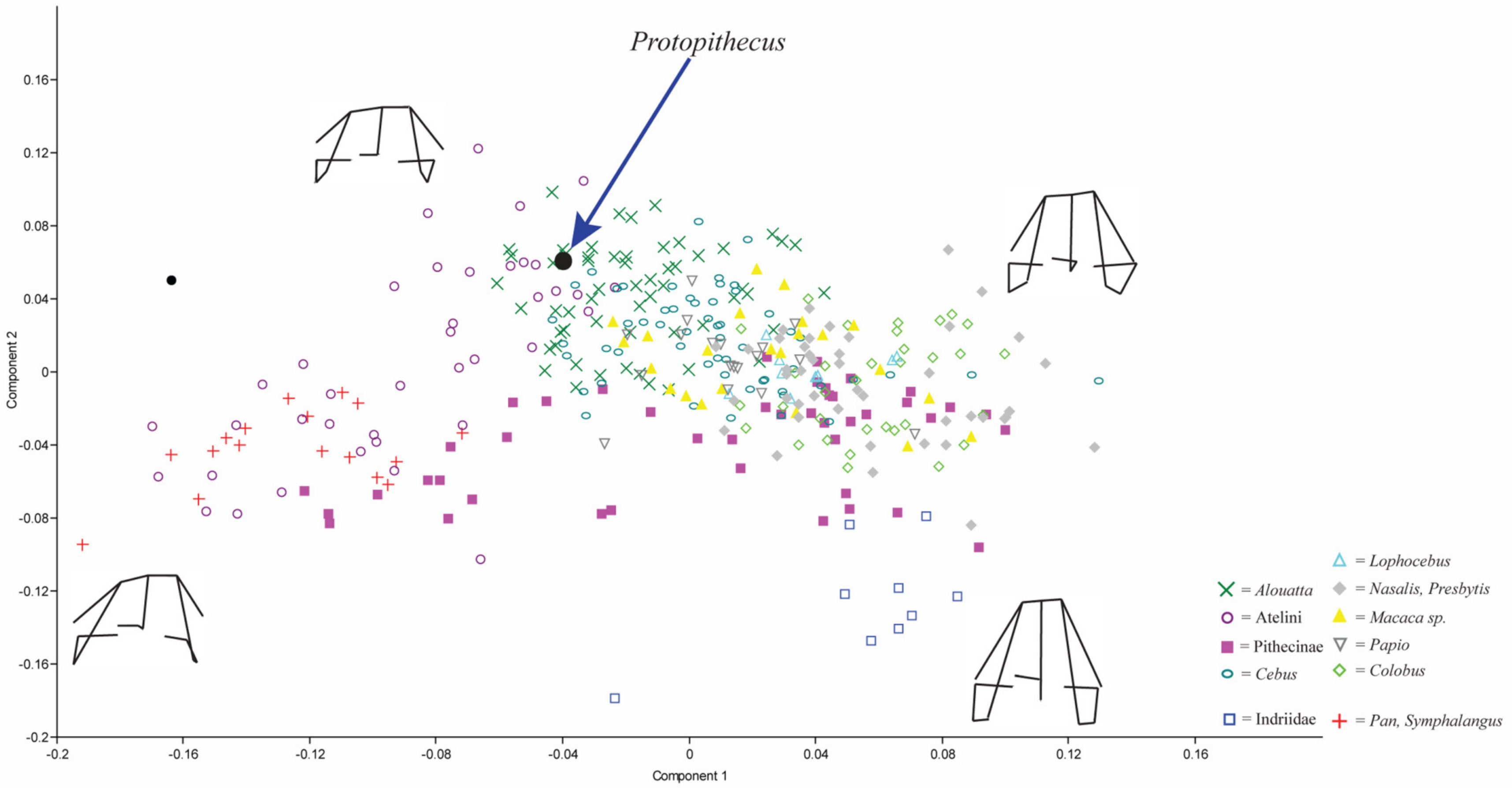

Figure 4.26. PCA results for the distal femur using the entire comparative sample.
PC1 (23% total variance) is being driven by the height and width of the patellar groove as well as the symmetry of the condyles; chimpanzees and suspensory atelines to the negative end of the axis have a shorter, wider groove and more asymmetrical condyles while smaller taxa that practice more leaping like *Propithecus, Indri*, and *Nasalis* are on the positive end of the axis with taller, narrower patellar grooves and more symmetrical condyles. PC2 (12%) relates to a more specific part of that morphological complex, reflecting variation in the width of the proximal border of the patellar groove. *Protopithecus* is in a rarely seen position nearest a cluster of *Alouatta,* while *Caipora* is isolated from the rest of the sample, perhaps due to the poor preservation of this particular epiphysis. Wireframes represent a left femur in anterior view (see Fig. 4.10 for reference).

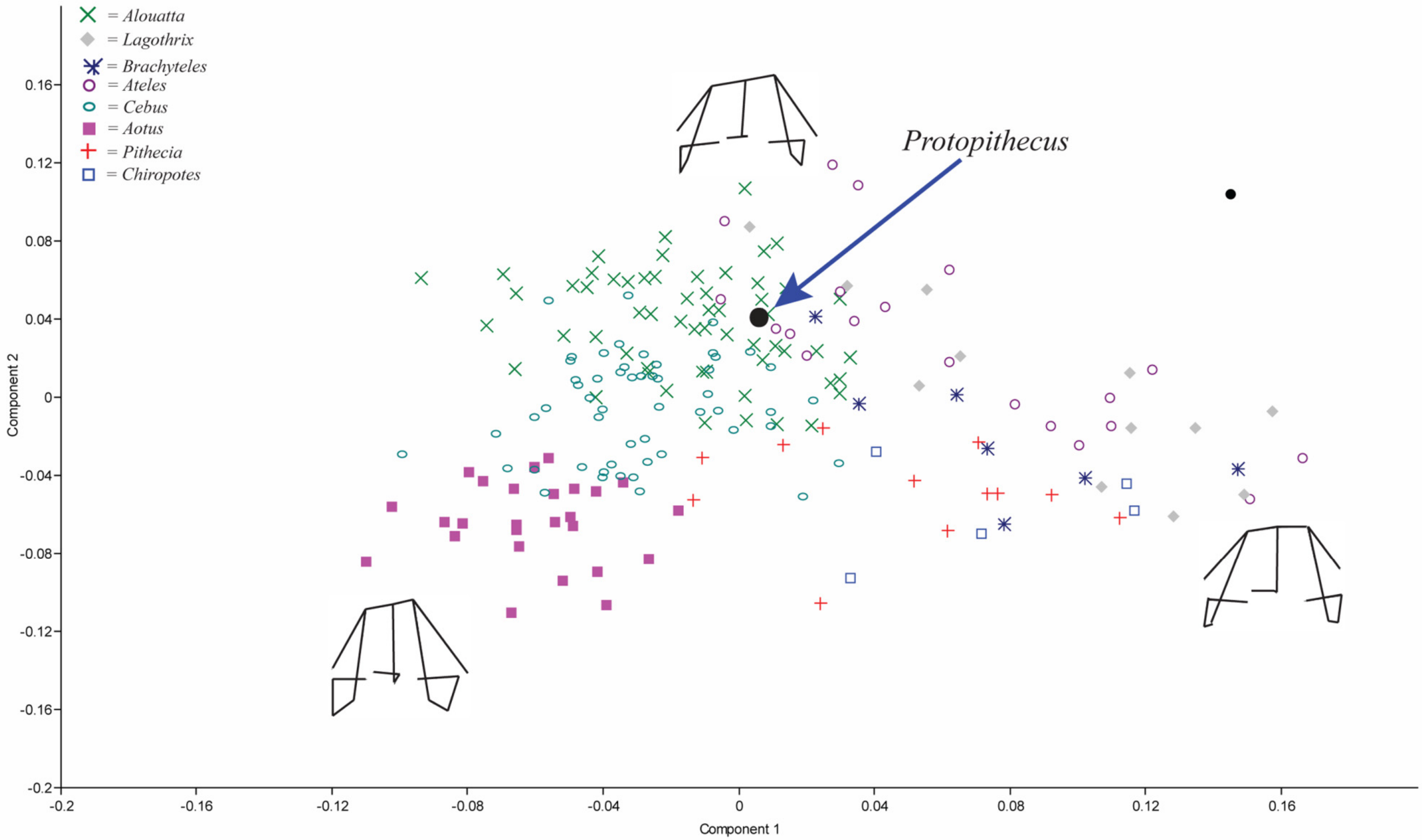

Figure 4.27. PCA results for the distal femur using the platyrrhine taxa only. *Protopithecus* falls closer to *Alouatta* than in the analyses of other skeletal elements, reflecting the more asymmetrical condyles shared by the two taxa for increased rotation along with flexion/extension of the knee during climbing. Similar distribution of morphology is seen on the two PC axes as in Fig. 4.26. Wireframes represent a left femur in anterior view (see Fig. 4.10 for reference).

species such as *A. seniculus* (30%; Fleagle and Mittermeier, 1980). However, the different definitions of "climbing" used by these authors render cross-study comparisons suspect and it is unknown whether the relatively small differences in the form of the distal femur seen here in each species correspond to differences in function.

While the proximal end of the knee joint of *Protopithecus* is very similar to *Alouatta*, the distal end is not. This, too, needs to be evaluated in a broader context, for the proximal tibia has the least influence on separating taxa from one another in the PCAs. Perhaps the simplicity of the tibial plateau, two relatively flat circles, makes this element less amenable to three-dimensional geometric morphometric analyses. Taxa are arrayed across PC1 somewhat in reference to body size (although the R^2 value for a regression of PC1 against ln centroid size is relatively low at 0.2) with the subfossil lemurs, apes, and larger atelines to the negative end and smaller *Cebus* and *Aotus* to the positive end (Fig. 4.29). Old World and New World monkeys show considerably more overlap than in the other analyses. *Protopithecus* falls close to many cercopithecoid species due to their shared slightly asymmetrical articular surfaces and a wide anterior portion of the tibial plateau, but this could be said of many of the taxa in the sample (Fig. 4.29).

There is less overlap between the groups when the platyrrhines are considered on their own, and *Protopithecus* still seems to belong to a non-ateline cluster (Fig. 4.30). The minimum spanning tree links the *Protopithecus* proximal tibia directly with the more quadrupedal *Chiropotes* in a group of other platyrrhines that use leaping more frequently, a completely anomalous result that again seems based on the relatively more asymmetrical and widely spaced articular surfaces of those taxa (Fig. 4.31).

It is both interesting and unexpected that the two ends of the knee joint are similar to

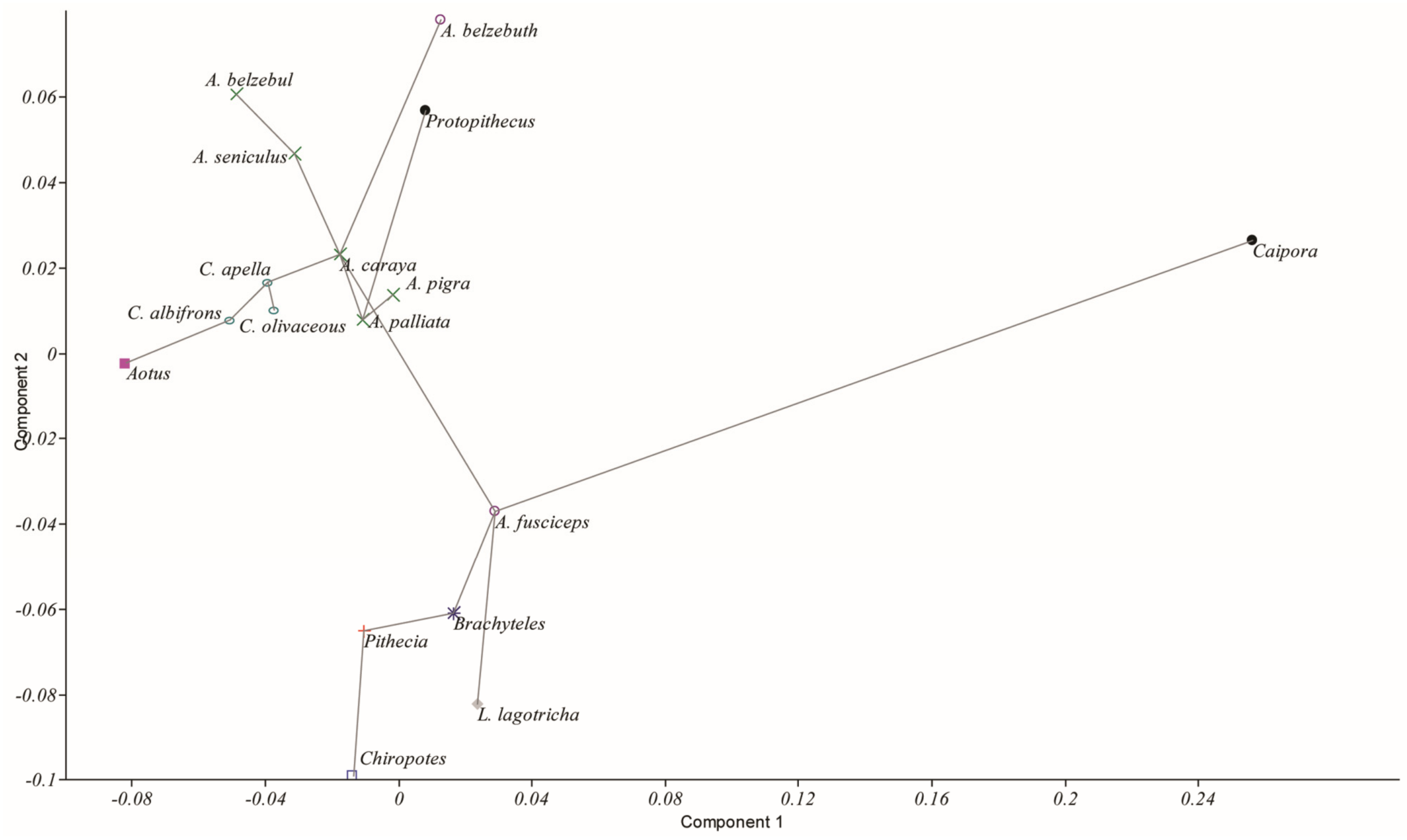

Figure 4.28. PCA results for the average male distal femur shape using all platyrrhine species.
A minimum spanning tree connects the shapes with the shortest Procrustes distance between them. *Protopithecus* is nearest to *Alouatta* instead of the more suspensory atelines, while *Caipora* continues to show unique morphology because of poor preservation.

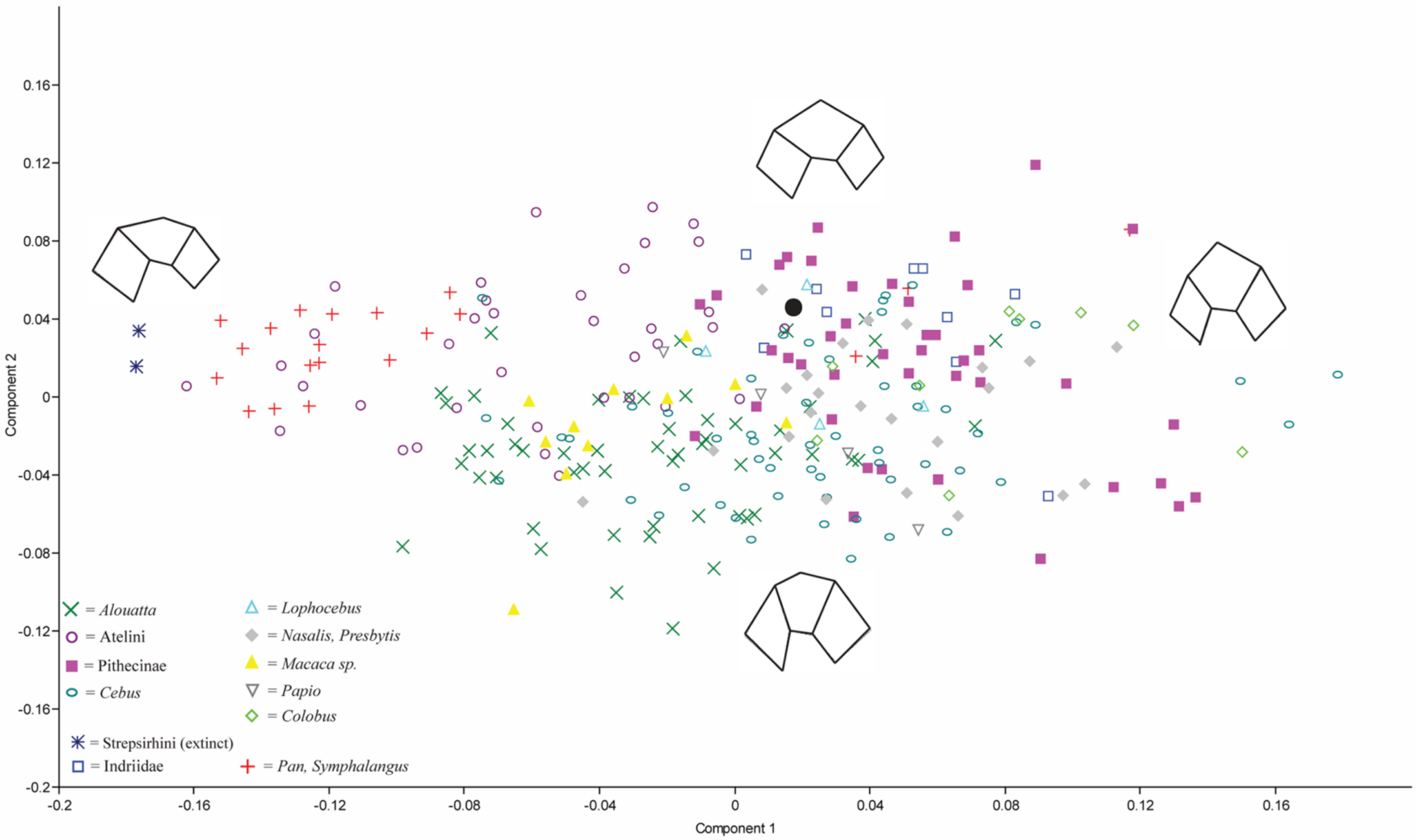

Figure 4.29. PCA results for the proximal tibia using the entire comparative sample.
The relatively simple geometry of the tibial plateau does not separate functional or phylogenetic groups in the comparative sample as well as the other skeletal elements. The overlap between Old World and New World monkeys makes placing *Protopithecus* with one particular taxon difficult. The fossil shares relatively asymmetrical articular surfaces and a wide anterior portion of the joint surface with many taxa in the sample. PC1 (28% total variance) is being driven by the relative size of the medial articular surface which is especially large in the subfossil lemurs and chimpanzees on the negative end of the axis. PC2 (11%) reflects the width of the anterior portion of the joint surface and the position of the tibial tuberosity. Wireframes represent a right tibia in superior view (see Fig. 4.10 for reference).

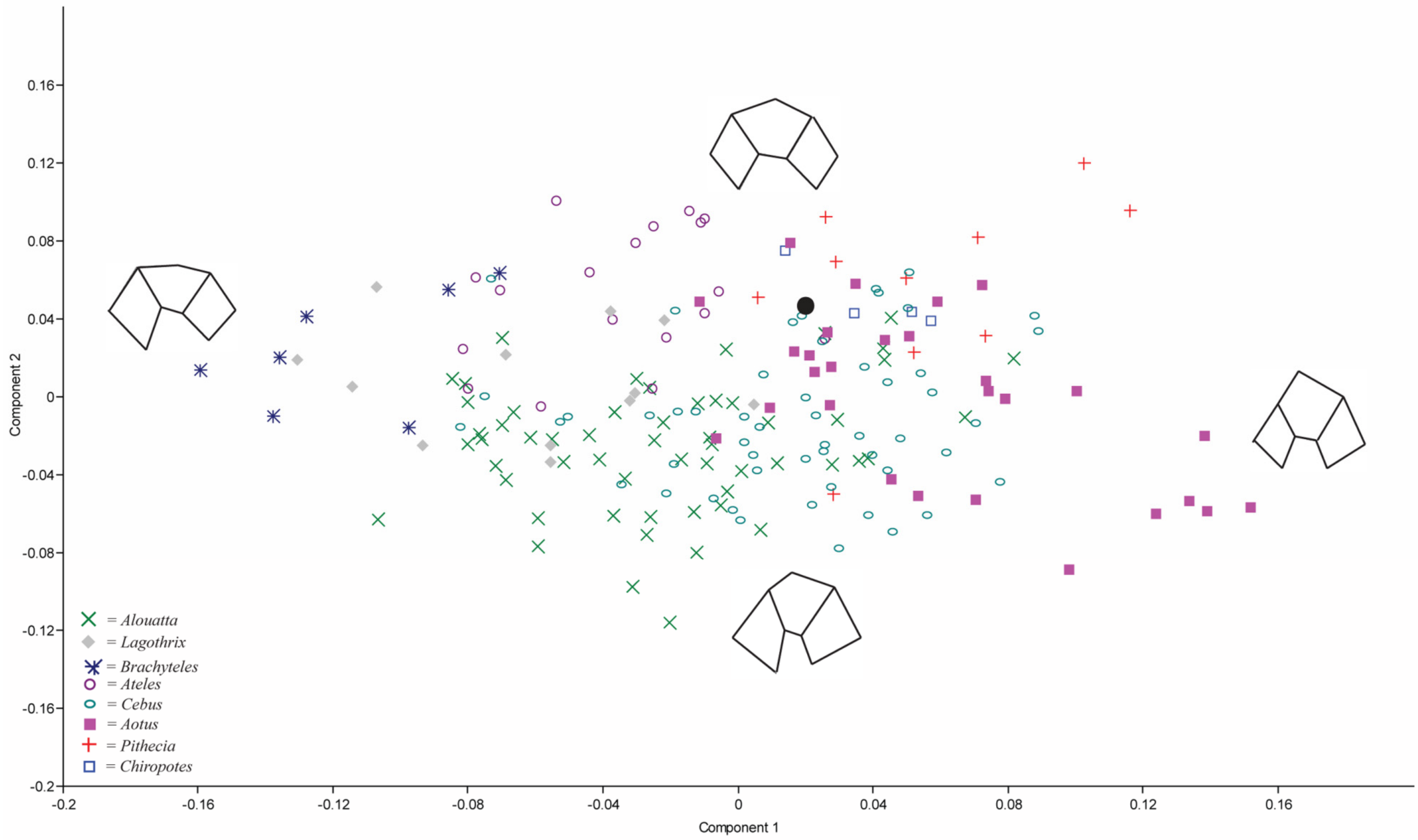

Figure 4.30. PCA results for the proximal tibia using the platyrrhine taxa only.
Groups are slightly more distinct than in Fig. 4.29 with suspensory atelines to the negative end of PC1 (25% total variance) and taxa that practice more leaping, like *Aotus* and *Pithecia,* to the positive end with smaller medial articular surfaces and a tibial tuberosity positioned lower down the shaft of the bone. PC2 (14%) is again being driven by the width of the anterior portion of the plateau. *Protopithecus* is in a cluster of multiple taxa almost directly in the middle of the plot. Wireframes represent a right tibia in superior view (see Fig. 4.10 for reference).

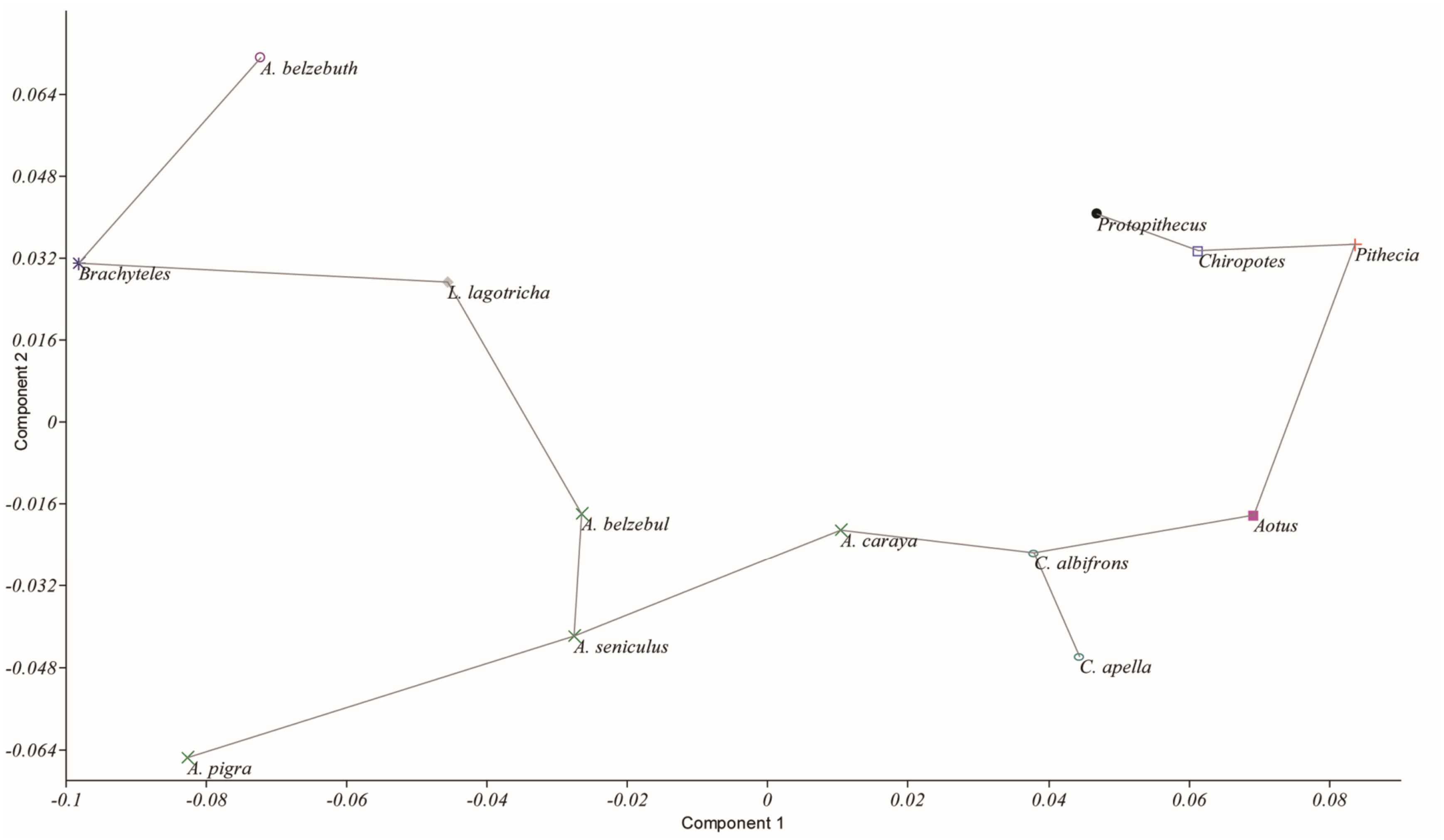

Figure 4.31. PCA results for the male average proximal tibia shape using all platyrrhine species.
A minimum spanning tree connects the shapes with the shortest Procrustes distance between them. All links are as expected based on phylogeny and function except for the connection between *Protopithecus* and *Chiropotes*.

different taxa. The two ends of the ankle joint present the same dilemma, although concerns with the distal tibia measurements might be a factor. As with the proximal femur, *Aotus* in particular seems to be clustering based on museum of origin, suggesting that at least some of the data are not reflecting genuine morphological variation (Fig. 4.32). A potential explanation lies in the position of *Aotus* as the smallest taxon in the comparative sample, at the likely minimum size threshold where collecting reliable measurements via Microscribe is feasible. *Protopithecus* is relatively isolated from all other taxa in the comparative sample and the reduction of data points to the mean male landmark configurations is necessary to see that its nearest neighbors are *Brachyteles* and *Cebus* (Fig. 4.33).

Landmarks placed on the talus, with its multiple complex articular surfaces, should do a better job at separating the taxa in the comparative sample and producing a clearer result for the fossil, and this does in fact seem to be the case. It should be noted that the sample size here is smaller than the other skeletal elements as tali are not as often preserved in the museum collections. When compared to the full sample, *Protopithecus* falls near the suspensory atelines, and this relationship is also seen when the platyrrhines are analyzed separately (Figs. 4.34-35). These taxa share a relatively wide and symmetrical trochlea and short talar neck. The minimum spanning tree connects *Protopithecus* with *A. fusciceps* (and *Caipora*), as was seen for many of the other elements (Fig. 4.36). Similar clusters are recovered when only the landmarks on the dorsal surface of the bone are examined (Fig. 4.37). However, it is obvious at first glance that the full sample PCA scatter is arranged across PC1 in body size order; a regression of PC1 on ln centroid size yields an R^2 value of 0.7, the highest in any analysis performed here. Variation in the length of the talar neck, width of the trochlea, and relative sizes of both the medial and lateral malleolar facets are clear when warping the shape change along both PC1 and PC2. This

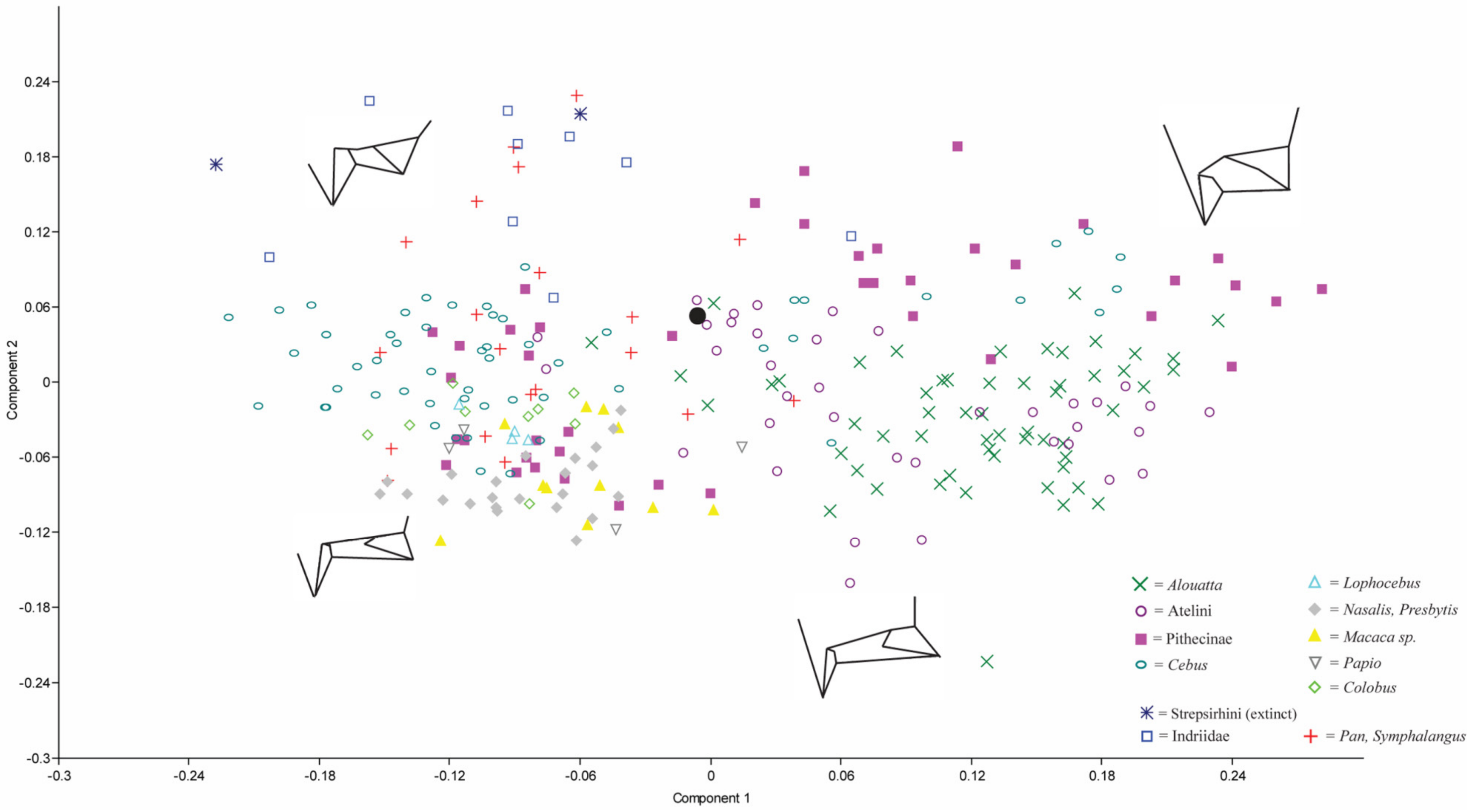

Figure 4.32. PCA results for the distal tibia using the entire comparative sample.
While the wireframes (here representing a right tibia in posterior, slightly oblique view) show some expected morphological variation along each axis (in dimensions of the medial malleolus and trochlear facet for articulation with the talus), some taxa are again clustering based on artifacts of the data collection process. For example, the two clusters of *Aotus*, one on the far right and the other to the left overlapping the Old World monkeys, are from the AMNH and NMNH, respectively. *Protopithecus* again falls in the center of the plot, close to various other ateline specimens.

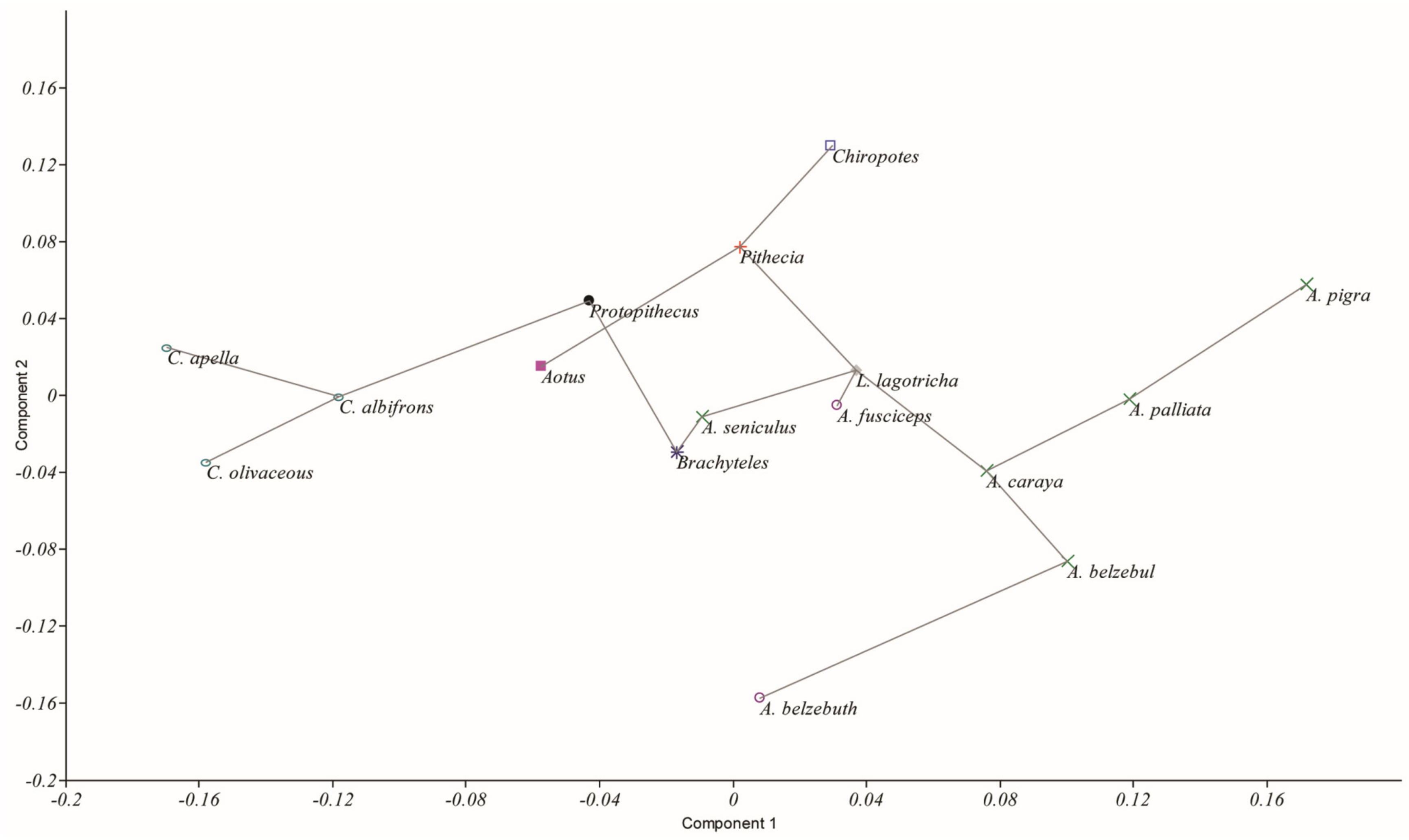

Figure 4.33. PCA results for the average male distal tibia shape using all platyrrhine species.
A minimum spanning tree connects the shapes with the shortest Procrustes distance between them. *Protopithecus* is nearest to *Brachyteles*, as expected from other analyses, but also to *Cebus*, a result not seen elsewhere.

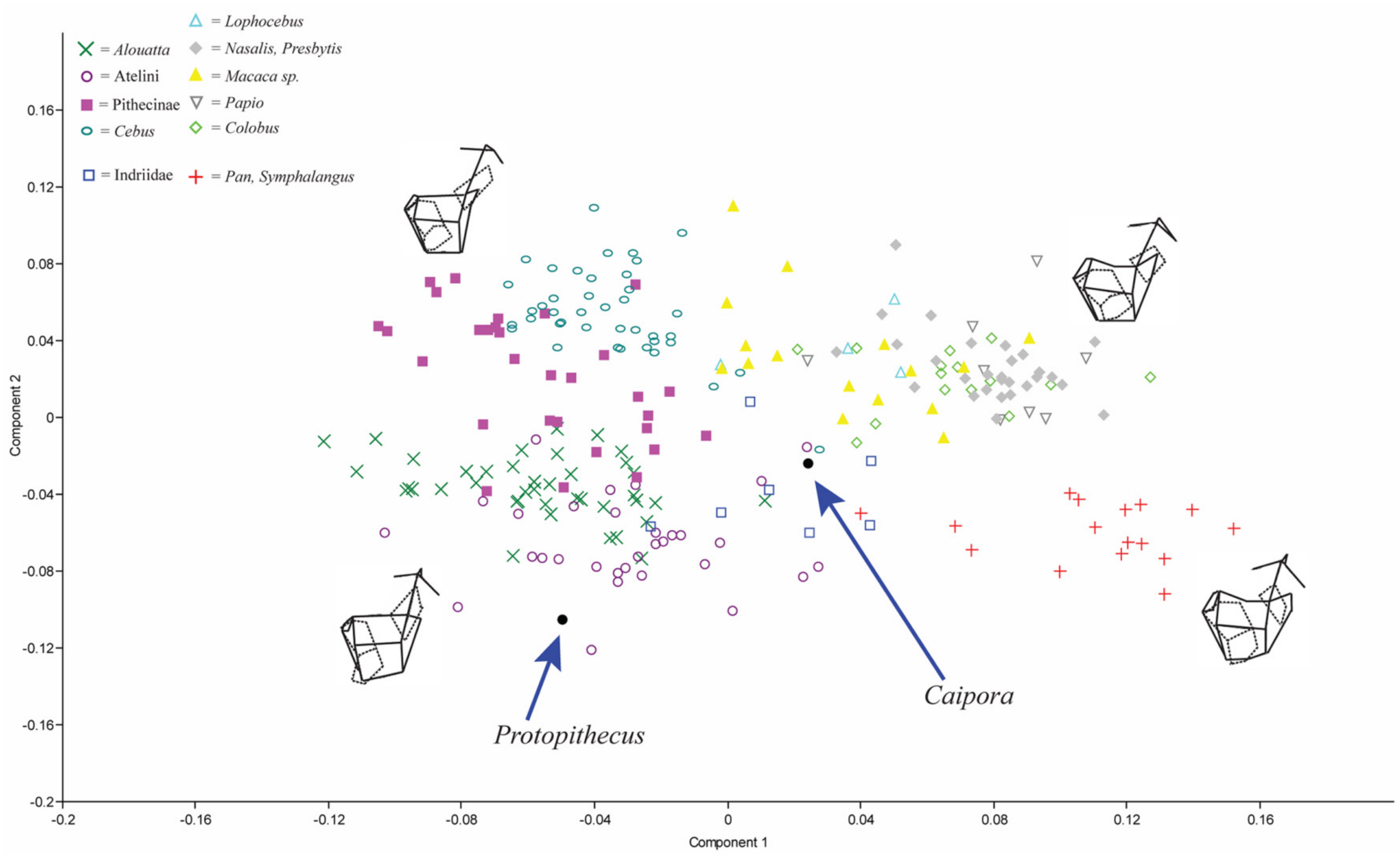

Figure 4.34. PCA results for the talus using the entire comparative sample.
The negative end of PC1 (20% total variance) includes taxa that have a symmetrical trochlea and long anterior calcaneal facet and talar neck while the positive end of the axis includes taxa that have a much wide anterior portion of the trochlea, medial and lateral malleolar facets that extend further from the sides of the bone, and a much shorter anterior calcaneal facet and talar neck. PC2 (12%) is also related to neck proportions and torsion of the talar head as well as the size of the posterior calcaneal facet. Wireframes represent a left talus in superior view with landmarks on both the dorsal (solid line) and plantar (dashed line) surfaces visible (see Fig. 4.10 for reference).

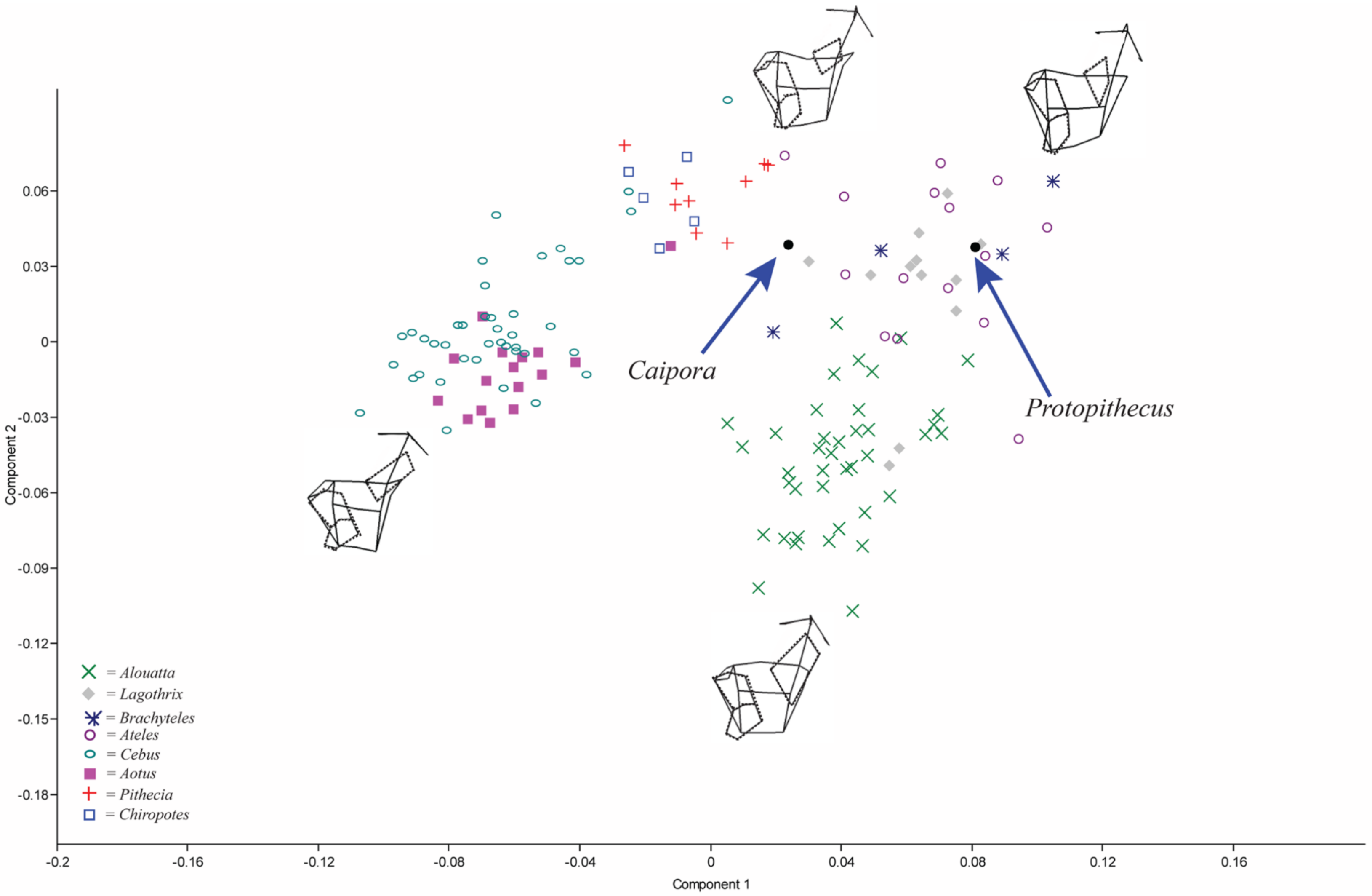

Figure 4.35. PCA results for the talus using the platyrrhine taxa only.
PC axes represent similar morphological variation as in Fig. 4.34. *Protopithecus* shares a wide trochlea and short talar neck with the suspensory atelines. Wireframes represent a left talus in superior view with landmarks on both the dorsal (solid line) and plantar (dashed line) surfaces visible (see Fig. 4.10 for reference).

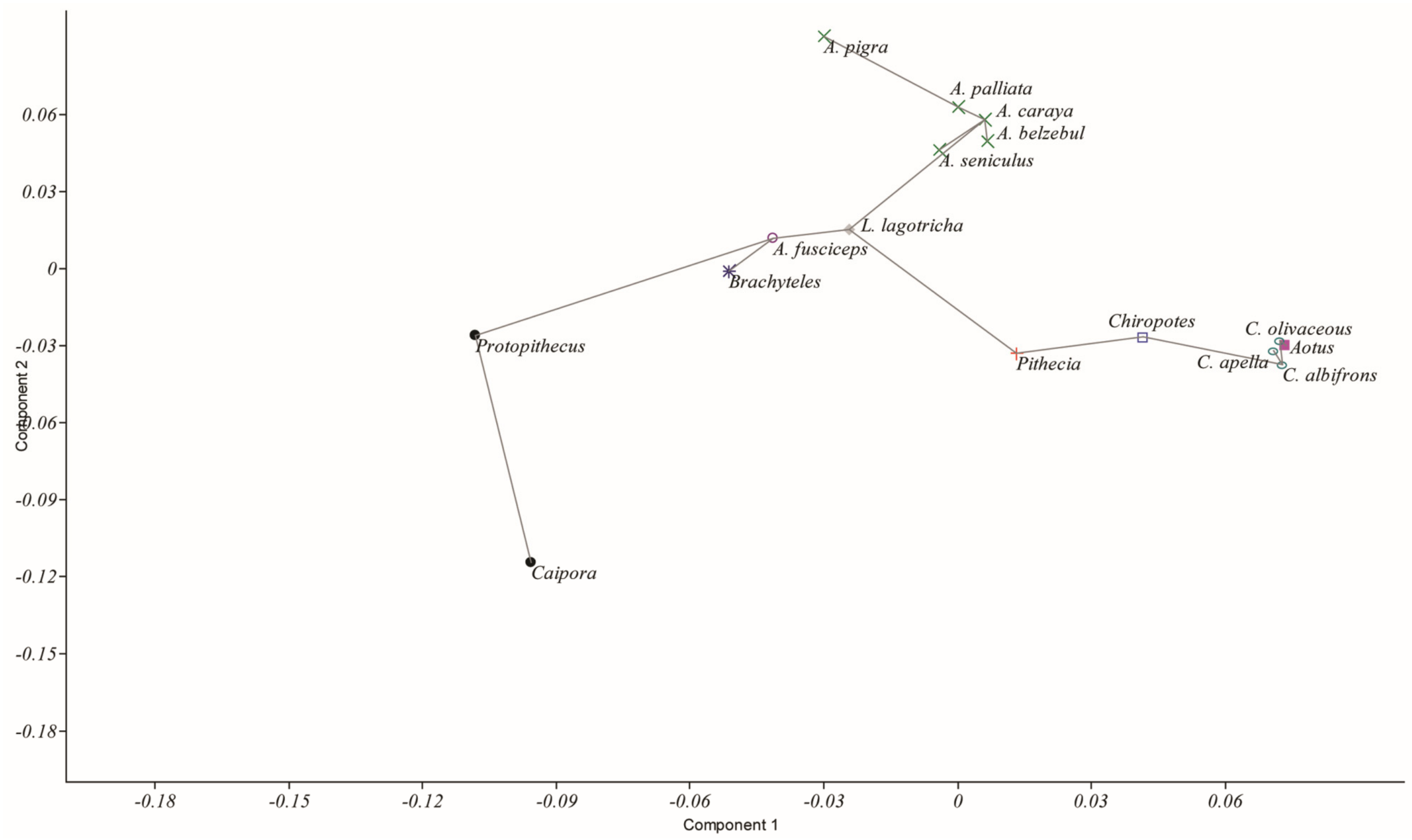

Figure 4.36. PCA results for the average male talus shape using all platyrrhine species.
A minimum spanning tree connects the shapes with the shortest Procrustes distance between them. The large size of the fossil tali is separating them from the extant species, but *Protopithecus* is most similar to *Ateles* as in other elements.

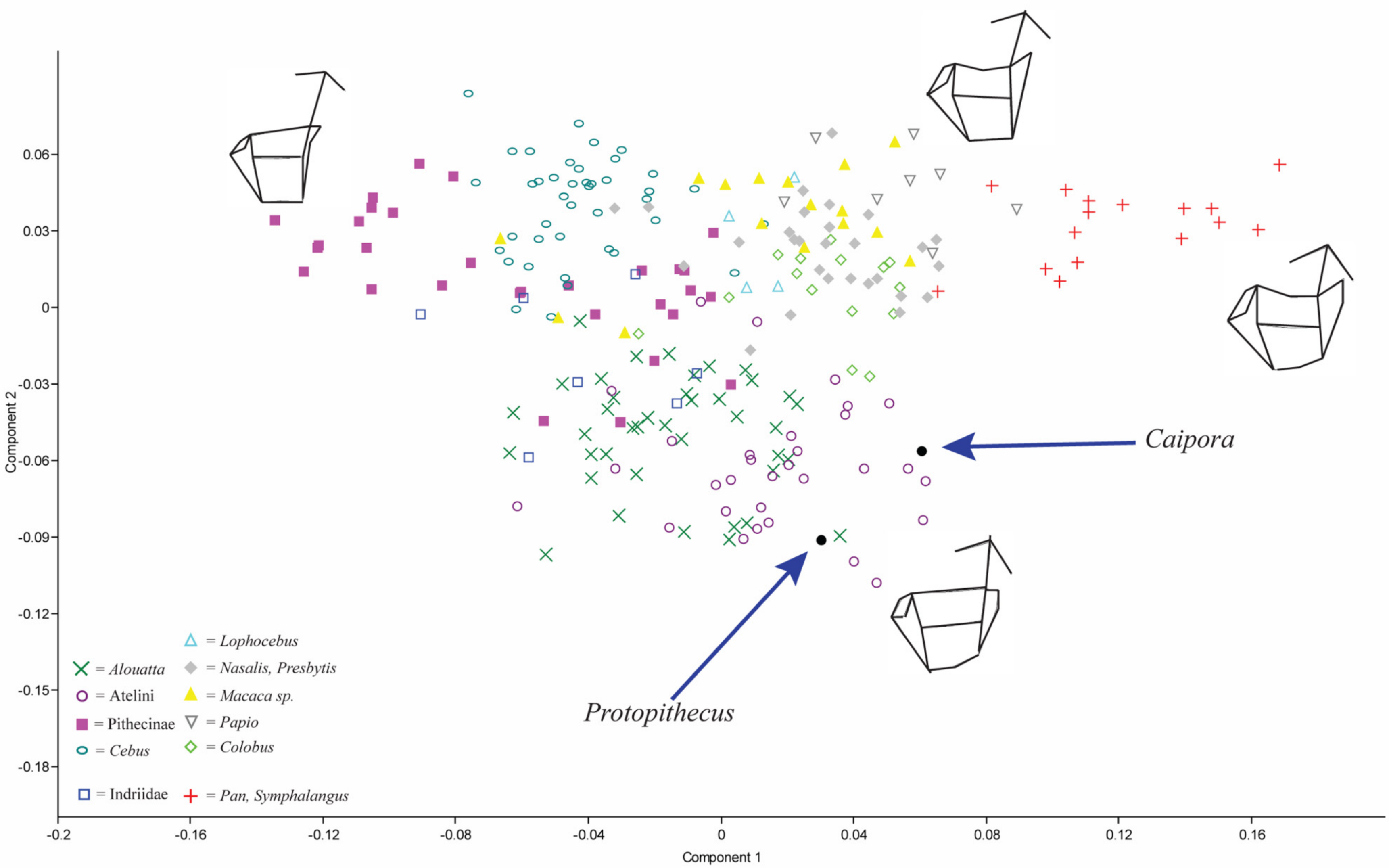

Figure 4.37. PCA results for the dorsal talar surface using the entire comparative sample.
While PC1 (19% total variance) is highly correlated with centroid size ($R^2 = 0.7$), morphological variation related to function is still visible in this plot. The length of the talar neck, torsion of the talar head, and relative proportions of the trochlea vary predictably from group to group. Wireframes represent a left talus in superior view (see Fig. 4.10 for reference).

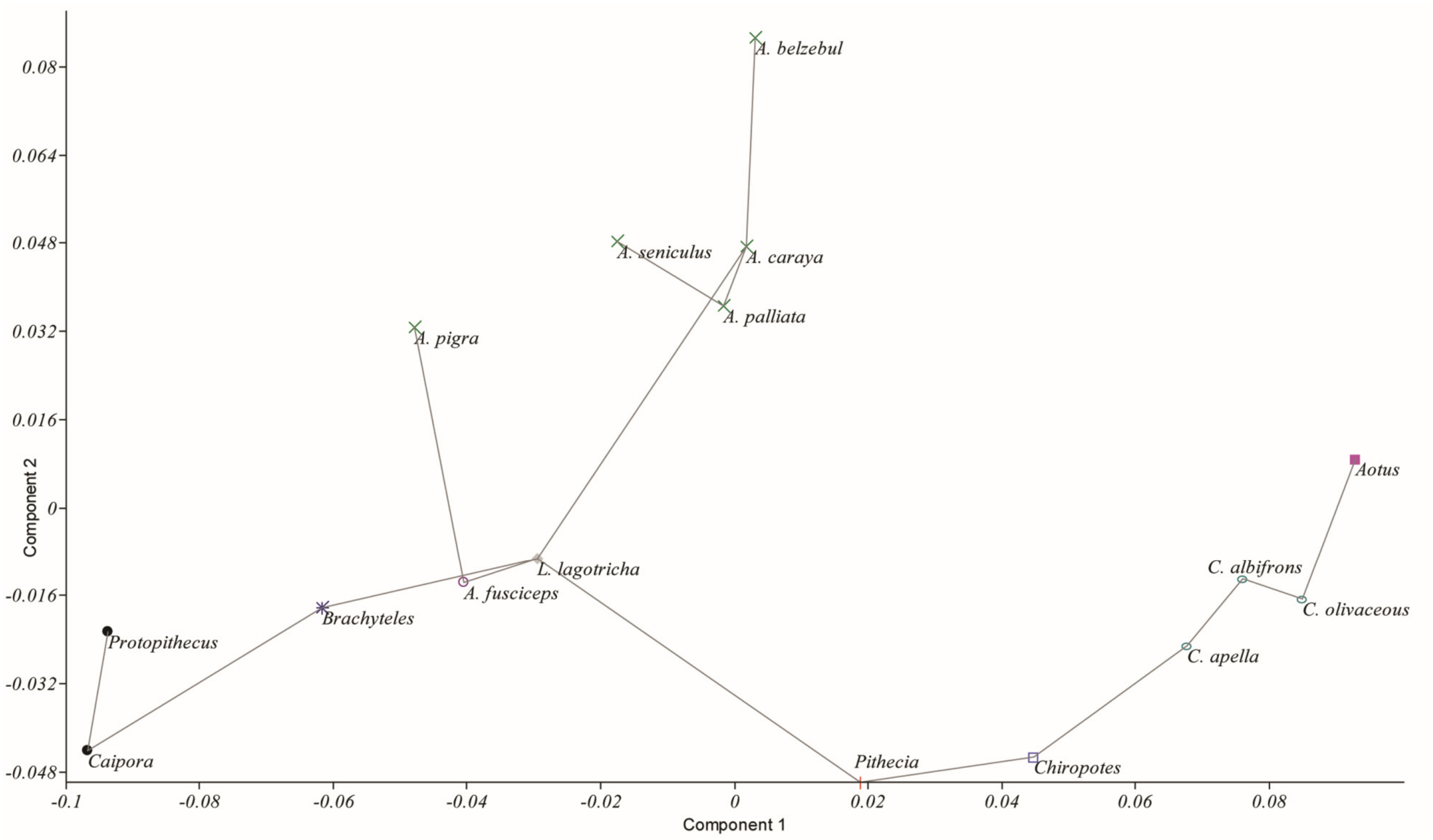

Figure 4.38. PCA results for the average male dorsal talar surface shape using all platyrrhine species.
A minimum spanning tree connects the shapes with the shortest Procrustes distance between them. The distribution across PC1 is arranged according to body size, which explains the links between *Protopithecus* and *Caipora* and then *Brachyteles*. *Alouatta* is distinct on PC2 due to their parallel-sided trochlea with very little lateral expansion of either malleolar facet (see wireframes on Fig. 4.39).

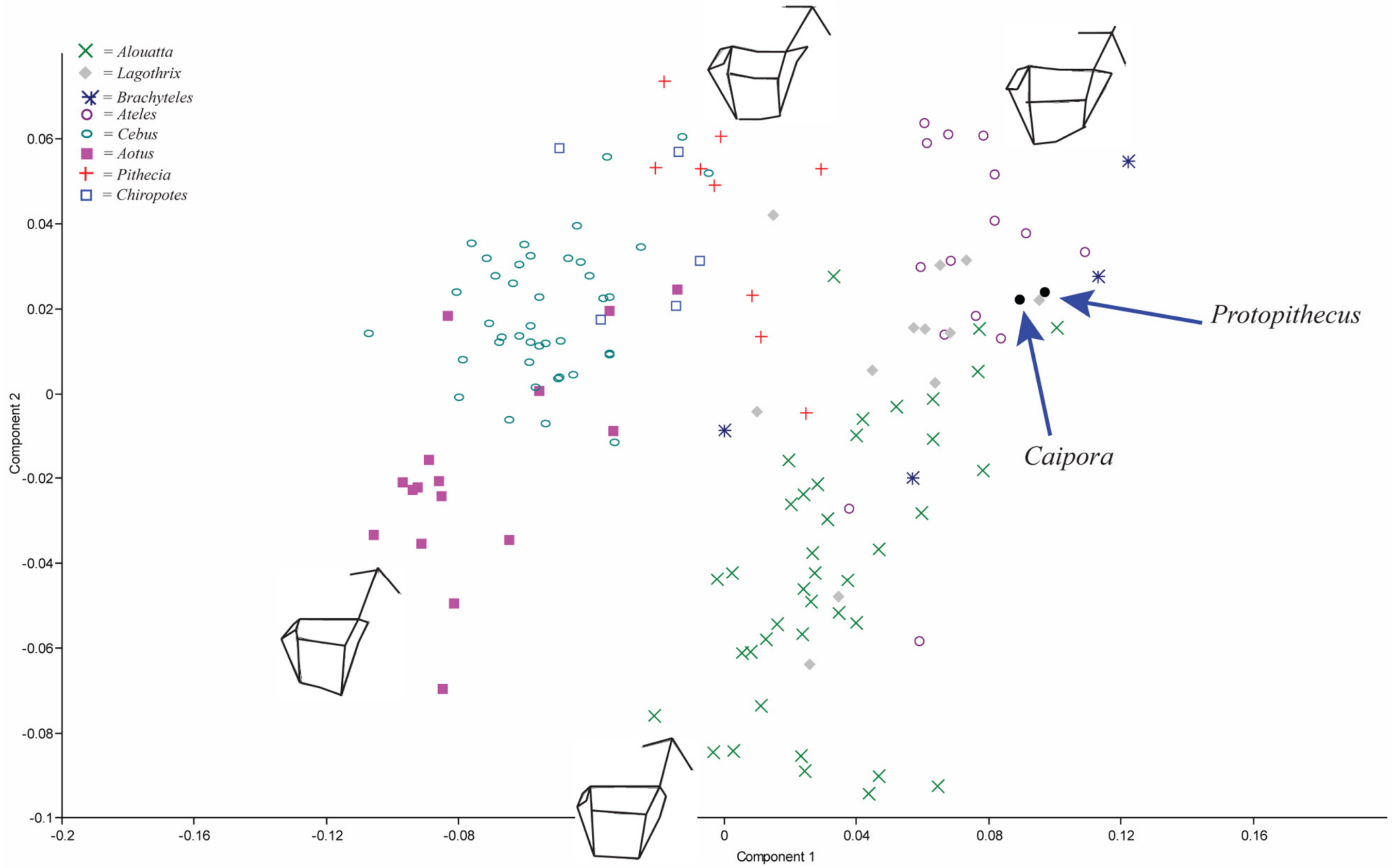

Figure 4.39. PCA results for the dorsal talar surface using the platyrrhine taxa only.
The distribution of taxa on PC1 and PC2 is the same as in Fig. 4.35, but slightly more diffuse as compared to when the plantar surface landmarks were included in the analysis. Wireframes represent a left talus in superior view (see Fig. 4.10 for reference).

minimum spanning tree connects the dorsal surface of the talus of *Protopithecus* with that of *Caipora*, emphasizing the large size and short, squat nature of this bone in the two fossils compared to the extant taxa (Fig. 4.38). The platyrrhine-only analysis of the landmarks on the dorsal talus also has a relatively high R^2 value (= 0.6) when PC1 is regressed against ln centroid size and it is clear that size is driving the grouping patterns, especially on the diagonals seen in the ateline vs non-ateline clusters (Fig. 4.39). For example, one would expect *Pithecia* to group with *Aotus* as they use leaping more frequently, while *Chiropotes* should be with the atelines because of their shared use of hindlimb suspension. Instead, the signal contained in the talar morphology examined here seems to be one of both body size and phylogenetic affinity.

To summarize, based on the PCA results described here, the *Protopithecus* postcranial skeleton is most similar to that of the extant suspensory atelines (Table 4.4). As noted above for the qualitative description of the fossil material, several elements show isolated similarities to taxa that practice other locomotor behaviors, but none strongly suggest any new or unexpected interpretations for the fossil material. Based on these quantitative results, as well as the qualitative observations described above concerning the large muscle attachment sites on the robust humerus and femur, a combination of suspension, by both the fore- and hindlimbs, and quadrupedal climbing was most likely used by the large-bodied *Protopithecus* to navigate its arboreal habitat.

Table 4.4. Summary of quantitative postcranial analyses.

	Distal Humerus	Proximal Ulna	Proximal Femur	Distal Femur	Proximal Tibia	Distal Tibia	Talus
Propithecus							
Indri					Pb[1]		
Archaeolemur							
Megaladapis							
Palaeopropithecus							
Aotus					Pb	Pb	
Pithecia					Pb		
Chiropotes					**Pb**[2]		
Cebus					Pb	**Pb**	
Alouatta				**Pb**	Pb	Pb	
Lagothrix	Pb		**Pb**				Pb
Ateles	**Pb**	**Pb**	Pb	Pb	Pb	Pb	**Pb**
Brachyteles	Pb	Pb	**Pb**			**Pb**	Pb
Caipora		**Pb**	**Pb**				**Pb**
Presbytis							
Lophocebus					Pb		
Macaca							
Colobus							
Nasalis					Pb		
Papio							
Symphalangus							
Pan							

[1] Pb indicates taxon closest to *Protopithecus* in PCA

[2] **Pb** indicates taxon linked to *Protopithecus* in minimum spanning tree

Discussion

Broad categories of locomotor behavior, i.e., “quadrupedal”, “arboreal”, “terrestrial”, “leaper”, are not necessarily useful when it comes to describing the complex behavior of living or fossil primates (e.g., Prost, 1965; Stern and Oxnard, 1973; Hunt et al., 1996). The entire locomotor repertoire of an individual or a species might be different from the locomotor behavior it uses most often on a daily basis. This creates a situation akin to that surrounding “fallback foods” (e.g., Marshall and Wrangham, 2007) and the “critical function” hypothesis (Rosenberger and Kinzey, 1976); the morphology preserved in a fossil of the postcranial skeleton could be reflecting adaptations to the way the animal moves most often while traveling or, instead, to those parts of the behavioral profile that could be most important to survival, such as fleeing predators or feeding. This is especially important for a fossil like *Protopithecus*, which presents a mosaic of traits that could fall under several different, commonly recognized locomotor categories. Another relevant issue involves work done on comparing ateline “brachiation” to hylobatid “brachiation”. Historically the term “semi-brachiation” has been used for the atelines (Ashton and Oxnard, 1963; Napier, 1963; Ashton and Oxnard, 1964; Ashton et al., 1965; Rose, 1973), but there are several problems with this conceptualization, most notably the fact that further detailed behavioral studies have shown that the animals that have been included in this category all move in very different ways (e.g., Stern and Oxnard, 1973; Mittermeier and Fleagle, 1976).

Protopithecus has fallen victim to this terminological chaos as well and has been lumped together with the *Ateles*-style “brachiators” based on possession of a suite of traits associated with this genus, including: long forelimbs relative to hindlimbs, long and straight diaphyses, mobile shoulder joints, curved phalanges, and a prehensile tail (Hartwig and Cartelle, 1996;

Jones, 2008). However, Hartwig and Cartelle (1996) also point out unique features of the *Protopithecus* postcranium, such as the well-developed brachioradialis flange on the distal humerus and the large attachment site for the gluteus medius muscle on the ilium, that could suggest climbing as an adaptively important part of the locomotor repertoire in addition to suspension. The presence of morphological features suggested to be related to both suspensory locomotion and deliberate quadrupedal climbing in *Protopithecus* is confirmed here, both qualitatively and quantitatively.

Terrestrial platyrrhines?

One of the most intriguing aspects of the evolutionary history of New World monkeys is the lack of terrestrial species. To date, no fossil or living South American primate has been described as spending the majority of its daily activity budget on the ground, as do many Old World monkeys and strepsirhines of Madagascar. This is not for lack of open habitat; there are, and have been for approximately 25 million years (MacFadden, 1997), plenty of grasslands in South America that are home to many diverse mammal species, but no primates. Several suggestions have been given to explain why the platyrrhines are restricted to an arboreal lifestyle: for example, some argue that the South American forest structure is more conducive to suspensory behavior with the aid of a prehensile tail (Emmons and Gentry, 1983; Lockwood, 1999) while others point to the high predator pressure on the ground for the relatively small-bodied taxa that are found in the New World (Di Fiore, 2002; Campbell et al., 2005).

Recently, several fossil platyrrhines have been suggested to have been either terrestrial or “semi-terrestrial” (Heymann, 1998; Kay et al., 2002; MacPhee and Meldrum, 2006; Kay, 2010). “Semi-terrestrial” has been defined as a separate locomotor category for Old World monkeys that have adaptations for transitioning between the trees and the ground by climbing and leaping as well as adaptations for quadrupedal running (Gebo and Sargis, 1994; Anapol et al., 2005). A combination of terrestrial and arboreal traits such as relatively long distal limb segments, a long tail, and smaller body size would indicate membership in this group; an example in the Old World is *Cercopithecus aethiops*, the vervet monkey (Anapol et al., 2005). In their study of the *Paralouatta* postcranium, MacPhee and Meldrum (2006) compared several morphological features of the elbow joint, ankle joint, and digits to the same elements in living New World and Old World primates of various locomotor patterns. Due to its unique combination of skeletal features that includes a retroflexed medial epicondyle and short straight phalanges, *Paralouatta's* postcranial skeleton was suggested to function more like that of a cercopithecine than any platyrrhine. Whether this means that *Paralouatta* is directly analogous to the vervet monkey as another "semi-terrestrial" species is not exactly clear. But it is worth noting that *Paralouatta*, like *Protopithecus*, does not seem to be moving around in its environment in the same way as any extant ateline.

Spending at least some time on the ground has also been suggested for the oldest platyrrhine, *Branisella boliviana* (Kay et al., 2002). However, this was based on its high-crowned and heavily worn molars (the assumption being that grit in the terrestrial diet would wear teeth faster, necessitating higher crowns) combined with paleoenvironmental reconstruction of a more open habitat, as no postcranial remains are yet known for this taxon. Similar reasoning has been used to infer "scansorial" behavior from the high crowned molars of the newly discovered Argentinian primate *Mazzonicebus almendrae* (Kay, 2010). *Protopithecus,* and *Caipora,* provide new morphological information relevant to this topic. Since these taxa are both represented by nearly complete skeletons, hypotheses about locomotor adaptations can be tested by looking directly at the joint surfaces themselves, instead of distant functional systems such as teeth.

To this point, Heymann (1998) proposed that *Protopithecus,* and *Caipora,* were not as suspensory as Hartwig and Cartelle (1996) originally believed and instead would have practiced a "high degree" of terrestriality. Most of the evidence presented in the short paper is intended to counter the pendulum model of brachiation as practiced by gibbons and siamangs as the main mode of locomotion for the fossils. For example, as plotted in Heymann's Figure 1, the intermembral indices of the fossils, when taking into account their extremely large body size for New World primates, make them look more similar to chimps or bonobos than to spider monkeys. In fact, if the ateline portion of that figure is isolated, *Protopithecus* and *Caipora* seem to fall on a line with *Alouatta* and *Lagothrix*, the less-acrobatic atelines, while *Ateles* and *Brachyteles* are the more specialized suspensory outliers (Fig. 4.40). While the intermembral index of *Protopithecus*, at 104, is within the range of values for *Ateles* (e.g., Erikson, 1963), this value could more correctly be seen as being in line with expectations for its body size based on a regression model restricted to the non-specialized extant ateline genera. However, this is simply evidence *against* suspensory locomotion for the fossil, not *for* terrestriality. The intermembral index is a gross indicator of limb proportions and, hence, locomotor capabilities, but not of substrate or micro-habitat preferences. Interpretations about locomotion in fossil taxa should not weigh heavily on this value as it can mask subtler differences in limb structure and behavior.

Nor can body size alone provide a smoking gun for locomotor capabilities. Many other variables, both intrinsic to the skeletal system like joint surface morphology and extrinsic, like habitat type and social behavior, can influence how an animal moves (Remis, 1995). However, regarding suspensory locomotion, there is some evidence that siamangs, at 10-12 kg, are at the

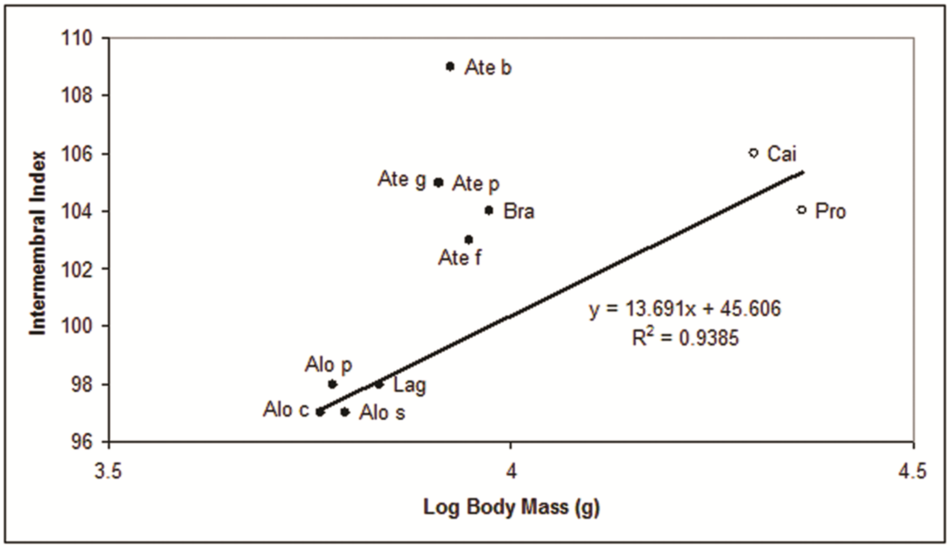

Figure 4.40. Bivariate plot of log body mass and intermembral index in atelines. The regression line added through the less suspensory taxa, although driven by the marked contrast between species of two different size classes, still suggests that the intermembral index of *Protopithecus* and *Caipora* is on trend for their larger body size. Despite having high intermembral indices in the range of the more suspensory taxa, when their body size is taken into account, the fossils appear more similar to the slower, more quadrupedal atelines. Modified from Heymann (1998).

body size limit for biomechanically efficient ricochetal brachiation (Preuschoft and Demes, 1985). Even the largest New World suspensory taxa, *Ateles* and *Brachyteles*, do not exceed more than about 12 kg (DiFiore and Campbell, 2007) despite possessing a prehensile tail which provides more support and weight distribution throughout the canopy and allowing them to move in a more flexible way at a larger size, more similar to an orangutan than to a gibbon. *Protopithecus*, at an estimated 20-23 kg (Hartwig, 1995a; Hartwig and Cartelle, 1996; see Chapter 2), is well above this proposed 10-12 kg threshold and within a body size range where behaviors like climbing become more important (Fleagle and Mittermeier, 1980; Gebo, 1992; Lockwood, 1999).

While the combined limb proportions and large body size of *Protopithecus* may point to a non-suspensory mode of locomotion, this does not automatically mean that *Protopithecus* was terrestrial. The picture is most certainly more complicated than a strict dichotomy between arboreality and terrestriality. A primate probably cannot be an efficient ricochetal brachiator at 20-23 kg, but that does not make terrestriality its only other option. Other large-bodied primates, like orangutans and the truly giant subfossil "sloth" lemurs, have found other ways to move around successfully in the trees (e.g., Godfrey and Jungers, 2003; Thorpe and Crompton, 2006). Heymann (1998) points out that the great apes, while being skeletally well-adapted for brachiating, do not actually use brachiation as their main mode of locomotion. Most primates have a flexible locomotor repertoire, the full range of which might not be represented in their postcranial morphology. Analogy suggests that, perhaps, *Protopithecus* was not completely arboreal or terrestrial but could be better compared to a versatile great ape, such as the chimpanzee. This would just be one more example of convergence between atelines and hominoids (for a review, see DiFiore and Campbell, 2007).

Other evidence presented for a "high degree" of terrestriality in the fossil repertoire is largely reliant on circular logic: for example, *if Protopithecus* was terrestrial, its large body size would be a good defense against predators such as jaguars and other large cats. Heymann (1998) also brings up contradictory statements made by Cartelle and Hartwig (1996) about the paleoenvironmental reconstructions of the area. They appear to vacillate between an interpretation of the area as being more open and similar to the *cerrado* vegetation that exists in parts of Bahia and Minas Gerais today while also inferring that the existence of the large-bodied suspensory primates is evidence for a more closed forest habitat type. The paleoenvironment in the Toca da Boa Vista and Lagoa Santa areas relevant to *Protopithecus* is hard to pin down, especially as the fossils have not been dated directly (see Chapter 1). If the climate was more dry and the habitat more open at the time the fossils were extant, the primates would have had an opportunity to spend more time on the ground. Even if the habitat was more closed, Heymann (1998) suggests that the New World forest structure, with its lack of lianas and more fragile branches (Emmons and Gentry, 1983), cannot support a large-bodied suspensory taxon, even one with a prehensile tail. Both of these points, potential for predator defense and the possible existence of a more open habitat, are valid considerations but do not prove that *Protopithecus* was terrestrial.

As mentioned above regarding "brachiation", the terminology being used here, and elsewhere in the literature, can benefit from clarification. Even though the quantitative results presented here do not ally *Protopithecus* with terrestrial Old World monkeys like some macaques and baboons, none have suggested that these extinct animals did not use the ground at all. Several other ateline species, while not "terrestrial" in their dominant pattern of substrate use, come to the ground for many reasons during daily activities. In the Atlantic Coastal Forest, both *Brachyteles* and *Alouatta guariba* come to the ground, especially in more disturbed parts of the habitat to cross cleared patches (Mourthe et al., 2007). Even *Ateles*, the most suspensory and highly reliant on an arboreal habitat, does come to the ground, most often for reasons related to specialized feeding behaviors such as drinking water during the dry season and geophagy at mineral licks (Campbell et al., 2005). Some of these mineral licks are even in small caves (Link et al., 2011), an interesting point to consider regarding the taphonomy of the nearly complete *Protopithecus* and *Caipora* skeletons from Toca da Boa Vista (see Chapter 1). The majority of these behaviors are described in the literature as opportunistic and more properly called facultative "ground use", not "terrestrial locomotion", and as such they may not leave a morphological or adaptive signal on a fossilized skeleton. There is a difference between being labeled a terrestrial primate in the manner of an Old World monkey and allowing for ground use as part of a more flexible locomotor repertoire that could be more appropriately given a different categorization. Perhaps “semi-terrestrial” could be used, but as with “semi-brachiation”, lumping taxa into a catchall intermediate category can obscure distinctions between them and caution should be exercised; a description of a range of possible behaviors may be preferable to a single categorical label.

Protopithecus and the prehensile tail: Part 2

The locomotor behavior of *Protopithecus* has in the past been described as “ateline-like” (Harwig and Cartelle, 1996). An important part of “ateline-like” locomotion is the use of the prehensile tail. As mentioned previously, it is therefore important to reevaluate the inference of a prehensile tail in *Protopithecus*. The tail to trunk length ratio calculated in Chapter 2 suggests that the *Protopithecus* tail was at least elongated, if not prehensile. The ensuing discussion should make it even clearer that this ratio is insufficient and further detailed work needs to be done to settle this question.

Prehensile tails have evolved several times in South American mammals. This is potentially due to the lack of lianas and more fragile branches of the forests on this continent, which are often flooded requiring foraging in the understory layers to be done by hanging from the branches above (Emmons and Gentry, 1983; Lockwood, 1999; Rosenberger et al., 2009). Other prehensile tailed mammals are of approximately the same size as the modern atelines; the largest is the binturong, a carnivoran of the genus *Arctictis*, which weighs 9-14 kg, approximately the size of a *Brachyteles* (Youlatos, 2003). With this in mind, it would be of interest to model the biomechanics of tail suspension and propulsion of a 20-25 kg primate to determine the size of the vertebrae and musculature necessary to support this large body weight and compare that with the size of the known fossil vertebrae.

Behavioral studies of both captive and wild populations have shown quantitative and qualitative differences in tail use among the four ateline genera (e.g., Cant, 1986; Bergeson, 1998; Youlatos, 2002; Schmitt et al., 2005), so the conceptual problem arises that, like "semi-brachiation", there is no uniform set of behaviors that one can term "ateline-like" on account of a prehensile tail. Despite being less suspensory and acrobatic than the other ateline primates, *Alouatta* uses its prehensile tail just as frequently: "A howler monkey might well survive with a paralyzed hand or foot; but were his tail injured, the animal would probably be severely handicapped" (Grand, 1967: 111). However, *Alouatta* does not usually hang solely by the tail and their body weight is therefore also distributed across the hindlimbs (Schön Ybarra, 1984; Cant, 1986). Hoisting the body up out of suspension by the hindlimbs and prehensile tail during feeding is done by large muscle masses in the hip (Stern, 1971; Stern and Oxnard, 1973) which would have to have been even larger if *Protopithecus* was engaging in similar positional behaviors. As described above, the fossil does have a very large gluteal tuberosity suggesting that foraging postures, such as pedal hanging, are just as important to consider when interpreting morphological adaptations in the postcranial skeleton. This is especially relevant when they are different than those used during travel, as is the case for *Alouatta* (e.g., Schön Ybarra, 1984; Gebo, 1992).

Unlike *Ateles*, which uses its tail mostly as a third propulsive force during forelimb suspensory locomotion (Schmitt et al., 2005), *Alouatta*'s prehensile tail is used most often in conjunction with its hindlimbs in suspensory foraging postures (Stern, 1971; Gebo, 1992; Lawler and Stamps, 2002). The prehensile tail should therefore be considered with the hindlimbs as a functional unit in *Alouatta* and any locomotor reconstructions for *Protopithecus* need to take this morphological relationship into account. This could be part of the reason why the hindlimb is not producing the clear picture seen in the forelimb PCAs. There are non-locomotor factors influencing hindlimb morphology, especially in the atelines which are using the prehensile tail/hindlimb complex for feeding and other postural behaviors. As *Protopithecus* is an ateline, it most likely had a prehensile tail that it would have been using at least in these postural behaviors, if not also as an aid in the suspensory locomotion indicated by the rest of its postcranial skeleton. The combination of spider monkey arms and howler monkey legs posited here is another interesting mosaicism in the fossil that could suggest a primitive position in the alouattin lineage. It also highlights the fossil's overall transitional nature between the ateline last common ancestor and something we would more easily recognize as a modern alouattin.

CHAPTER 5

SUMMARY AND CONCLUSION S

What we know about *Protopithecus*

Although specimens of *Protopithecus brasiliensis* have been known to paleontology since the middle of the 19th century, little detailed analysis of these remains has been done. This study aimed to fill in many of the gaps in our knowledge of not only the paleobiology of this taxon, but also the evolutionary history of its extant ateline relatives. Linear regression and three-dimensional geometric morphometric techniques were used to test hypotheses regarding the body size, craniomandibular, and postcranial morphology of the fossil. Linear regression equations based on platyrrhine postcranial dimensions, data that have not existed up until now, were generated and used to confirm the hypothesis that *Protopithecus* belongs to a large size class of platyrrhines that no longer survives. While mean values inferred for body weight, head and body length, and total body length vary, *Protopithecus* is estimated to be in the size range of a large male baboon or proboscis monkey, approximately 20-23 kg.

While this large body size prompted a previous suggestion in the literature that *Protopithecus* would have spent more time traveling on the ground than any living platyrrhine does today, detailed investigation of the morphology of the postcranial skeleton did not show any adaptations to terrestriality. The hypothesis put forth by Heymann (1998) is thus falsified. The original hypotheses of Hartwig (1995) and Hartwig and Cartelle (1996) are supported, suggesting that *Protopithecus* was a suspensory animal that moved in a way similar to extant *Ateles* and *Brachyteles*, with the addition of muscular *Alouatta*-like climbing. Based on both qualitative descriptions and quantitative analyses, the forelimb of *Protopithecus*, specifically the shape of the distal humerus and proximal ulna, was shown to be very similar to that of the atelin genera. The curved phalanges with large flexor sheath ridges are also strong evidence for the fossil's arboreal niche. One of the distal humeri attributed to *Protopithecus* has a very large brachioradialis flange, which suggests that forelimb flexion, important either during climbing or suspension, would most likely have been an essential part of the locomotor repertoire.

The femur and pelvis of *Protopithecus* are two of the only elements of the postcranial skeleton evaluated in this study that show similarities to *Alouatta*; the proximal end of the Toca da Boa Vista femur has a very large gluteal tuberosity and proximally placed lesser trochanter, and the pelvis has a large, deeply concave iliac fossa. The size and position of these muscle attachment sites indicate *Protopithecus* also had large, powerful muscle masses in the hip, hypothesized to be important for "antipronograde" positional behaviors such as hindlimb suspension and climbing. *Alouatta* hangs by their feet and prehensile tail during foraging in the outer canopy and uses powerful hindlimb-assisted climbing more than any other ateline. These behaviors could also have been advantageous for maneuvering the fossil's large body through the trees.

Other positional behaviors, like those used during howling bouts, also could have had an important impact on the evolution of the *Alouatta* skeleton. The cranial base and mandible of *Protopithecus* were examined in order to test the hypothesis that the fossil shares morphological features with *Alouatta* that could indicate the presence of an enlarged hyoid bone. As *Alouatta* is the only extant primate to howl using a greatly enlarged, hollowed out hyoid bone, finding this feature in the fossil would provide evidence for a similar behavior as well as a robust phylogenetic marker. However, while there were relatively high correlations among variables describing the size and geometry of the cranial base, mandible, and hyoid in extant *Alouatta*, those anatomical areas are not so tightly integrated that confident, exacting predictions can be made about the size and shape of the *Protopithecus* hyoid. The fossil's cranial base is not as elongated and unflexed as in *Alouatta* and there is evidence to suggest that the gonial region and ascending ramus of the mandible would not have been as expanded as original reconstructions had assumed. In terms of the hyoid, this seems to suggest that while *Protopithecus* would have had an *absolutely* large hyoid in concert with its large body size, it did not have a *relatively* greatly enlarged *Alouatta*-like hyolaryngeal apparatus. The shape of the cranial base as defined by the landmarks used here is more similar to *Lagothrix* than any other living ateline, thus throwing doubt on previous hypotheses that the *Protopithecus* basicranial morphology belongs on the list of alouattin synapomorphies. However, the large body size of the fossil is a confounding variable when making decisions about the functional and phylogenetic significance of many of its cranial traits. It is possible that at 23 kg, *Protopithecus* had enough subbasal space to support a relatively large hyoid without subsequent modifications to the cranial base and mandible.

There were some similarities shared with *Alouatta*, however, that can more confidently be interpreted as alouattin synapomorphies. For example, the occipital region of the *Protopithecus* skull is expanded and rugose and the foramen magnum is more posteriorly directed than in the atelin primates. This suggests that *Protopithecus* would have carried its large head in a way more similar to *Alouatta*, stretching it out in front of the cervical spine. This could be related to increasing space in the throat for a new type of vocal apparatus, protecting the integrity of the airway during respiration, or it could be an architectural side-effect of having a relatively small brain sitting posterior to a relatively large face. Based on the unexpected association in *Protopithecus* of non-folivorous, non-*Alouatta*-like teeth with a small brain, it is possible that small brain size is primitive for the atelines as a group, instead of being a derived consequence of *Alouatta's* mostly folivorous, low quality diet. If this is the case, then the cantilevered head carriage of both taxa was also already in place before the rest of the skull was modified. It is thus possible that in the *Protopithecus* skull we are seeing preadaptations for the unique hyolaryngeal morphology of extant *Alouatta*.

What we think we know about ***Protopithecus***

Data from this study suggest that the *Protopithecus* cranial and postcranial morphology represents a combination of primitive ateline, derived alouattin, and autapomorphic traits (Table 5.1). There are thus several options for the fossil's placement on the ateline cladogram that can be treated as competing hypotheses that need to be tested. While this dissertation was not a phylogenetic analysis, its results can offer some insight into which of these is the most likely scenario. The traits listed in Table 5.1 can be used to extend the character analysis done by Rosenberger and Strier (1989), using similar methodology to inform decisions about character polarity and reconstructing ancestral morphotypes. The modified nuchal region of the fossil that partially surrounds its relatively small brain, as well as the muscle attachment sites on the pelvis and femur indicating large powerful climbing muscles, are traits shared with *Alouatta* that are presumed to be derived and certainly unlike the extant atelin condition. Many of the other anatomical areas described here, such as the forelimb adapted to suspensory locomotion and moderately airorynchous face, agree with previous reconstructions of the ateline morphotype (e.g., Rosenberger and Strier, 1989; Jones, 2008). The polarity of body size in the alouattins is harder to determine. Interpreting the large body size of *Protopithecus* as an autapomorphic size increase from a medium-sized alouattin last common ancestor seems as equally plausible as the

Table 5.1. The *Protopithecus* pattern.

	Protopithecus	**Ateline Morphotype**[1]	**Alouattin Morphotype**[2]	***Paralouatta***	***Alouatta***	***Lagothrix***	***Brachyteles***	***Ateles***
Body Size	Large[3]	Medium	Medium/Large?	Medium	Medium	Medium	Medium	Medium
Facial Proportions	Moderately large	Moderately large	Moderately Large	Large	Large	Moderately large	Moderately large	Small
Craniofacial Haft	Intermediate	Intermediate	Intermediate	Airorynchous	Airorynchous	Intermediate	Intermediate	Non-airorynchous
Postorbital Constriction	Marked	Moderate	Marked	Marked	Marked	Moderate	Absent	Absent
Cranial Crests	Marked, compound	Moderate	Marked lines	Marked lines	Marked lines	Moderate	Absent	Absent
Nuchal Plane	Flat, enlarged, subvertical	Flat, unreduced, subvertical	Flat, reduced, subvertical	Flat, reduced, vertical	Flat, reduced, vertical	Flat, unreduced, subvertical	Flat, unreduced, subvertical	Rounded, unreduced
Foramen Magnum	Reduced, posterior	Unreduced?, posterior	Reduced, posterior	Reduced, far posterior	Reduced, far posterior	Unreduced, posterior	Unreduced, posterior	Unreduced, central
Brain Size and Shape	Reduced, cylindrical	Unreduced?, non-cylindrical	Reduced, cylindrical	Reduced, cylindrical	Reduced, cylindrical	Unreduced, non-cylindrical	Enlarged, non-cylindrical	Enlarged, globular
Basicranial Shape	Intermediate	Intermediate	Elongate	Elongate	Elongate	Intermediate	Intermediate	Shortened
Incisor Proportions	Enlarged	Enlarged	Enlarged	Reduced	Reduced	Enlarged	Reduced	Enlarged
Molar Relief	Reduced relief	Reduced relief	Reduced relief	Reduced relief	Cristodont	Reduced relief	Cristodont	Bunodont
Forelimb	Moderately elongated Adaptations for suspension and climbing	Moderately elongated Adaptations for suspension and climbing	Not elongated Adaptations for quadrupedalism and climbing	? Adaptations for semiterrestriality ?	Not elongated Adaptations for quadrupedalism and climbing	Moderately elongated Adaptations for suspension and climbing	Elongated Adaptations for suspension	Elongated Adaptations for suspension
Hindlimb	Adaptations for suspension and powerful climbing	Adaptations for suspension and climbing	Adaptations for suspension and powerful climbing	Adaptations for semiterrestriality ?	Adaptations for suspension and powerful climbing	Adaptations for suspension	Adaptations for suspension	Adaptations for suspension
Tail	Prehensile	Prehensile	Prehensile	Prehensile	Prehensile	Prehensile	Prehensile	Prehensile

[1] Rosenberger and Strier (1989) (also for extant taxa), Jones (2008), Rosenberger et al (in press)

[2] Results presented here and Rosenberger et al (in press) (see this as well as Cooke (2011) for further explanation and justification for some of these craniodental traits)

[3] See text for explanation of presumed body size polarity

more modern-looking alouattins reflecting a body size decrease from a larger *Protopithecus*-sized ancestor (see below for further explanation of the latter option).

Based on the postcranial results presented here, the original phylogenetic hypothesis proposed by Hartwig (1995a) needs to be considered. He argued from the morphology of the Lagoa Santa specimens, as well as their shared geographic location in the Atlantic Coastal Forest, that *Protopithecus* is most closely related to *Brachyteles*. However, despite the many postcranial similarities functionally linking *Protopithecus* to *Brachyteles*, and *Ateles*, especially in the forelimb, a phylogenetic relationship is not strongly supported. Postcranial traits related to suspensory behaviors have been shown to be quite homoplastic in the Atelidae (e.g., Lockwood, 1999) and therefore could be less useful as phylogenetic indicators. They also could be primitive for the ateline subfamily (e.g., Jones, 2008), meaning they cannot be used to link a fossil to a specific extant genus. Also, *Protopithecus* does not share any cranial traits with *Brachyteles,* such as a relatively large brain or lack of cranial cresting and postorbital constriction (Table 5.1). Results of this study make the hypothesis of a sister taxon relationship between *Protopithecus* and *Brachyteles* no longer tenable.

The most widely cited hypothesis, and the one supported here, places *Protopithecus* as a basal member of the alouattin tribe (Fig. 5.1; Hartwig and Cartelle, 1996; Rosenberger et al., 2011, in press). This view is based on suggested synapomorphies shared between the TBV *Protopithecus* skull and extant *Alouatta* (see Table 1.3), while recognizing that none of them are as extremely derived as the condition seen in the living howler monkey. Results of this study show that several of these traits are actually similarities that *Protopithecus* shares with *Lagothrix*, instead of *Alouatta*. The moderate degree of airorynchy and cranial base elongation and flexion shared by *Protopithecus* and *Lagothrix* are traits suggested by Rosenberger and Strier (1989) to

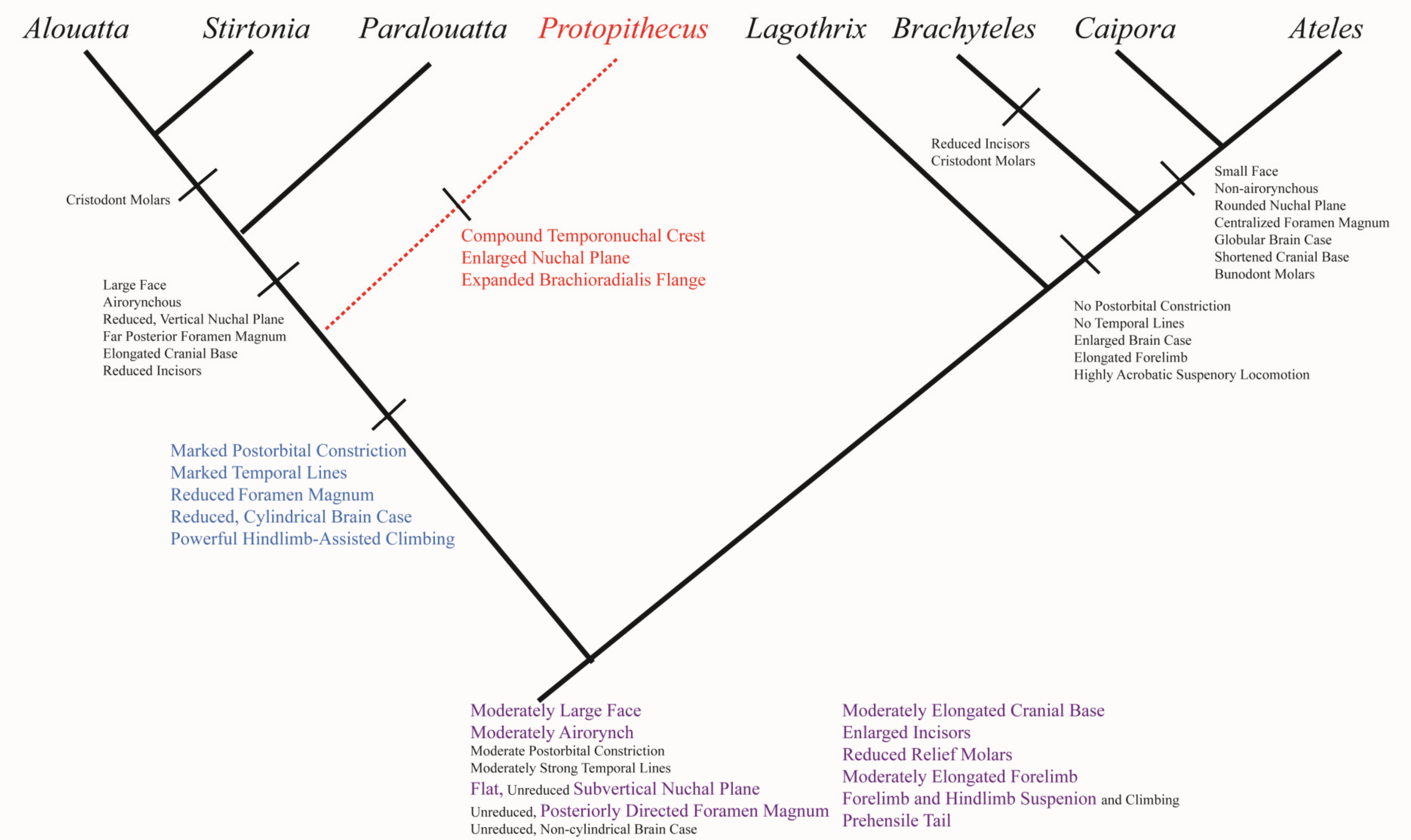

Figure 5.1 Ateline cladogram with proposed position for *Protopithecus*.
The branching pattern drawn here is based on morphological character analysis from this study (see Table 5.1), Rosenberger and Strier (1989), Jones (2008), and Rosenberger et al. (in press). The red dotted line is the phylogenetic hypothesis most strongly supported by the results of this study. Characters listed in red are autapomorphic for *Protopithecus*, those in blue are shared with the alouattin morphotype, and those in purple are primitive for all atelines. Only the most informative characters from Table 5.1 are listed here. See text for specific postcranial characters used to infer the locomotor behaviors listed in the table and on the figure.

characterize the ateline last common ancestor. These shared primitive traits between *Protopithecus* and *Lagothrix* bring up a third hypothesis that places *Protopithecus* at this basal ateline position. However, the morphology of the pelvis and femur mentioned above continue to link *Protopithecus* with the alouattins, as they are most likely derived traits potentially related to a functional complex that signals a shared reliance on both exaggerated climbing and hindlimb suspension not seen in the atelins. Similarly, the small brain size, marked cranial cresting and postorbital constriction, as well as the expanded, rugose nuchal plane are traits seen in the fossil that place it on the alouattin side of the tree (Fig. 5.1).

Because of the morphocline described here in cranial, and to some extent postcranial morphology, putting a strict dividing line between primitive alouattins and primitive atelins is difficult. As with any fossil, the closer it is to the last common ancestor of two groups, the less predictable is its particular combination of traits. The morphological pattern expressed by *Protopithecus* was certainly unexpected based on observations of only the extant atelines. As mentioned in Chapter 1 when discussing the disagreement between ateline molecular and morphological phylogenies, a rapid adaptive radiation at the base of the ateline tree could be the root cause of this uncertainty.

This hypothesized quick burst of evolutionary separation has been dated to approximately 16 Ma (Meireles et al., 1999; Cortes-Ortiz et al., 2003). *Paralouatta* and *Stirtonia*, smaller-bodied species with skulls and teeth, respectively, much more similar to those of *Alouatta* than *Protopithecus*, appear in the Miocene, a relatively short time after this date. If *Protopithecus* is provisionally positioned as transitional between the ateline last common ancestor and the more derived alouattins, this suggests that the actual fossil material that exists with its Pleistocene date is the remains of a platyrrhine “living fossil” (see Delson and Rosenberger, 1984). The more primitive craniodental morphology of *Protopithecus* led to previous suggestions that it is part of the Miocene alouattin radiation (Rosenberger et al., 2009), and the same could potentially be said of *Paralouatta*, which is also represented by Pleistocene material as well as the Miocene talus referred to *P. marianae* (Rivero and Arredondo, 1991; MacPhee et al., 2003). *Protopithecus* is a New World example of a lesson that has also been learned in studying the Old World monkey fossil record (regarding, for example, the relationship of taxa such as *Pliopithecus* and *Saadanius*; Begun (2002); Zalmout et al. (2010)): a geologically recent date for a fossil does not mean it cannot be part of an older, more primitive radiation, and vice versa.

Evolutionary implications

The fossil record preserves evidence of changes in body size, locomotion, diet, and vocal tract morphology over the course of the evolutionary history of the ateline subfamily. *Protopithecus* fits in well with a scenario proposed by Schön that integrates several of these functional systems (Schön, 1971, 1976; Schön Ybarra, 1984, 1995). He proposed that howler monkey ancestors were adapted for suspensory locomotion before the greatly enlarged hyoid complex evolved. A similar proposal of howler monkeys passing through a “brachiating stage” was made by Campbell (1937) based on the similar shoulder musculature of *Alouatta, Ateles*, and *Lagothrix*. As the hyoid became larger and took up more space in the throat as a permanently inflated air sac, the cranial base was modified to open the subbasal space and maintain a clear airway during howling bouts (Biegert, 1963). Part of this modification included a flattening of the nuchal region which would have been functionally associated with the posterior displacement of the foramen magnum and occipital condyles, thereby changing the neutral orientation of the head on the neck. Schön has suggested that this made acrobatic maneuvering more challenging, as the animals' visual field was no longer oriented anteriorly while using forelimb suspension (Schön Ybarra, 1984; see also Strait and Ross, 1999). As a consequence, howler locomotion evolved into the more deliberate slow quadrupedalism that is evident in *Alouatta* today.

As Schön's original hypothesis was articulated before the large body size of *Protopithecus* was fully appreciated, this potentially important aspect of alouattin evolutionary history was not incorporated into his proposed scenario. A change in body size could be an important piece of the selective puzzle missing between the suspensory howler monkey ancestor with a relatively small, unmodified hyoid and the development of the derived suite of craniomandibular characters found in the more advanced members of the alouattin tribe. I hypothesize that if *Paralouatta, Stirtonia,* and the extant howler monkeys represent the results of a body size decrease over evolutionary time, characters like airorynchy, expanded gonial angles, and an unflexed cranial base could have been necessary to open up the volume of the subbasal space even more in order to support the morphology underlying the howling ability that had become selectively important for aspects of their social behavior. As this change took place, selection no longer favored maintaining the use of forelimb suspensory locomotion. Previous methods for reorienting the animals' visual field, such as bending the neck or flexing the cranial base, were no longer efficient due to the placement of the newly enlarged hyolaryngeal structures.

Of course, this scenario still leaves unanswered many morphological questions. As discussed in many places throughout this dissertation, there are a multitude of variables exerting selective pressure on aspects of craniomandibular morphology in the alouattins (see Fig. 5.2). While the Schön-Biegert hypothesis, which underlines the unique *Alouatta* cranial morphology

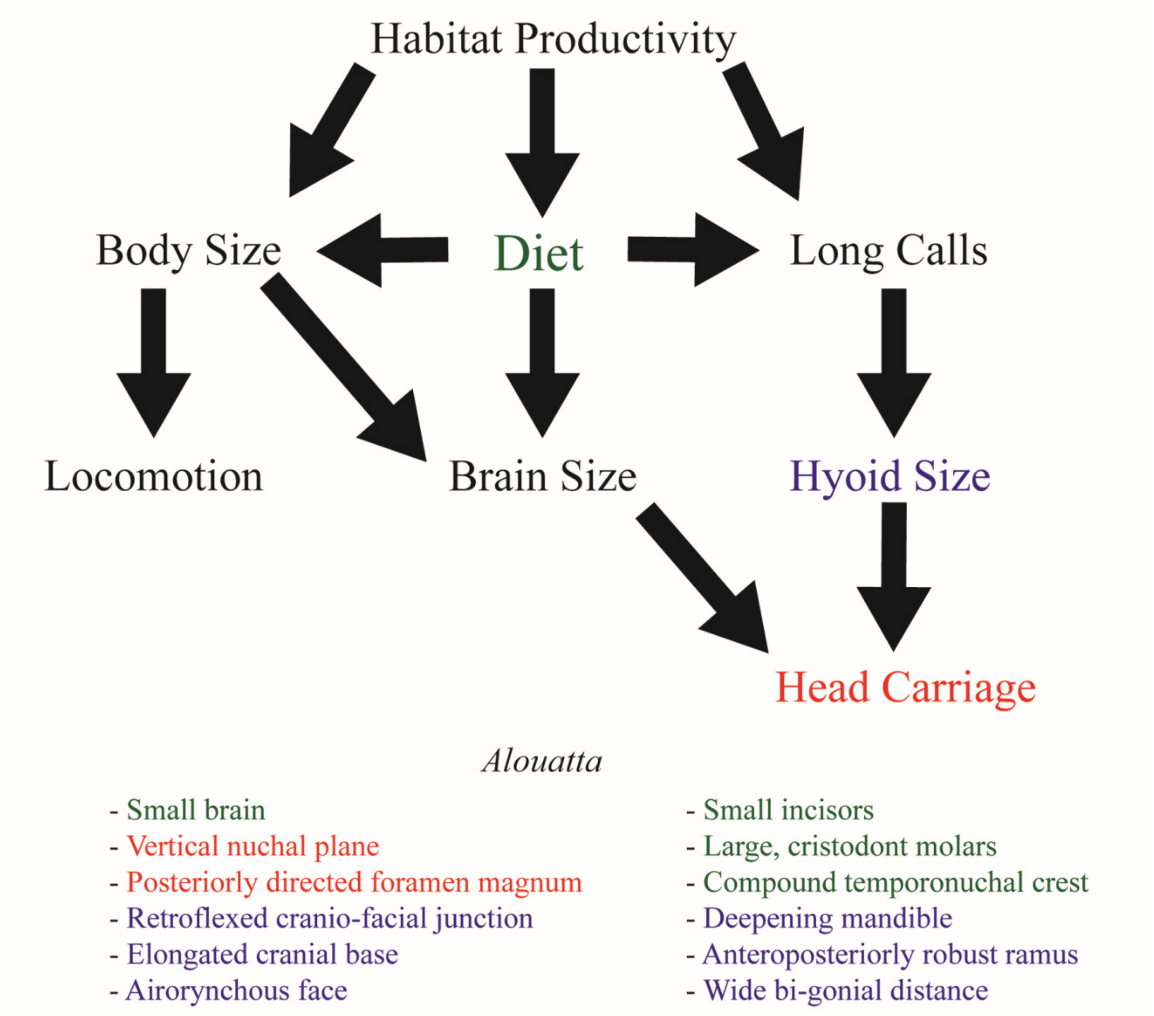

Figure 5.2. A model of some selective pressures influencing *Alouatta* morphology. Green indicates cranial morphology influenced by diet, red is for head carriage and how the cranium is attached to the vertebral column, and blue are unique *Alouatta* traits potentially related to hyoid size and shape. *Protopithecus*, with its mosaic of characters, some shared with *Alouatta* and some not (see Table 5.1), provides crucial evidence for the interrelationships between these selective pressures. Some arrows should most likely be pointing in both directions and some of the traits on the list are also most likely interrelated. For example, the small brain and retroflexed cranial base are found together as predicted by the "spatial packing" hypothesis (see Chapter 3). These caveats serve to emphasize the complex nature of evolutionary morphology.

as being driven by a spatial adjustment to a hypertrophied hyolaryngeal apparatus, remains appealing, there are other, related possibilities. For example, while reorientation of the head and modification of the cranio-facial junction may have been advantageous for positioning the hyoid in a more beneficial place to act as a sound resonator (Schön, 1986; Whitehead, 1995), the opening of the airway for the aerodigestive tract is also an important consideration (Laitman and Reidenberg, 2009). An animal needs to be able to breathe and swallow properly before it can evolve any specializations for producing vocalizations; the larynx and its associated structures, like the hyoid, need to be functional for these primary directives first, and then they can be modified for other purposes. Why howler monkey relatives and their ancestors evolved an enlarged hyoid and increased reliance on howling in the first place is yet to be determined, but it could have something to do with the history of alouattins as ecologically flexible, pioneering marginal habitat colonizers (Rosenberger et al., 2009).

While the diet of *Protopithecus* was not specifically investigated here, it is also an important piece of the paleoecological puzzle. A frugivorous diet usually includes a significant amount of time spent feeding in thinner terminal branches (Grand, 1972; Dunbar and Badam, 2000; Cant et al., 2001), potentially inducing the large-bodied *Protopithecus* to use more suspensory postures during foraging. The prehensile tail would have been particularly helpful in this regard, along with the large muscle masses in the hip of *Protopithecus* which are comparable to those in *Alouatta*, which are presumed to be important for tail and hindlimb suspension during foraging (Stern, 1971; Stern and Oxnard, 1973; Gebo, 1992). Foraging in the thin outer branches assisted by a prehensile tail could have been the situation in which leaf eating became more prevalent, as those outer canopy branches are also where extant ateline semi-folivores find the young leaves that they prefer (Rosenberger and Strier, 1989; Rosenberger, 1992; Jones, 2008).

A largely frugivorous diet during the early periods of alouattin evolutionary history also fits into the sequence of transformational events involving the hyoid and cranial base. If howling contributes selectively as a way to avoid conflict with neighboring groups (Carpenter, 1934; Chivers, 1969; Baldwin and Baldwin, 1976; Sekulic, 1982), then its appearance first in a frugivorous taxon that makes use of clumped defendable resources is a reasonable hypothesis. As the percent of leaves included in the diet continued to increase in the howler lineage as they expanded their range into less productive habitats, selection for behaviors that conserve energy would also have increased (also see Rosenberger et al, 2011; Rosenberger et al., in press). This may explain the howler's relatively small brain size, more deliberate locomotion, and minimizing of travel expenditures, all of which could place a premium on evolving an inexpensive manner of spatial advertisement and defense – howling. Thus, increased folivory may have been the catalyst for the positive feedback loop continuing selection for many of *Alouatta's* derived cranial and postcranial traits.

For the *Alouatta* lineage, this evolutionary transition may have begun in an ancestor similar to *Protopithecus*, a large-bodied animal that would need to limit its reliance on acrobatic behaviors to preserve energetic efficiency. Modifications to the proximal femur and pelvis to enhance the efficiency of the hindlimbs as a compliment to the forelimbs in suspension and climbing would have helped the large-bodied monkey to support its weight in the trees. Perhaps as *Alouatta* ancestors began to expand their ranges and colonize more marginal habitats (Eisenberg, 1979; Rosenberger and Strier, 1989; Rosenberger et al., 2009), a body size decrease could have been selectively advantageous as a response to the less abundant resources they encountered. During this period of body size change, powerful hindlimb-assisted climbing and deliberate quadrupedalism, as well as howling, could have become even more prevalent as an increase in percent of leaves included in the diet began to enhance the energy-minimizing strategy that *Alouatta* follows today (Rosenberger and Strier, 1989; Rosenberger et al., 2011; Rosenberger et al., in press). As subbasal space decreased with decreasing body size over evolutionary time, and semi-folivory became more entrenched, selecting for relatively larger cheek teeth and a large face to accommodate them, the degree of airorynchy in the face became more extreme and the cranial base elongated and unflexed. At the same time, the gonial angles and ascending ramus of the mandible expanded their lateral span and antero-posterior width, respectively, to match the stretching of the basicranium above. These shape changes would have served to maintain the volume necessary for the enlarged hyoid that could have developed by this time as well as a way to produce even louder long calls.

This evolutionary scenario needs to be tested further with embryological and developmental work on aspects of *Alouatta* cranial morphology, ontogenetic samples, biomechanical studies, and a full-scale phylogenetic analysis based on a character matrix including both cranial and postcranial traits of atelines and pitheciines. This would lead to more confidence in reconstructing character state polarities based on the variation seen in a diverse array of related extant taxa. The data presented here provide a jumping off point for pursuing such work in the future, promising that *Protopithecus* will not be forgotten and ignored for another 150 years.

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