# Stony Brook University

# MORPHOLOGICAL DISPARITY AND MACROEVOLUTION IN STREPSIRRHINES, PLATYRRHINES, AND PLESIADAPIFORMS

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Abstract of the Dissertation

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The level of adaptive diversity within an ecosystem or natural group is an aspect of biodiversity that is not necessarily available from counts of species or higher taxa. One method of estimating adaptive diversity is to measure the morphological disparity, or the range of variation observed in the sample. Morphological disparity can be used to investigate large-scale evolutionary changes in the fossil record, and has also been applied to a number of questions in extant organisms, ranging from investigations of diversification through time to understanding ecological community structure. In this dissertation, I investigated the potential for application of morphological disparity methods to understanding diversification in extant and fossil primates. I assessed the degree to which the fragmentary dental remains available for fossil mammals may represent skeletal diversity in other regions, and the extent to which ecological diversity in diet and activity pattern is captured by morphological disparity. I also investigated the relative influence of diet and size on dental morphology. Finally, I applied measurements of morphological disparity in the dentition to understanding the adaptive diversification of a radiation of primate-like mammals, the plesiadapiforms.

Ecological distances and morphological distances were correlated in the two extant radiations examined, and gave similar assessments of the pattern of diversification through time in the extant radiations. Comparisons of morphological diversity in molar morphology compared to other regions indicated that, while not necessarily representative of diversity in other regions, molar morphological disparity is particularly useful for identifying adaptive diversity in both analyses of diversification through time, and identification of unusually diverse clades.

Geometric morphometric analysis was found to be an effective method to assess dietary signal in molar morphology. Analyses of morphological disparity in plesiadapiforms indicate that over the course of the Paleocene sufficient diversity in molar morphology was accumulated such that the plesiadapiforms achieved levels of molar disparity comparable to those of extant groups such as strepsirrhines, even given their much shorter temporal range. Morphological disparity and taxonomic richness were not entirely concordant with maximum disparity in the Plesiadapoidea, with the highest taxonomic diversity occurring earlier than greatest morphological disparity. The latter result indicates that molar morphological variation may add information to analyses of diversity through time in this group, including evaluating hypotheses regarding extinction and diversification in this group and other fossil mammals.

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## Chapter 1. Introduction - Biodiversity and morphological disparity in fossil and extant organisms

Biodiversity can be defined as the complex variation exhibited by biological organisms; "the variety of morphology, behaviour, physiology, and biochemistry in living things" (Mallet, 1996:13). Measurement of biodiversity is often discussed in the context of setting priorities for conservation (e.g., Vane-Wright et al., 1991; Crozier, 1992). However, understanding of biodiversity can also contribute to biological theory; for example, the level of biodiversity interacts with elements of ecosystem function (e.g., McCann, 2000). Biodiversity is often measured in terms of counts of species (or other taxonomic levels) numbers, but taxonomic richness does not capture every aspect of diversity that may be of interest (Purvis and Hector, 2000); for example, taxon counts provide little direct information on ecological variation or unique phylogenetic history.

Diversity is an important topic in the paleontological literature, because the diversity present at any point in time provides the material for future evolutionary radiations. One avenue of research has examined the manner in which biodiversity differs among localities or over evolutionary time in relation to geologic or climatic factors (e.g., Bambach, 1977; Sepkowski et al., 1981; Sepkowski, 1984; Jackson and Johnson, 2001). Currently such paleontological studies focus overwhelmingly on richness at a chosen taxonomic level, even though there is evidence indicating that other aspects of biodiversity, such as morphological variation, may not always be closely related to the observed level of taxonomic richness (Foote, 1991; Lupia, 1999; Roy et al., 2001; Eble, 2000).

Alternative measurements of biodiversity include phylogenetic diversity, which incorporates consideration of the total branch lengths represented within a group of species. Faith (1994) suggested that phylogenetic diversity is particularly useful for estimating functional diversity, or the range of organismal traits that influence ecosystem function (Tilman, 2001) on the grounds that if unusual organisms, or organisms with few close relatives, become extinct, biodiversity in terms of the range of forms or number of features is likely to be affected. It is also likely that organisms with unique adaptations may play similarly unique roles within ecosystems, and that ecosystem function would therefore be disproportionately affected by their removal (Jernvall and Wright, 1998).

The lemuriform radiation in Madagascar provides a good example of some of the differences between considering biodiversity as a sum of the numbers of species compared to other aspects of biodiversity. Of around 100 species included in Mittermeier et al. (2010), there are 18 species of *Microcebus* (more have been described since this volume was published) and 26 species of *Lepilemur*. In contrast, there is only one extant species of the genus *Daubentonia*. The species diversity in *Lepilemur* and *Microcebus* has primarily been supported by karyotypic analysis (e.g., Rumpler and Albignac, 1975, 1978) and mitochondrial sequence data (e.g., Louis et al., 2006a,b) , even though some species can also be distinguished by morphological characters (Jungers and Rumpler, 1975; Yoder et al., 2000). If biodiversity is estimated by species richness, the loss of one species of *Microcebus* would cause an equal reduction in biodiversity to the loss of the aye-aye. However, in terms of ecological roles, morphological peculiarity, or phylogenetic history, loss of the aye-aye would result in a much greater loss to the biodiversity of Madagascar.

**Morphological disparity**

Morphological disparity, the range in form exhibited by organisms, forms the basis of all comparative anatomy. Measurements of morphological disparity have been argued to provide an additional, intuitive method of estimating biodiversity that may effectively capture ecological variation, and does not require a known phylogeny (Roy and Foote, 1997). Morphological disparity can provide insights into diversification and extinction patterns that may be related to functional roles. The application of morphological disparity measurements across a taxonomically broad sample is limited by the difficulty of measuring morphological differences in the absence of homologous features. However, within a group of species, morphological variation may allow considerable potential to analyze diversification (see overviews by Foote 1997; Erwin 2007). [1]

The analysis of morphological variation in paleontological studies holds considerable potential to add information to the study of evolutionary processes in biological groups (e.g., Saunders and Swan, 1984; Foote, 1991, 1992, 1993; Van Valkenburgh, 1994; Wesley-Hunt, 2005), but currently few such studies have been carried out in mammals. Van Valkenburgh and Janis (1993) emphasized the importance of evaluating ecological roles to understand diversification over evolutionary time. However, the use of morphological disparity to analyze

[1] The term "morphological diversity" is sometimes used to refer to a count of morphological "types" (e.g., Jernvall et al., [1996] use this term to refer to the number of different molar crown types in their ungulate samples). If this usage of morphological diversity is followed, "morphological disparity" then refers to a comparative quantitative estimate of the range of variation in morphospace. A more general usage of "morphological diversity" refers to variation within *and* between types. I find the diversity/disparity distinction somewhat artificial, because apparent discontinuity and subsequent identification of "types" becomes complex if an intermediate morphology is subsequently identified, but in subsequent chapters I try to use "morphological disparity" rather than "morphological diversity" to avoid confusion. This has the additional benefit of not conflicting with existing usage of "diversity" to indicate species-richness.

evolutionary diversification in mammals such as primates, will likely be limited to skeletal morphology (Van Valkenburgh, 1994), specifically those skeletal regions most often preserved in the fossil record, such as the dentition (e.g., Jernvall et al., 1996; 2000; Wesley-Hunt, 2005; Wilson et al., 2012). Jernvall et al. (1996, 2000) examined taxonomic diversity, morphological diversity in numbers of molar crown types, and morphological disparity from molar measurements in perissodactyls and artiodactyls. From the pattern of molar morphological disparity, these authors concluded that a shift in the predominant ecological strategies in ungulates occurred at the transition between the Oligocene and Miocene. In another recently published example, Wilson et al. (2012) analyzed morphological disparity in multituberculate mammals, and identified an adaptive radiation, possibly associated with the rise in angiosperm resources, beginning prior to the Cretaceous/Tertiary boundary.

Morphological disparity can be quantified through any summary variable that provides an estimate of the morphological variation within a group of organisms. If a morphospace is defined by a single variable, the degree of dispersion from the mean value for that variable could be considered morphological disparity (standard deviation, coefficient of variation). One example of this is provided by the recent analysis of multituberculate dental complexity by Wilson et al., 2012). More often, morphological disparity is calculated from a combination of multiple variables, and therefore measurements of disparity are made based on the distances between species in a multivariate space. Morphological disparity has also been used to analyze levels of diversity and reconstruct diversification patterns in extant organisms. Losos and Miles (2002) used the average morphological distances between members of a clade to identify clades as possessing unusually high levels of disparity, in order to provide a test of the hypothesis that a clade constitutes an adaptive radiation. Harmon et al. (2003) also used morphological distances

in combination with a phylogeny to reconstruct patterns of diversification in extant taxa by examining the distribution of morphological disparity within and between subclades, at various points from root to tip of the tree.

**Goals of this dissertation**

This dissertation will investigate the potential and limitations for the application of morphological distances to analyze macroevolution in the mammalian, and particularly the primate, fossil record, using the examples of extant strepsirrhine and platyrrhine primates, and the Paleocene radiation of plesiadapiforms. Following this introductory chapter, Chapters 2 and 3 explore two possible factors limiting the interpretation of morphological disparity in fossil mammalian species: 1) the degree of correspondence between ecological disparity and morphological disparity, and 2) the limitation to specific regions of the skeleton such as the dentition. Chapter 4 explores factors underlying morphological variation in the molars of primates, and introduces a method of quantifying dental morphology, geometric morphometric analysis, that has only recently begun to be applied to occlusal morphology. Chapter 5 applies a geometric morphometric analysis of plesiadapiform molar morphology to quantify disparity in molar shape within and between North American plesiadapoids in the Paleocene.

**Chapter 2: Ecological and morphological distances in extant primates**

As discussed above, morphological disparity is often used to assess ecological breadth or range of adaptive specialization in the clade studied. However, many factors may interact to reduce the level of correspondence between intertaxon distances in morphological space compared to ecological space and, as noted by Foote (1997), the relationship between the two is

often assumed rather than verified empirically. Factors such as phylogenetic relatedness and size-associated shape change may affect the association between measurements of morphology and function. Such differences may also occur even if morphological measurements are closely associated with function. These include diverse morphological solutions that produce similar performance in functionally important variables (Wainwright et al., 2005) or, conversely, morphological similarity between species that differ in ecological specialization.

Primates provide an ideal opportunity to investigate such a possible discrepancy in a mammalian radiation given the large amount of data available on both ecological variation in wild species, and the relationships between morphological variation and adaptive differences. In this chapter, morphological measurements of the cranium, mandible, and molar morphology are compared with ecological variables representing diet in two clades of primates, strepsirrhines and platyrrhines. Ecological and morphological distances are compared directly, and I also compare ecological and morphological distances in analyses used in previous literature to 1) identify particular clades as adaptive radiations, and 2) to estimate the pattern of diversification through time.

**Chapter 3: Morphological distances from different skeletal regions**

The goals of this chapter are to investigate the degree to which the region studied influences conclusions concerning the relative amount of morphological disparity in particular groups. In neontological analyses of vertebrate morphological disparity, measurements can consist of variables that combine several different skeletal elements, for example, measurements of limb lengths, can be combined with head length, or total body length, to give a measurement of body proportions. In contrast, for analyses of fossil taxa, measurements from different skeletal

regions are likely only available for a small proportion of species in any group. Instead, analysis of morphological disparity in clades will likely be limited to the dentition, or to isolated postcranial elements such as proximal and distal ends of limb bones or tarsal bones, because it is necessary to have the same morphological region available for analysis for all included taxa. In this chapter, morphological distances calculated from the molar, mandible and cranium will be compared with each other, and to matrices derived from phylogenetic distances. Methods used to assess morphological diversification in extant animals will be applied to different skeletal regions to investigate any differences between the patterns of diversification revealed.

**Chapter 4: Geometric morphometric analysis of the mandibular second molar**

Decades of research have shown that molar morphology shows a clear dietary signal. However, phylogenetic differences between clades can also be seen in molar morphology, for example, the presence or absence of cusps such as the paraconid on the lower molar and the hypocone on the upper molar. Furthermore, it has also been suggested that some components of molar morphology may be the result of shape changes associated with increasing and decreasing size. In this chapter a more detailed investigation of association between dietary variables, size, and tooth shape is conducted. It also introduces the use of geometric morphometric methods for the analysis of 3D tooth shape, in an attempt to capture dental morphological shape more thoroughly than is possible using linear measurements.

**Chapter 5: Dental morphological disparity analysis in plesiadapiforms.**

The goal of this chapter is to evaluate the information that may be added by the analysis of morphological distances to investigation of disparity through time in primate/mammalian

radiations. This chapter will use dental morphological distances to evaluate changes in morphological disparity through the late Paleocene in plesiadapiforms, concentrating on the two most species-rich families of plesiadapoid plesiadapiforms, carpolestids and plesiadapids. Geometric morphometric methods, demonstrated in the previous chapter to successfully capture dietary variation in extant prosimian and platyrrhine primates, are used to represent tooth shape. The position of plesiadapiform species in morphospace is compared to those of extant archontan mammals (treeshrews, dermopterans, and prosimian primates) and fossil euprimates. The relative disparity in molar morphology in Plesiadapoidea and its two major subclades, plesiadapids and carpolestids, is compared to that seen in extant strepsirrhines and strepsirrhine subclades. Morphological disparity among plesiadapoid taxa is measured for the Torrejonian, early Tiffanian, late Tiffanian, and Clarkforkian North American Land Mammal "Ages" and compared to generic richness during these time periods.

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## Chapter 2: Macroevolutionary comparisons of ecological disparity and craniodental disparity in primates

*ABSTRACT: Morphological distances between taxa are used in macroevolutionary analyses to provide insights into the processes underlying adaptive diversification. However, even when morphological variation can be clearly related to functional performance, morphological distances between species may not represent differences in ecology or adaptation. In this analysis activity profile and diet are used to create a matrix of ecological distances between species that are compared to craniodental morphological distances in two clades of primates, platyrrhines and strepsirrhines. Analyses include direct comparison of the distance matrices, analyses of disparity through time, and comparisons of relative amounts of disparity in clades at the family level.*

*Direct comparisons of the distance matrices indicate significant associations between morphological and ecological distances. In strepsirrhines these occur in the absence of a significant correlation between morphological and phylogenetic distances, which may indicate some independence of phylogenetic history. In both clades, most of the deviation from the diagonal occurred in cases of high ecological distances in species pairs that were more morphologically similar. Disparity through time curves were somewhat consistent between ecological and morphological distances, particularly when comparisons are made between clades. However, in both clades, some contour changes are present only in the ecological distance matrix. Clades identified as possessing unusual levels of disparity were not consistent between the two analyses. These results indicate that while morphological distances may be broadly representative of ecological distances, results may vary depending on the type of analysis performed.*

Measurements of morphological disparity, defined as the range of morphological forms within a group of species, have been frequently applied to macroevolutionary analyses of fossil radiations in a wide array of organisms; very recent examples of such studies have been conducted on the teeth of multituberculate mammals (Wilson et al., 2012) and the platform elements of conodonts (Girard and Renaud, 2012). Morphological disparity, often with measurement choices informed by ecomorphological relationships observed in extant forms, has been considered to represent adaptive diversity. As such, morphological disparity is compared with counts of species or higher taxa for analyses of disparity through time that aim to compare changes in taxonomic diversity with the expansion and contraction of ecological niche space within a radiation (e.g., Foote, 1992a,b, 1993; Jernvall et al., 1996; Wesley-Hunt, 2005).

Morphological disparity has also been used as a proxy for ecological variation in studies that aimed to quantify ecological community structure among extant species (Ricklefs and Travis, 1980) or to estimate ecological aspects of biodiversity (Roy and Foote, 1997). Ricklefs and Travis proposed that, given the ready availability of morphological measurements from museum specimens and the difficulties associated with directly quantifying ecological niche characteristics to compare communities, morphological analyses might be usefully employed in both evolutionary and ecological studies of species assemblages. For example, morphological phenotypic resemblances between species with similar ecological roles in geographically separated ecosystems have been used to identify the degree of convergence between communities (e.g., Mares, 1976; Hertel, 1994). More recently, morphological distances have been used to investigate macroevolutionary processes underlying observed disparity in extant clades (e.g., Losos and Miles, 2002; Harmon et al., 2003).

The extent to which morphological distances are representative of ecological variation is relevant to the use of morphological disparity for such studies, but is rarely tested. In studies that have made such a test, morphological distances are not always directly representative of ecological variation (e.g., Douglas and Matthews, 1992). The relationship between morphology and ecological or behavioral variation has been a topic of much study in numerous groups, often with the intention of identifying morphological adaptations, and predicting ecological roles in extinct taxa (e.g., Kay and Cartmill, 1977). The framework for the identification of ecomorphological associations most often employed in the primate literature is that of Kay and Cartmill (1977), who provided a list of criteria for considering morphological traits as adaptations for particular functions. Their criteria focus on the distribution of the trait amongst extant taxa, observed functional associations in extant taxa, and an apparent historical co-appearance of the trait and function. Under this model, a close association between morphology and ecology would be predicted if the traits that represent morphological variation are well chosen to represent function, and can therefore be considered to represent adaptations.

Insights into factors that may disrupt the association between ecological variation and morphological variation, even under conditions in which function is closely associated with a particular trait or set of traits, can be gained from consideration of a more general ecomorphological framework. Arnold (1983) presented a model for the association between phenotype and environment that incorporates the level of performance into consideration, in that the phenotypic diversity creates differences in functional parameters, and selection acts at the level of the interaction between performance and ecological variation. Reilly and Wainwright (1994) expanded this model and illustrated levels of analysis for ecomorphological studies, with the additional levels of the "fundamental niche" and the "realized niche" (redrawn in Fig. 2.1,

with annotation). The realized niche is defined as the actual resource use of the organism, while the fundamental niche describes potential resource use, based on performance capacity.

There are several points in this ecomorphological pathway at which an association between ecological/behavioral variation and morphological variation might be disrupted. At the most basic level (A in Fig. 2.1), other influences on morphology may affect the degree of morphological similarity between species with similar ecological profiles. These include the tendency of closely related organisms to resemble each other ("phylogenetic signal", Blomberg et al., 2003). This could create both morphological similarity among closely related species that have nevertheless diverged ecologically, or apparent morphological differences between more distantly related species possessing a similar ecological profile (Losos and Miles, 1994). Additionally, non-isometric scaling relationships between traits such as brain size or eye size, could lead to morphological similarity between similarly sized organisms, even if they differ in related ecological parameters. Finally, there may be geographic variation in limb proportions or body size within species, such that some component of morphological variation between species can be ascribed to environmental factors rather than to similarity in ecological roles (Mosimann and James, 1979)

An additional factor that may affect ecomorphological associations is provided by instances of functional equivalence among varying morphological configurations, described as "many-to-one mapping" (Alfaro et al., 2004; Wainwright et al., 2005; Young et al., 2007). This could potentially intervene between a close association of morphological similarity and functional similarity (B in Fig. 2.1). For example, a parameter such as increased bite force might be achieved either through increases in the physiological cross sectional area of jaw adductor muscles, or through altering their mechanical advantage by changes in location of the bite point.

Young et al. (2007) provide one such example, finding that shared dietary group in soricid shrews resulted in functional but not morphological similarity in the mandible. The degree to which the morphological similarity reflects functional similarity should relate to the degree to which the system is canalized to evolve toward a particular morphological solution, by the presence of other constraints on the system or by correlated changes through integration. In contrast to possible disruptions due to phylogenetic signal, issues of "many-to-one mapping" make a prediction about the direction of deviation from a situation in which ecological differences are proportional to morphological differences. Morphologically similar species should still be similar functionally (in as much as morphological traits are associated with function), but similarity in function might exist in the absence of similar morphology. Thus, many-to-one mapping should create instances in which small ecological distances are associated with larger differences in morphology, but not the reverse.

However, another situation might arise that would create the alternative prediction. While different morphological configurations may be functionally equivalent, it is also possible that similar morphological/functional configurations may result from different selective environments (disrupting the ecomorphological association at point C in Fig. 2.1). This could occur through a similarity in functional requirements, such as the higher summed crest lengths and occlusal relief of both folivorous and insectivorous primate species (Kay, 1975; Boyer, 2008). In this case, even though the dietary substrate differs, both dietary groups feed on ductile foods that may be best divided by a bladed dentition (Lucas, 2004). Additionally, even contrasting functional demands may result in similar morphologies. The locomotor patterns of human bipedalism and the frequent saltation of some prosimian primates are both associated with a reduced length of the forelimbs relative to the hind limbs, often expressed in the intermembral index (sum of humeral

length and radius length/sum of femoral length and tibial length). In this case, despite an association between proportions of the limbs and locomotor performance, a similar morphology is associated with two distinct locomotor strategies.

A final issue affecting associations between ecology and morphology may arise in situations in which morphology appears to create performance capacities that are infrequently exploited in an organism's resource use. The fit between the total range of ecological behavior that is available to an organism based on performance capacity and the range of behaviors performed (level D in Fig. 2.1) may be affected by the degree to which frequent behaviors are the driving factor in selection on morphology (Wainwright, 1994). For example, the capacity to deal with food items relied upon during periods of food scarcity ("fallback foods") may exert a strong influence on associated dental morphology (Lambert et al., 2004; Marshall and Wrangham, 2007; Constantino et al. 2009). This might particularly apply to primate dietary ecology; most primates include fruits in their diet when available, but may use other resources when fruit is scarce (Terborgh, 1986). Ripe fruit may require less processing to extract energy than other food sources, and therefore exert less selection on morphology than might be expected by its prevalence in the diet. Additionally, even within a seemingly consistent ecological group, such as a dietary description of "folivore," demands on morphology may not be homogeneous – mechanical properties of foods can vary within a category, for example (Yamashita, 1996). Such situations could create apparent differences between ecology and morphology even if evolution is highly canalized toward particular anatomical solutions to meet demands on performance, and morphological traits adequately capture functional/adaptive parameters.

## Aims

The aims of this study are to compare ecological and morphological disparity and diversification, and to evaluate the degree to which craniodental distances between species can be considered representative of ecological distances in primates.

# METHODS

This study uses craniodental measurements to capture morphological disparity, and the proportions of different foods in the diet combined with activity profile to represent ecological diversification in two clades of primates. Strepsirrhine and platyrrhine primates are monophyletic clades of primates that contrast in some aspects of their radiation. Platyrrhines diverged relatively recently (20–25 mya; Steiper and Seiffert, 2012) and occupy a single landmass (South America) while strepsirrhine primates have a deeper divergence (ca. 55 mya; Steiper and Seiffert, 2012) and are comprised of the lemuriforms of Madagascar and the lorisiforms of Asia and mainland Africa. Both radiations display variation in their diet and activity profile (Table 2.1). Like most primates, the majority of strepsirrhine species include some fruit in their diet, but the radiation also includes specialized folivores (*Avahi*, *Lepilemur*), dedicated gummivores (*Phaner*), and species with an almost entirely animal-based diet (*Loris*). The extant small-bodied strepsirrhine clades (*Lepilemur* species, cheirogaleids, galagids, and lorisids) are exclusively nocturnal. Nocturnal or cathemeral species are also found in the remaining clades (nocturnal *Avahi* among the indriids, cathemeral *Hapalemur* and *Eulemur* among the lemurids). Platyrrhine communities generally show more limited ecological variation (Fleagle and Reed, 1996) with fruit as a substantial component of the diet in most species, but the radiation still contains

committed gummivores (*Callithrix*, *Cebuella*) and highly folivorous taxa (*Brachyteles*, *Alouatta*), as well as some frugivores that are specialized toward seed predation (*Pithecia*, *Cacajao*, *Chiropotes*). Platyrrhines are predominantly diurnal, but also contain cathemeral and nocturnal species among the owl monkeys, *Aotus*.

**Ecological variables**

Ecological variables included diet and activity pattern (diurnal, cathemeral, nocturnal). Activity pattern was scored as 0 for diurnal species, 1 for nocturnal species, and 0.5 for cathemeral species; species identified as cathemeral include *Eulemur* sp. (Curtis and Rasmussen, 2002; Donati et al., 2009) and *Aotus azarae* (Fernandez-Duque and Erkert, 2006). *Hapalemur* species were also scored as cathemeral; this is true for *H. simus* and some subspecies of *H. griseus*, but not all (Wright, 1999; Curtis and Rasmussen, 2002). The decision to score *H. griseus* as cathemeral is based on the uncertainty to subspecies of the morphological sample, and the possibility that cathemerality/diurnality within the species is locality or population specific; it appears that the evolutionary potential is present to exploit cathemerality under certain environmental conditions. This categorization is consistent with that used by other researchers (e.g., Heesy and Ross, 2001).

Dietary data were collated from published studies of wild platyrrhines and strepsirrhines, many of which provide the proportion of the diet composed of different classes of food item (e.g., fruit, leaves, gums, animal prey). In primate studies, diet is quantified through a number of different methods, most commonly either representing feeding activity budget (time spent feeding on particular items) or the quantity of items consumed in each category; stomach content data is also sometimes provided (Charles-Dominique, 1977). These methods are not necessarily directly comparable (Chivers, 1998). For example, time spent feeding may overestimate the

contribution to the diet of items with high search times relative to ingestion (e.g., insectivory); energetic gain from such dietary items may be better represented by methods that use ingestion rates (Janson, 1985). However, restricting the dataset to only methodologically similar studies (e.g., proportion of items ingested) biases against the inclusion of nocturnal species and other species on which a limited number of field studies have been conducted. Therefore, for the present study, it is assumed that dietary proportions from different methods are broadly representative of differences between species, with the recognition that this may affect the degree of accuracy in the reconstruction of ecological similarity. This approach avoids a categorical treatment of diet (e.g., folivore, frugivore), but allows input from studies using disparate methods of quantification or description of ecological variation such as stomach contents (e.g., Charles-Dominique, 1977), %feeding time (e.g., Pollock, 1977), or more precise estimates of food intake that combine intake rate and energetic value (e.g., Janson, 1985). When possible, studies providing quantitative estimates of the diet were verified by comparison with more qualitative, but more widely available, descriptions of species' diet. Data used in the analyses presented are shown in Table 2.1, which also lists the species included. Verbal summaries of dietary components are available in Appendix 1, together with references for dietary data in Table 2.1. Dietary proportions were arcsine transformed prior to data analysis.

**Morphological variables**

Measurements were taken from the cranium, mandible, and mandibular second molar for the species of primates included (measurements illustrated in Fig. 2.2). Specimens included in the sample come from the American Museum of Natural History, New York; the Natural History Museum, London; the Field Museum, Chicago; the Smithsonian Museum of Natural History, Washington, D.C.; and the Museum of Comparative Zoology, Harvard University, Cambridge.

Total sample sizes were 267 individuals for the mandible and cranium, and 270 individuals for the molar measurements.

Cranial and mandibular measurements were taken with digital calipers to the nearest 0.1mm, with the exception of the height of the condyle above the tooth row, which was taken from a photograph of the mandible in lateral view using SigmaScan Pro 5. The measurement of condylar height was taken in reference to a line drawn through the crown base of the most mesial mandibular premolar and the second molar (marked by a horizontal dashed line in Fig. 2.2). Dental measurements from photographs taken with a Zeiss digital microscope were taken using AxioVision Release 4.8.2 and measurements from μCT generated surface models were taken using the surface projection tools in Geomagic, following methods described in Bunn et al. (2011). Cranial measurements were: 1) orbit height, 2) facial height, 3) zygomatic arch length, 4) biparietal breadth, 5) palatal width at the 1st molar, 6) zygomatic width across the skull, 7) skull length, and 8) width of the skull at postorbital constriction. These were chosen to represent the relative size of the brain case, orbit size, face size, and information on the space available for masticatory muscles. Mandibular measurements were 1) corpus breadth, 2) corpus height, 3) symphyseal height 4) symphyseal depth, 5) ramus height, 6) ramus breadth, 7) condyle height above tooth row, and 8) mandibular length. These were chosen to capture information relevant to resistance to bending/ shear resistance of the mandibular corpus and symphysis, insertion areas of masticatory muscles, and gape. Lower second molar measurements were 1) mesiodistal length, 2) trigonid width, 3) trigonid height 4) talonid height 5) square root of talonid area, 6) postmetacristid length, 7) length of buccal section of protocristid (from protoconid to notch/lowest point between protoconid and metaconid), and 8) cristid obliqua length. These measurements are designed to capture crest development, occlusal relief, and crushing area.

In this analysis, morphological shape is considered in isolation from interspecific variation in size, through conversion to ratios using geometric means local to the morphological region (cranium, mandible, or molar). Each measurement was divided by a geometric mean prior to the calculation of species averages. This approach does not remove any associations between size and shape, but allows species to be compared as if of equal size, and has been shown to perform well at identifying similar shapes (Jungers et al., 1995). Under this approach, somatic size is treated as a possible contributing factor to observed morphological disparity. Strepsirrhines typically show little or no sexual dimorphism in the cranium or mandible, whereas some species of platyrrhines are markedly dimorphic. For this reason, species averages for the cranial and mandibular measurements were calculated from a combined sex sample for strepsirrhine species, and from females only for platyrrhine species.

**Data analyses**

All data analyses were performed in the statistical computing environment "R" (R Development Core Team, 2011). The aims of the present analysis are to provide insights into the use of morphological distances as representative of adaptive diversity, by assessing the degree to which morphological distances and ecological distances lead to similar conclusions regarding the distribution of disparity amongst species. Statistical methods often utilized in ecomorphological studies to identify axes that maximize the association between two datasets, such as canonical correlation analyses, will not necessarily answer this question. Instead, morphological and ecological distance matrices will be created, and distance-based methods designed to investigate macroevolution will be applied to both. If morphological distances are representative of ecological distances, similar results are predicted.

Phylogenetic principal components analysis (pPCA, Revell 2009) in the "phytools" package (Revell, 2012) was performed on the correlation matrix to create orthogonal axes from which morphological and ecological distances were calculated (squared euclidean distances). Phylogenetic principal components analysis incorporates the phylogenetic covariance structure into the calculation of axes and factor loadings, and produces axes that are orthogonal (uncorrelated) when phylogenetic structure of the data is recognized in a measurement of correlation (Revell, 2009). Following the protocol of studies developing the methods applied here to investigate macroevolutionary questions (Losos and Miles, 2002; Harmon et al., 2003), pPC axes summing to explain either 85% or 95% of the variance in the sample were retained for the calculation of distances. Principal components were scaled to be equal in length to their eigenvalues prior to distance calculations.

The pPCA was performed on a combined taxonomic sample for the two clades, with the phylogenetic covariance matrix derived from the phylogeny shown in Figure 2.3. The phylogenetic tree was downloaded from the 10kTrees website (Arnold et al., 2010; version 3 dataset, consensus tree); branch lengths represent time since divergence. The dataset for this phylogenetic analysis is entirely molecular, with data from both mitochondria and autosomal DNA when available. Two species in the ecological and morphological datasets, *Pithecia monachus* and *Chiropotes albinasus*, are not currently available in the 10kTrees dataset. The divergence date for *Pithecia pithecia*/*Pithecia irrorata* was used as a proxy for *Pithecia pithecia*/*Pithecia monachus*. *Chiropotes albinasus* was added as an additional species at a polytomy in the consensus tree between *Chiropotes satanas*, *Cacajao melanocephalus*, and *Cacajao calvus*. The phylogenetic tree was subdivided into platyrrhine and strepsirrhine clades for the analysis of disparity through time described below.

***Correlations between morphological distances and ecological distances.*** In order to investigate whether morphological distances and ecological distances provide similar estimates of the degree of separation among species, Mantel matrix correlations were performed on ecological and morphological distances for platyrrhines and strepsirrhines. The calculation of morphological distances followed the procedure of Losos and Miles (2002), except for the use of the pPCA described above. To test whether morphological and/or ecological distances are correlated with phylogenetic distances, phylogenetic tree files were first converted to distance matrices, using the cophenetic values (summed branch lengths uniting the species, equal to twice the age of the node at which they diverge), prior to performing correlations using the same method. The partial Mantel test (Smouse et al., 1986), which can include phylogenetic distance as a third matrix, was also performed for comparison, even though this test has recently been shown to have poor experimental error rates (Harmon and Glor, 2010). In the absence of an appropriately rigorous phylogenetic control for tests of association between distance matrices, the Mantel test results presented here should not be over-interpreted, and are presented primarily for comparison with the other methods.

***Disparity through time.*** The analysis of disparity through time used the same distance matrices calculated for the comparisons of morphological and ecological distances, and followed the methods of Harmon et al. (2003), available in the R package "geiger" (Harmon et al., 2008). Because the species comprising the present sample exclude a large group of anthropoids (catarrhines), these analyses were performed separately for the platyrrhine and strepsirrhine clades, rather than the full sample. This method requires a phylogeny and a set of variables from which to calculate distance metrics. Using the phylogeny as a framework, disparity (measured as the average pairwise Euclidean distance) is calculated for the entire clade, and for every subclade

nested within it. For each subclade, disparity is divided by the average disparity for the whole clade to create a relative disparity index (RDI) for that subclade. The "disparity through time" curve is created by taking the phylogeny and, at each divergence event, calculating the average RDI for all subclades with ancestral lineages present at that time. For example, in the phylogeny of taxa in the present analysis shown in Figure 2.3, at 70 mya there are two subclades present (Haplorrhini and Strepsirrhini), at 60 mya there are three (Anthropoidea, Lemuriforms, Lorisiforms). Comparisons can then be made between the observed distribution of RDI values and an average of repeated simulations under a Brownian motion model of morphospace occupation. The difference between the observed and predicted disparity curves can be quantified through the morphological disparity index (MDI), the area between the two curves.

As only extant species are included, it is difficult to ascertain whether this method provides a true reflection of changes in disparity occurring in a lineage through time; however, Harmon et al.'s method does provide a visualization of phylogenetic structure in the distribution extant taxa in morphospace and the extent to which subclades disparity matches up to a simulation of evolution under a null model (Brownian motion). This approach may therefore have the potential to provide insights into contrasting evolutionary processes when comparing radiations. Comparisons between "disparity through time" curves in ecospace and morphospace will indicate the degree to which the distribution of morphological disparity among subclades matches the ecological disparity; Harmon et al. (2003) related morphological disparity to ecological disparity, but did not test the strength of association.

***Identification of diverse clades.*** Losos and Miles (2002) developed a method to identify clades with unusual levels of disparity, with a stated aim of developing a method to test the hypothesis that a clade has adaptively radiated. They identified unusually diverse clades through

the use of resampling procedures to create expected distributions of average diversity among groups of varying numbers of species. The average disparity of a clade is then compared to that which would be expected for a group of *n* species, and concluded to be unusual in the amount of disparity if it falls in the tails of the distribution from the resampling exercise. Losos and Miles use the upper and lower 2.5% of the distribution as evidence of unusually low or high morphological diversity within a clade, which is followed here.

Following the methods of Losos and Miles (2002), PC scores for the components comprising 85% of the variance in the whole sample were retained, and PC axes were scaled to be equal in length to their eigenvalues. To create a sample for the expected distribution of average intertaxon distances for *n* species, the dataset was adjusted to remove interfamilial differences by calculating the family mean score for each PC, and subtracting it from the PC score for each species within that family. This creates a distribution of points in which family means are centered on the origin for all components, but interspecific distances within families are preserved. A function was written in R to sample, with replacement, sets of *n* species and calculate the average distance between the species in that set. This was then replicated for 1000 iterations. This process is illustrated in Figure 2.4. The resampling function was run with *n* set equal to four, five, six, nine, and ten, to match the range of variation for numbers of species within families in this sample. Families were considered to have unusually high morphological diversity if the average intertaxon distance exceeds the 95$^{th}$ percentile for the bootstrap sample with the same number of species as in the family (e.g., Lorisidae was compared with the distribution for four species, Cebidae with the distributions for six species)**.**

In this analysis, families were chosen as the clades to be compared using this approach (Atelidae, n=6 species; Cebidae, n=6 (excluding Callitrichidae); Callitrichidae, n=10;

Pitheciidae, n=9; Cheirogaleidae, n=5; Indriidae, n=4; Lemuridae, n=6; Lorisidae, n=4; Galagidae, n=6). For platyrrhines, the taxonomy for grouping genera into families follows Rylands and Mittermeier (2009), with the exception that *Aotus* species are included in the Cebidae, rather than as a separate family. For strepsirrhines, the taxonomy for grouping genera into families follows Fleagle (1999). Species included in each family are listed in Tables 1 and 2. The current focus of investigation is on the effects that differences between ecological and morphological disparity may have on conclusions for macroevolutionary analyses. A detailed investigation of diversification within platyrrhines or strepsirrhines might require different species groupings. For example, some phylogenetic hypotheses (including the one employed for the pPCA) suggest that Callitrichidae are phylogenetically embedded within the Cebidae (*Aotus*, *Saimiri,* and *Cebus*), but they are analyzed separately because they have traditionally been recognized at a taxonomic rank similar to that of other species groups used here (e.g., Fleagle, 1999; Rylands and Mittermeier, 2009) and their phylogenetic position relative to other cebids is not certain; recent analyses have placed Callitrichidae as the sister taxon to *Aotus* (10kTrees Version 3 consensus tree, Figure 2.3), to *Saimiri*/*Cebus* (Wildman et al., 2009), and to a clade of *Aotus*, *Saimiri* and *Cebus* (Fabre et al., 2009). Similarly, *Phaner,* but not *Lepilemur,* was included in Cheirogaleidae, despite some evidence from mitochondrial sequences that these two genera possibly form a clade (e.g., Roos et al., 2004; Fabre et al., 2009). Molecular sequences for *Phaner* are very limited, with only seven nucleotide sequences stored on GenBank (information retrieved: June, 2012), of which only two exceed 1000 base pairs. The nodes defining the families used in this analysis ranged in estimated age between 34.6 mya (lorisids) and 14.8 (atelids), with an average age of 17.5 mya for the platyrrhine families, and 24.3 mya for the strepsirrhine families.

# RESULTS

## PCA results

Results from the pPCA analyses of morphological and ecological variables are provided in Tables 2.2 and 2.3, respectively, and plots of the first two principal component axes for each pPCA are shown in Figures 2.5 and 2.6. The morphological pPCA of 24 variables produced 10 PCAs that summarized 85% of the variance and 14 PCAs that summarized 95%. The 14 PCAs were used to calculate distances for comparisons of pairwise intertaxon distances and disparity through time, while only the first 10 PCs were used for the comparisons of disparity within clades, following the methods of Losos and Miles (2002). The ecological pPCA produced seven PCs to summarize just over 85% of the variance and eight PCs to summarize close to 95%. The ecological pPCA differed somewhat from the similar analysis of Fleagle and Reed (1996) in the degree to which closely related species cluster together in different groups. For example, in the present analysis the first two principal components separate cheirogaleid species to a greater degree, but show a similar amount of variation within the indriids . This may reflect the differences in the variables included (i.e., not including locomotor variables) and/or the narrower taxonomic focus of the sample, or may reflect the use of the pPCA in this study.

## Matrix correlations

Mantel matrix correlations between morphological and ecological data are presented in Figure 2.7; the correlation coefficients and probability estimates of these comparisons are presented in Table 2.4, with additional comparisons between phylogenetic distance and morphological or ecological variation, and the results of the partial Mantel tests. Significant associations between morphological and ecological distances were found in both the platyrrhine

and strepsirrhine clades. Both morphological distances and ecological distances were significantly correlated with phylogenetic distances in platyrrhines, but only the ecological distances were significantly correlated with phylogenetic distance in strepsirrhines. This suggests that, at least for the latter clade, the correlation between morphological and dietary distances is unlikely to be purely a result of phylogenetic structure in the two datasets. In the partial Mantel test, the association between strepsirrhine ecological and morphological distances is significant even after a correction for multiple comparisons, while in platyrrhines the partial Mantel produced a coefficient that is significant at the 0.05 level, but fails to reach significance under the Bonferroni-Holm correction (alpha =0.025 for this comparison). The scatter plots of ecological distances against morphological distances indicate that in both clades there are relatively few instances of larger morphological distances associated with low ecological distances (lower right portion of the plot). Most of the points away from the diagonal are concentrated in species showing higher ecological distances at lower morphological distances (upper left portion of the plot).

**Disparity through time**

The results of the disparity through time analyses are shown in Figure 2.8, with morphological curves on the left and ecological curves on the right. In platyrrhines the morphological curve follows that predicted by the simulations under a Brownian motion model until quite late in the clade's history (0.6–1.0 of the proportion of time since taxon origin). In this section of the plot, corresponding to approximately 9 mya to present the average relative disparity index (RDI) within the clade remains constant or increases slightly, rather than following the decline of the predicted slope. In the ecological dataset, the same is broadly true in the earlier part of the disparity curve, but with some deviation both above and below the

predicted curve and a slight peak and then decline in average RDI at 0.4. Between 0.6 – 1.0 of the time since clade origin, the ecological disparity curve is similar to that of the morphological curve in remaining steady or increasing, and showing a slight decline immediately before present.

In the strepsirrhine comparison, the morphological curve remains approximately parallel with the predicted curve from the simulations, but is consistently elevated above the line, indicating relative disparity within subclades greater than expected. Between 0.8 and 1.0 of the time since clade origin, the relative disparity declines sharply to fall below the predicted line. The curve from the ecological data is more markedly different from the morphological curve in strepsirrhines than in platyrrhines, specifically in being higher relative to the predicted line from 0.4 – 0.6 of the time since taxon origin, with a sharp decline in average RDI occurring at 0.6 of the time since taxon origin. This decline would occur at around 30-25 mya and by comparison with the phylogeny in Figure 2.3, may be associated with the separation of the indriid subclade from that of the cheirogaleids/*Lepilemur*, and subsequently the separation of *Lepilemur* and *Phaner* from the *Microcebus*/*Mirza*/*Cheirogaleus* clade. Between 0.6 and 1.0 of the proportion of time since clade origin, the ecological and morphological curves are similar in being elevated above the predicted curve until 0.8 on the x-axis and then declining sharply.

**Analysis of unusual levels of disparity**

In the analysis to identify unusual levels of disparity, each family was compared to a bootstrap distribution of intertaxon distances for a corresponding number of species. Under this comparison, only the family Lemuridae was identified as particularly diverse for morphological distances (left on Fig. 2.9), and only the family Cheirogaleidae was identified as particularly diverse for ecological distances. Therefore, the two analyses of intrafamilial disparity provide

contrasting conclusions about which families should be considered as possessing "unusual" disparity.

## DISCUSSION

The aims of this analysis were to evaluate whether morphological distances represent ecological distances in macroevolutionary analyses. Morphological measurements were chosen to capture functionally relevant information from the skull, mandible and molar. Ecological variables were taken from the literature, related to diet and activity pattern, traits that should be associated with measurements of the morphology responsible for ingestion and mastication, and possibly relative orbit size (at least at the lower end of the body size range – Heesy and Ross, 2001; Kirk, 2006). Comparisons of ecological and morphological distances between pairs of species will only provide some of the information necessary to evaluate the use of morphological distances. A significant correlation can potentially be associated with a lot of scatter in ecological and morphological distances, which could affect the degree to which the two distance matrices provide similar information about diversification within the clade.

Mantel tests of matrix correlation between the morphological and ecological distances calculated here were found to be significant. It is possible that, in part, this association is due to shared phylogenetic history, given that ecological distances were also significantly correlated with phylogenetic distances in both clades tested (platyrrhines and strepsirrhines). However, the lack of a significant association between phylogenetic distance and morphological distance in strepsirrhines indicates that, in this clade at least, morphological and ecological association may be somewhat independent. In the partial Mantel test, with phylogenetic distance included as a

third distance matrix, the association of ecological and morphological distances was, indeed, significant in strepsirrhines. In platyrrhines, this comparison narrowly missed significance under the Bonferroni-Holm correction for multiple comparisons. It is difficult to interpret this difference, given the potential problems associated with the partial Mantel (Harmon and Glor, 2010) and arguments made by some researchers rejecting the use of sequential Bonferroni adjustment as overly conservative (e.g., Moran, 2003). The difference is probably not sufficient to argue that the two clades show different patterns, given that the non-significant analysis in platyrrhines is close to criterion for significance (0.047 relative to 0.025 for this comparison in the Bonferroni adjustment). Thus, the platyrrhine analysis might better be considered as weaker than in strepsirrhines, but showing a similar trend of correlation between ecological and morphological distances, when phylogenetic structure is incorporated using this method.

One interesting aspect of the association between morphological and ecological distances is the pattern of points off the diagonal in Figure 2.7. Relatively few instances of species with high morphological distances but low ecological distances appear in the plots in either platyrrhine or strepsirrhine clades in comparison to the reverse situation. This may provide some indication that, in the primate radiations examined here, there are relatively few instances of contrasting morphological configurations associated with similar ecological strategies, as might have been predicted under a "many-to-one" mapping hypothesis (Wainwright et al., 2005). Several explanations are possible for instances in which similar morphology is associated with differing ecological profiles. Firstly, these species may be more closely related to each other, and share similar morphological features despite ecological differences. Secondly, and not exclusive with the prior explanation, the morphological traits used here may not adequately capture the ecological variation in these species. Species may share ecological strategies in times of low

resource availability resulting in morphological traits that do not match up with a more general ecological profile (e.g., Constantino et al., 2009). Lastly, it also seems likely that some dietary items require fewer specializations in morphological systems than others, or have requirements for morphological specialization that are limited to particular regions of the anatomy; for example, gummivory is associated with changes in mandibular shape (Vinyard et al., 2003) but has limited apparent influence on molar morphology (Nash, 1986).

The disparity through time analyses also indicated some degree of correspondence between the calculated morphological and ecological distances. Here, there can be more confidence that the similarities in the results are not an artifact of phylogenetic structure, because in this analysis the predicted disparity curve is constructed from simulations along the phylogeny under an evolutionary model of Brownian motion (i.e., strong phylogenetic signal). Similarity in the way in which the observed curve corresponds to the predicted curve can therefore not be explained by phylogenetic signal. If comparisons are made between the two clades, the disparity curves based on ecology and morphology paint a similar picture of differences between the two clades – in platyrrhines, morphology and ecology both indicate approximate correspondence (closer in morphology than ecology) with the predicted curve. This may indicate that in the early portion of the radiation expansion of both ecospace and morphospace approximately followed a Brownian motion model of evolution, at least in regards to the lineages that survived to present day. In the last 40% of the clades history, both analyses indicate that within-subclade disparity was greater than expected, and average disparity within subclades remained relatively constant until the present day. Higher disparity than expected indicates greater overlap in ecospace/morphospace between clades than would be expected to occur through the Brownian motion model (Harmon et al., 2003). If the manner in which disparity is partitioned among extant

species accurately represents the process of platyrrhine diversification, it might be hypothesized that, during early platyrrhine evolution, species radiated into available morphospace/ecospace through a relatively random Brownian motion-like process, while more recent evolutionary processes have maintained dietary disparity within subclades above that expected by chance.

In contrast, in strepsirrhines the disparity curves are elevated above the predicted curve for the majority of the time period, only falling below predicted levels in the most recent portion of the time since clade origin. While this aspect of the observed curve was shared by the morphological and ecological datasets, the two are less similar to each other in the strepsirrhine dataset than in platyrrhine disparity through time analysis. Specifically, in the ecological disparity curve, within subclade disparity was particularly high in the 0.4 – 0.6 (time since clade origin) region of the plot, and a similar increase in relative within subclade disparity was not observed from the morphological data. In comparison to the phylogeny, this period corresponds to the base of the lemuriform radiation (strepsirrhine divergence occurs at approximately 65 million years so each tenth of the time since origin corresponds to ca. 6.5 million years, and the period 0.4 – 0.6 corresponds to 39–26 mya). Within-subclade ecological disparity levels decline when the clades corresponding to the extant lemurid families of cheirogaleids, indriids and lemurids are established. A rapid shift decline in subclade ecological disparity associated with the base of a clade might be expected to be associated with an adaptive radiation, given that it suggests rapid establishment of ecological partitioning, followed by reduced ecological disparity within each subclade.

The analysis that assessed whether primate families showed unusual levels of disparity in the variables included here were less consistent between ecological disparity and morphological disparity than the previous analyses (Fig. 2.8). For example, Lemuridae show a high degree of

craniodental disparity, but were not found to be ecologically variable to the same degree, though still in the upper portion of the bootstrap samples. In contrast, cheirogaleids were identified as unusually diverse ecologically, but not morphologically. This may reflect the fact that ecological specializations in this group are not strongly related to obvious craniodental specializations. For example, *Microcebus* consumed a high proportion of sugary insect secretions (honeydew), *Phaner* is a specialized exudativore, and *Cheirogaleus* is a specialized frugivore. Nectar and exudates require little postcanine processing to increase digestibility, and might not be as easy to distinguish in masticatory morphology as other food items. Some associations between mandibular morphology and gummivory exist related to intake of food, such as low condylar height (Vinyard et al., 2003), but these may not have made a sufficient contribution to morphological disparity to be detected.

It is possible that some of these analyses would produce different results with alternative morphological or ecological variables, or with more comparable dietary data for all species. For example, gummivory may be better represented morphologically by dental measurements that include information from anterior teeth (Burrows and Nash, 2010) and the use of stomach content data, for example, likely limits the degree to which some feeding behaviors can be represented, such as nectivory. Additionally, studies of primate feeding ecology are increasingly assessing mechanical properties of food items (e.g., Lucas and Pereira, 1993; Strait and Vincent, 1998; Elgart-Berry, 2004; Vogel et al. 2008; Wieczkowski, 2009). Such data should be more directly related to selection on performance, and therefore may show a closer association between morphology and ecology than was found here. The application of such variables to analyses across a wide range of taxa is prevented both by the unavailability of such data for most

primate species, and by the choice of different metrics for quantification of mechanical properties between different studies.

## CONCLUSIONS

In conclusion, these results suggest that, while morphological distances capture some of the variation in ecological data necessary to be considered as proxies for adaptive diversity, results are not always interchangeable with those derived from more direct ecological variables. Analyses of disparity through time using morphological variables were similar but not identical. Conclusions about how the two primate radiations included here (platyrrhines and strepsirrhines) differ from each other were fairly comparable between ecological and morphological data, but ecological data appeared to capture aspects of diversification that were not observable from the analyses of morphological disparity. Conclusions about which clades show unusual levels of disparity were not consistent between ecological and morphological data, at least with the present samples and sample sizes. It is possible that conclusions may alter in the future as more data become available, including additional methods of quantifying functional demands of the diet, and increased comparability of feeding data from different species.

One potential avenue of future research concerns the wider application of macroevolutionary methods based upon the analysis of extant species. These methods have primarily been developed to analyze morphological systems (e.g., Losos and Miles, 2002; Harmon et al., 2003; Cooper and Purvis, 2009) but as long as data can be expressed quantitatively, this need not be the case. The application of such methods to non-morphological aspects of the phenotype, such as the ecological variables used here, is somewhat novel to the

present study. This component of the dataset could be usefully expanded in future work to assess evolutionary patterns and disparity through time in other aspects of primate biology. For example, it is possible that some variables that have previously been collated for comparative analyses such as that of Di Fiore and Rendall (1994) could also be analyzed in a macroevolutionary framework to provide additional insights into primate diversification.

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*Table 2.1. Ecological variables used in the analysis. When more than one source is available for a species diet, proportions were calculated as averages of the values from these sources. Full references are provided in Appendix 1. Activity pattern D=diurnal, C=cathemeral, N=nocturnal*

| Taxon | fruit | leaves/ buds | flowers | faunivory | nectar/ honeydew | seeds | exudates | fungi | bamboo | activity pattern | References |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Indri indri* | 21.06 | 70.43 | 4.58 | 0.00 | 0.00 | 2.70 | 0.00 | 0.00 | 0.00 | D | Britt et al., 2002; Pollock, 1977; Powzyk and Mowry, 2003 |
| *Avahi laniger* | 0.00 | 93.20 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | N | Harcourt, 1991; Faulkner and Lehman, 2006; Thalmann, 2001 |
| *Propithecus diadema* | 20.22 | 43.30 | 9.02 | 0.00 | 0.00 | 25.84 | 0.00 | 0.00 | 0.00 | D | Hemingway, 1995, 1998; Irwin, 2006; Meyers and Wright, 1993; Powzyk, 1997; Powzyk and Mowry, 2003 |
| *Propithecus verreauxi* | 26.90 | 57.25 | 12.20 | 0.00 | 0.00 | 4.70 | 0.00 | 0.00 | 0.00 | D | Norscia et al., 2006; Simmen et al., 2003 |
| *Eulemur fulvus* | 70.59 | 22.07 | 6.16 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | C | Nègre et al., 2006; Rasmussen, 1999 |
| *Eulemur rufus* | 57.56 | 38.25 | 2.58 | 0.60 | 0.00 | 0.30 | 0.00 | 0.00 | 0.00 | C | Donati et al., 1999; Overdorff, 1993; Simmen et al., 2003; Sussman, 1972, 1977 |
| *Hapalemur griseus* | 13.00 | 12.00 | 3.30 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 71.67 | C | Grassi, 2006; Tan, 1999 |
| *Hapalemur simus* | 0.50 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 98.00 | C | Tan, 1999 |
| *Lemur catta* | 53.08 | 36.00 | 6.24 | 2.15 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | D | Goodman et al., 2006; Simmen et al., 2003; Soma, 2006; Sussman, 1972, 1977 |
| *Varecia variegata* | 80.00 | 15.97 | 0.00 | 0.00 | 4.65 | 0.00 | 0.00 | 1.00 | 0.00 | D | Britt, 2000; Morland, 1991; Ratsimbazafy, 2006 |
| *Lepilemur mustelinus* | 0.00 | 90.00 | 10.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | N | Nash, 1998 |
| *Cheirogaleus major* | 86.00 | 3.00 | 0.00 | 0.00 | 11.00 | 0.00 | 0.00 | 0.00 | 0.00 | N | Wright and Martin, 1985 |
| *Cheirogaleus medius* | 74.50 | 0.00 | 2.10 | 19.70 | 3.60 | 0.00 | 0.00 | 0.00 | 0.00 | N | Fietz and Ganzhorn, 1999 |
| *Microcebus griseorufus** | 12.50 | 0.00 | 0.00 | 7.85 | 56.35 | 0.00 | 13.15 | 0.00 | 0.00 | N | Dammhahn and Kappeler, 2008; Radespiel et al., 2006 |
| *Phaner furcifer* | 0.37 | 0.00 | 1.40 | 0.22 | 8.20 | 0.00 | 85.80 | 0.00 | 0.00 | N | Schulke, 2003 |
| *Arctocebus calabarensis* | 13.04 | 0.00 | 0.00 | 86.96 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | N | Charles-Dominique, 1977 |
| *Loris tardigradus* | 0.00 | 0.00 | 0.00 | 96.00 | 2.80 | 0.00 | 0.00 | 0.00 | 0.00 | N | Nekaris and Rasmussen, 2003 |

*Dietary data are for the closely related species, *M. murinus*.

| Taxon | fruit | leaves/ buds | flowers | faunivory | nectar/ honeydew | seeds | exudates | fungi | bamboo | activity pattern | References |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Nycticebus coucang* | 22.50 | 0.00 | 0.00 | 2.50 | 31.70 | 0.00 | 43.30 | 0.00 | 0.00 | N | Wiens, 2002 |
| *Perodicticus potto* | 66.88 | 0.00 | 0.00 | 10.83 | 0.00 | 0.00 | 22.29 | 0.00 | 0.00 | N | Charles-Dominique, 1977 |
| *Euoticus elegantulus* | 4.01 | 0.00 | 0.00 | 18.94 | 0.00 | 0.00 | 77.05 | 0.00 | 0.00 | N | Charles-Dominique, 1977 |
| *Galago alleni* | 80.56 | 0.00 | 0.00 | 19.44 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | N | Charles-Dominique, 1977 |
| *Galago demidoff* | 18.63 | 0.00 | 0.00 | 72.05 | 0.00 | 0.00 | 9.32 | 0.00 | 0.00 | N | Charles-Dominique, 1977 |
| *Otolemur crassicaudatus* | 21.00 | 0.00 | 0.00 | 5.00 | 8.00 | 4.00 | 62.00 | 0.00 | 0.00 | N | Charles-Dominique and Bearder, 1979 |
| *Alouatta palliata* | 33.23 | 54.98 | 11.14 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | D | Estrada et al., 1999; Glander, 1978; Smith, 1977; Milton, 1980 |
| *Alouatta seniculus* | 43.70 | 43.28 | 6.37 | 1.50 | 0.00 | 7.65 | 0.00 | 0.00 | 0.00 | D | Gaulin and Gaulin, 1982; Julliot and Sabatier, 1993; Mittermeier and van Roosmalen, 1981; Palacios and Rodriguez, 2001 |
| *Ateles belzebuth* | 84.25 | 8.00 | 0.80 | 1.00 | 1.90 | 0.00 | 0.00 | 0.10 | 0.00 | D | Dew, 2005; Klein and Klein, 1977; Nunes, 1998; Suarez, 2006 |
| *Ateles geoffroyi* | 67.00 | 21.00 | 7.10 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | D | Gonzalez-Zamora et al., 2009 (collated wild feeding data from multiple studies) |
| *Brachyteles arachnoides* | 46.28 | 43.23 | 7.25 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | D | Carvalho et al., 2004; Milton, 1984; Strier, 1991; Talebi et al., 2005 |
| *Lagothrix lagotricha* | 72.62 | 12.41 | 3.87 | 10.80 | 0.00 | 4.30 | 6.20 | 0.00 | 0.00 | D | Defler and Defler, 1996; Dew, 2005; Di Fiore, 2004; Peres, 1994; Stevenson et al., 1994 |
| *Cacajao calvus* | 18.40 | 0.00 | 0.00 | 5.20 | 6.20 | 66.90 | 0.00 | 0.00 | 0.00 | D | Ayres, 1989 |
| *Cacajao melanocephalus* | 16.91 | 4.00 | 5.00 | 0.00 | 0.00 | 72.09 | 0.00 | 0.00 | 0.00 | D | Boubli, 1999 |
| *Chiropotes albinasus* | 53.90 | 0.00 | 3.00 | 0.00 | 0.00 | 35.90 | 0.00 | 0.00 | 0.00 | D | Ayres, 1989 |
| *Chiropotes satanas* | 31.00 | 1.04 | 4.48 | 2.20 | 0.00 | 58.75 | 0.00 | 0.00 | 0.00 | D | Ayres, 1981; Kinzey and Norconk, 1993; Mittermeier and van Roosmalen, 1981; van Roosmalen et al., 1988 |
| *Pithecia monachus* | 53.00 | 16.00 | 13.00 | 0.00 | 0.00 | 18.00 | 0.00 | 0.00 | 0.00 | D | Happel, 1982 |
| *Pithecia pithecia* | 43.90 | 3.55 | 4.45 | 2.30 | 0.00 | 46.95 | 0.00 | 0.00 | 0.00 | D | Kinzey and Norconk, 1993; Mittermeier and van Roosmalen, 1981 |
| *Callicebus moloch* | 46.00 | 31.00 | 0.00 | 20.00 | 2.00 | 0.00 | 0.00 | 0.00 | 0.00 | D | Wright, 1985 |

| Taxon | fruit | leaves/ buds | flowers | faunivory | nectar/ honeydew | seeds | exudates | fungi | bamboo | activity pattern | References |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Callicebus torquatus* | 63.20 | 9.70 | 3.90 | 8.70 | 0.00 | 26.90 | 0.00 | 0.00 | 0.00 | D | Kinzey, 1977; Palacios et al., 1997 |
| *Aotus azarae* | 45.00 | 41.00 | 0.00 | 0.00 | 14.00 | 0.00 | 0.00 | 0.00 | 0.00 | C | Arditi et al., 1992 cited in Fernandez-Duque, 2007 |
| *Aotus nigriceps* | 60.00 | 7.50 | 0.00 | 17.50 | 14.00 | 0.00 | 0.00 | 0.00 | 0.00 | N | Wright, 1985 (values for leaves and insects are midpoints of the estimated dietary contribution) |
| *Cebus apella* | 44.13 | 8.20 | 4.39 | 38.87 | 9.40 | 9.80 | 0.00 | 0.00 | 0.00 | D | Brown and Zunino, 1990; Galetti and Pedroni, 1994; Janson, 1985; Scarry, unpublished data |
| *Cebus capucinus* | 69.27 | 0.48 | 0.20 | 26.59 | 0.00 | 10.57 | 0.00 | 0.00 | 0.00 | D | Chapman, 1987; Chapman and Fedigan, 1990; Mackinnon, 2005 (only adult data used) |
| *Saimiri sciureus* | 41.60 | 0.00 | 10.40 | 53.20 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | D | Lima and Ferrari, 2002; Stone, 2007 |
| *Cebuella pygmaea* | 0.00 | 0.00 | 0.00 | 33.00 | 0.00 | 0.00 | 67.00 | 0.00 | 0.00 | D | Ramirez et al., 1977 |
| *Callimico goeldii* | 26.00 | 0.00 | 0.00 | 43.50 | 0.00 | 0.00 | 3.00 | 24.00 | 0.00 | D | Porter, 2001, 2007; Rehg, 2003 |
| *Callithrix penicillata* | 0.00 | 0.00 | 0.00 | 28.98 | 0.00 | 0.00 | 71.02 | 0.00 | 0.00 | D | Alonso and Langguth, 1989; Fonseca and Lacher, 1984 |
| *Leontopithecus rosalia* | 66.35 | 0.00 | 0.30 | 15.35 | 17.20 | 0.00 | 1.40 | 0.00 | 0.00 | D | Dietz et al., 2007; Kierrulf et al., 2002 |
| *Mico argentata* | 36.00 | 0.00 | 0.00 | 5.00 | 0.00 | 0.00 | 59.00 | 0.00 | 0.00 | D | Veracini, 1997, cited in Correa et al., 2000 |
| *Saguinus fuscicollis* | 47.47 | 0.00 | 0.00 | 31.40 | 4.52 | 0.00 | 15.65 | 0.00 | 0.00 | D | Garber 1988, 1993; Knogge and Heymann, 2003; Lopes and Ferrari, 1994; Porter, 2001, 2007; Rehg, 2003 |
| *Saguinus geoffroyi* | 38.40 | 0.00 | 0.00 | 39.40 | 0.00 | 0.00 | 14.40 | 0.00 | 0.00 | D | Garber, 1980, 1984 |
| *Saguinus midas* | 68.15 | 0.00 | 0.00 | 6.95 | 22.30 | 0.00 | 13.45 | 0.00 | 0.00 | D | Oliveira and Ferrari, 2000; Veracini, 2000 |
| *Saguinus mystax* | 54.17 | 0.00 | 0.00 | 30.30 | 6.80 | 0.00 | 10.93 | 0.00 | 0.00 | D | Garber, 1988, 1993; Knogge and Heymann, 2003 |

*Table 2.2. Summary of pPCA results from morphological variables*

| PC | Eigenvalue | Cumulative variance | Factor loadings* |
|---|---|---|---|
| PC1 | 4.875 | 20.31% | Ramus height (-0.82), Facial height (-0.73), Biparietal breadth (0.72), Zygomatic arch length (-0.72), Mandibular length (0.69), Width of skull at postorbital constriction (0.65), Skull length (0.52), Trigonid height (-0.52) |
| PC2 | 3.824 | 36.24% | Trigonid width (0.74), Mandibular length (-0.61), Corpus breadth (0.59), Corpus height (0.59), Skull length (-0.56), Ramus breadth (-0.54), Talonid area (0.53) |
| PC3 | 3.112 | 49.21% | Orbital height (0.64), Postmetacristid length (0.54), Ramus breadth (-0.52), Width of skull at postorbital constriction (0.50) |
| PC4 | 2.221 | 58.46% | Symphyseal depth (0.72), Corpus height (-0.53), Condyle height above tooth row (-0.53) |
| PC5 | 1.617 | 65.20% | Cristid obliqua length (-0.60), Protocristid length (-0.56), Molar mesiodistal length (-0.47), Metacristid length (-0.37) |
| PC6 | 1.520 | 71.54% | Symphyseal height (-0.61), Cristid obliqua length (-0.47), Palatal width (0.43) |
| PC7 | 1.144 | 76.30% | Protocristid length(-0.51), Bizygomatic breadth (0.42), Condyle height above tooth row (0.39) |
| PC8 | 1.012 | 80.52% | Palatal width (0.56), Symphyseal height (0.50), Facial height (-0.29) |
| PC9 | 0.814 | 83.91% | Orbital height (0.36), Protocristid length (-0.33), Symphyseal height (0.30) |
| PC10 | 0.759 | 87.07% | Trigonid height (-0.45), Talonid height (0.39), Bizygomatic breadth (0.31) |
| PC11 | 0.601 | 89.58% | Corpus height (0.39), Metacristid length (0.34), Condyle height above tooth row (-0.24) |
| PC12 | 0.529 | 91.78% | Molar mesiodistal length (0.30), Skull length (-0.27), Width of skull at postorbital constriction (0.26) |
| PC13 | 0.428 | 93.56% | Cristid obliqua length (-0.29), Orbital height (0.25), Symphyseal depth (0.23) |
| PC14 | 0.342 | 94.99% | Symphyseal depth (-0.26), Ramus breadth (0.23), Orbital height (0.20) |

*Variables listed are those with a factor loading >|0.5| or the three greatest factor loadings.

*Table 2.3. Summary of pPCA results from ecological variables (diet and activity pattern)*

| PC | Eigenvalue | Cumulative variance | Factor loadings* |
|---|---|---|---|
| PC1 | 1.802 | 18.02% | Leaves/buds (0.83), Flowers (0.69), Activity pattern (-0.53) |
| PC2 | 1.611 | 34.13% | Fruit (0.73), Exudates (-0.63), Seeds (-0.46) |
| PC3 | 1.458 | 48.71% | Faunivory (0.70), Fungi (0.48), Fruit (-0.48) |
| PC4 | 1.085 | 59.56% | Activity pattern (-0.53), Exudates (-0.48), Faunivory (-0.38) |
| PC5 | 1.030 | 69.86% | Bamboo (-0.63), Seeds (0.63), Nectar/honeydew (0.30) |
| PC6 | 0.911 | 78.97% | Fungi (-0.62), Seeds (0.45), Nectar/honeydew (-0.41) |
| PC7 | 0.824 | 87.21% | Exudates (-0.49), Fungi (-0.42), Nectar/honeydew (0.37) |
| PC8 | 0.642 | 93.64% | Flowers (0.59), Leaves/ buds (-0.42), Nectar/honeydew (0.26) |

*Variables listed are all variables with a factor loading >|0.5|, or the three greatest factor loadings.

*Table 2.4. Results of Mantel matrix correlations (10,000 replicates). Results in bold text remain significant under a Bonferroni-Holm control for multiple comparisons (alpha=0.05).*

| **Comparison** | **Correlation coefficient** | **Probability** |
|---|---|---|
| Platyrrhine: diet+activity / morphology | **0.3089** | **0.0132** |
| Strepsirrhine: diet+activity / morphology | **0.2948** | **0.0012** |
| Platyrrhine: morphology / phylogeny | **0.4208** | **<0.0001** |
| Strepsirrhine: morphology / phylogeny | -0.0090 | 0.5140 |
| Platyrrhine: diet+activity / phylogeny | **0.2352** | **<0.0001** |
| Strepsirrhine: diet+activity / phylogeny | **0.2459** | **0.0046** |
| Platyrrhine: diet+activity/morphology/phylogeny | 0.2381 | 0.0470 |
| **Strepsirrhine: diet+activity/morphology/phylogeny** | **0.2917** | **0.0011** |

**Fig. 2.1.** General framework for ecomorphological relationships, redrawn from Reilly and Wainwright (1994). Letters represent levels at which potential factors may lead to a disruption of a close association between morphological and ecological variation, discussed in the text.

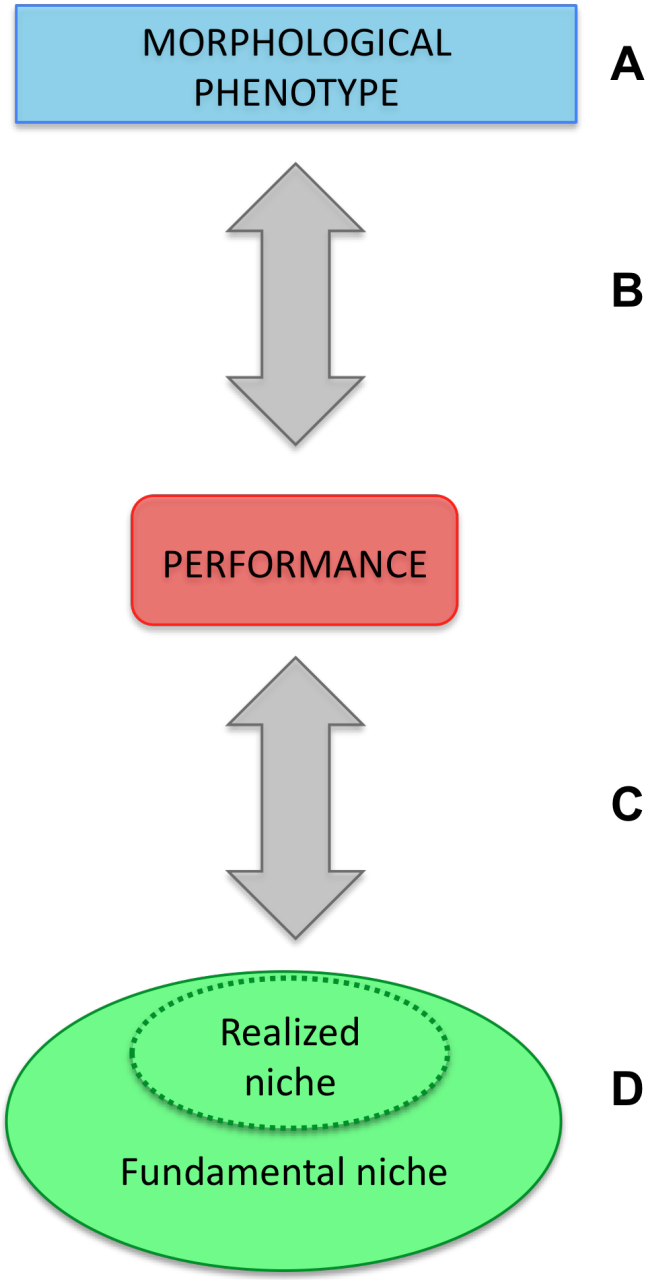


**Fig. 2.2.** Measurements used in the morphological data set illustrated on the cranium (above, left to right: anterior, superior and inferior views), mandible (middle, left to right: superior and lateral views) and mandibular right lower molar (below, left to right: occlusal, oblique distobuccal, and lingual views).

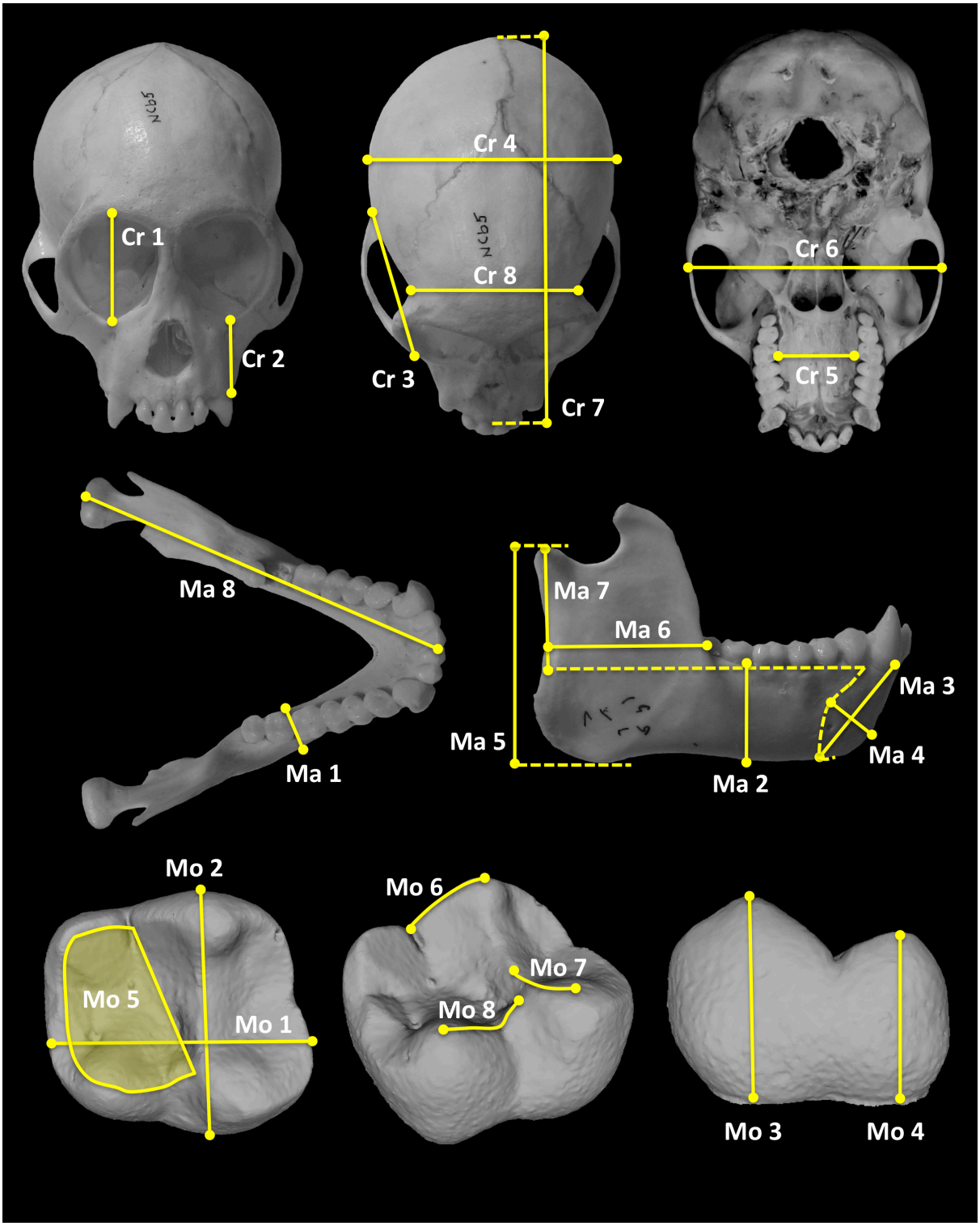


**Fig. 2.3.** Phylogenetic relationships of taxa in this sample. The x-axis represents time before present in millions of years.

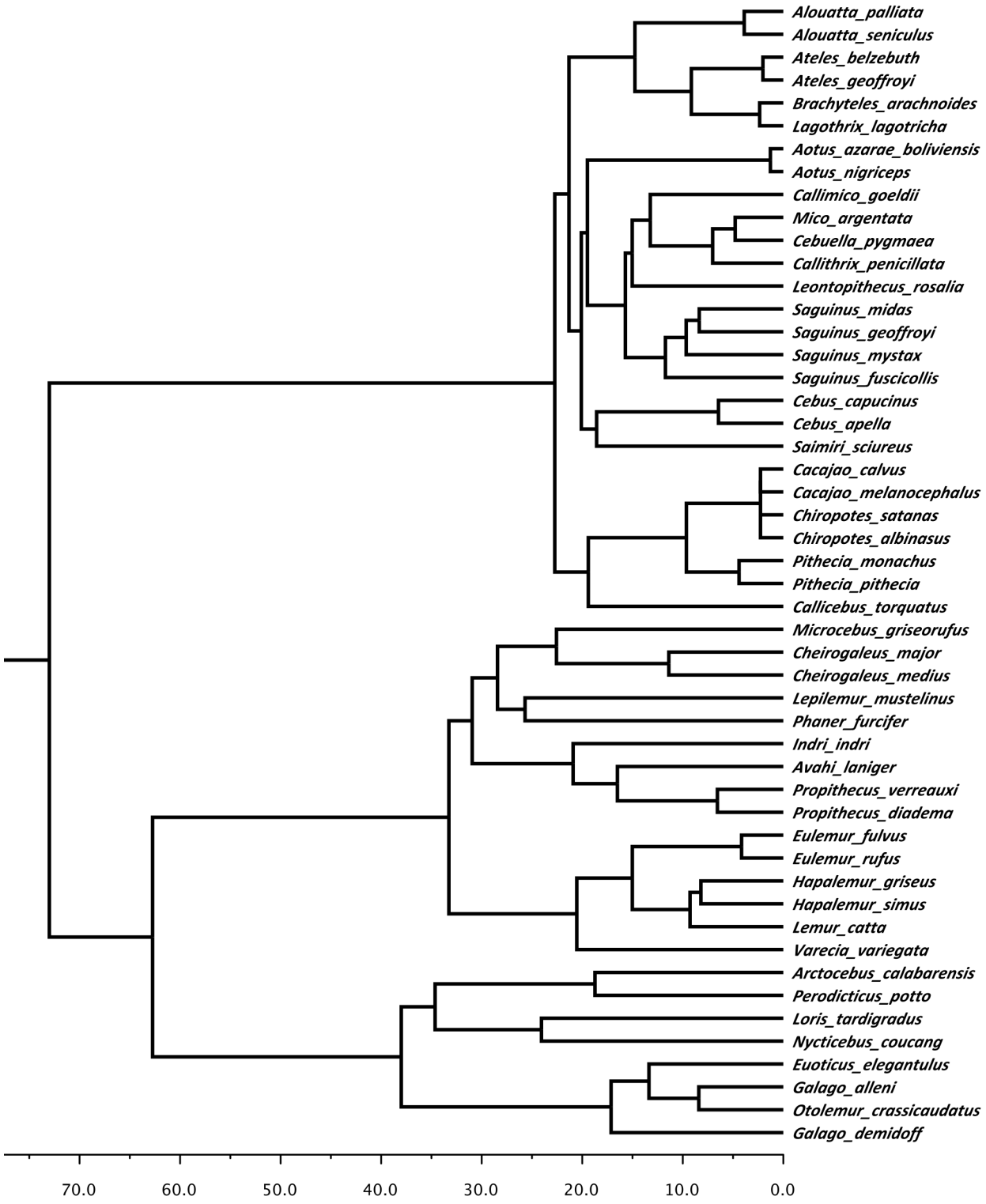


**Fig. 2.4.** Illustration of the method used by Losos and Miles (2002) to create a distribution of values against which disparity within a clade (in this case, family) can be compared. The centroids (black dots) for each family are centered on the origin for each PC to create a distribution in which family means are equal (0 for all components), but the distances among species within a family are preserved. Repeated random samples of a set number of species allow a distribution of mean distances to be created.

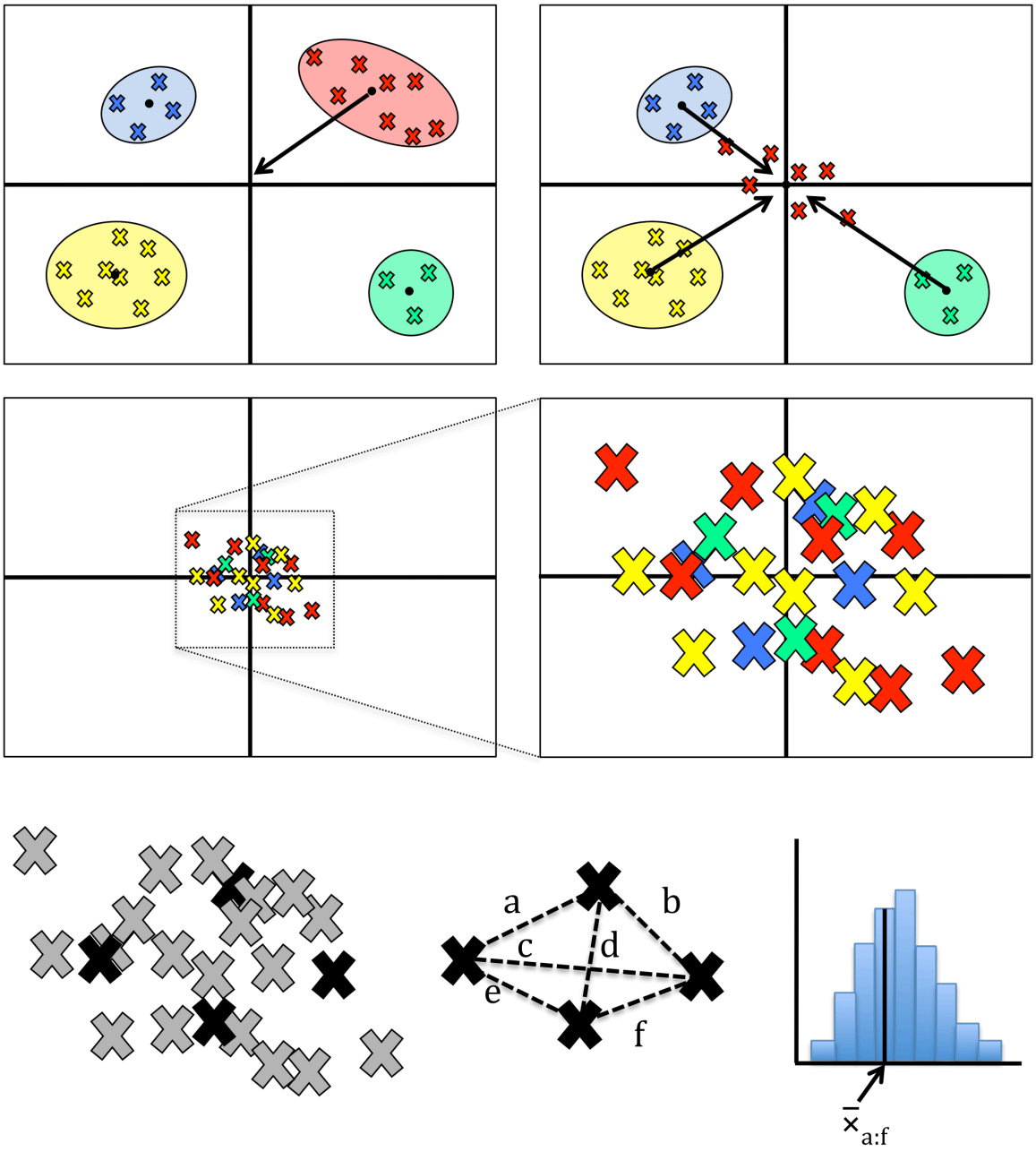
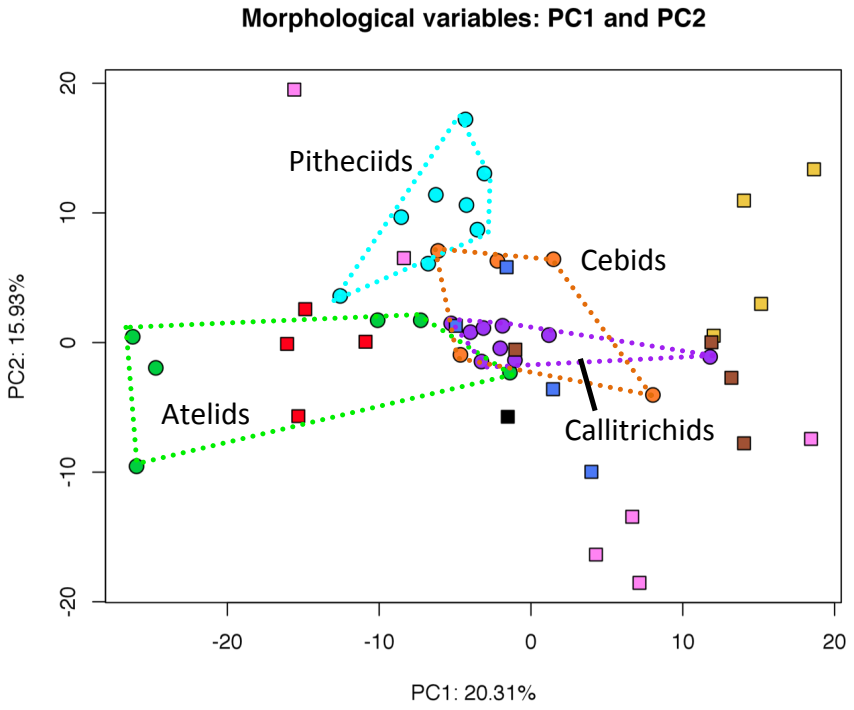


**Fig. 2.5.** First two principal components derived from the pPCA of morphological variables. The above plot shows the variation among platyrrhine families, while the lower plot shows strepsirrhines.



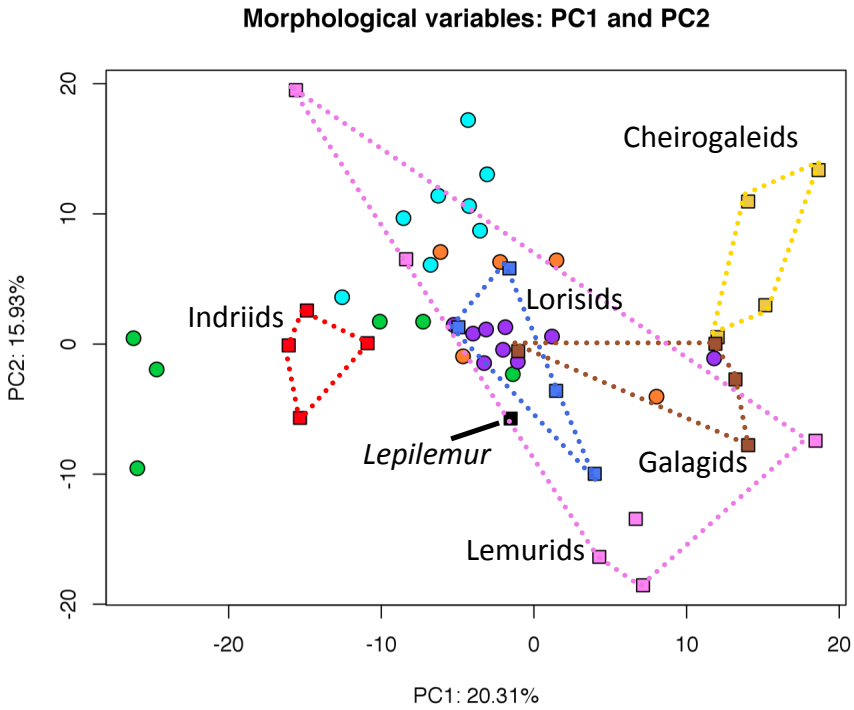
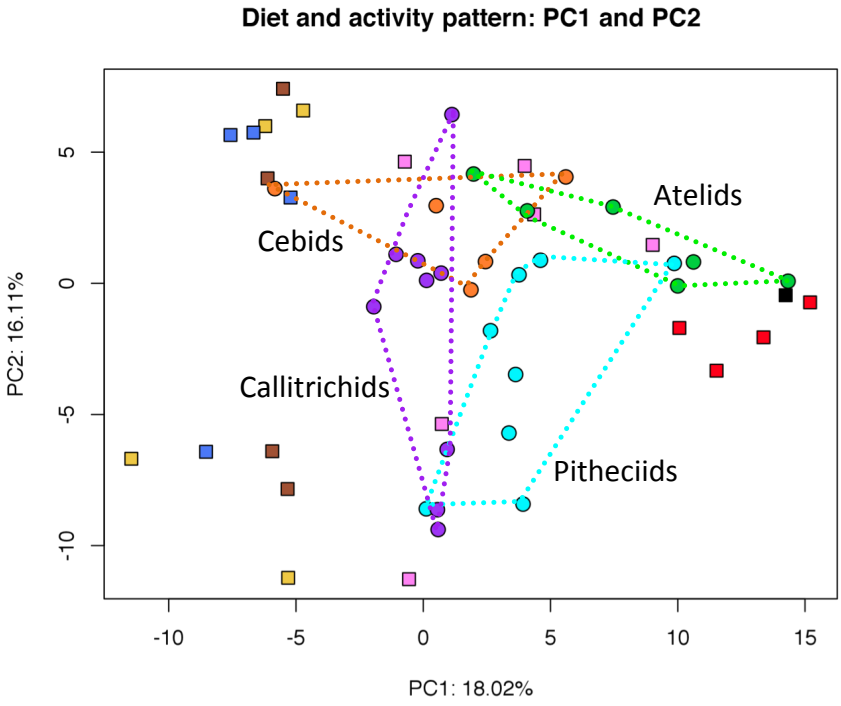



**Fig. 2.6.** First two principal components derived from the pPCA of ecological variables. The above plot shows the variation among platyrrhine families, while the lower plot shows strepsirrhines.



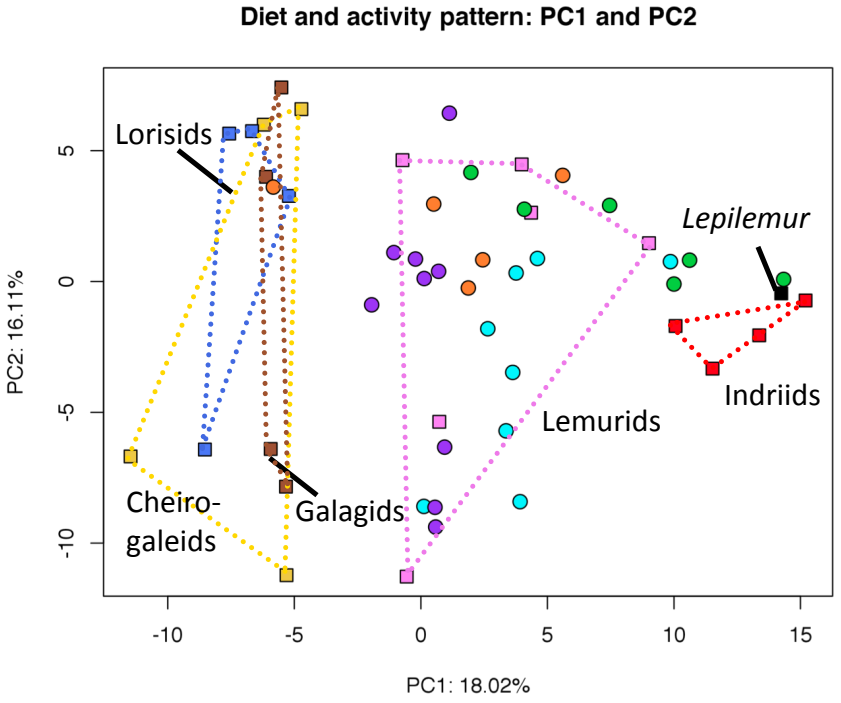



**Fig. 2.7.** Mantel matrix correlations of morphological and ecological distances in platyrrhines (above) and strepsirrhines (below).

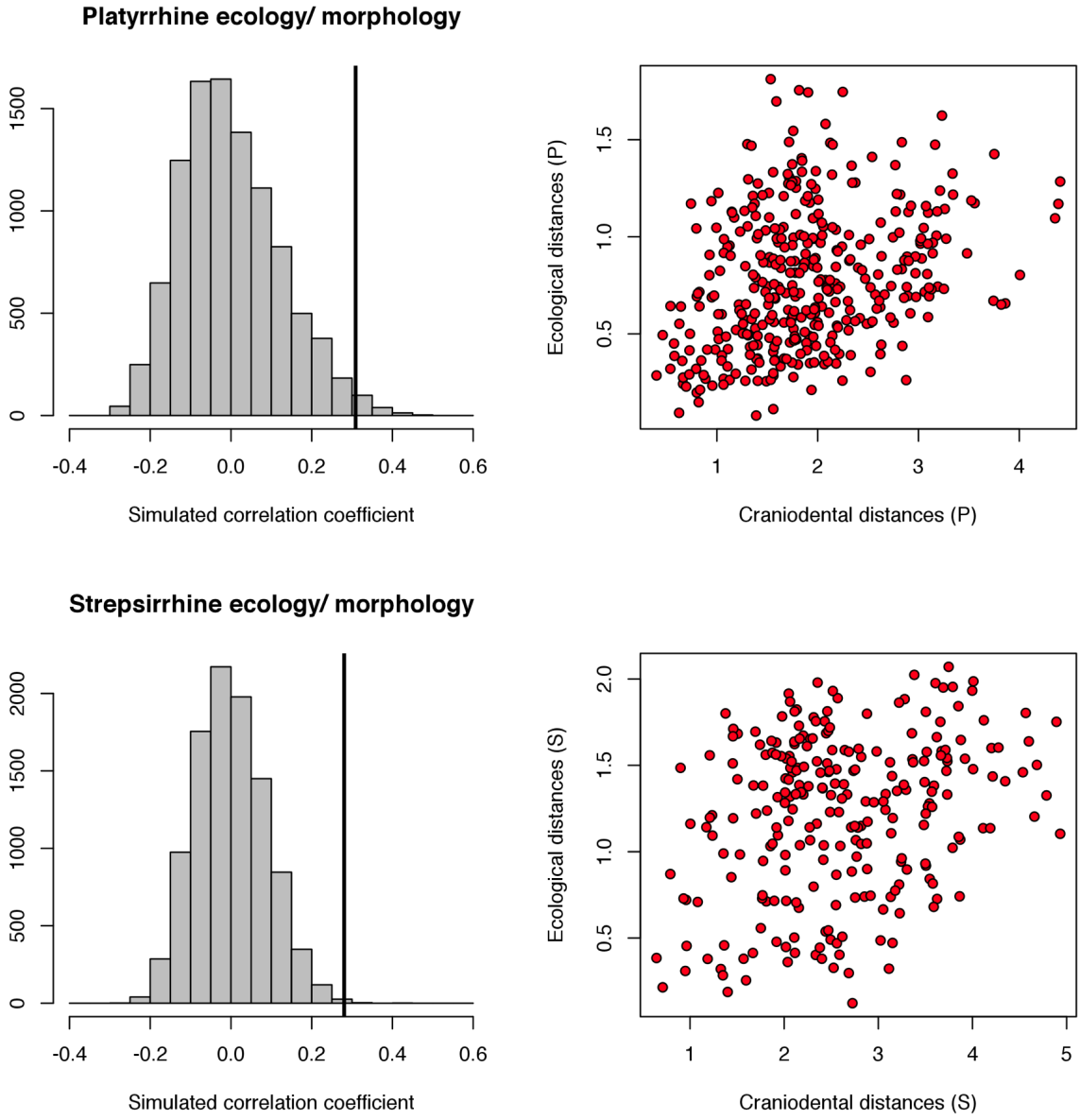


**Fig. 2.8.** Disparity through time analyses. The area between the curves is summarized as the morphological disparity index (MDI). MDI values are calculated from the 0.2–0.8 portion of the range.

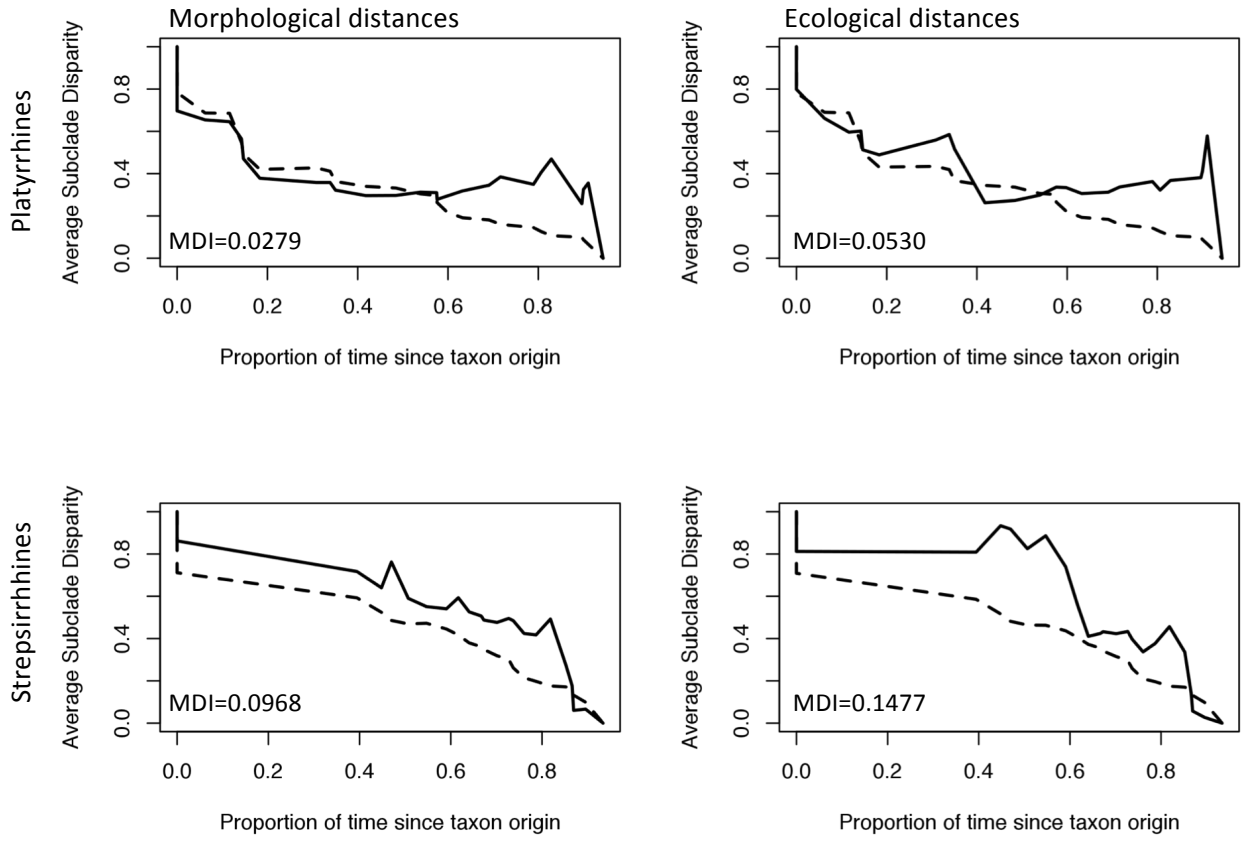
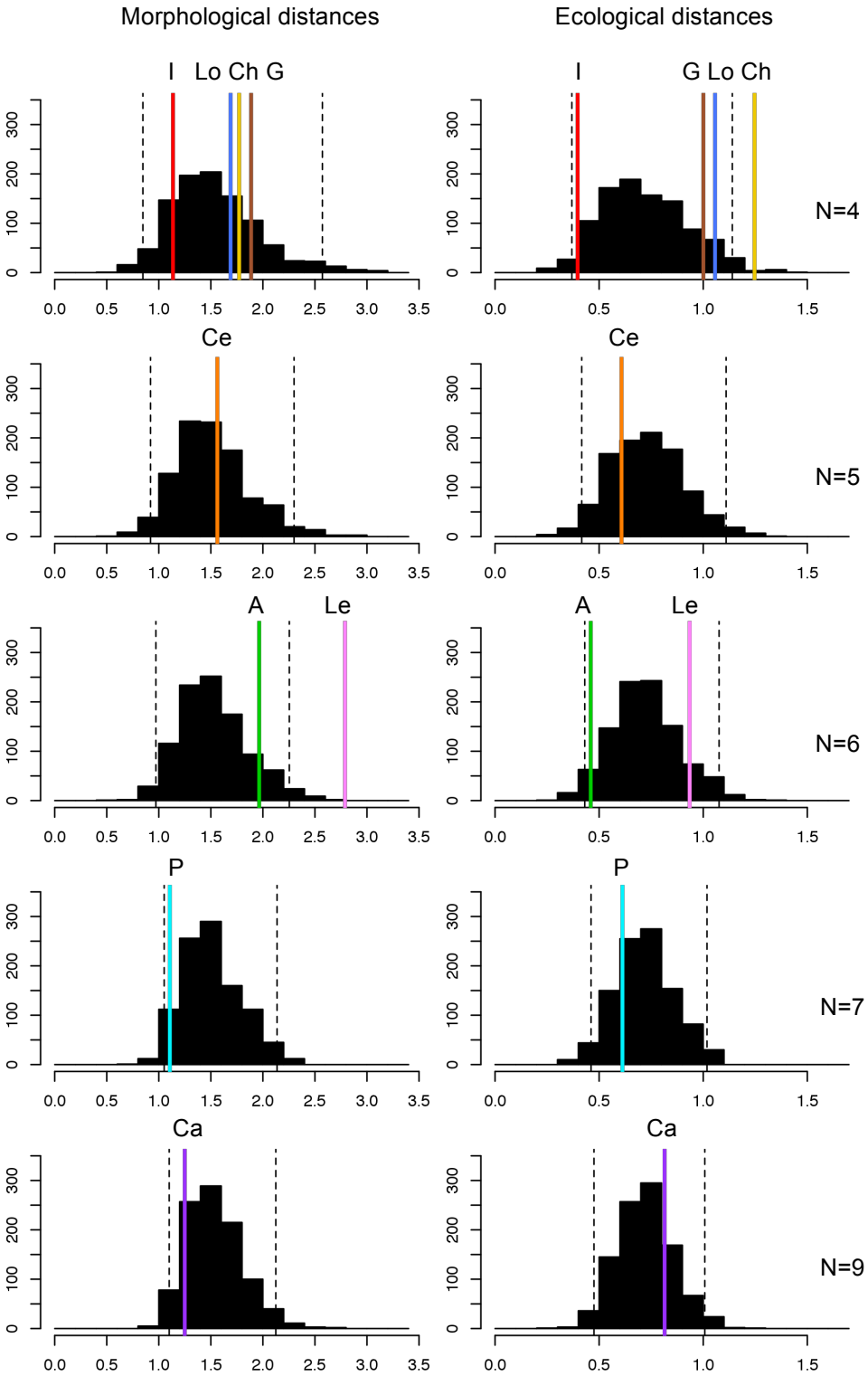


**Fig. 2.9.** Comparisons of average intertaxon distances in primate families. Dashed lines demarcate the upper and lower 2.5% of values from the bootstrap sample. A=Atelidae, Ca=Callitrichidae, Ce= Cebidae, Ch=Cheirogaleidae, G=Galagidae, I=Indriidae, Le=Lemuridae, Lo=Lorisidae, P=Pitheciidae.



## Chapter 3: Regional differences in morphological distances, disparity, and diversification among the primate cranium, mandible, and molar

*ABSTRACT: Macroevolutionary analyses of morphological disparity in mammalian fossil radiations are inevitably limited to those skeletal elements preserved for the greatest number of taxa. For most mammalian groups, including primates, the region most commonly preserved is the dentition. In this analysis, morphological distances calculated from molar measurements were compared to cranial and mandibular morphological distances, and the effects on conclusions regarding diversification and levels of disparity were evaluated for the three regions. Two extant clades of primates were compared, strepsirrhines and platyrrhines. Morphological measurements were converted to shape variables by dividing each variable within a region by a geometric mean specific to that region. Following phylogenetic Principal Components Analysis to reduce dimensionality and create orthogonal axes, Euclidean distances were calculated for each region.*

*Morphological distances calculated from different regions were not found to be correlated with those from other regions consistently, but were correlated with phylogenetic distances, at least in platyrrhines. These differences in the patterning of morphological disparity resulted in some differences among regions in the conclusions regarding the pattern of disparity through time, particularly in the molar. The region examined also affects conclusions regarding which clades can be considered as possessing unusually high morphological disparity. Such variation should be considered as a potential limitation of analyses examining diversity in fossil mammal radiations, in which information may be limited. However, molar morphological distances were more independent of phylogenetic distances and possibly more indicative of ecological variation within clades, which indicates that they may have the potential to add otherwise unavailable information to macroevolutionary analyses, even within those limitations.*

Morphological disparity, defined as quantitative morphological variation within groups, has been used to assess the tempo, mode, and extent of evolutionary radiation within and across clades in both fossil and extant organisms (Foote, 1993, 1997; Roy and Foote, 1997; Losos and Miles, 2002; Harmon et al., 2003; Erwin, 2007; Cooper and Purvis, 2009). When studying extant organisms, data can be collected from any aspect of morphology, including soft tissues, but quantification of morphological differences among fossil species will inevitably be confined to those hard tissue regions preserved through fossilization for a large number of species in the group of interest. Macroevolutionary analyses of changes in morphological disparity in fossil mammals have been restricted to the dentition (e.g., Jernvall et al., 1996, 2000; Wesley-Hunt, 2005; Gilbert, 2005; Wilson et al., 2012). Dental morphology is a valuable and much utilized source of information for taxonomic identification and phylogenetic reconstruction for fossil mammals, including primates (e.g., character matrices of Bloch et al., 2007; Seiffert et al., 2005, 2009). Teeth provide additional insights into ecology through established relationships with diet (e.g., shearing crest lengths in relation to insectivory and folivory, Kay, 1975). However, the extent to which diversification in the dentition is similar to that of other morphological regions is not known. In this chapter, I use methods developed for the analysis of macroevolutionary processes from morphological distances to assess the extent to which conclusions may be affected by regional differences, using the examples of extant radiations of strepsirrhine and platyrrhine primates.

## Morphological distances and macroevolution

While morphological differences between extant organisms have been used as the basis for analyses of ecological convergence and adaptation, the use of morphological disparity to study biodiversity and diversification was developed primarily within the field of invertebrate

paleontology (e.g., Saunders and Swan, 1984; Foote, 1991). Such studies became particularly important when it was recognized that previous methods of estimating adaptive diversity. For example, counts of higher taxa such as families (e.g., Sepkowski, 1984) did not adequately capture the relationship between the number of taxa within a clade (taxonomic diversity) and the amount of variation in morphology among those taxa (morphological disparity) (Foote, 1991, 1997). The interaction of taxonomic and morphological diversification has been examined in various invertebrates such as echinoderms, trilobites, crinoids, and snails (e.g., Foote, 1991, 1992a,b, 1993; Wagner, 1997). In such cases, the entire morphology of the animals' exoskeleton may be available for study and estimates of morphological disparity for fossil samples may be highly comparable to those that could be made for similar animals alive today. In contrast, much of the fossil record for terrestrial vertebrates, including fossil primates and other mammals, is relatively fragmentary. In order to have sufficient samples for meaningful analyses of morphological diversification among species, investigators are limited to particular regions that are well represented in the fossil record, such as dental and gnathic remains (Van Valkenburgh, 1988; Jernvall et al., 1996, 2000; Wesley-Hunt, 2005).

With paleobiological research on morphological disparity as a model, Roy and Foote (1997) argued that morphological disparity could also have considerable potential for a range of studies in extant organisms, particularly as a method of incorporating variation related to function and adaptation into estimates of biodiversity within groups. Recent studies have applied analysis of morphological distances to questions related to diversification and biodiversity among extant organisms (e.g., Roy et al., 2001; Losos and Miles, 2002; Harmon et al., 2003; Cooper and Purvis, 2009), in addition to estimates of phylogenetic signal within morphological regions (e.g., Cardini and Elton, 2008). Losos and Miles (2002) used morphological distances in

different clades of iguanid lizards to determine whether the disparity observed within a group of species was unusually high or low. With a similar taxonomic sample, Harmon et al. (2003) employed morphological distances to compare taxonomic diversification and morphological disparity through time. The goal of such studies is often to establish whether there are general patterns and processes underlying diversification among species. For example, are there identifiable common factors shared by clades that acquire greater species richness or adaptive diversity, compared to those that remain relatively conservative (e.g., Lovette et al., 2002; Dumont et al., 2012)?

**Regional differences in morphological disparity**

As discussed above, estimates of morphological disparity among fossil mammal species are likely to be limited to isolated morphological regions, in order that a high enough proportion of taxa can be sampled to provide a reasonable estimate of total diversity. Even when the study taxa are extant, some macroevolutionary analyses of morphological diversification are based on measurements from a limited region of the skeleton (e.g., Cooper and Purvis, 2009). Morphological similarity amongst organisms is likely to be related to several interacting factors that could include shared phylogenetic history, similarity in body size, and similarity in ecological parameters such as habitat use or diet. If morphological disparity primarily reflects phylogenetic proximity or similarity in overall body size, it might be predicted that the patterns observed from one area of the skeleton would be consistent with those seen in other regions. In such a scenario, a regional estimate of morphological disparity, for example, from the dentition, could lead to conclusions regarding diversification that are consistent with those that would be made with a wider range of morphological measurements. In contrast, if morphology is largely

influenced by functional requirements specific to that region, it is possible that different regions would indicate quite different patterns of diversification.

Morphological integration, defined as the correlations among traits derived from shared ontogenetic developmental pathways or evolutionary selection upon function (Goswami, 2006), may also influence variation in morphological disparity among different regions. Research in the field of morphological integration posits that many skeletal elements consist of several relatively independent modules defined by separate clusters of correlated traits. The level of correlation among the traits within these modules has been suggested to lead to differences in disparity among different modules (Goswami and Polly, 2010); if this is true, it may also apply to disparity among the skeletal regions containing those modules. Goswami and Polly (2010) describe two potential competing models for the way in which the level of morphological integration might influence disparity, summarized as the constraint and facilitation models. Under the constraint model, high correlations among traits within a module would limit variation in those traits and lead to lower total disparity. Conversely, under the facilitation model, high correlations among traits within a module would be expected to lead to higher disparity as changes in one trait result in a coordinated transformation of the tightly associated traits. In their analysis, Goswami and Polly (2010) predominantly found support for the constraint model in the cranial modules they analyzed (higher correlated modules with restricted disparity), but noted that landmarks placed in the regions of the skull supporting the maxillary molars were more consistent with the facilitation model (highly correlated module with high disparity). It is possible, therefore, that even within a region such as the cranium, similar amounts of morphological integration can be associated with different patterns of disparity.

Analyses of skeletal areas at a regional rather than modular level also indicate that differences in morphological disparity may occur among even associated skeletal elements. In an investigation of the cranium, mandible, and molar of Eurasian marmots, three regions that might be expected to be functionally associated, Caumul and Polly (2005) found that the three regions differed in the degree of phylogenetic signal, and relationships between morphology and diet or body size. They predicted that variation among these three structures would be seen because of differences in "genetic, developmental and functional controls" (p. 2461), i.e., the number of independent genetic loci likely to be involved in development, differences between the regions in the degree of ontogenetic association with surrounding structures, and relative amounts of exposure to environmental influences during growth. For example, while the morphology of the cranium (e.g., Lieberman et al., 2004) and the mandible (e.g., Holmes and Ruff, 2011) may respond to environmental influences while maintaining function, this is not necessarily the case for molar shape. In mammals the dentition develops within crypts located within the upper and lower jaws, and in most, tooth crowns are completely formed prior to dental eruption. While enamel mineralization of permanent teeth continues after birth, and environmental factors such as disease or other stresses may cause macroscopic features in crown anatomy (Guatelli-Steinberg, 2001), tooth morphology is largely buffered from direct environmental influences, at least prior to the point that teeth occlude and enamel wear begins.

In this study, the three regions studied by Caumul and Polly (2005) will be compared in a broader phylogenetic context in two clades of primates to investigate the impact that the anatomical region examined may have on conclusions regarding morphological disparity and macroevolutionary patterns. Strepsirrhine and platyrrhine primates are two monophyletic clades that differ in the depth of temporal divergence, and also in the degree of vicariance in their

radiation, with platyrrhine primates diverging relatively recently (20–25 mya) and occupying a single landmass (South America) while the strepsirrhine clade has a deeper divergence (ca. 60 mya) and is composed of three (currently) geographically isolated radiations, the lemuriforms of Madagascar and the lorisiforms of Asia and sub-Saharan Africa.

## Macroevolutionary questions

An initial insight into whether one region is likely to represent wider morphological disparity may be obtained from whether morphological distances between species are correlated when calculated from different regions. However, it is possible that, even if interspecific morphological distances are not well correlated between regions, the pattern of diversification and the distribution of diversity within the sample might be similar. In order to further investigate the degree to which any differences among skeletal regions may affect conclusions regarding morphological diversification and amount of diversity, two approaches employing morphological distances to investigate macroevolutionary questions in extant taxa will be applied to the three regions under investigation: analysis of disparity through time (Harmon et al., 2003) and comparisons of morphological disparity within clades (Losos and Miles, 2002).

The "disparity through time" (DTT) analysis described by Harmon et al. (2003) attempts to estimate the pattern of diversification, using the distribution of morphological disparity among extant members of the clade, with a known phylogeny. The observed pattern of morphospace occupation is compared to that predicted by simulations under a Brownian motion evolutionary model. Under a Brownian motion model, morphological traits are assumed to evolve along a random path; successive changes in a trait value are independent of any preceding changes (Felsenstein, 1985). Under this evolutionary model, variance among species for a given trait would be predicted to be proportional to the branch lengths connecting them (Harvey and Pagel,

1991) and the degree to which individual traits fit a Brownian motion model can be used to assess the level of phylogenetic signal in that trait (Pagel, 1999). In the DTT analyses, if a clade has a morphological diversification curve above the simulated curve, subgroups within that clade would typically exhibit a greater amount of morphological disparity relative to the total morphospace occupied, suggesting overlap in morphospace between different subclades. Lower morphological disparity than expected from simulations indicates that greater morphological distances are found between different subclades than within them, indicating partitioning of the morphospace along phylogenetic lines. Thus, the DTT analysis provides an indication of how morphological disparity is distributed within the clade studied.

Losos and Miles (2002) applied morphological distances to the investigation of a macroevolutionary question in order to test hypotheses of adaptive radiation. While it is relatively common in comparative biology to refer to clades with some degree of ecological diversification as "adaptive radiations," the original concept of adaptive radiation had a more specific definition as "more or less simultaneous divergence of numerous lines all from the same ancestral type into different, also diverging, adaptive zones" (Simpson, 1953:223). A more recent modification of this definition by Schluter (2000:10) describes adaptive radiation as "evolution of ecological and phenotypic diversity within a rapidly multiplying lineage," and gave four criteria that could be used to identify adaptive radiation: 1) descent from a common ancestor, 2) the presence of correlation between the phenotype and environment in the descendent species, 3) clear associations of trait variation and a fitness advantage, and 4) rapid speciation. Losos and Miles (2002) additionally surmised that the amount of variation within a sample may also be an important component of the definition of adaptive diversity. When measurements are informed by consideration of functional importance, morphological diversity may be an appropriate proxy

for diversity in adaptive zones. Losos and Miles generated expected distributions for morphological disparity within clades using resampling procedures, and compared the observed amounts within taxonomic groups to the distribution. Under this method, species groups with unusually high level of disparity are identified as possible adaptive radiations.

### Aims

The aims of this study are to investigate regional variation in morphological disparity, specifically the effect that differences among regions in the amount and distribution of morphological disparity may have on the perceived pattern or extent of diversification. This will be assessed using three methods: 1) direct comparisons of morphological distances with those calculated from different regions, and with phylogenetic distances; 2) investigation of changes in diversity through time in different regions; and 3) identification of unusually diverse clades.

## METHODS

Measurements were taken on skulls, mandibles, and lower second molars (m/2) of platyrrhine and strepsirrhine primates. Museums contributing to the sample included the American Museum of Natural History, New York; the Natural History Museum, London; The Field Museum, Chicago; the Smithsonian Museum of Natural History, Washington, D.C.; and the Museum of Comparative Zoology, Harvard University, Cambridge. The lists of strepsirrhine and platyrrhine taxa and sample sizes for each species are listed in Tables 3.1 and 3.2, respectively, and their phylogenetic relationships are illustrated in Figure 3.1. Skull and mandibular measurements were taken from the same individuals, selected on the basis of preservation, and possession of a fully erupted adult dentition. Total sample sizes were 289 total

individuals from 31 species of platyrrhines (avg. sample size: males=4.6, females=4.7), and 147 individuals in 26 species of strepsirrhines (avg. sample size=5.7, males and females combined). The molar sample was selected based on presence and preservation of the target tooth, m/2. In order to secure undamaged teeth with limited post-eruptive modification of crown anatomy due to wear, these individuals were not necessarily the same as those in the cranial/mandibular sample but were taken from individuals of the same species and, where possible, subspecies. The total sample sizes for the molars were 190 individuals (avg. sample size=6.1) for platyrrhines, and 107 (avg. sample size=4.0) for strepsirrhines. Species were typically sampled at a density of two to three species per genus when genera are polytypic, and included the majority of genera in these clades for which museum material is readily available, with the exception of the strepsirrhine *Daubentonia*. *Daubentonia* molars are highly derived and lack homologous measurement landmarks for tooth crests and areas of molar basins, and could therefore not be included in the present comparison of disparity in the cranium, mandible, and molar. Other genera omitted include *Allocebus* and *Callibella*, due to limited availability, and *Oreonax*, which is also poorly represented in museum collections and may not be distinct at the generic level from *Lagothrix* (Matthews and Rosenberger, 2008). Finally, additional species of *Saguinus* were sampled, in recognition of the fact that the depth of divergence between species within this genus is similar to the divergence between genera in some other clades of platyrrhine primates.

**Measurements**

Measurements were designed to capture overall variation in shape and to represent traits previously described as functionally important, such as crest lengths on the molars or robusticity of the mandibular corpus. Descriptions of the measurements are provided in Tables 3.3–3.5 and the measurements are illustrated in Figures 3.2–3.4. Skulls and mandibles were measured to the

nearest 0.1 mm using Mitutoyo digital calipers, with two additional measurements on the mandible taken from digital photographs of the mandible in lateral view (heights of the condyle and coronoid process above the tooth row). Digital photographs of the mandible in lateral view were taken with Canon G6 or G11 cameras, with a scale placed level with the mandibular ramus.

To capture dental morphology, vinyl polysiloxane molds were made of the lower postcanine dentition during museum visits, and grey-pigmented epoxy resin casts were made in the Vertebrate Fossil Preparation Laboratory at Stony Brook University. Casts were photographed in occlusal and lingual views using a Zeiss Discovery.V12 stereomicroscope, for measurements of linear dimensions and areas in occlusal and lingual view[2]. Epoxy resin casts of the mandibular dentition were manually reduced to isolate the m/2, and 20–30 individual tooth casts were mounted on foam board discs for scanning with a ScanCoMedical μCT 40 machine at 8–18 μm slice resolution in the facilities of the Department of Biomedical Imaging at Stony Brook University (for a description of the scanning protocol followed, see Boyer, 2008). Stacks of DICOM images were segmented in ImageJ to isolate individual teeth; digital models were created after importing these image stacks into the software Avizo with voxel size set by the scanning resolution to maintain scale. Digital models were then downsampled to 150,000 faces and subjected to 20 iterations of smoothing (lambda=0.6). Measurements of crest lengths followed procedures that have been shown to be highly replicable within and between observers (Bunn et al., 2011, supplementary information).

[2] In order to be comparable with the cranial and mandibular datasets, quantification of molar morphology is limited to linear and area measurements, rather than the landmark-based geometric morphometric methods used in later chapters.

## Data analysis

Geometric means for the cranium, mandible, and molar were calculated from selected measurements (marked with asterisks in Tables 3.3–3.5). In order to analyze diversity in shape, data were converted to Mosimann shape variables (Mosimann and James, 1979) by dividing each variable by the geometric mean for that region. The square root of area measurements was calculated prior to ratio calculation. Ratios were used rather than residuals because they more effectively capture geometric similarity (Jungers et al., 1995) and are not dependent on the specific set of species selected for analysis. Additionally, the use of ratios to create size-adjusted variables avoids assumptions concerning the causative factors underlying observed correlations between shape and size. Mosimann shape variables therefore allow shape to be analyzed without being overwhelmed by variance in absolute size, but do not attempt to remove any possible effects of size on the observed morphological diversity. Thus, if changes in absolute size are associated with changes in shape, that shape variation will be present in the sample. Using this approach, size can be considered one possible source of morphological disparity.

Species averages were created for each variable after conversion to shape variables. In platyrrhines, while some species show relatively little sexual dimorphism, others have considerable dimorphism in body size or canine size (Kay et al., 1988), or in other features that may influence cranial or mandibular shape, such as the enlarged hyoid bones in *Alouatta* males. Therefore, as averaging values for males and females might result in the analysis of morphological shapes that are not present in nature, platyrrhine males and females were averaged separately for the skull and cranium. Dimorphism in molar shape would not be expected, and sexes were pooled in the dental sample. Among extant strepsirrhines, sexual dimorphism in skull size has been described in a small number of species (Jenkins and Albrecht, 1991), but the

degree of dimorphism in skull size is low if present, and canine dimorphism is usually absent (Plavcan et al., 1995). In the absence of substantial dimorphism in size or secondary sexual characteristics such as canine size, sexual dimorphism in cranial or mandibular shape would not be expected. Species averages for strepsirrhines were created without separating males and females. As the phylogenetic principal components analysis (pPCA) used in the creation of morphological distances limits the number of rows in the data matrix to a single entry for each species, each analysis was conducted once with female platyrrhines and once with males.

All analyses were performed in the statistical computing environment "R" (R Development Core Team, 2011); functions described below are available in the base stats-package (*ibid.*) unless otherwise stated. Phylogenetic trees were imported using the package "ape" (Paradis et al., 2004). Region specific Principal Components Analyses (PCA) were then performed on the correlation matrix, using the phylogenetic PCA (pPCA) developed by Revell (2009), available in the R package "phytools" (Revell, 2012), to correct for non-independence of species points when calculating factors summarizing variation in the sample. The correlation matrix was used because even though the variables are measured in the same units (mm), some are quite small compared to the geometric mean (e.g., condyle width in the mandible dataset) while others are much larger (e.g., mandible length). Using the correlation matrix standardizes the measurements as standard deviation units, and therefore gives more equal weight to all variables. Under the pPCA, species scores on PC axes would still be expected to retain any phylogenetic structure present in the original dataset[3], but the loadings of variables on

[3] While the computation of the principal component axis is made incorporating phylogenetic covariance, the projections of species scores onto PCA axes occur from the original data space, and may therefore retain phylogenetic structure (Revell, 2009). Similarly, residuals from a regression line may retain phylogenetic structure, even when the slope and intercept are calculated using phylogenetically informed methods.

components are calculated incorporating phylogenetic relatedness, and axes should be truly orthogonal (uncorrelated) when phylogenetic structure is incorporated into the analysis. For the first and second analyses described below, pPCAs were performed on strepsirrhine and platyrrhine clades separately (with the platyrrhine analysis performed for males and females also separately). However, for the third analysis of relative morphological diversity, a combined analysis of both clades together was performed, as comparisons of intertaxon distances in different clades require that all taxa are in the same shape space. The full phylogenetic tree presented in Figure 3.1 was used for the latter; the topology of the trees used for the separate clades matches the branching pattern and distances in this tree. As in previous studies using the selected methods (Losos and Miles, 2002; Harmon et al., 2003), the principal components summing to explain 85% or 95% of the variance cumulatively were used to calculate squared Euclidean distances between species. Prior to distance calculation, each PC axis was scaled to be equal in length to its eigenvalue in order that each component contributes to the distance calculation in proportion to the variance explained by that component.

To assess the concordance in morphological disparity among regions, several different analyses were conducted, similar to those described for ecological and morphological disparity in the previous chapter. The first analysis compared morphological pairwise interspecies distances from different regions using Mantel tests of matrix correlation in the R package "ade4" (Dray and Dufour, 2007). After separate pPCAs on the platyrrhines and strepsirrhines, the principal components cumulatively representing 95% of the total sample variance were retained for calculation of morphological distances (Euclidean distances); pPCs were first scaled to be equal in length to their eigenvalues. After Mantel matrix correlations were carried out for each pair of morphological regions, correlations were also performed between morphological and

phylogenetic distances. The Mantel test is not a powerful test of association between two datasets (Peres-Neto and Jackson, 2001), but does allow analysis of distances, which are key to the questions examined here relating to the measurement of disparity in a sample.

Secondly, "disparity through time" plots were produced for platyrrhines and strepsirrhines separately, following the methods of Harmon et al. (2003) in the R package "geiger" (Harmon et al. 2008). This approach, described at greater length in the preceding chapter, takes a phylogeny and at each point of divergence calculates the amount of disparity within each subclade relative to the total sample (relative disparity index, RDI), and provides an average value for all subclades present at that time point. The observed curve is then compared to an average curve from simulations under a Brownian motion evolutionary model. To assess the degree to which the simulated curve and the observed curve are similar, the area between the two is measured by the morphological disparity index (MDI). Disparity through time curves were created for the three regions under investigation for both platyrrhines and strepsirrhines.

Finally, the method developed by Losos and Miles (2002) was used to identify clades with unusually high levels of morphological disparity. The clades analyzed consisted of nine primate families (Cheirogaleidae, Indriidae, Lemuridae, Galagidae, Lorisidae, Cebidae, Callitrichidae, Pitheciidae, Atelidae), each of which had at least four species included in the sample. Grouping of species within families followed traditional primate taxonomy (strepsirrhines – Fleagle, 1999; Mittermeier et al., 2010; platyrrhines – Rylands and Mittermeier, 2009), i.e., despite its position within several molecular phylogenies (e.g., Horvath et al., 2008; Fabre et al., 2009) *Lepilemur* was not included in the Cheirogaleidae, and Callitrichidae was considered separately from Cebidae. This method, developed by Losos and Miles (2002) to assess the level of adaptive diversity within a clade, uses a resampling approach to create

expected distributions of average distances within a clade of *n* species. Principal components are calculated from a set of morphological variables, and clade mean values for each component are centered on the origin for all clades in the analysis. This preserves intertaxon distances within each family, but removes interfamily differences. Samples of *n* species are randomly drawn from the mean centered distribution, and a range of intertaxon distances for samples of n species is created. The observed values for each group of species are then compared to the distribution from the resampling procedure to identify clades with unusual levels of disparity (in the 2.5% tails of the distribution). To test a hypothesis that a clade possesses unusually high disparity, a one tailed hypothesis may be appropriate, and the latter approach is used here.

Distances were calculated in a similar way to the previous analyses; this analysis was performed twice for the skull and mandible, with platyrrhines represented by either females or males only. Following the procedures used by Losos and Miles (2002), PC scores for the components comprising 85% of the variance in the sample were retained, and PC axes were scaled to be equal in length to their eigenvalues. To create a sample for the expected distribution of average intertaxon distances for *n* species, the dataset was adjusted to remove interfamilial differences by calculating the family mean score for each PC, and subtracting it from the PC score for each species within that family. This creates a distribution of points in which family means are centered on the origin for all components, but interspecific distances within families are preserved. A function was written in R (Supplemental 2) to sample, with replacement, sets of *n* species and calculate the average distance between the species in that set. This was then replicated for 1000 iterations. This process is illustrated in Chapter Two, Figure 2.4. The resampling function was run with *n* set equal to four, five, six, nine, and ten, to match the range of variation for numbers of species within families in this sample. Families were considered to

have unusually high morphological diversity if the average intertaxon distance exceeds the 95$^{th}$ percentile for the bootstrap sample with the same number of species as in the family (e.g., Lorisidae was compared with the distribution for four species, Cebidae with the distributions for six species)**.**

## Phylogenetic relationships

Phylogenetic trees, constructed using molecular sequence data, for platyrrhines, strepsirrhines, and the combined sample were downloaded from the 10kTrees website (Arnold et al., 2010) using the most recent available dataset (Version 3). The consensus tree for the combined sample is shown in Figure 3.1. Branch lengths were based on divergence dates rather than genetic distances; calibration points for this analysis include *Cebus*/*Saimiri* at 12.5 mya and *Loris/Galago* at 38–42 mya. Two species in the morphological dataset, *Pithecia monachus* and *Chiropotes albinasus*, are not currently available in the 10kTrees database. The divergence date for *P. irrorata/P. pithecia* was used as a proxy for *P. monachus/P. pithecia*. If *Pithecia irrorata* is correctly interpreted as more closely related to *P. monachus* than to *P. pithecia* (Hershkovitz, 1987), the divergence date for *P. monachus/P. pithecia* will be identical. In the consensus tree from 10kTrees Version 3, the relationships between *Cacajao melanocephalus*, *Cacajao calvus*, and *Chiropotes satanas* are represented by a trichotomy. *Chiropotes albinasus* was added to the tree with the same branch length, creating a polytomy of the four species. More data are needed to resolve the relationships within these species and genera. Because some analytic methods are intolerant of polytomies, this polytomy was resolved for computational purposes by pairing species by genus with branch lengths set to zero.

# RESULTS

The first two analyses, correlations of morphological distances between regions and examination of disparity through time curves, were based on distances calculated from phylogenetic principal components analyses (pPCAs) in platyrrhines and strepsirrhines separately, while the third analysis comparing amounts of morphological diversity in different regions used a pPCA of all taxa. The results of the principal components analyses are summarized in Appendix 2. In all analyses, prior to the calculation of morphological distances, the PC axes were rescaled to be equal in length to their associated eigenvalues, by dividing the PC score for each species by the range of values on that axis and multiplying by the eigenvalue. Within and between family mean morphological distances (Euclidean distances), calculated as described for the analyses below, are shown in Tables 3.6–3.10. In platyrrhines the greatest within family mean distances are seen in the Atelidae for the cranium and molar, and in the Cebidae for the mandible. In strepsirrhines, the Galagidae have the greatest average intertaxon distance in the cranium, while the Lemuridae have the greatest average distances in the mandible and molar. These hold whether the pPCA is of platyrrhines alone, lemuriforms alone, or the combined sample.

***Correlations between morphological distances from different regions.*** The summary of Mantel matrix correlations between different regions is presented in Table 3.11; scatter plots of interspecies distances and histograms of the simulated correlation coefficients following 10,000 permutations of the matrices are shown in Figures 3.5 and 3.6 for the platyrrhines and Figure 3.7 for the analysis of strepsirrhine species. At a significance level of alpha=0.05, significant correlations were found between morphological distances for the cranium and mandible, and

cranium and molar in platyrrhines (using both male and female specimens), and between the cranium and mandible in strepsirrhines. Only the correlation between cranial and mandibular distances in male platyrrhines remains significant under a Bonferroni-Holm correction for multiple comparisons; however, given the consistency between the male and female dataset in platyrrhines, and the potentially low power of the Mantel test (Peres-Neto and Jackson, 2001), it may be overly conservative to dismiss the results that miss significance under this correction. Mantel correlations between the male and female matrices indicated a high degree of association between morphological distances from male and females, with a correlation coefficient of 0.934 ($p<0.0001$) for the cranial distances and 0.8930 ($p<0.0001$) for the mandibular distances. The pattern of correlations with phylogenetic distances (Table 3.12, Figs. 3.8 and 3.9) contrasted in the two clades. In platyrrhines, all three regions under analysis showed significant correlations with phylogenetic distances, while in strepsirrhines only cranial morphological distances correlated significantly; the results were not affected by a correction for multiple comparisons.

***Disparity through time.*** The disparity through time (DTT) curves for the three regions are shown in Figure 3.10, with the morphological disparity index (MDI) for each curve included. The MDI is a measure devised by Harmon et al. (2003) to quantify the difference between the simulated curve and that observed, calculated as the area between the two curves. The MDI values for the three regions are also provided in Figure 3.10. In the platyrrhines, the DTT curves for the three regions shared a similar contour of an initial sharp decline in subclade diversity associated with the initial branching events, but had a consistent level of subclade diversity persisting through subsequent diversification until the last fifth of the time since taxon origin shown on the x axis. When compared to the simulated DTT curve, the three regions are quite distinct. In the cranium, the observed curve in platyrrhines is below the predicted curve for most

of the clade's history; subclade diversity is typically lower than would be expected under the Brownian motion model. In contrast, the molar diversity within subclades is typically higher than expected under the simulation, with average diversity among subclades well above the predicted level, particularly in the later portion of the clade's history. The mandible results are somewhat intermediate, with lower diversity than predicted close to the initial divergence but higher than predicted diversity later. The results presented in Figure 3.10 are the female platyrrhine curves for cranium and mandible. Figure 3.11 shows the disparity through time plots for both female and male platyrrhines in the cranium and mandible. The shape of the curves and the MDI values are similar, with approximately the same MDI in the diversification curves of male and female crania and slightly less difference between the observed and expected curves in the male mandible diversification curve than in the female.

In the strepsirrhine sample (also shown in Fig. 3.10), the three regional disparity curves are also quite similar to each other in pattern. Both cranial and mandibular disparity curves are almost entirely above the simulated diversity curve, but have a similar contour. In these two curves the greatest departures from the simulation occur in the most recent portion of the curve, around 0.8 on the axis representing proportion of time since taxon origin. The molar diversification curve has a similar value for the area between the simulated and calculated diversification curves (MDI) as the other two regions, and the greatest differences between the observed and simulated curves are seen deeper in time, around 0.4 – 0.5. Similar to the platyrrhines, the departure from the simulated curve based on the Brownian motion model is greatest in the strepsirrhine molar sample, but the difference is not as great as in the platyrrhine analysis.

***Identification of diverse clades.*** As in the previous analyses, separate species averages for male and female platyrrhines were created for the cranium and mandible. Because comparisons of relative diversity would be made for all taxa, and the phylogenetic PCA (see Appendix 2) can only have one set of data for each species, the sample was comprised of 1) strepsirrhines and female platyrrhines, and 2) strepsirrhines and male platyrrhines. Figures 3.12–3.14 show the histograms from bootstrapped distributions of 1000 samples of four, five, six, nine, or ten species, with colored lines indicating the intertaxon distances found in each group. In Figure 3.12 (cranium) and Figure 3.13 (mandible) the analysis with female platyrrhines is shown to the left, and that using male platyrrhines is shown to the right.

In the cranial analysis (Figure 3.12), none of the families included were identified as possessing significantly greater diversity in the analysis that used the sample of female platyrrhines; when the sample was constructed using male platyrrhines, the atelids were identified as being unusually diverse following the criterion of falling above the 95th percentile in the distribution of average taxonomic distances based on a sample of six species. In contrast, in the analysis of mandibular data (Figure 3.13), the results were consistent between the sample with female versus male platyrrhines, and the only group identified as possessing unusual levels of morphological diversity was the lemurid family. Finally, the results of the analysis of molar morphology (Figure 3.14) were similar to those from the mandible, with the lemurids identified as possessing unusual morphological diversity; the cheirogaleids also fell just above the 95th percentile for the bootstrapped sample.

# DISCUSSION

The results of the analyses described here have a number of implications for the application of morphological distances to macroevolutionary analysis of the mammalian fossil record, and may also provide insights for future research for studies measuring morphological disparity amongst extant organisms, given that museum collections of mammals are also often limited to specific skeletal regions such as the skull (e.g., Cooper and Purvis, 2009). Additionally, while the focus of this investigation was on the comparison of morphological distances from different regions and their relevance to analysis of morphological disparity in past faunal assemblages, these analyses of diversification within platyrrhines and strepsirrhines indicate potential avenues for future analyses of morphological diversification in these groups.

***Correlations of morphological distances.*** Prior to correcting for multiple comparisons, a number of significant correlations between the regional morphological distances were found in both clades of primates, and a similar pattern was seen from male and female platyrrhine species averages, as would be expected given the high association between distances in males and females for both cranium and mandible. In both male and female platyrrhines, morphological distances from the cranium were correlated with morphological distances calculated from the mandible and molar, but no significant association was seen between the mandible and molar distance matrices. Following a correction for multiple comparisons, only the platyrrhine male mandible-cranium comparison remained significant. While the Mantel test is necessary to test associations between distances, as required in the present comparison focused on morphological disparity, as mentioned previously it is not a powerful test (Peres-Neto and Jackson, 2001). Therefore, applying an additional correction to significance may not be appropriate, particularly

as in this case it leads to a possibly misleading inference of contrasting patterns in male and female platyrrhines. Additionally, corrections for multiple comparisons have been suggested to be overly conservative in this type of study (e.g., Moran, 2003; Nakagawa, 2004; but see Garcia, 2004).

Whether or not a correction for multiple comparisons is applied, these results indicate that morphological distances calculated from different regions of the skull can be relatively uncorrelated or weakly correlated. Furthermore, such differences in the distance matrices can occur even when two regions are functionally associated, such as is the case for the mandibular molar and the mandible (insignificant in all comparisons). In the mandible and molar, points were distributed relatively evenly on both sides of the diagonal, i.e., close similarity in either region can be matched with very distinct anatomy in the other. Inspection of the plots of the PCs (Appendix 2) supplies some explanation for this observation. For example, in the strepsirrhine mandible pPCA, the indriids (*Avahi*, *Propithecus*, and *Indri*) have almost no overlap with other families of strepsirrhines in the morphospace defined by the first three PCs. In dental morphology, indriids (highly folivorous) have similar scores on the first PC to several other groups, including the insectivorous galagids, some lorisids, and another folivore, *Lepilemur*. This axis principally summarizes variation in occlusal height, relative width of the tooth, and isolated crest lengths. As noted in previous research, relief of the tooth (Boyer, 2008) and relative crest lengths (Kay, 1975) can be similar in folivores and insectivores. However, requirements for behaviors related to ingestion (for example, morphological features related to gape) might well differ.

Additionally, correlations among the three regions included appeared generally higher in platyrrhines than in strepsirrhines. It is not obvious why one clade should have greater

association between regions in morphological similarity among species, but this phenomenon may bear further investigation. Platyrrhines diverged from a common ancestor more recently than strepsirrhines, and show low overall ecological diversity when compared to other groups of primates (Fleagle and Reed, 1999). If correlations between morphological distances in different regions are due to disparate functional demands on those regions, limited ecological variation could result in a relatively greater influence of factors that are shared across the skeleton, such as somatic size or phylogenetic relatedness. Notably, correlations between morphological and phylogenetic distances were found in all three regions in platyrrhines, but in strepsirrhines such a correlation was only found in the cranium.

The lack of significant correlations with phylogeny for the mandibular and molar regions in strepsirrhines may also reflect specific aspects of the distribution of morphological diversity in this clade. The plots of phylogenetic distances relative to the morphological distances show a large range of values for morphological similarity at the greatest phylogenetic distance, that uniting examples of lorisiforms and lemuriforms. Lorisiforms are often described as being very similar to cheirogaleids in their morphology and ecology, to the point that some researchers have considered them to be sister taxa within the strepsirrhine radiation (e.g., Tattersall and Schwartz, 1974), or concluded that their similarities must reflect the primitive state for the clade (Charles-Dominique and Martin, 1970). Cheirogaleids and lorisiforms are not notably closer in the morphological distances calculated here, except perhaps in the mandibular morphological distances, but it does seem that low values for morphological distances between lemuriform/lorisiform pairs of species may have reduced the correlation between morphological and phylogenetic distances; there may be a closer association of phylogenetic distance with

morphological distances within lorisiforms and lemuriforms separately than in strepsirrhines as a whole.

***Disparity through time.*** The analyses of disparity through time provide some interesting complementary insights and contrasts to the results of the previous section. The disparity through time curves are compared to the expected pattern of diversification derived from simulations based on a Brownian motion model of trait evolution along the entered phylogeny. As described earlier, if the calculated pattern of morphological diversification falls above the simulated curve, subclades have greater than expected levels of morphological disparity while a morphological diversification curve lower than expected indicates that subclades are more restricted in morphological disparity. Despite a general similarity across the three regions in the contour of the disparity curve, in platyrrhines the three regions differed in respect to the position of the morphological diversification curve relative to that expected under the Brownian motion model. In the cranium, the morphological curve fell below the line while the mandibular disparity curve was very close to that predicted; the molar disparity curve contrasted with both these patterns and showed greater than expected disparity within subclades. Despite the fact that morphological distances had lower correlations between regions in strepsirrhines, the three regions were consistent in that they all showed morphological diversification curves above that expected, and the degree of difference from the line was more consistent.

It might have been predicted from the lower correlations between morphological distances and phylogenetic distances in strepsirrhines, and the fact that the simulation curves represent those expected by evolution under a Brownian motion models along a known phylogeny, that the strepsirrhines would show greater separation (higher MDI values) from the simulated curves than the platyrrhines. However, this was only true in the cranium and mandible.

In the molar analyses, the platyrrhines had a greater difference from the expected, both relative to the other two morphological regions and to the strepsirrhines. This result would not necessarily be expected from the observation that morphological distances in all three regions are correlated with phylogenetic distances in platyrrhines. Additionally, the MDI values for the cranium, mandible, and molar in strepsirrhines are quite similar despite differences among regions in the degree of correlation with phylogenetic distance.

Despite the differences among the regional DTT curves within platyrrhines and strepsirrhines in the pattern and degree of difference from the predicted curves under the simulations, it is notable that the three regions do share some features of their DTT curves. For example, all three curves for strepsirrhine taxa follow the contour of the predicted curve quite closely, and the decline in average subclade diversity is relatively consistent. In contrast, all three platyrrhine curves have some degree of a plateau in the average subclade diversity between 0.2–0.8 of the total time since the clade's origin. Comparison to the phylogeny shown in Figure 3.1 indicates that this plateau is not a result of few instances of cladogenesis in this time period, but rather seems to indicate that during that time period, the average amount of diversity in the subclades compared to the total remains constant.

In the original paper that introduced this method of examining diversification, Harmon et al. (2003) compared patterns of cladogenesis with the disparity curves in iguanian lizards, and found that clades that had a history of early cladogenesis shared a pattern of more morphological diversity among rather than within subclades. This pattern of morphological disparity is indicative of little overlap in morphological space between the members of different subclades. However, the results here show that, given the same underlying pattern of cladogenesis, different morphological regions can show different patterns of within/among subclade disparity. This

argues for a less deterministic interaction between the pattern of cladogenesis and the distribution of morphological diversity. The platyrrhine radiation had lower than predicted variation in the cranium within subclades, but more than predicted variation in molar morphology. In strepsirrhines, the direction of difference between the molar and other regions was similar, but all regions had greater than expected diversity within subclades. The analysis of Harmon et al. (2003) used measurements of limb and other body segment proportions, rather than details of skeletal regions as considered here, and their morphological disparity estimates might therefore be considered more "general." However, given the differences observed here, even between different components of the same functional system, it would be interesting to recreate their analysis partitioning measurements of limb proportions and measurements of jaw architecture to see if their conclusions regarding the relationship between disparity and cladogenesis are affected by the region examined in those clades.

***Identification of diverse clades.*** The final analysis compared the amount of disparity in families of platyrrhine and strepsirrhine primates. The cranial analysis based on the pPCA using female averages for platyrrhines found no family that could be considered unusually diverse relative to the distribution of values for intertaxon distances calculated for groups of *n* species. In the analysis that used males, atelids were found to be the only clade with exceptional cranial disparity. The analyses of disparity in the mandible and molar identified lemurids as unusually diverse in both regions, and the average intertaxon distance among the cheirogaleids also fell just above the threshold. The lemurid result is interesting, given that in strepsirrhines molar and mandibular morphological distances were not correlated. Even so, the choice of region used for this analysis does affect the clades that are identified as exceptional in degree of morphological

disparity. In addition, the use of males or females in radiations that exhibit sexual dimorphism may also influence the conclusions concerning relative diversity.

It is possible, given the use here of Mosimann shape variables, that size-related shape changes might lead to families with a large amount of variation in body size being found to be more morphologically diverse. However, this hypothesis is not supported by detailed examination of the body size range in the families identified as unusually diverse (atelid males, lemurids for mandible and molar, cheirogaleids for molar morphology). It is true that the two lemuriform clades identified as unusually diverse in one or more of the regions studied show variation in their body mass. Extant lemurids in this sample range between the smallest species, *Hapalemur griseus*, at around 700g, and the largest species, *Varecia variegata,* which has five times this mass at 3.5 kg. Cheirogaleids included here range between *Microcebus griseorufus* at 50–60g (Genin, 2008) and *Cheirogaleus major,* which is nearly six times greater at 350 g (all body mass values from Smith and Jungers [1997] unless otherwise noted). These two clades do show some considerable variation in mass, but a third group found to be unusually diverse, atelid males, occupies a much more limited range of values, between 6.7 kg (*Alouatta seniculus*) and 9.6 kg (*Brachyteles arachnoides*). Additionally, several clades show greater diversity in body mass without being identified as unusually diverse in their morphology, including the indriids, which have a seven-fold increase from the body mass of *Avahi* (1kg) to the *Indri* (7kg) and the galagids, which range between *Galagoides demidoff* at 60g and *Otolemur* at 1.2kg. Thus, this sample has examples of families with both high morphological disparity and low body mass range, and high body mass range with lower morphological disparity. Additionally, of the three regions examined in this study, the cranium could be argued to be the most likely region to show shape variation associated with body mass, given non-isometric scaling of cranial vault (e.g.,

Isler et al., 2008) and eye size (e.g., Ross and Kirk, 2007), and in this region the only sample identified as being unusually diverse consisted of male atelids, with the aforementioned limited body size range.

Whether or not the families identified here as possessing high levels of morphological disparity can be considered as adaptive radiations, under the definitions discussed earlier, is open to question. Most definitions include the element of rapid diversification, which cannot be addressed without some consideration of the relative timing of the clade origin, and the speed at which diversity was acquired. As discussed by Losos and Miles (2002), if comparisons are limited to clades of similar age, a morphologically diverse group must presumably have undergone morphological divergence at a greater rate than other clades at some point in its history. It is possible that those clades identified here as unusually diverse might have acquired their disparity over a longer period of time than others in the analysis. Using the divergence dates from the molecular phylogenetic analysis (Figure 3.1) as an indication of the age of the clades, it does not seem that this hypothesis would be tenable. The lemurids are a similar age to the indriids within the strepsirrhines, and to the pitheciids within the platyrrhines, but show a greater degree of morphological disparity, while the clade with the deepest divergence among the families considered here, the lorisids, did not show exceptional diversity relative to the histogram generated by the bootstrap analysis. Ideally, analyses of disparity through time could be performed at the same taxonomic level as comparisons of levels of morphological diversity, to address both the pace and amount of diversification. However, the present focus was on comparisons of skeletal regions.

Rather than being the result of effects of body size or age of the clade, the families identified as possessing exceptional morphological disparity appear to be those that contain some

species that are very distinct from their close relatives in their ecology or other aspects of their adaptation. Within the lemurids, the bamboo lemurs, *Hapalemur griseus* and *H. simus*, have very distinct mandibular and molar morphology from their close relative *Lemur* (see PCA plots in Appendix 1), and *Varecia* also has quite distinct molar morphology in the low crown relief found in this species, presumably associated with the high degree of frugivory (Britt, 2000; Vasey, 2004). The high diversity in cheirogaleid molar shape is similarly likely related to the very low crown relief found in *Cheirogaleus* compared to the other species. In atelids, the genus *Alouatta* differs from other species in relative encephalization (Martin, 1990; Hartwig et al., 2011) and in the high degree of folivory in the diet. Additionally, the cranium shows some modifications due to the enlarged air spaces within the hyoid, which is particularly great in males. Thus, those clades identified as diverse here do provide some evidence that morphological disparity in these regions can be primarily linked to ecological diversity or other adaptive variation. The possible role of sexual dimorphism in increasing diversity in males rather than females would be worth investigation in future studies, particularly of the catarrhine primates.

It would be particularly interesting to perform comparisons of morphological disparity within strepsirrhine families when including the recently extinct subfossil lemurs from Madagascar with their living relatives, to investigate how the degree of morphological variation within clades was affected by the reduction in diversity. The lemuriforms of Madagascar are often described as one of the most adaptively diverse radiations in primates (e.g., Martin, 2000). In order to evaluate the morphological disparity within the entire clade quantitatively, it would be necessary to have a similar amount of information on additional clades of primates, as in the present sample only the lorisiforms and platyrrhines are comparable in taxonomic rank, and even

platyrrhines are considerably more recent in divergence. It would also be necessary to use methods for quantifying morphology that can be measured in *Daubentonia.*

## CONCLUSIONS

The avenues of investigation applied here to three skeletal regions, the cranium, mandible, and lower second molar, revealed differences amongst regions in the distribution of morphological disparity. Morphological distances calculated from molar dental morphology are not necessarily correlated with those from the mandible or cranium included here, and few significant correlations were identified between regions, despite the functional association of the mandible and mandibular molar. In the two clades studied, the three regions also differed in the degree of covariation between morphological and phylogenetic distances. Additionally, while the contours of the disparity through time curves were broadly similar across the three regions in strepsirrhines and platyrrhines, the position of the calculated curves relative to the curves based on simulations under a Brownian motion model differed between regions, affecting conclusions about how morphological variation is partitioned amongst subclades within the radiation. Similarly, conclusions concerning the amount of disparity within a group such as a primate family were affected by region analyzed. Non-redundancy of skeletal regions in analyses of diversification may limit the wider applicability of conclusions from particular regions such as the dentition. If this is true of other mammalian groups, conclusions made on the basis of dental disparity regarding the timing and extent of adaptive radiations in groups such as multituberculates (Wilson et al., 2012) or ungulates (Jernvall et al., 1996) might alter if other regions are examined.

The results presented here suggest that caution should be taken when inferring the timing or causation of organismal diversification from an isolated region, as it may not be representative of wider morphological disparity. However, it is possible that diversity in one region reflects a particular aspect of ecological adaptation or evolutionary history more strongly than in others, and such a case could be argued for mammalian dentition and diet. Some aspects of the analyses of dental morphology discussed above do indicate that consideration of diversification in the dentition has the potential to add information to other types of analyses, for example alteration in the body size range or in numbers of taxa. Firstly, the lower association between the phylogenetic distance and the molar morphological distances, and the wider separation of the molar diversification curve from the predicted curve in both clades, indicate that the information from molar shape is not redundant with respect to information on phylogenetic history. Additionally, the fact that diversity in dental morphology can be related to diversity in ecological adaptation, but not obviously to the age of the clade or the body size range, (e.g., the unusually high disparity of the lemurids) might indicate that dental morphology and possibly also mandibular disparity, when available, are particularly useful to indicate ecological diversity.

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*Table 3.1. List of strepsirrhine species and sample sizes*

| **Family** | **Species** | **Skull/Mandible** | **Molar** |
|---|---|---|---|
| Lorisidae | *Arctocebus calabarensis* | 6 | 4 |
| | *Loris tardigradus* | 5 | 4 |
| | *Nycticebus coucang* | 11 | 4 |
| | *Perodicticus potto* | 5 | 5 |
| Galagidae | *Euoticus elegantulus* | 6 | 5 |
| | *Galago alleni* | 5 | 5 |
| | *Galago moholi* | 5 | 4 |
| | *Galago gallarum* | 5 | 2 |
| | *Galagoides demidoff* | 6 | 4 |
| | *Otolemur crassicaudatus* | 7 | 5 |
| Cheirogaleidae | *Cheirogaleus major* | 6 | 2 |
| | *Cheirogaleus medius* | 5 | 1 |
| | *Microcebus griseorufus* | 5 | 9 |
| | *Mirza coquereli* | 3 | 2 |
| | *Phaner furcifer* | 5 | 2 |
| Indriidae | *Avahi laniger* | 6 | 8 |
| | *Indri indri* | 7 | 3 |
| | *Propithecus diadema* | 7 | 3 |
| | *Propithecus verreauxi* | 8 | 3 |
| Lemuridae | *Eulemur fulvus* | 3 | 2 |
| | *Eulemur rufus* | 4 | 3 |
| | *Hapalemur griseus* | 7 | 8 |
| | *Hapalemur simus* | 2 | 2 |
| | *Lemur catta* | 6 | 4 |
| | *Varecia variegata* | 6 | 5 |
| Lepilemuridae | *Lepilemur mustelinus* | 6 | 5 |

*Table 3.2. List of platyrrhine species and sample size*

| **Family** | **Species** | **Skull/Mandible** | | **Molar** |
|---|---|---|---|---|
| | | **M** | **F** | |
| Atelidae | *Alouatta palliata* | 5 | 5 | 7 |
| | *Alouatta seniculus* | 6 | 6 | 9 |
| | *Ateles belzebuth* | 5 | 6 | 6 |
| | *Ateles geoffroyi* | 4 | 5 | 7 |
| | *Brachyteles arachnoides* | 3 | 5 | 1 |
| | *Lagothrix lagotricha* | 10 | 10 | 9 |
| Pitheciidae | *Cacajao calvus* | 5 | 5 | 7 |
| | *Cacajao melanocephalus* | 5 | 4 | 5 |
| | *Chiropotes albinasus* | 3 | 5 | 6 |
| | *Chiropotes satanas* | 5 | 5 | 6 |
| | *Pithecia monachus* | 6 | 6 | 8 |
| | *Pithecia pithecia* | 5 | 5 | 7 |
| | *Callicebus donacophilus* | 3 | 3 | 4 |
| | *Callicebus moloch* | 8 | 5 | 11 |
| | *Callicebus torquatus* | 3 | 3 | 7 |
| Cebidae | *Aotus azarae* | 5 | 5 | 5 |
| | *Aotus nigriceps* | 5 | 4 | 13 |
| | *Cebus apella* | 4 | 4 | 10 |
| | *Cebus capucinus* | 4 | 4 | 7 |
| | *Saimiri boliviensis* | 5 | 5 | 9 |
| | *Saimiri sciureus* | 5 | 5 | 8 |
| Callitrichidae | *Cebuella pygmaea* | 6 | 6 | 4 |
| | *Callimico goeldii* | 2 | 1 | 6 |
| | *Callithrix penicillata* | 2 | 3 | 2 |
| | *Leontopithecus rosalia* | 1 | 1 | 6 |
| | *Mico argentata* | 3 | 5 | 5 |
| | *Saguinus fuscicollis* | 4 | 4 | 4 |
| | *Saguinus geoffroyi* | 6 | 4 | 3 |
| | *Saguinus midas* | 6 | 8 | 3 |
| | *Saguinus mystax* | 4 | 4 | 2 |
| | *Saguinus oedipus* | 5 | 5 | 3 |

*Table 3.3. Cranial measurements, as illustrated in Figure 3.2 (*=contributing to the geometric mean)*

| Number | Measurement | Description |
|---|---|---|
| C01 | Orbital height* | Maximum vertical dimension of orbit |
| C02 | Orbital breadth | Width of orbit, orthogonal to C01, at superior margin of lacrimal bone |
| C03 | Lower facial height* | From inferior limit of orbit to inferior edge of maxilla |
| C04 | Interorbital breadth | Distance between orbits, at upper limit of lacrimal bone |
| C05 | Biparietal breadth* | Maximum width across calvarium |
| C06 | Bizygomatic breadth | Maximum width across the left and right zygomatic arches, orthogonal to long axis of skull |
| C07 | Width at postorbital constriction | Minimum width at postorbital constriction |
| C08 | Skull length* | Distance from the base of the incisors (prosthion) to the most posterior point on the occiput in the median sagittal plane (opisthocranion) |
| C09 | Calvarial length | From median sagittal junction of nasal and frontal bones (nasion) to opisthocranion |
| C10 | Anterior palatal width | Width of palate immediately posterior to upper incisors, between canines. |
| C11 | Posterior palatal width* | Width of palate at first molar |
| C12 | Zygomatic arch length* | From external acoustic meatus to anterior edge of zygomatic arch (anterior termination of masseter origin scar) |
| C13 | Snout length | C8 minus C9 (not illustrated) |

*Table 3.4. Mandibular measurements, as illustrated in Figure 3.3 (P=taken from a digital photograph, *= contributing to the geometric mean)*

| Number | Measurement | Description |
|---|---|---|
| Ma01 | Breadth of mandibular corpus* | Thickness of the body of mandible measured between m1 and m2 or at m1 (callitrichids) |
| Ma02 | Height of mandibular corpus* | Height of mandibular body, from inferior edge to base of teeth, at same point as Ma01 |
| Ma03 | Symphyseal height | Long axis of mandibular symphysis, from base of first lower incisors (lingual) to inferior edge of the symphysis |
| Ma04 | Symphyseal thickness | Maximum anteroposterior thickness of mandibular symphysis, orthogonal to Ma03 |
| Ma05 | Height of mandibular ramus* | From inferior edge of mandibular ramus, to condylar process perpendicular to occlusal plane. |
| Ma06 | Width of mandibular ramus* | Width of mandibular ramus, at level of molar occlusal surface, parallel to occlusal plane. |
| Ma07 | Condyle height (P) | Height of condyle, perpendicular from line intersecting crown base of first postcanine tooth and second molar |
| Ma08 | Coronoid height (P) | Height of coronoid process, perpendicular from same reference line as Ma07 |
| Ma09 | Maximum length of mandible* | Distance from condyle to base of lower first incisors (labial side) |
| Ma10 | Length of postcanine tooth row | Length from most anterior premolar to most posterior molar. |
| Ma11 | Width of postcanine tooth row | Greatest width of the dentition orthogonal to Ma10 |
| Ma12 | Width of mandibular condyle | Maximum mediolateral diameter of condylar head |
| Ma13 | Length of mandibular condyle | Maximum anteroposterior diameter of condylar head, orthogonal to Ma12 |
| Ma14 | Anterior dentition width | From medial edge of the canine or second premolar (in strepsirrhines) to midline of mandible |
| Ma15 | Temporalis lever arm | Measured with cranium and mandible in articulation, teeth in centric relation - from external acoustic meatus to the tip of the coronoid process of the mandible (not illustrated) |

*Table 3.5: Molar measurements, as illustrated in Figure 3.4 (P=taken from a photograph, CT=taken on a 3D digital model, * =contributing to the geometric mean)*

| Number | Measurement | Description |
|---|---|---|
| Mo01 | Molar length* (P) | Length of tooth parallel to long axis of tooth/tooth row from most mesial to most distal point visible in occlusal view. |
| Mo02 | Trigonid width * (P) | Width of trigonid region of tooth, orthogonal to Mo01 |
| Mo03 | Talonid width* (P) | Width of talonid region of tooth, orthogonal to Mo01 |
| Mo04 | Trigonid height * (P) | Height of trigonid, measured on lingual side of tooth (crown base to metaconid tip). Taken on photograph in lingual view |
| Mo05 | Talonid height* (P) | Height of talonid, measured on lingual side of tooth (crown base to entoconid tip). Taken on photograph in lingual view |
| Mo06 | Occlusal area (square root) (P) | Area of outline of tooth crown, taken from a photograph in occlusal view |
| Mo07 | Trigonid area (square root) (P) | Area within cusps and crests of trigonid basin |
| Mo08 | Talonid area (square root) (P) | Area within cusps and crests of talonid basin |
| Mo09 | Paracristid length (CT) | Length of crest issuing mesially from protoconid |
| Mo10 | Protocristid (CT) | Length of crest issuing lingually from protoconid; protoconid tip to notch/ lowest point between protoconid and metaconid (buccal section of protocristid) |
| Mo11 | Postmetacristid length (CT) | Length of crest issuing distally from metaconid; metaconid tip to lowest point on tooth crown between metaconid and entoconid (talonid notch) |
| Mo12 | Pre-entoconid length (CT) | Length of crest/distance from base of talonid notch to tip of entoconid |
| Mo13 | Posthypoconid length (CT) | Length of crest issuing distolingually from hypoconid; hypoconid tip to crest terminus on distal margin of talonid basin |
| Mo14 | Cristid obliqua length (CT) | Length of cristid obliqua, from hypoconid to point of contact with trigonid. |

*Table 3.6. Summary of within and between family mean morphological distances from the pPCA of platyrrhines alone.*

| | | Atelid | Callitrichid | Cebid | Pitheciid |
|---|---|---|---|---|---|
| Cranium (F) | Atelid | **1.6824** | | | |
| | Callitrichid | 2.9734 | **1.0806** | | |
| | Cebid | 3.0085 | 1.8123 | **1.6269** | |
| | Pitheciid | 1.9087 | 1.8035 | 1.6987 | **0.9933** |
| Cranium (M) | Atelid | **1.8963** | | | |
| | Callitrichid | 2.9322 | **0.9080** | | |
| | Cebid | 2.8066 | 1.7278 | **1.8921** | |
| | Pitheciid | 1.8112 | 1.8465 | 1.7651 | **0.9914** |
| Mandible (F) | Atelid | **1.3022** | | | |
| | Callitrichid | 2.0285 | **1.5872** | | |
| | Cebid | 2.0523 | 1.9092 | **2.0370** | |
| | Pitheciid | 1.7586 | 2.6401 | 2.4086 | **1.2574** |
| Mandible (M) | Atelid | **1.4860** | | | |
| | Callitrichid | 2.0709 | **1.3599** | | |
| | Cebid | 2.0680 | 1.7727 | **2.0934** | |
| | Pitheciid | 1.9277 | 2.7293 | 2.3496 | **1.1605** |
| Molar | Atelid | **2.5662** | | | |
| | Callitrichid | 2.2132 | **1.6491** | | |
| | Cebid | 2.0953 | 1.6809 | **1.1317** | |
| | Pitheciid | 2.2537 | 2.0276 | 1.7143 | **0.9947** |

*Table 3.7. Summary of within and between family mean morphological distances from the pPCA of strepsirrhines alone.*

| | | Cheirogaleid | Indriid | Lemurid | Lepilemurid | Galagid | Lorisid |
|---|---|---|---|---|---|---|---|
| Cranium | Cheirogaleid | **1.3894** | | | | | |
| | Indriid | 2.0478 | **1.3845** | | | | |
| | Lemurid | 1.9535 | 1.7132 | **1.5748** | | | |
| | Lepilemurid | 1.3194 | 2.2361 | 2.1397 | -- | | |
| | Galagid | 2.2750 | 3.4817 | 3.3832 | 1.8936 | **1.7050** | |
| | Lorisid | 1.7333 | 2.2332 | 2.3955 | 1.6777 | 2.4157 | **1.9835** |
| Mandible | Cheirogaleid | **1.0834** | | | | | |
| | Indriid | 3.9438 | **1.3497** | | | | |
| | Lemurid | 2.3282 | 4.1093 | **2.8657** | | | |
| | Lepilemurid | 1.2362 | 3.232 | 2.2307 | **--** | | |
| | Galagid | 1.1587 | 3.6756 | 2.2168 | 1.163 | **1.1755** | |
| | Lorisid | 1.6234 | 3.1927 | 2.6083 | 1.3572 | 1.5304 | **1.4786** |
| Molar | Cheirogaleid | **1.8019** | | | | | |
| | Indriid | 3.2252 | **0.9379** | | | | |
| | Lemurid | 2.5023 | 1.9036 | **2.1263** | | | |
| | Lepilemurid | 3.2890 | 1.4268 | 2.1458 | -- | | |
| | Galagid | 2.9042 | 1.3106 | 1.9251 | 1.6287 | **1.0850** | |
| | Lorisid | 2.9220 | 1.2133 | 1.9911 | 1.6785 | 1.3254 | **1.5977** |

*Table 3.8: Summary of within and between family mean morphological distances from the pPCA analysis of all species – cranium. The results from the pPCA using female platyrrhines are shown above and the results from the pPCA using male platyrrhines are below. The same specimens contributed to the strepsirrhine species averages for both, the details of the distances may vary, because the shape space is altered by the use of male or female platyrrhines. Abbreviations: A =Atelidae, Ca = Callitrichidae, Ce = Cebidae, P = Pitheciidae, Ch = Cheirogaleidae, I = Indriidae, Lem = Lemuridae, Lep = Lepilemuridae, Lo =Lorisidae, G =Galagidae. Only one species of Lepilemuridae was measured.*

| | | A | Ca | Ce | P | Ch | I | Lem | Lep | G | Lo |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Cranium (female platyrrhines) | A | **1.3994** | | | | | | | | | |
| | Ca | 2.3204 | **0.9135** | | | | | | | | |
| | Ce | 2.5605 | 1.3458 | **1.2725** | | | | | | | |
| | P | 1.5553 | 1.2220 | 1.3352 | **0.6668** | | | | | | |
| | Ch | 1.9381 | 1.5199 | 1.8252 | 1.2969 | **1.0864** | | | | | |
| | I | 1.6020 | 2.1144 | 2.6872 | 1.7904 | 2.3276 | **1.1266** | | | | |
| | Lem | 1.7334 | 2.3596 | 2.7810 | 1.8932 | 1.6868 | 1.4139 | **1.2113** | | | |
| | Lep | 2.2005 | 1.0790 | 1.5192 | 1.1600 | 0.9986 | 1.8353 | 1.9299 | -- | | |
| | G | 3.1403 | 1.8742 | 1.7331 | 2.0962 | 1.9720 | 2.9295 | 2.3708 | 1.6562 | **1.4905** | |
| | Lo | 1.8354 | 1.7070 | 1.8452 | 1.2699 | 1.2936 | 1.6856 | 1.8761 | 1.3662 | 2.1463 | **1.6093** |
| Cranium (male platyrrhines) | A | **1.5562** | | | | | | | | | |
| | Ca | 2.2180 | **0.6681** | | | | | | | | |
| | Ce | 2.1972 | 1.2477 | **1.3785** | | | | | | | |
| | P | 1.3892 | 1.2787 | 1.3015 | **0.6745** | | | | | | |
| | Ch | 1.9644 | 1.3913 | 1.5704 | 1.2932 | **0.8704** | | | | | |
| | I | 1.5591 | 1.6194 | 1.9365 | 1.3005 | 1.9344 | **0.9493** | | | | |
| | Lem | 1.7395 | 1.9063 | 2.1293 | 1.5248 | 1.4283 | 1.2020 | **1.0580** | | | |
| | Lep | 2.1131 | 0.9256 | 1.3174 | 1.2141 | 0.8670 | 1.4626 | 1.5631 | -- | | |
| | G | 2.8988 | 1.7252 | 1.6796 | 2.0162 | 1.6112 | 2.4024 | 1.9709 | 1.3939 | **1.2049** | |
| | Lo | 1.8058 | 1.6171 | 1.5859 | 1.1852 | 1.1659 | 1.4761 | 1.6602 | 1.2501 | 1.8010 | **1.3677** |

*Table 3.9: Summary of within and between family mean morphological distances from the pPCA analysis of all species – mandible. The results from the pPCA using female platyrrhines are shown above and the results from the pPCA using male platyrrhines are below. The same specimens contributed to the strepsirrhine species averages for both, the details of the distances may vary, because the shape space is altered by the use of male or female platyrrhines. Abbreviations: A =Atelidae, Ca = Callitrichidae, Ce = Cebidae, P = Pitheciidae, Ch = Cheirogaleidae, I = Indriidae, Lem = Lemuridae, Lep = Lepilemuridae, Lo =Lorisidae, G =Galagidae. Only one species of Lepilemuridae was measured.*

| | | A | Ca | Ce | P | Ch | I | Lem | Lep | G | Lo |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Mandible | A | **0.8353** | | | | | | | | | |
| | Ca | 1.4874 | **1.1048** | | | | | | | | |
| | Ce | 1.4278 | 1.2718 | **1.3951** | | | | | | | |
| | P | 1.2093 | 1.8361 | 1.7131 | **0.9895** | | | | | | |
| | Ch | 3.1486 | 2.2083 | 2.3295 | 3.5973 | **0.8831** | | | | | |
| | I | 1.1313 | 1.3197 | 1.3529 | 1.5807 | 2.5154 | **0.7686** | | | | |
| | Lem | 3.0177 | 2.3941 | 2.3923 | 3.4730 | 1.5889 | 2.6304 | **1.7790** | | | |
| | Lep | 2.5965 | 1.8498 | 1.8040 | 3.0613 | 1.0294 | 2.0916 | 1.4084 | **--** | | |
| | G | 2.8125 | 2.0519 | 2.1062 | 3.3187 | 0.9398 | 2.3735 | 1.9221 | 0.8866 | **0.8694** | |
| | Lo | 2.4368 | 1.6498 | 1.7894 | 2.8599 | 1.2561 | 2.1304 | 1.7704 | 1.1487 | 1.0901 | **1.0860** |
| Mandible | A | **0.9657** | | | | | | | | | |
| | Ca | 1.4505 | **1.0176** | | | | | | | | |
| | Ce | 1.4019 | 1.2134 | **1.3825** | | | | | | | |
| | P | 1.3389 | 1.8257 | 1.6292 | **1.0678** | | | | | | |
| | Ch | 3.0262 | 2.0882 | 2.3376 | 3.4509 | **0.9272** | | | | | |
| | I | 1.2890 | 1.2952 | 1.4132 | 1.7633 | 2.3526 | **0.7988** | | | | |
| | Lem | 3.0353 | 2.3563 | 2.5029 | 3.4618 | 1.6315 | 2.5701 | **1.8049** | | | |
| | Lep | 2.6212 | 1.7785 | 1.9466 | 3.0471 | 0.9830 | 2.0527 | 1.4366 | -- | | |
| | G | 2.7383 | 1.9584 | 2.1668 | 3.2380 | 1.0001 | 2.2077 | 1.9241 | 0.9560 | **0. 9278** | |
| | Lo | 2.3817 | 1.5847 | 1.8026 | 2.7635 | 1.2495 | 2.0355 | 1.8046 | 1.1562 | 1.1404 | **0.5314** |

*Table 3.10: Summary of within and between family mean morphological distances from the pPCA analysis of all species – molar. Abbreviations: A =Atelidae, Ca = Callitrichidae, Ce = Cebidae, P = Pitheciidae, Ch = Cheirogaleidae, I = Indriidae, Lem = Lemuridae, Lep = Lepilemuridae, Lo =Lorisidae, G =Galagidae. Only one species of Lepilemuridae was measured.*

| | | A | Ca | Ce | P | Ch | I | Lem | Lep | G | Lo |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Molar | A | **1.3007** | | | | | | | | | |
| | Ca | 1.2433 | **0.7882** | | | | | | | | |
| | Ce | 1.1649 | 0.7714 | **0.6128** | | | | | | | |
| | P | 1.2170 | 1.2024 | 1.0095 | **0.6358** | | | | | | |
| | Ch | 2.4381 | 2.3010 | 2.2805 | 1.7885 | **1.5081** | | | | | |
| | I | 1.3908 | 1.5065 | 1.6955 | 1.9579 | 1.9528 | **0.6927** | | | | |
| | Lem | 1.7807 | 1.6421 | 1.7852 | 1.7443 | 2.1131 | 1.6155 | **1.7140** | | | |
| | Lep | 1.7137 | 1.6751 | 1.9790 | 2.2255 | 3.0153 | 0.9388 | 1.7693 | -- | | |
| | G | 1.3847 | 1.0146 | 1.1951 | 1.6342 | 2.6036 | 1.1693 | 1.5990 | 1.3847 | **0.8910** | |
| | Lo | 1.3087 | 1.2380 | 1.3357 | 1.6199 | 2.6263 | 1.0171 | 1.6446 | 1.3577 | 1.1352 | **1.3496** |

*Table 3.11. Results of Mantel matrix correlation between morphological regions. Results in bold text are significant at an alpha=0.05 level. Under a Bonferroni-Holm correction for multiple comparisons, only the mandible/cranium comparison in male platyrrhines remains significant.*

| **Regions** | **Correlation coefficient** | **Probability** |
|---|---|---|
| Platyrrhine Cranial (F) - Mandible (F) | **0.264** | **0.0170** |
| Platyrrhine Cranial (F) - Molar | **0.360** | **0.0037** |
| Platyrrhine Mandible (F) - Molar (F) | 0.086 | 0.1583 |
| Platyrrhine Cranial (M) - Mandible (M) | **0.377** | **0.0007*** |
| Platyrrhine Cranial (M) - Molar | **0.307** | **0.0305** |
| Platyrrhine Mandible (M) - Molar | 0.135 | 0.0757 |
| Strepsirrhine Cranial-Mandible | **0.159** | **0.0442** |
| Strepsirrhine Cranial-Molar | -0.046 | 0.6748 |
| Strepsirrhine Mandible-Molar | 0.012 | 0.4202 |

*Table 3.12. Results of Mantel matrix correlation between morphological and phylogenetic distances. Results in bold text are significant at an alpha=0.05 level, and these results remain significant under a Bonferroni-Holm correction for multiple comparisons.*

| **Regions** | **Correlation coefficient** | **Probability** |
|---|---|---|
| Platyrrhine Cranial (F) | **0.372** | **<0.0001** |
| Platyrrhine Cranial (M) | **0.375** | **<0.0001** |
| Platyrrhine Mandible (F) | **0.402** | **<0.0001** |
| Platyrrhine Mandible (M) | **0.481** | **<0.0001** |
| Platyrrhine Molar | **0.240** | **<0.0001** |
| Strepsirrhine Cranial | **0.379** | **0.0005** |
| Strepsirrhine Mandible | -0.013 | 0.5126 |
| Strepsirrhine Molar | 0.067 | 0.1272 |

**Fig. 3.1.** Phylogeny of all taxa; horizontal axis indicates date of divergence (mya).

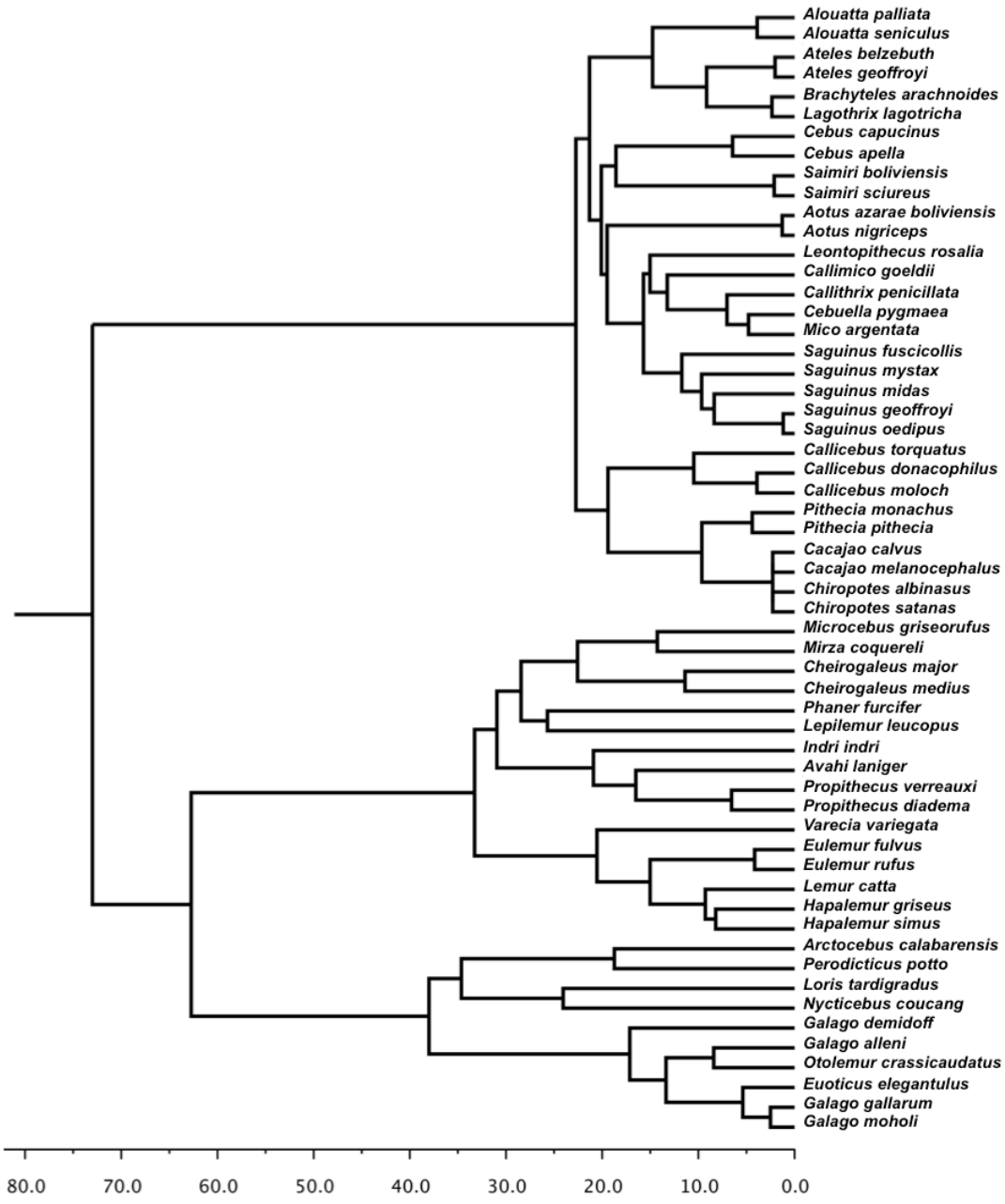


**Fig. 3.2.** Illustration of cranial measurements on a *Cebus* skull in anterior (top left), superior (top right) and ventral (bottom) views.

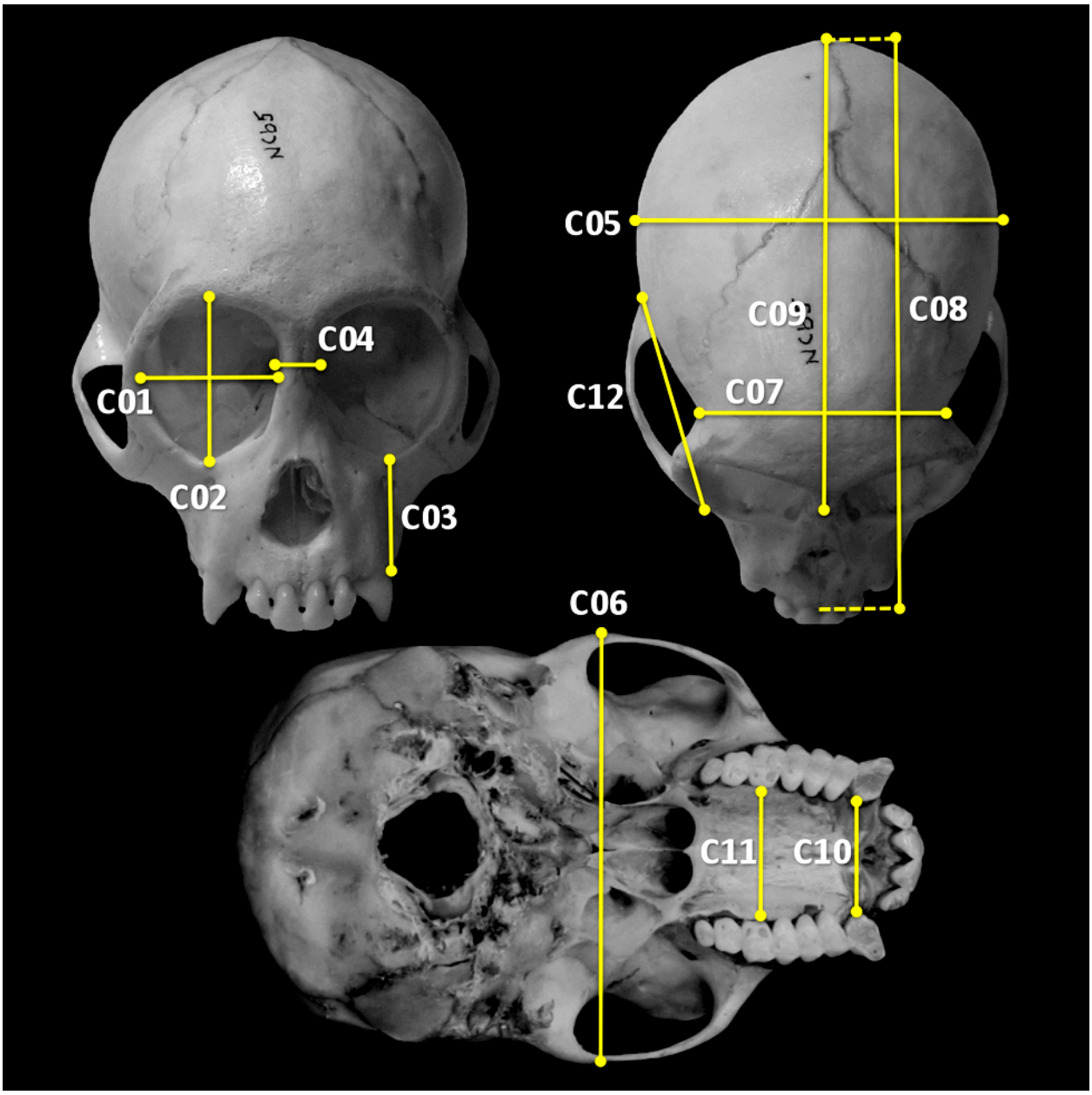


**Fig. 3.3.** Illustration of mandibular measurements on a *Cebus* mandible in superior/occlusal (left) and right lateral (top and bottom right) views.

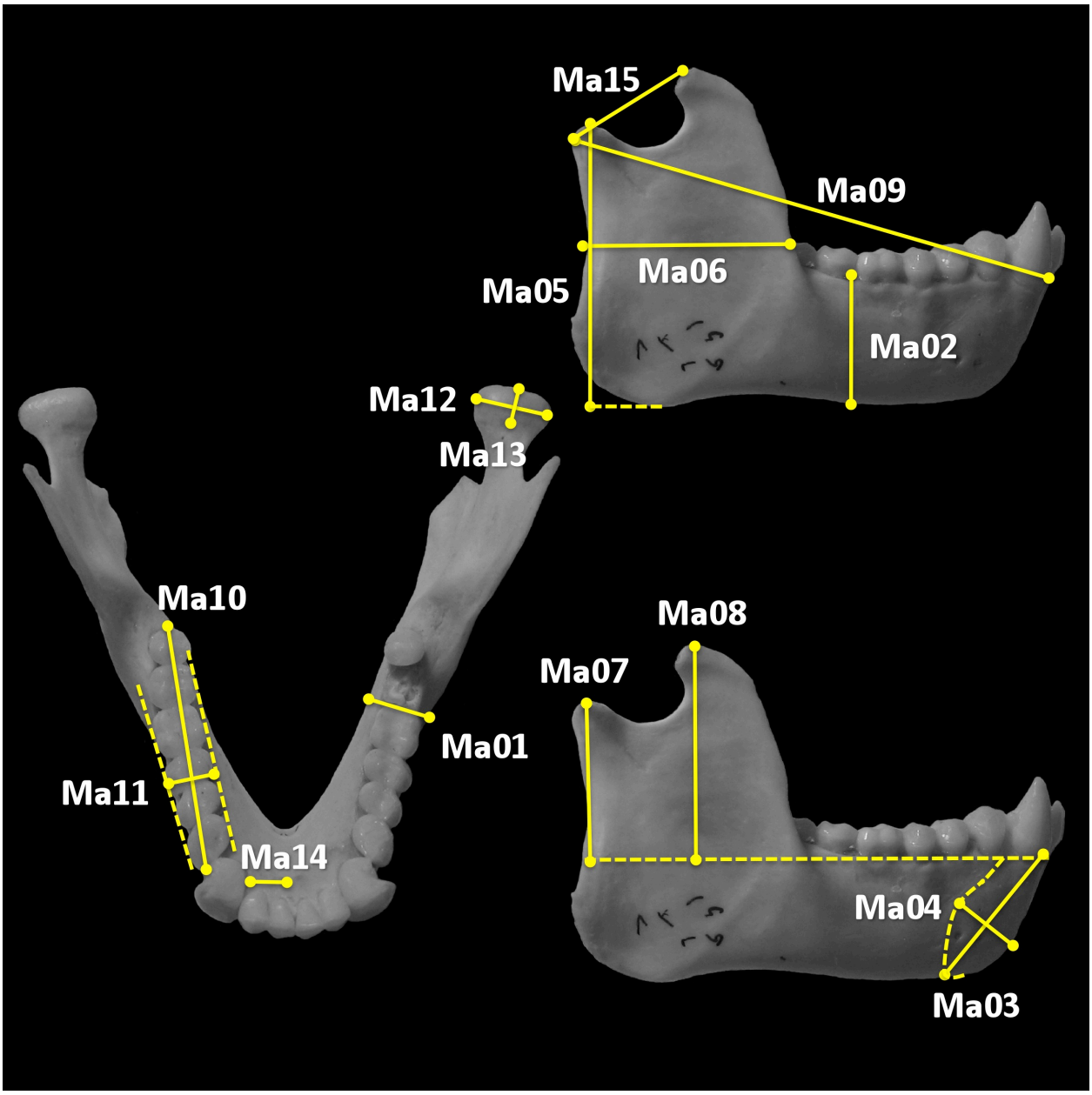


**Fig. 3.4.** Illustration of measurements on a *Cebus* right mandibular molar (m/2) in occlusal view (top left and top right), buccal/occlusal oblique view (bottom left), and lingual view (bottom right).

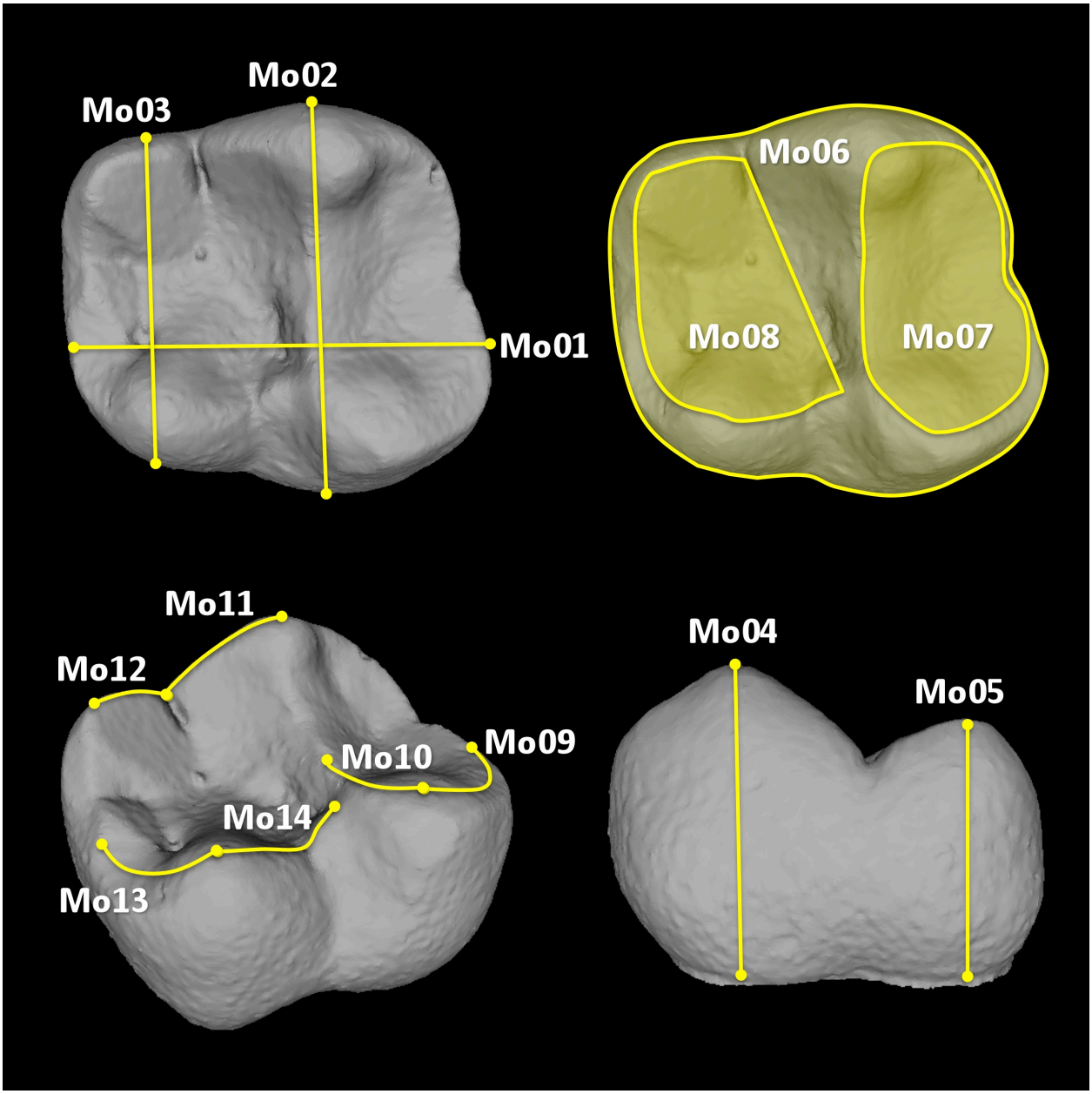


**Fig. 3.5.** Comparisons of regional morphological distances in platyrrhine females for cranial and mandibular morphological distances. Histograms of the simulated correlation coefficients shown on the left with a vertical line indicating the observed value. Scatterplots of the distance comparisons shown on the right.

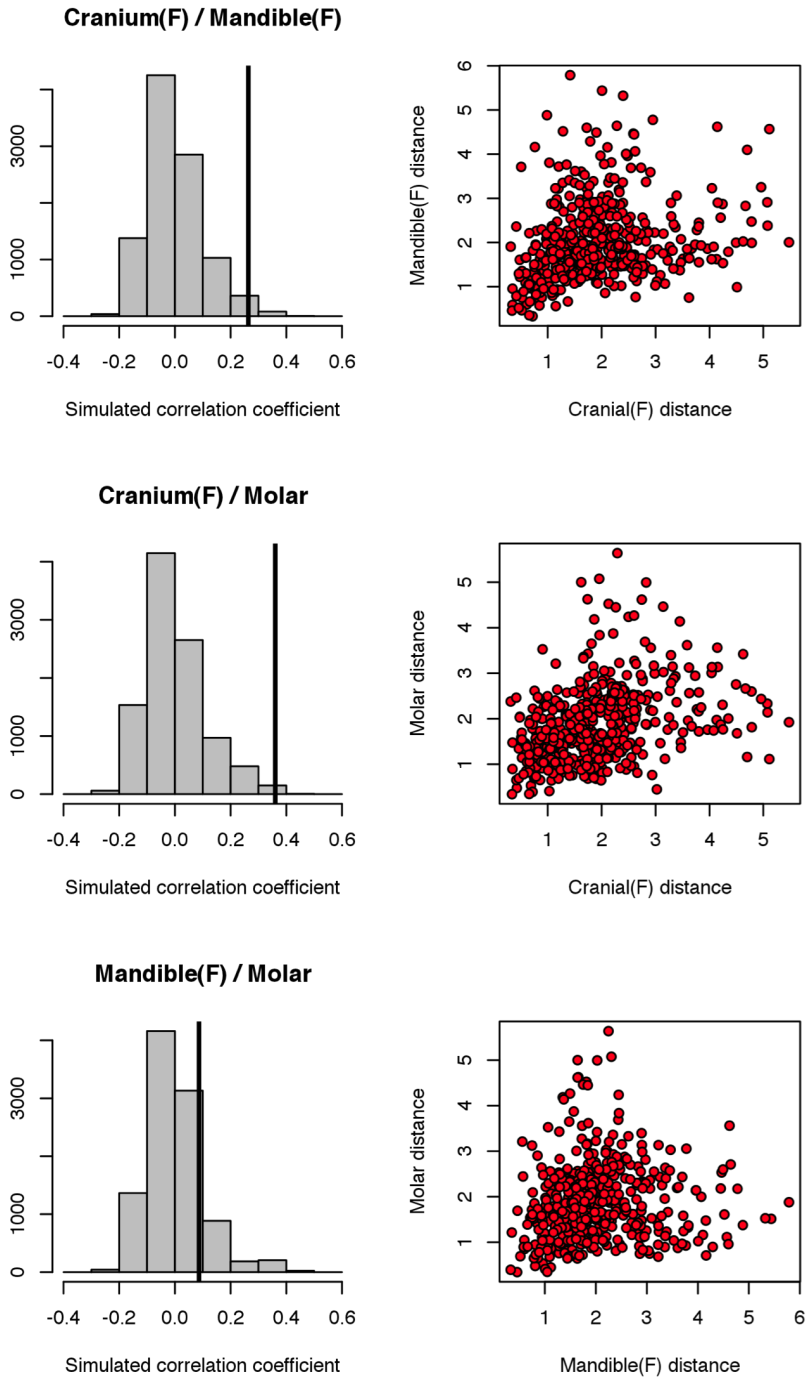


**Fig. 3.6.** Comparisons of regional morphological distances in platyrrhines using the male dataset for cranial and mandibular morphological distances. Histograms of the simulated correlation coefficients shown on the left with a vertical line indicating the observed value. Scatterplots of the distance comparisons shown on the right.

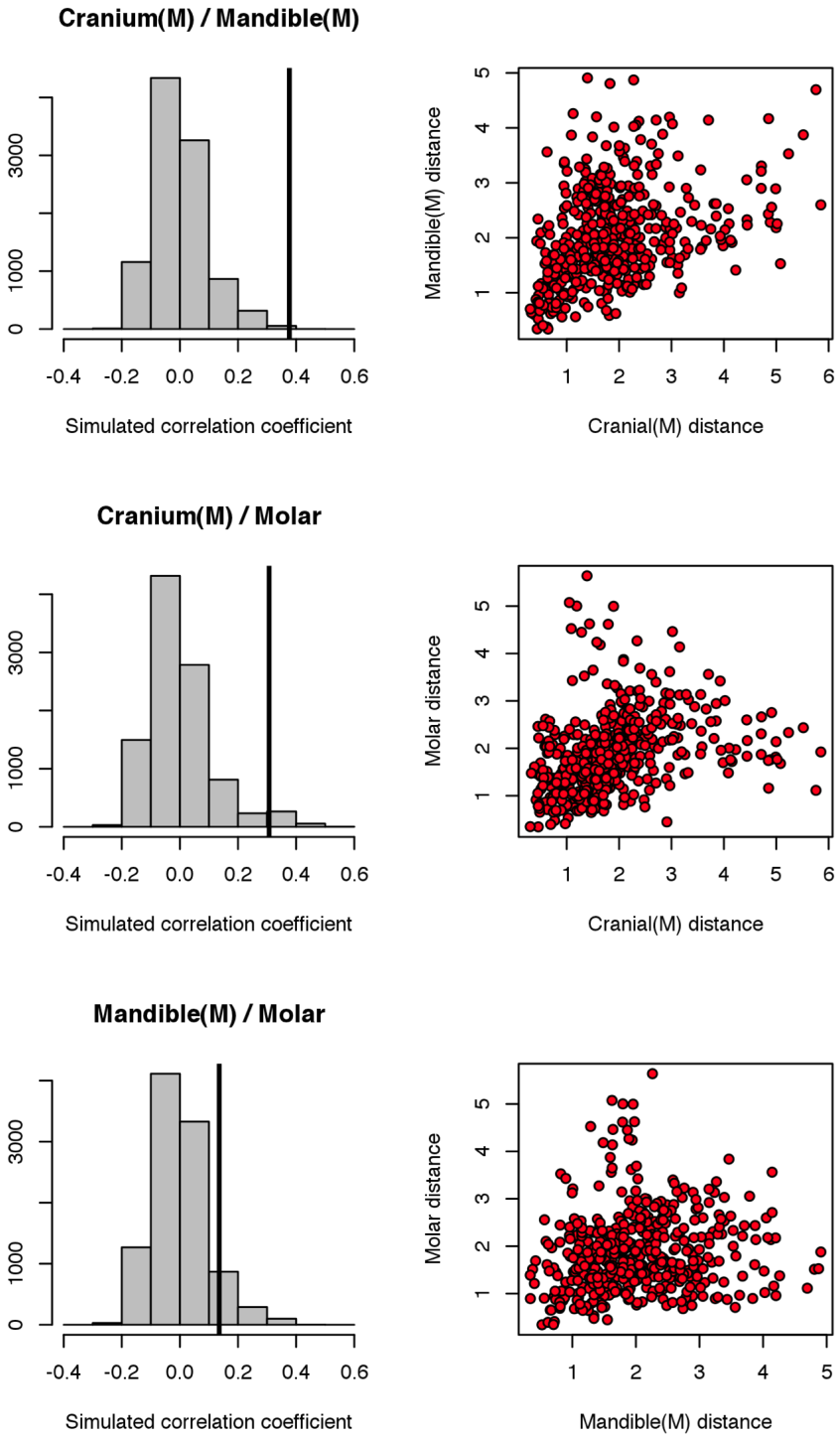


**Fig. 3.7.** Comparisons of regional morphological distances in strepsirrhines. Histograms of the simulated correlation coefficients shown on the left with a vertical line indicating the observed value. Scatterplots of the distance comparisons shown on the right.

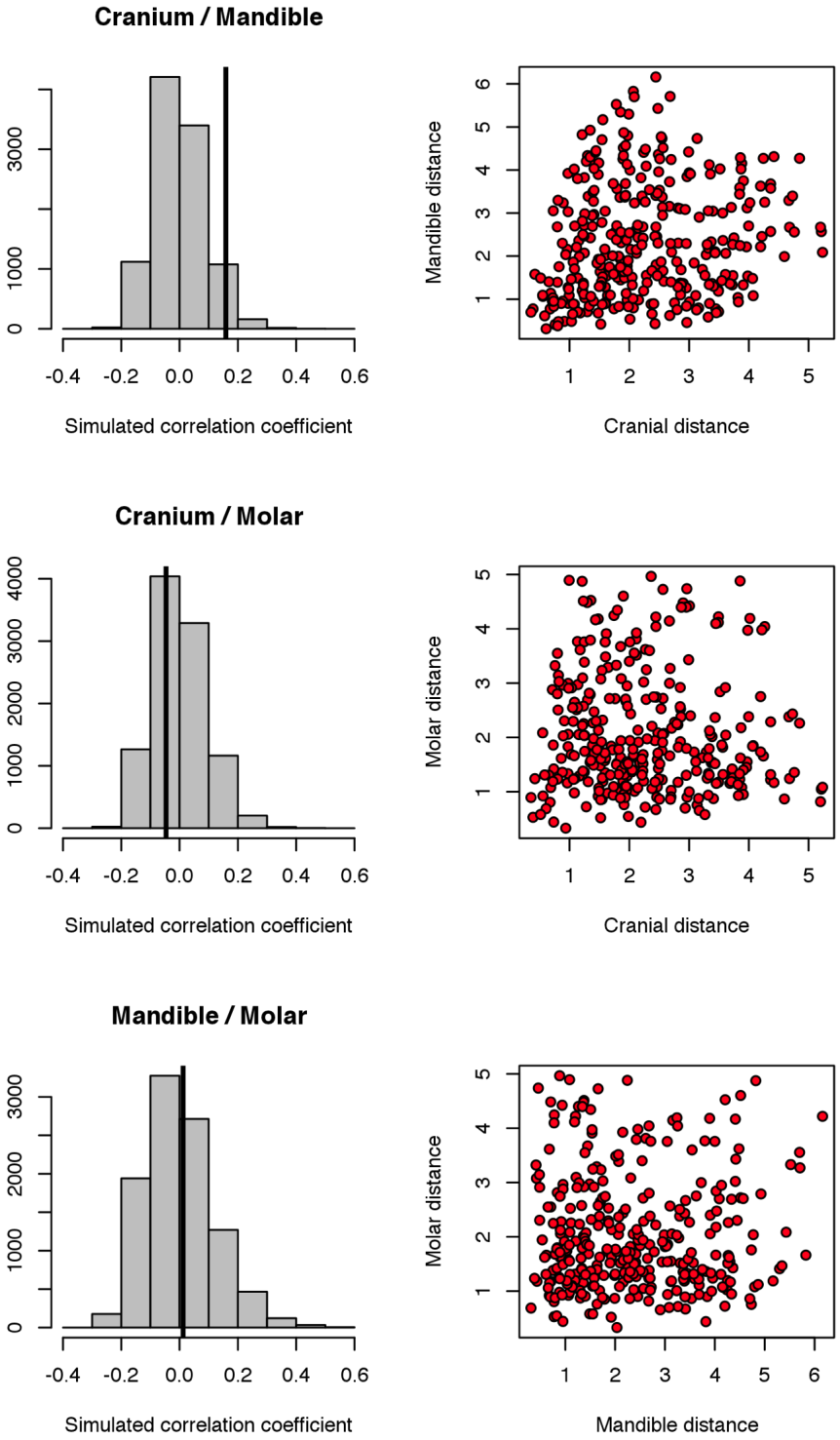


**Fig. 3.8.** Comparisons of regional morphological distances and phylogenetic distances in platyrrhines. Histograms of the simulated correlation coefficients shown above with a vertical line indicating the observed value. Scatterplots of the distance comparisons shown below.

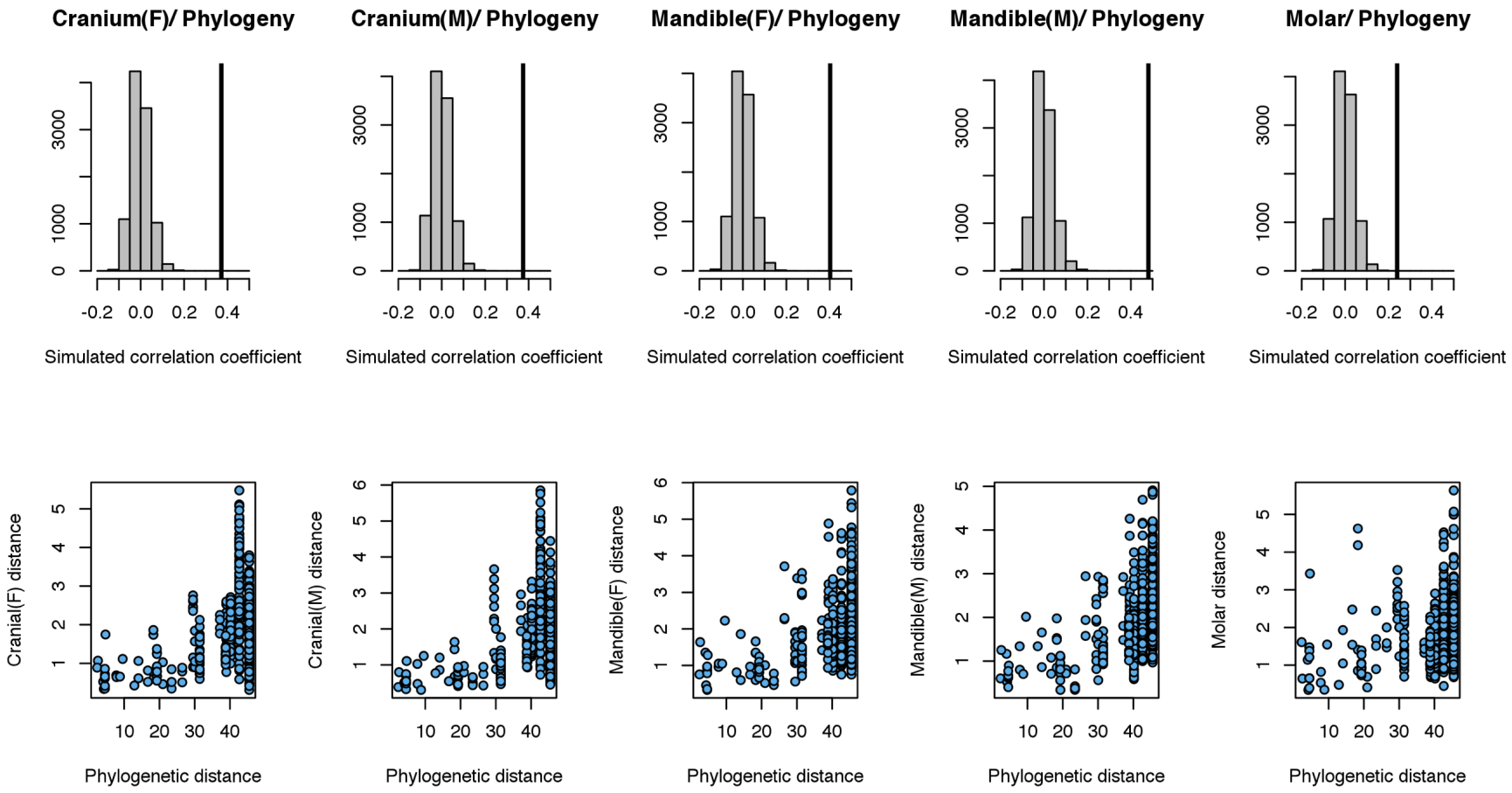


**Fig. 3.9.** Comparisons of regional morphological distances and phylogenetic distances in strepsirrhines. Histograms of the simulated correlation coefficients shown above with a vertical line indicating the observed value. Scatterplots of the distance comparisons shown below.

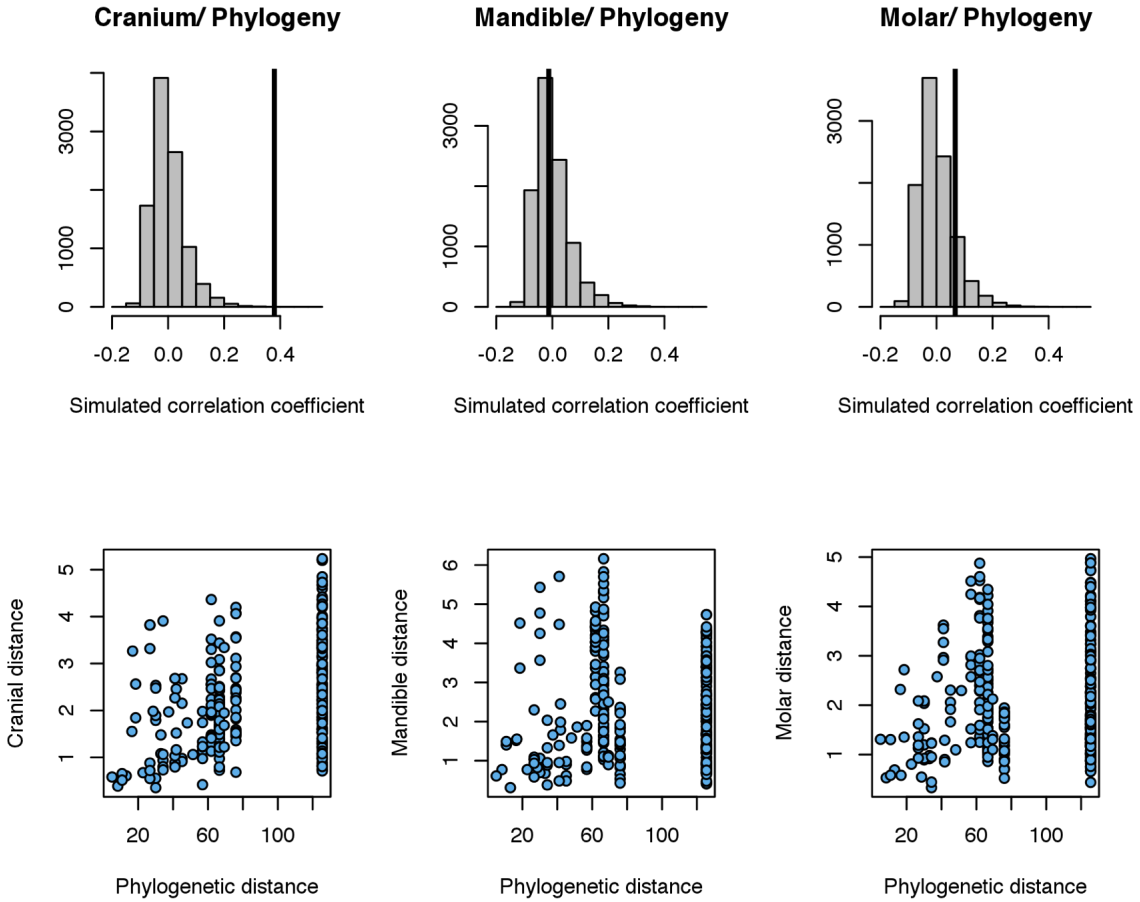


**Fig. 3.10.** Disparity through time analyses for the cranium, mandible, and molar. Platyrrhines are shown above (cranium and mandible are from the analysis of female platyrrhines) and results from strepsirrhines are shown below. Dashed lines represent the predicted patterns of diversification based on simulations under a Brownian motion model of morphospace occupation. MDI is the area between the simulated and observed curve, calculated for the time range between 0.2–0.8 of the time since taxon origin. In platyrrhines, time on the x axis represents approximately 25 mya (0) to present (1), while in strepsirrhines, time on the x axis represents approximately 63 mya (0) to present (1).

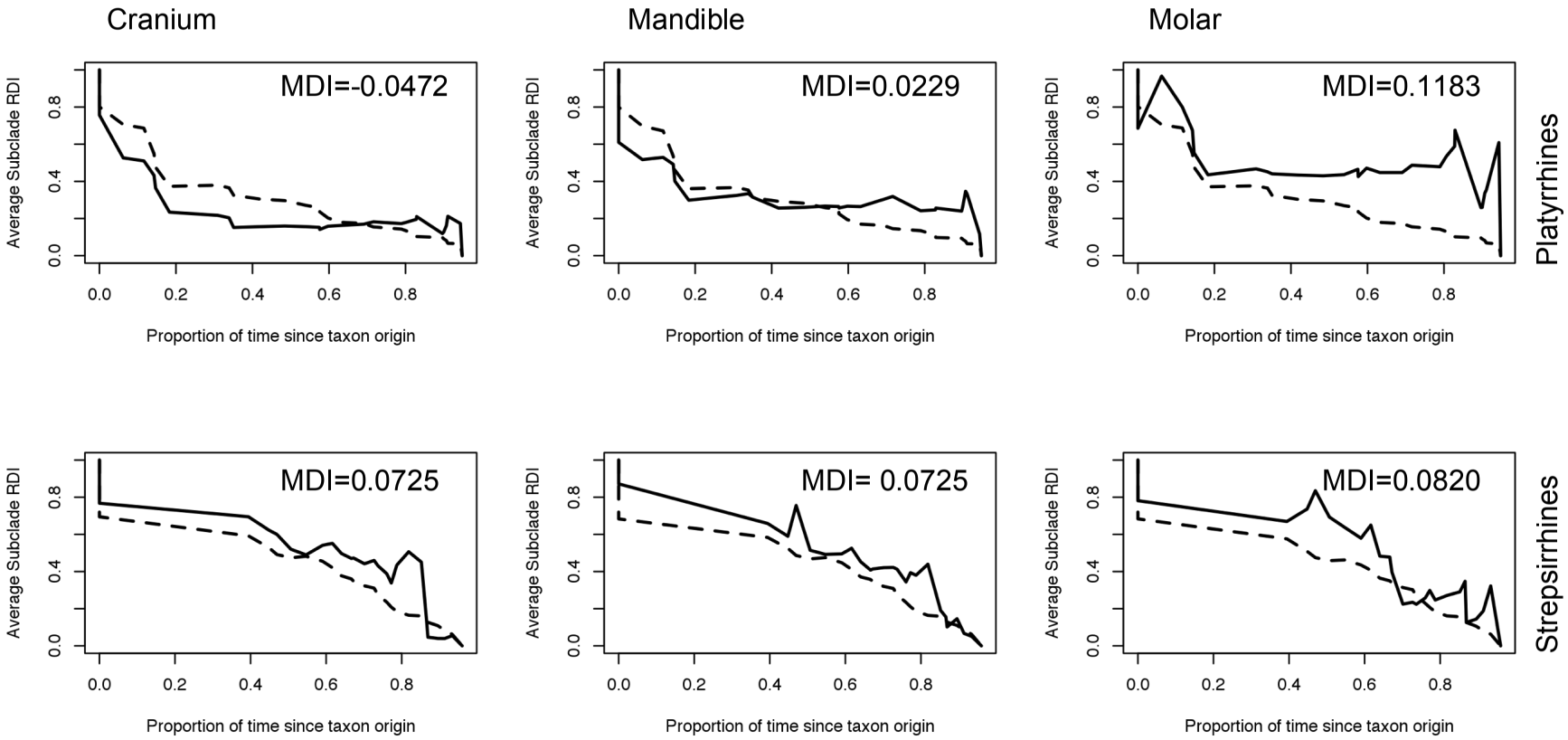


**Fig. 3.11.** Comparisons of disparity through time curves for the cranium and mandible obtained from platyrrhine females (above) and males (below).

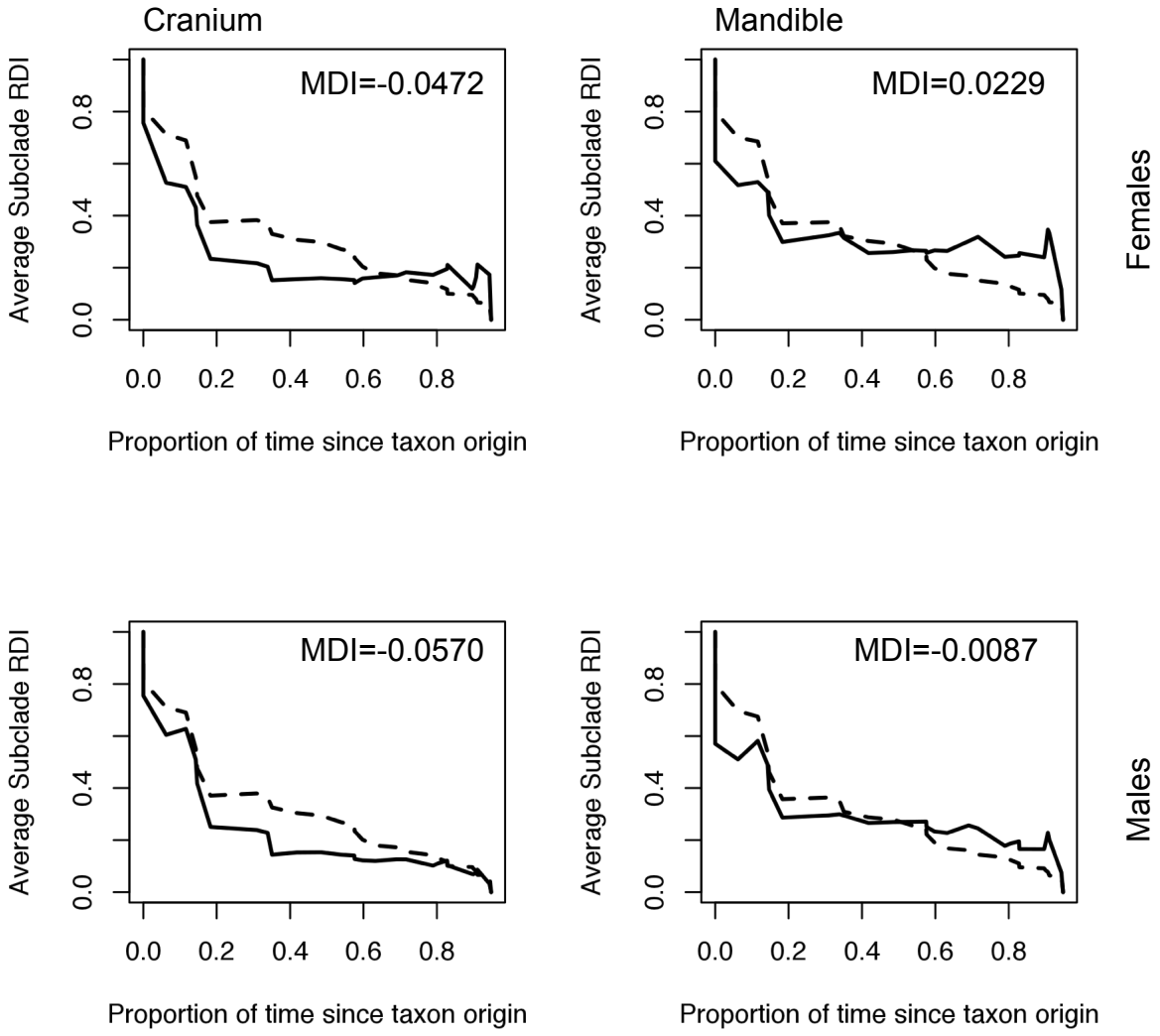


**Fig. 3.12.** Histograms of intertaxon distances for the cranial pPCA (analysis with female platyrrhines left, analysis with male platyrrhines right). Families: I = indriids (red), Lo =lorisids (dark blue), Ch = cheirogaleids (gold), Le = lemurids (pink), Ce = cebids (orange), A =atelids (green), G =galagids (brown), P = pitheciids (turquoise), Ca = callitrichids (purple). Dashed lines represent the 95$^{th}$ percentile.

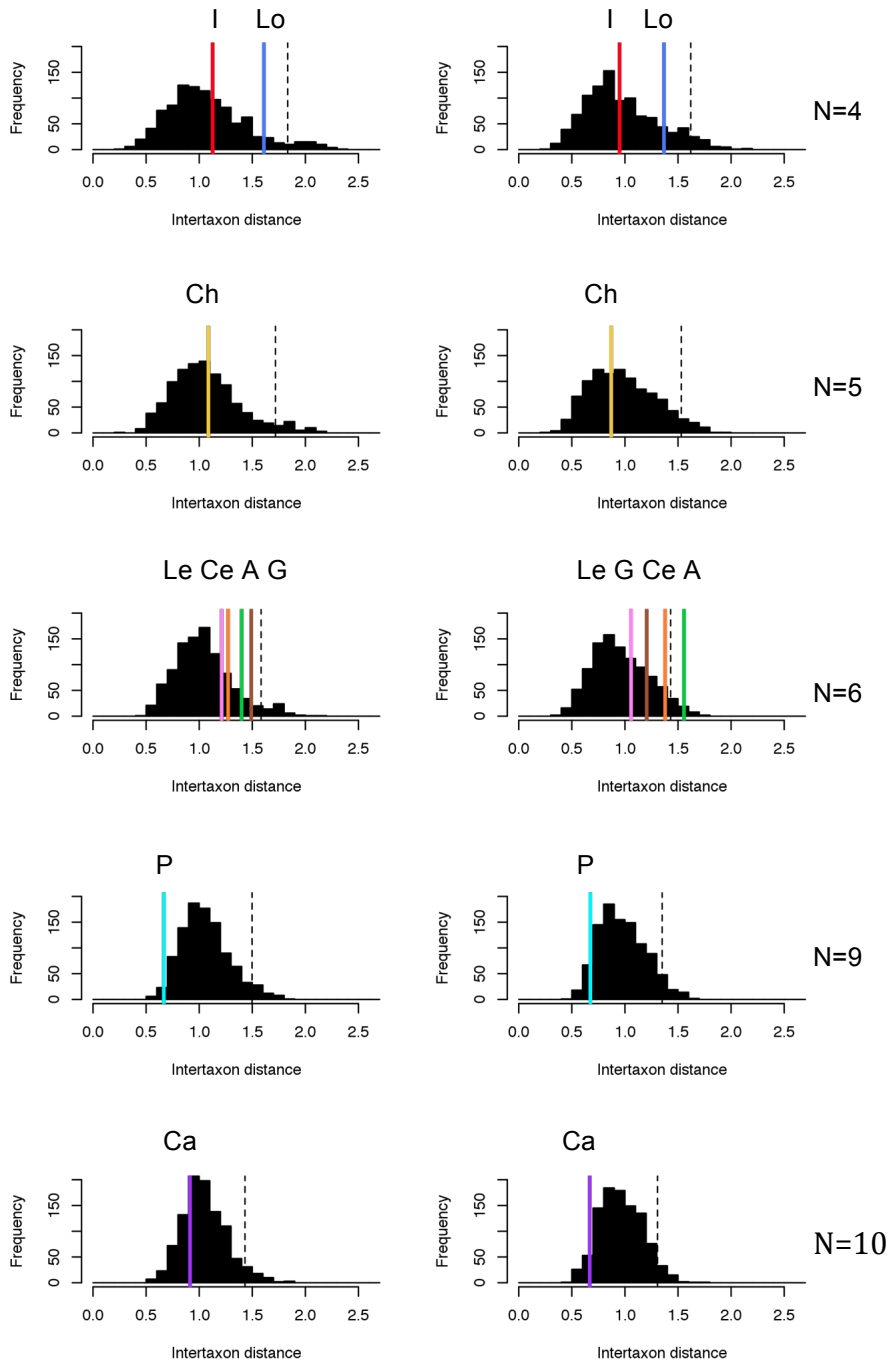


**Fig. 3.13.** Histograms of intertaxon distances for the mandible pPCA (analysis with female platyrrhines left, analysis with male platyrrhines right). Colors and family abbreviations as for Figure 3.12. Dashed lines represent the 95$^{th}$ percentile.

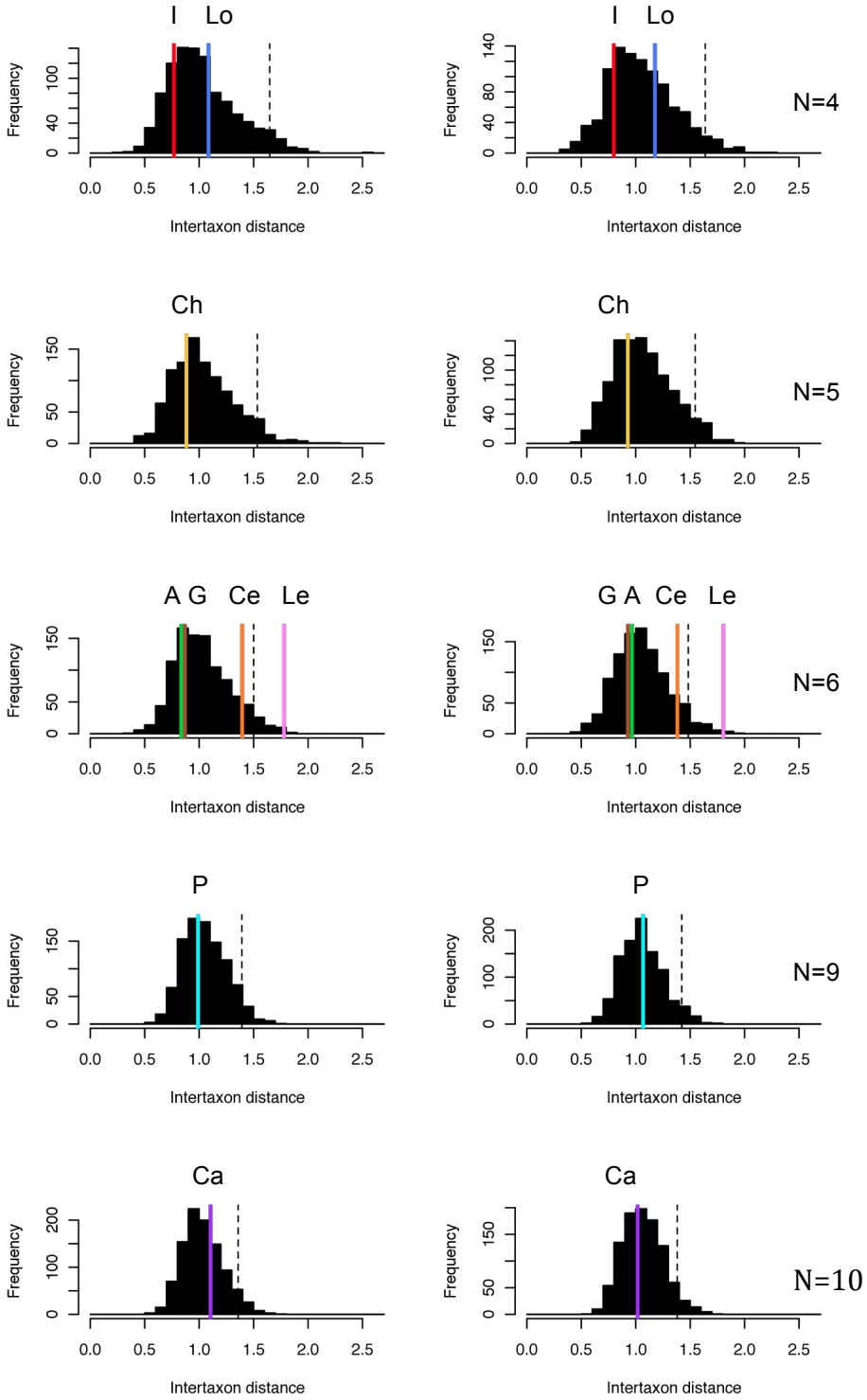
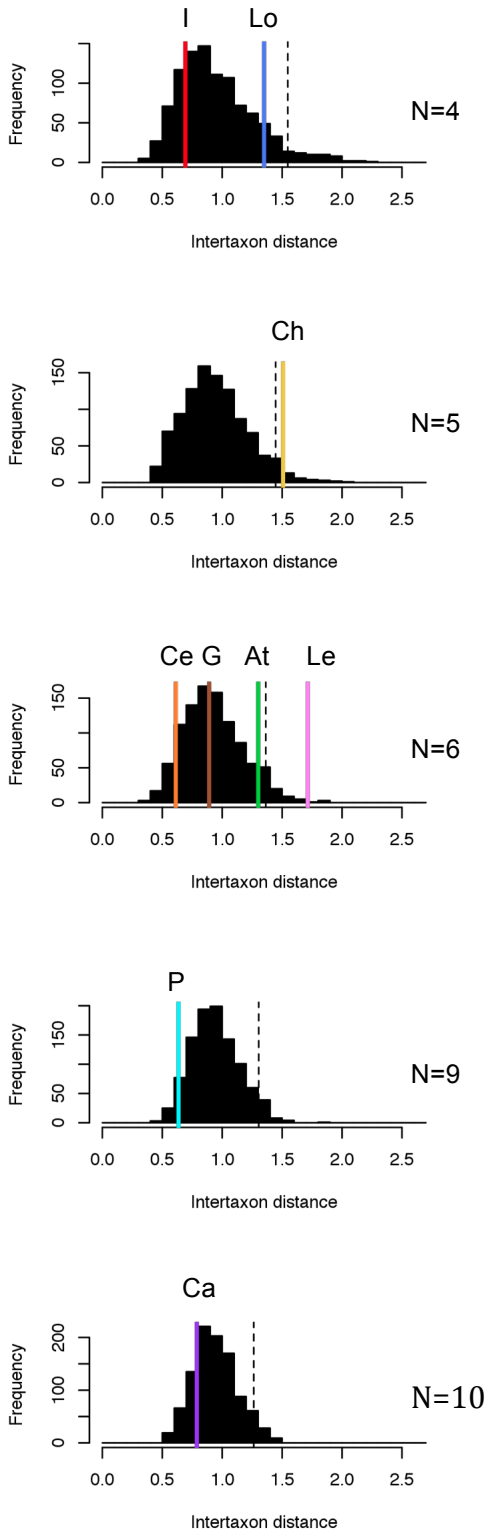


**Fig. 3.14.** Histograms of intertaxon distances for the molar pPCA. Colors and family abbreviations as for Figure 3.12. Dashed lines represent the 95$^{th}$ percentile.



**Supplemental:** R code for functions written for the analysis of relative diversity within subgroups

Function "center" to center PCs on the origin, run after dataset has been separated into families.

```
center <- function (X1){
avg<- mean (X1)
(X1 - avg)
}
```

Function "AvgDist" to select a set number of species and calculate the average distance between them.

```
#calculating average distances for different group sizes using euclidean
 distances

#X1=dataframe in which the species are in rows and the variables are in
 columns, X2=total rows in the dataframe (total number of species), X3=number
 of species to be sampled, X4=specifies the columns to be used for the
 distance calculation in the format "1:n" n will equal the triangular number
 of the number of species to be sampled (X3) minus one.

#first program a function for calculating a triangular number

triangular <-function(x1){
((x1)^2)/2+1/2*(x1)}


#then use the following (method of distance calculation - Euclidean)

AvgDist <- function (X1,X2,X3,X4) {
Sample <-X1[sample(X2,X3, replace=TRUE),]
Sample.D<-dist(Sample[,X4], method="euclidean",diag=FALSE,upper=FALSE, p=2)
mean(Sample.D[1:(triangular(X3-1))])
 }
```

## Chapter 4: 3D geometric morphometric analyses of size and shape diversity in the lower second molar of prosimians and platyrrhines

*ABSTRACT: Dental morphology contributes to the paleontological analysis of phylogenetic relationships and ecological variation, and is also utilized for the alpha taxonomy of fossil species. The utility of teeth for dietary analysis has motivated detailed investigation of dental shape in primates, but the relative strength of dietary influence compared to possible size-associated shape change or to phylogenetic signal has not been investigated to the same degree. This may influence best practice for dietary and phylogenetic analyses. In this study, geometric morphometric analysis is used to identify axes of shape variation in the lower second molars of 1) prosimian primates and non-primate archontans and 2) platyrrhines. Landmarks were placed on μCT generated 3D surface renderings. Landmark configurations were aligned using Generalized Procrustes Analysis; a principal components analysis (PCA) was performed on species average landmark co-ordinates. PCs were examined with phylogenetic generalized least squares analysis for association with size and with diet.*

*PCs from both analyses were sufficient to separate species by broad dietary categories. In both analyses, PC1 was not correlated with tooth size, but some PCs explaining a lower proportion of the variance were significantly correlated with size, specifically those separating folivores and insectivores. In multiple regression with centroid size and dietary variables included, the correlation of these PCs and size altered, indicating that dietary differences can both create and mask correlations between shape and size. These results indicate a dominant phylogenetic and dietary signal in molar shape but also show some shape change correlated with size in the absence of obvious dietary associations.*

The importance of the dentition for reconstruction of taxonomic affiliation, phylogenetic position, and dietary inferences of fossil primates, combined with wider interest in the comparative morphology of extant groups, has led to extensive investigation of primate dental anatomy. Despite this previous body of research, there are lingering questions about the selection of methods for quantification of dental morphology, and the extent to which similarities and differences in body size or phylogenetic history may constrain inference of ecological variation from dental morphology. This chapter investigates the associations and interactions among dental shape and diet, body size, and phylogenetic history in prosimian primates and New World monkeys using 3D geometric morphometric methods for the quantification of shape. It also evaluates the application and efficacy of these methods for assessing primate dietary variation.

## Dental shape and diet

The dentition is the first component of the digestive system that encounters food, and shows a suite of morphological adaptations to increase the efficiency of food processing during ingestion and mastication. Various methods to identify dietary indicators in the dentition and form inferences about the ecological variation of extinct mammals have been used. These range from qualitative comparisons of trait complexes that appear to recur in various lineages (e.g., the "plagiaulacoid dentition" described by Simpson, 1933), to the descriptive categorization of different molar types (Jernvall, 1995; Jernvall et al., 1996, 2000), and to more quantitative measurements of specific details of dental morphology. Crest lengths provide one such method that has been widely used in the primate literature (Kay, 1975, 1984; Strait, 1991, 1993a,b; Anthony and Kay, 1993). Recently, measurements of various aspects of surface topography have increased in popularity (e.g., Zuccotti et al., 1998; Ungar and M'Kirera, 2003; Dennis et al., 2004; Evans et al., 2007).

It is possible that when dietary similarity between species appears independently through convergent or parallel evolution, dental morphology will converge in functional properties but lineages will differ in the details of specific morphological changes. In order to compare functionally relevant properties of dental shape, approaches to reconstructing diet have frequently employed variables that circumvent the need to identify homologous landmarks for measurements, instead summarizing functionally relevant tooth properties for comparisons among taxa. One of the first such approaches to the analysis of primate dental morphology was the widely applied shearing quotient (SQ, e.g., Kay and Simons, 1980; Kay and Covert, 1984; Covert, 1986). While shearing crest lengths are based on measurements of homologous structures, summing crest lengths across the tooth allows animals that have achieved similar levels of crest development through different morphologies to be identified. The SQ is based upon a plot of summed shearing crest lengths against tooth length. Residuals from a regression line fitted to the frugivorous taxa are then calculated. Positive values (greater relative crest lengths) are associated with insectivory and folivory. This pattern of variation has been seen in many groups of primates (Kay and Simons, 1980; Kay and Covert, 1984; Anthony and Kay, 1993; Ungar and Kay, 1995), but as the regression line is calculated from a subset of the specific sample, values from different studies may not be directly comparable. To counter this issue, the shearing ratio (SR) was developed by Strait (1991, 1993a); this is a more direct comparison of total crest lengths to tooth size, measured as the square root of occlusal area (Strait 1991, 1993a) or molar length (Strait, 1993a; Bunn et al., 2011). The SR has not been as widely applied as the SQ, but has been shown to effectively distinguish between small-bodied frugivores and insectivores (Strait, 1991, 1993a,b; Bajpai et al., 2008).

Technological advances allowing the creation of digital models of morphological structures have resulted in the development of methods designed to recover dietary information from dental morphology that treat the tooth surface as a landscape. These new variables are collectively known as "dental topographic variables" (e.g., Zuccotti et al., 1998). Measurements that have been developed using this approach characterize such features as the relief of the tooth (Ungar and M'Kirera, 2003; Boyer, 2008), volumes of cusps and basins (Zuccotti et al., 1998), the complexity of the occlusal surface (Evans et al., 2007), or the changes in slope and elevation across the tooth surface (Dennis et al., 2004; Bunn et al., 2011). One advantage of using digital models to analyze the tooth as a surface is that a fully three dimensional representation of the morphology is used (Zuccotti et al., 1998). Furthermore, such approaches either do not require homologous measurement landmarks, or use them only for orientation of specimens prior to measurement. Such relative independence from homology makes topographic measures of tooth shape particularly useful for comparisons of animals with very divergent evolutionary histories, or for analyses in which homologous features are considerably modified by dental wear in some specimens (Ungar and M'Kirera, 2003; Evans et al., 2007; Boyer, 2008; Bunn and Ungar, 2009).

The use of such homology-free metrics has shifted the focus of comparative morphological analyses, at least those with a dietary focus, away from the analysis of resemblances in dental shape that result from a similar configuration of homologous features. However, when examining the evolution of form over time, tracking homologous features such as cusps and crests provides information on the relationships between species, and the trajectory of shape evolution, that is lost when summarizing a surface property across a tooth. As stated above, the purpose of using topographic variables or sums of crest lengths for dietary inference is that values may be similar across teeth that have distinct differences in shape, but converge in

functional properties. However, this very property may introduce problems when inferring an ancestral state. If two species with very distinct morphologies possess a similar value for a topographic variable or sum of shearing crests, the inference of the ancestral state from the extant or descendent species may be problematic.

Additionally, measures of shape that directly capture the geometry of cusps and crests may provide complementary insights into dental-dietary relationships compared to the above analyses (Evans and Sanson, 2003). These potentially include features of cusps (e.g., tip sharpness, radius of curvature, height, and spacing), crests or blades (variation in relative lengths and/or orientation of particular crests), and the area of crushing surfaces. Lucas (1979, 1982) and Lucas and Luke (1984) described morphological requirements necessary to propagate fractures through foods of different properties. The processing of hard, brittle foods is accomplished most efficiently using relatively flat occlusal surfaces, with cusps that have a large radius of curvature for a pestle and mortar action. A similarly flat structure with a higher surrounding rim can be used for the expression of juice from ripe fruit (Lucas and Luke, 1984; Freeman, 1988).

In contrast, a tooth with more emphasis on blades may be more efficient for processing tough and/or ductile foods requiring reduction to fine particles; variation in relative blade lengths and orientation may be informative for more detailed dietary analysis. Strait (1993a) found that taxa that feed on insects with hard carapaces (both brittle and tough, Strait and Vincent, 1998) have shorter crests than faunivores specializing on more ductile prey such as caterpillars. She inferred that this morphology would both reduce the risk of damage to tooth cusps, and also reduce the area of occlusal contact for more efficient crack propagation through the brittle exoskeleton. This conclusion was challenged by Evans and Sanson (1998), who view the shorter crests in hard-object insectivores as a compromise between the need for tall sharp cusps to pierce

and fragment both exoskeleton and internal visceral structures, and the need for crushing surface to further reduce the brittle exoskeleton; they stressed the importance of sharp cusps to initiate fracture in ductile materials, prior to division by blades. Evans and Sanson (2005) further demonstrated that even hard-carapaced beetles may not necessarily be considered "brittle" given the layered structure of the cuticle limiting brittle fracture, and the more ductile internal structures.

Seligsohn (1977) presented data from strepsirrhine primates suggesting that primarily insectivorous and primarily folivorous species can be differentiated on the basis of dental morphology alone, without reference to size. Factors that separated the two dietary groups included the orientation of the crests and the shape of the basins. Measurements of summed crest lengths, in contrast, often lead to inferences of predominant convergence in dental morphology between dietary groups (e.g., Kay, 1975; Kay and Covert, 1984; Strait, 1993a,b). The similar mechanical properties of chitin and cellulose, and the need for both to be reduced to fine particles for digestion to occur, led Kay (1979) to state that, given the similarity in predicted functional requirements between insectivory and folivory, Seligsohn's conclusion was probably due to misinterpretation of size-related variation (see below).

Geometric properties such as the radius of curvature of cusps may also interact with enamel thickness and microstructure to influence the resistance to fracture of the tooth itself (Lawn and Lee, 2009). Enamel properties likely interact with food properties; the mechanical properties and particle size of the food affect the distribution of occlusal forces, thereby influencing which areas of the tooth are vulnerable to enamel damage (Lucas et al., 2008). Evolutionary responses to such factors could include changes in geometric shape of the tooth crown such as an increase in the size of the cingulum, as may be predicted to occur in animals

feeding on ductile foods in which enamel cracks are likely to occur around the crown base (Lucas et al., 2008).

## Dental shape and allometry

Body size is often described as a significant contributing factor, "the single most important determinant" (Gingerich and Smith, 1985, p.257), to a range of biological parameters, including variation in morphology, physiology, reproductive biology, and life history. Allometric variation is defined as change in proportion associated with change in size (Gould, 1966). Studies identifying a correlation between size and shape often assume that size is the causal factor driving the association; size subsequently may be treated as a problem variable, the effects of which must be removed or controlled before other components of variation can be examined to identify adaptations (e.g., Gould, 1975; Clutton-Brock and Harvey, 1979). In such cases, changes of proportions with size are deemed to be necessary to maintain functional equivalence with changes in size (Gould, 1966). However, a distinction can be drawn between this type of explanation for observed allometry, described by Fleagle (1985) as "engineering allometry," and variation that has a correlation with size as a result of behavioral differences between animals of large and small body size ("behavioral allometry"). This distinction between underlying processes driving correlations with size has implications for the use of morphology to form functional inferences relating to behavior. The assumption that a regression line fitted to the data indicates functional equivalence is fundamental to methods using a "criterion of subtraction" to identify adaptation. In contrast, if a correlation between shape and size results from behavioral differences, it would be predicted that discarding variation correlated with size could lead to misleading functional inferences. Distinguishing between the two is likely to be intractable; even approaches that use one functional category to define the allometric line, such as the use of

frugivorous taxa only in the calculation of shearing quotients (Kay and Simons, 1980), do not necessarily avoid discarding variation associated with dental function. Within primates classed as frugivores, the mechanical properties of fruits included in the diet might vary with body (and fruit) size; it is also very likely that any non-fruit component of the diet will differ (e.g., that fruit is supplemented with gums or insects at small body sizes, and leaves at larger body sizes).

The main focus of previous analyses of scaling or allometry in the dentition has been on relative tooth area (e.g., Gould, 1975; Creighton, 1980; Gingerich and Smith, 1985; Copes and Schwartz, 2010). There have been various conclusions concerning the generality and nature of scaling of postcanine occlusal area in primates. In particular, attention has focused on predictions resulting from "Kleiber's Law," that metabolic rate scales to body mass at the 0.75 power (Kleiber, 1932, 1947, 1975). Pilbeam and Gould (1974) predicted that postcanine occlusal area would scale with positive allometry because a geometric relationship between area and volume would result in a 0.66 slope of occlusal area to body mass, which they hypothesized would be inadequate to meeting the metabolic needs of the animal. This hypothesis is referred to as "metabolic scaling" hypothesis. However, empirical data failed to confirm the prediction of positive allometry in many mammalian groups (Creighton, 1980; Fortelius, 1985; Vinyard and Hanna, 2005; Copes and Schwartz, 2010) and the original prediction was later countered by Fortelius (1989, 1990) with the argument that the amount of food processed by the teeth should be proportional to the volume enclosed by the teeth, rather than the tooth area, and thus isometric scaling of tooth area would be sufficient for meeting metabolic requirements. Additionally, a large body of literature has now called into question the validity of the 0.75 exponent for mammalian metabolic rate for a variety of reasons, including problems with the mathematical methods used to arrive at the value (e.g., Packard and Birchard, 2008), the effect of specific

categories of taxa on the analysis (e.g., White and Seymour, 2003), and because analyses incorporating phylogenetic structure fail to exclude alternative values (e.g., Symonds and Elgar, 2002).

One important question relating to dental morphology is whether there is shape variation associated with size, independent of dietary variation. The assumption of descriptions of "engineering allometry", i.e., that allometric scaling maintains functional equivalence, is directly relevant to the choice between methods using ratios and quotients, and to interpretation of any differences between the two that may be found. Additionally, analyses that attempt to identify size-related variation and compare it to dietary structure in molar morphology are needed to resolve the question raised by the conclusions of Seligsohn (1977) and re-interpretation by Kay (1979) concerning possible shape differences between folivores and insectivores. This is likely not important for formation of dietary inference in extinct primates, due to size differences between folivores and insectivores (Kay and Hylander, 1978). On the other hand, any shape differences between the two broad dietary categories *are* relevant to understanding the way in which tooth shape and dietary items interact during the reduction of food particle size. They are also directly relevant to the use of morphological diversity as a proxy for ecological variation within a primate radiation.

The impact of size-shape correlations is not limited to inferences of function; inference of phylogeny might also be affected. For fossil taxa much of the inference regarding taxonomy and phylogeny is based on dental morphology, with exhaustive descriptions of cusp and crest patterns used not only for alpha taxonomy but also for reconstructing relationships. Gilbert and Rossie (2007) demonstrated that co-evolution of size and morphological traits in the cranium of papionin primates could lead to multiple coding of size-associated traits and that such non-

independence of characters may result in a lack of concordance between molecular- and morphology-based phylogenetic inferences. Any relationship between dental shape and size may therefore also affect the interpretation of phylogenetic analyses using dental morphology.

Little attention has been paid to the investigation of size-related changes in tooth shape or functional characteristics in primates, with some exceptions (Kay, 1975, 1978; Seligsohn, 1977; Strait, 1993a; Yamashita, 1998; White, 2009). There are some reasons to predict that size-related shape changes in dental morphology may occur, independent of differences in diet at different body sizes. Very generally, growing or shrinking an identically shaped object will alter the relationships between lengths, areas, and volumes within that object. If tooth function or mechanical integrity is limited by any of the many possible relationships between a linear dimension (e.g., enamel thickness), an area (e.g., crown area, enamel dentine junction area), and/or a volumetric amount (total tooth size, enamel volume), size-associated shape changes would be predicted. However, the dental morphological literature is generally vague on the type of changes with size that might be predicted to occur from a theoretical perspective, with more focus being given to purely descriptive accounts of size-associated shape change (e.g. Kay, 1975; 1978). Evans et al. (2005) described possible relationships between tooth sharpness, bite force, and body size; these factors may interact with fracture resistance of both the food (Lucas, 1979; 1982; 2004) and dental enamel (Lawn and Lee, 2009) to drive changes in dental morphology that are associated with size. Jernvall (1995) predicted that in animals that rely on mechanical breakdown of cell walls of their plant-based food, larger body size might require more efficient molars, not because of "metabolic scaling" (discussed above), but because a consistent plant cell size means that large teeth encounter a greater number of cell walls, more of which would fall between the crest edges that drive cracks through the food item.

Some researchers have investigated allometric variation in primate dental shape empirically, but conclusions have been mixed. Kay found differing regression coefficients of crushing surface and crest lengths against body mass in both non-cercopithecoid (Kay, 1975) and cercopithecid (Kay, 1978) primates, and interpreted this result as an indication that primates of different body sizes will have different molar morphology regardless of diet. Seligsohn (1977) described apparent size-related patterns of variation in cusp acuity and relief in strepsirrhine primates, particularly in the lower second molar (m/2), which is the primary tooth used for dietary reconstruction of fossil primates. Recently, White (2009) presented evidence for a relationship between body size and dental shape in a 2D geometric morphometric analysis of prosimian primate molars. The first principal component (PC) recovered in this analysis appeared to be related to tooth size in bivariate plots, and a multivariate regression of partial warp scores with centroid size showed that the covariation of size and shape was significant, though it explained less than 30% of the variance in the sample. In contrast, Strait (1993a) found that shearing ratios (crest length/square root of tooth area) did not vary predictably with tooth or body size, suggesting a "general independence of size and shape," at least in her sample of frugivorous and insectivorous small-bodied primates. Yamashita (1998) also found that size related shape changes did not appear to provide explanations for the patterns of tooth shape in lemurid and indriid molars.

**Phylogenetic methods**

Correct identification and interpretation of co-variation between morphology and variables such as body size or diet in interspecific analyses requires consideration of phylogenetic history (Felsenstein, 1985; Harvey and Pagel, 1991; Martins and Garland, 1991; Freckleton et al., 2002). The constraint of phylogenetic relatedness on independence of data

points applies to any interspecific comparative analysis, but may be particularly applicable to allometric analyses of extant primates given that there are relatively few instances of wide variation in body size within clades at the family level and below. For example, while White (2009) found an association between size and PC1, PC1 in that analysis also separated lemuriforms and non-lemuriforms. The smallest lemuriform included was *Lepilemur mustelinus* (777g, Smith and Jungers, 1997) and the largest non-lemuriform taxon was *Otolemur crassicaudatus* (1110–1190g, Smith and Jungers, 1997), resulting in only a small degree of overlap in body mass between these groups. Thus, the association of size and shape identified by White's analysis could have been due in part to phylogenetic factors.

### Aims

The goals of this analysis are to 1) evaluate the degree to which dietary information can be captured by overall geometric shape, and 2) test for relationships between molar morphological variation and size using analytic methods that incorporate phylogenetic structure.

## METHODS

The lower second molar (m/2) is the tooth most commonly used in analyses of dental shape and diet (e.g., Kay, 1975; Covert, 1986; Ungar and M'Kirera, 2003; Boyer, 2008; Bunn and Ungar, 2009; Bunn et al., 2011), and was selected for the present analyses of geometric shape. Lower postcanine dentitions were molded and cast for two groups of primates and related archontan taxa (defining Archonta as a clade composed of primates, dermopterans, and scandentians). For comparisons with previous research (e.g., White, 2009), and to provide a suitable comparative extant sample for future analyses of fossil primates, one dataset consisted of

a range of non-primate archontan genera (*Tupaia*, *Ptilocercus*, *Dendrogale*, *Galeopterus*, and *Cynocephalus*) and prosimian primates (*Tarsius*, lemuriforms, lorisiforms). Tarsiers are likely a sister taxon to anthropoid primates in the clade Haplorrhini, as indicated by both cladistic analyses using morphological traits (e.g., Ross, 1994; Ross et al., 1998), and most recent phylogenetic hypotheses generated from molecular data (e.g., Bininda-Emonds et al., 2007; Fabre et al., 2009). "Prosimian" is thus a paraphyletic classification. Even so, tarsiers are closer to some strepsirrhines in their high degree of faunivory/insectivory, and in body size, and prosimians thus form a convenient gradistic group to use for a comparative analysis with particular relevance to the molar morphology of early fossil primates. Tarsiers also possess relatively primitive lower molars that retain the paraconid as a distinct cusp (Swindler, 2002).

The second dataset consisted of a monophyletic clade of anthropoid primates, the platyrrhines, to provide a test of the degree to which conclusions are applicable to different groups of primates. Platyrrhine teeth share some features with those of strepsirrhines, including loss of the paraconid cusp, but this morphology was likely acquired independently, as a paraconid is present in tarsiers and the earliest fossil anthropoids such as eosimiids (Beard et al., 1994; Beard and Wang, 2004) and *Qatrania* (Simons and Kay, 1983). Platyrrhine taxa range in body mass from the small callitrichids, represented in this sample by *Callimico goeldii* at 300–500g (Encarnación and Heymann, 1998), to the largest ateline, *Brachyteles arachnoides* at 8–10 kg (Smith and Jungers, 1997). While all species consume fruit in some proportion of their diet, they display a range of dietary adaptations, including ripe fruit specialists, specialized seed predators, and species with relatively high folivory and insectivory (see Appendix 1).

Taxonomic sampling included the majority of genera within the primate families studied. Taxa and sample sizes are listed in Tables 4.1 and 4.2. *Daubentonia* molars lack clearly

homologous landmarks when compared to molars of other primates, and this genus was excluded. Additionally, most callitrichid platyrrhines have lost the third molar, which may impact m/2 morphology; to maintain focus on dietary and size-related shape change, the only callitrichid genus included was *Callimico geoldii*, which either retains or has re-evolved the third molar.

## Morphological methods

Geometric morphometric (GM) analysis was selected for the analysis of dental shape because it provides a methodological approach that preserves the original geometry of the tooth throughout the analysis, in contrast to the use of linear measurements or a few angles to record shape (Slice, 2005). GM methods have shown considerable promise for exploring shape variation in studies of the evolutionary morphology of the cranium (e.g. Fleagle et al., 2010) and postcranium (e.g., Milne et al., 2009) and have recently been applied to comparative analysis of dental morphology, primarily using photographs of teeth in occlusal view (e.g., Wood et al., 2007; Gomez-Robles et al., 2007; 2008; Piras et al., 2009; White, 2009). Potentially informative variation is discarded without considering variation in the third dimension of occlusal relief. The availability of techniques for creating three-dimensional digital images has provided the resources necessary for 3D landmark placement (e.g., Skinner et al., 2009; Cooke, 2011; Singleton et al., 2011), allowing a more complete representation of dental shape to be captured.

## Creation of digital models

Teeth selected for inclusion in this sample were undamaged and at early wear stages, for accuracy and consistency of landmark identification and because the unworn or little-worn morphological state is of greatest relevance to the questions under investigation. Molds were made using Coltene-Whaledent President Jet light body polyvinylsiloxane molding gel from the

skeletal collections of the American Museum of Natural History, Smithsonian Museum (Natural History), and Museum of Comparative Zoology, Harvard University. The prosimian/ archontan sample expanded that of Boyer (2008), both taxonomically and in the number of individuals; the platyrrhine sample was collected purely for this analysis. Epoxy resin casts of the mandibular dentition were manually reduced to isolate the m/2. Casts of 20–30 individual teeth were then mounted on foam discs. The discs of tooth casts were scanned using a ScanCoMedical μCT 40 machine at 8–18 μm slice resolution (for a detailed description of the scanning protocol followed, see Boyer, 2008). Stacks of DICOM images of the entire disc were segmented using the software ImageJ and digital models were created after importing these DICOM stacks into the software Avizo; voxel size was set by the scanning resolution to maintain scale.

**Landmark collection**

Landmark Version 3.0 (Institute for Data Analysis and Visualization, UC Davis) was used to place 14 (platyrrhine) or 15 (prosimian/archontan) landmarks on surface files. Surface files were saved and imported into Landmark with file names constructed from the scan number and plate position alone; thus, at the time of initial landmark acquisition, the taxon of any one specimen was unknown without reference to the master database. Such reference was only made in the event that cusp homology was not clear (see below). Landmarks included the tips of major cusps and end points of crests, in addition to extremes of curvature on the tooth surface. By capturing both the cusp tips and endpoints of crests issuing from the cusps, shape variation related to cusp sharpness and radius of curvature and to the lengths, angles, and inclination of crests can be represented.

Landmark selection differed between the sample combining prosimian primates and other archontan mammals and the sample containing platyrrhines. This is because the range of

morphological variation affects the availability of landmarks, and because there were some differences in the anatomical features that were of interest. Anatomical nomenclature used in the text follows Strait (2001), and is illustrated in Figure 4.1. The landmarks are illustrated in Figure 4.2A (archontans and prosimians) and 2B (platyrrhines) and defined as follows:

Prosimian/Archontan (PA) landmarks — (PA1) Mesial/lingual terminus of paracristid, equivalent to tip of paraconid, when present; (PA2) Protoconid tip; (PA3) Metaconid tip; (PA4) Hypoconid tip; (PA5) Entoconid tip; (PA6) Distal/lingual terminus of postcristid; (PA7) Notch/lowest point of protocristid; (PA8) Talonid notch (deepest point between metaconid and entoconid); (PA9) Contact of cristid obliqua and trigonid; (PA10) Most buccal point on trigonid; (PA11) Most buccal point on talonid; (PA12) Most lingual point on trigonid; (PA13) Most lingual point on talonid; (PA14) Base of the crown on buccal side, where trigonid meets talonid; and (PA15) Base of the crown on lingual side, where trigonid meets talonid.

Platyrrhine (PL) landmarks — (PL1) Mesial/lingual terminus of paracristid; (PL2) Protoconid tip; (PL3) Metaconid tip; (PL4) Hypoconid tip; (PL5) Entoconid tip; (PL6) Distal/lingual terminus of postcristid; (PL7) Notch/ lowest point of protocristid; (PL8) Contact of cristid obliqua and trigonid; (PL9) Talonid notch (deepest point between metaconid and entoconid); (PL10) Terminus of crest issuing mesially from metaconid; (PL11) Base of protoconid in trigonid basin; (PL12) Deepest point on cristid obliqua; (PL13) Base of the crown on buccal side, where trigonid meets talonid; and (PA15) Base of the crown on lingual side, where trigonid meets talonid.

Recognition of homologous points was relatively straightforward for most species. In the case of *Lepilemur*, there are differences of opinion pertaining to the identity of the cusp immediately distal to the metaconid (Schwartz and Tattersall, 1985; Swindler, 2002). This cusp

occupies a location relative to the rest of the tooth that is normally associated with the entoconid. Unusually though, the cusp is linked to the metaconid by a crest, and thus the lingual opening of the talonid basin is located distal to it, rather than mesially. In other lemuriform taxa, the talonid is open lingually between the metaconid and entoconid. Schwartz and Tattersall (1985) describe this cusp as an exaggerated metastylid, and the entoconid as reduced or absent in *Lepilemur*, while Swindler (2002) names this cusp the entoconid (Figure 4.3A). The identification of cusps as homologous is problematic without information on evolutionary history or clear patterns in extant variation (Jernvall et al., 2008). *Lepilemur* has been referred to as the "bouncing ball of lemuriform phylogenetics" (Yoder, 1997, p. 18) because of the lack of resolution over the phylogenetic position of this genus, which makes such comparisons difficult. Comparisons with the molar morphology of the extinct genus *Megaladapis* (Figure 4.3B), proposed to be related to *Lepilemur*, support the interpretation of Schwartz and Tattersall (1985); in this genus the entoconid is very small and the talonid notch quite distally located, with a distinct metastylid visible distal to the metaconid. However, apparent similarity of molar morphology is one of the characteristics supporting the hypothesis that *Megaladapis* and *Lepilemur* are phylogenetically linked (Tattersall and Schwartz, 1974), which introduces circularity if using *Megaladapis* to inform assessments of cusp homology. Moreover, molecular analyses of ancient DNA have failed to show any strong association between *Megaladapis* and *Lepilemur* (Karanth et al., 2005; Orlando et al., 2008).

Given the absence of an adequate fossil record for identification of primitive lemuriform molar morphology and evolutionary trends, analyses for the prosimian/archontan group were carried out using two hypotheses for cusp homology in *Lepilemur*; "*Lepilemur* homology 1" represents the cusp in question as an entoconid and "*Lepilemur* homology 2" follows the

hypothesis of Schwartz and Tattersall (1985). The diagrams illustrating cusp landmarks in White (2009) suggest that she followed the latter hypothesis (for plots using *Lepilemur* homology 1, see Supplemental Information 1).

**Diet**

Dietary groupings used common categories for such analyses (Table 4.1 and 4.2, Appendix 1). Within the non-primate archontan and strepsirrhine sample, each dietary category (except for bamboo feeding) incorporates taxa from different phyletic groups. For example "folivore" includes *Cynocephalus*, *Lepilemur*, indriids, and some lemurids, while "insectivore" includes *Tarsius*, scandentians, and some galagids and lorisids. Thus, separation of dietary groups would require some convergent evolution of shape. Platyrrhines show relatively few examples of extreme specialization in diet, with all species consuming fruit for some proportion of feeding records. Assuming that, in general, insects and leaves represent greater mechanical challenges to primate dentitions than most fruits, it is possible that reliance on such resources at certain seasons (fallback foods) or for a substantial component of the diet may exert a stronger selective influence on morphology, even if consumed in lower overall quantity (Robinson and Wilson, 1998). This assumption may be questioned given that some species include unripe fruit, or hard fruit/seeds, and that these may be included in the "fruit" section of the diet rather than considered separately. In the absence of wide availability of data representing mechanical properties of food items for the species included, some compromises are necessary. Taxa were allocated to the folivore or insectivore categories if field reports indicated that the species showed a seasonal increase of these items in the feeding records, even if the average annual value was < 50%.

## Phylogenetic relationships

The phylogenetic trees used for data analysis (Figures 4 and 5) are based on the consensus tree from the 10kTrees Version 3 dataset for all primate taxa, with branch lengths calculated from estimated divergence dates. The 10kTrees website is an online resource for primate phylogeny (Arnold et al., 2010) providing a Bayesian inference of phylogenetic relationships based on molecular data; Version 3 of this database provides a more comprehensive taxonomic sample than Version 1 or 2, and combines information from eleven mitochondrial and six autosomal genes (Arnold et al., 2012). Molecular trees were used because dental morphology contributes substantially to most morphological phylogenetic analyses, and it is preferable to use an independent source of phylogenetic data to analyze dental diversification. For the analysis including tree shrews and other archontan mammals, divergence dates for the nodes at the base of archonta and for the topology of extant treeshrews were taken from Roberts et al. (2011). The point estimate for the base of the primate radiation is very similar in the two analyses, with the 10kTrees analysis placing the divergence of strepsirrhines and haplorrhines at 73 mya, and the Roberts et al. analysis placing this node approximately equidistant between 70 and 75 mya (Figure 4.3 of Roberts et al., 2011). Divergence dates in these analyses are for the most part also consistent (similar point estimates, and substantial overlap in the 95% confidence or credibility intervals) with those from other recent analyses of primate and archontan phylogeny (e.g., Janecka et al. 2007; Fabre et al. 2009), although differ somewhat from the strepsirrhine specific analysis of Horvath et al. (2008). Some modifications were made to include the maximum possible number of species. An estimate from Janecka et al. (2007) was used for the divergence of *Cynocephalus* from *Galeopterus* as other analyses included at most only one dermopteran. *Tarsius spectrum* is not available in the 10kTrees database, but Shekelle et al. (2010) provide a

divergence date of this species from other *Tarsius*. When incorporating this datum, some incongruity was noted between tree divergence dates, as the estimated divergence date for *T. bancanus*/*T. syrichta* from the 10ktrees analysis (16.31 mya) is close to the older 95% confidence interval of the estimate for the same two species in the Shekelle et al. analysis (11.1 mya, confidence intervals 4.8 – 18.6 mya). In order to preserve the relative spacing of nodes within the *Tarsius* clade, the older limit from Shekelle et al. for the divergence between *T. spectrum* and these species was therefore selected (32.1 mya). For the platyrrhine analysis *Pithecia irrorata* was used as a proxy for *P. monachus*, as it can be assumed to have diverged from *P. pithecia* at the same node (Hershkovitz, 1987). *Chiropotes albinasus* was added as an additional species at the polytomy in the 10kTrees consensus tree comprised of Cac*ajao melanocephalus, Cacajao calvus* and *Chiropotes satanas*.

**Data analysis**

Landmark data were imported into MorphoJ (Klingenberg, 2011) and subjected to Generalized Procrustes Superimposition to remove differences in orientation, translation, and absolute size of the specimens. Due to specimen availability, sample sizes are unequal for different species (see Table 4.1 and 4.2). Species with larger samples could disproportionately influence the ordination process if individual data were used for the PCA. Therefore, species average coordinates were used for the PCA; the use of species averages also permits the use of methods that incorporate phylogenetic structure. Species average centroid size and Procrustes co-ordinates were calculated in MorphoJ.

In order to be able to visualize shape changes along axes summarizing shape variation, regular PCAs were performed in MorphoJ to produce plots of the species positions in shape space and examine shape changes separating dietary groups. However, to analyze the

associations between tooth shape, size and diet, data were then imported into R and a phylogenetic Principal Components Analysis (pPCA; Revell, 2009) was used to produce orthogonal variables summarizing the shape variation within the sample. The pPCA developed by Revell incorporates a phylogenetic covariance matrix in the calculation of covariance between landmark co-ordinates, and thus produces axes that are orthogonal (uncorrelated) in a phylogenetic correlation, with factor loadings also calculated incorporating the phylogenetic structure. The projection of species onto the PC axes (PC scores) may still retain phylogenetic structure and should be analyzed accordingly (Revell 2009).

**Testing for variation associated with size and diet**

If somatic size influences molar morphology, then it would be predicted that the size-related shape variation might be sufficient to lead to correlations between size and the PCs describing variation in the sample. Frequently, shape variables such as PCs are highly correlated with size – often this applies to PC1 (e.g., Singleton, 2002). To test this prediction, PCs explaining more than 5% of the variation in the sample were regressed against the natural logarithm (Ln) of average centroid size using phylogenetic generalized least squares analysis (PGLS). For species with body mass available, Ln centroid size was also regressed against the cube root of species average female body mass (Table 4.1 and 4.2), to evaluate the degree to which tooth centroid size is likely to be representative of other proxies for body size. Unfortunately, equivalent body mass data are not available for the non-primate archontan sample, so female body mass could not be used for all comparisons.

While correlations between size and shape variables may indicate the presence of allometry, a correlation is not necessarily sufficient to identify shape variation as being a consequence of body size variation. In the case of potential differences between folivores and

insectivores, as identified by Seligsohn (1977) in a strepsirrhine sample, it may be particularly difficult to differentiate between morphological variation resulting from size and from dietary differences. If Kay (1979) is correct that any differences between folivores and insectivores are due to allometry, size correlation would be predicted for any axis of shape variation separating insectivores and folivores. However, with the marked differences in body mass between the two dietary groups (Kay and Hylander, 1978), any shape variation due to dietary differences would also likely be correlated with size, so size correlation alone does not differentiate the two hypotheses. The hypothesis that the dietary categories of insectivores and folivores would only differ in molar shape as a result of size differences results in the additional prediction that in a regression model that incorporates both dietary variation and size, size would add a significant explanatory component to the model. Thus, testing the shape variables for association with size in a regression model that also incorporates dietary information should allow the two hypotheses to be distinguished.

Multiple regression of each PC explaining >5% of the variance was performed using PGLS in the R package "caper" (Orme et al., 2012). Predictor variables included LnCS, and categorical variables representing dietary groups coded as 0 or 1. Each analysis had five dietary groups identified by the dominant item in the diet (prosimian/archontan: frugivory, folivory, insectivory, omnivory, and bamboo feeding; platyrrhine: folivory, frugivory, insectivory, omnivory, and seed predation). The taxa considered as "omnivores" (*Nycticebus*, *Otolemur*, *Microcebus*, *Mirza*, and *Cebus*) all consume primarily insects and fruit/gums. This category was combined with insectivory, as "omnivory" generates few predictions concerning molar morphology, and the insect component of the diet is likely more important for selection on molar morphology, as insects presumably require more postcanine processing to obtain nutrients than

most fruit. This assumption may not be warranted if fruits are particularly hard, as may be the case if the plant component of the diet is particularly hard or tough e.g., those consumed by some species of *Cebus* (Wright, 2005), which introduces a potential source of error in combining insectivory and omnivory. However, given a relatively small number of species, further division of dietary categories seems problematic. To avoid redundancy, three categorical variables of binary states can be used to represent the remaining four dietary states, just as two exclusive categories can be represented by 0 and 1 in one dummy variable. The categories represented by dummy variables coded in the prosimian/archontan analysis were "fruits", "leaves", and "insects", while in the platyrrhine analysis the variables coded were "fruits", "insects", and "seeds"; in both analyses the "uncoded" variable was the dietary category with fewest species included (bamboo, folivory). Residuals from the phylogenetic regression were inspected for normality and for outliers. Additionally, the "caper" package allows both multiple response variables and multiple predictor variables to be incorporated into the model. These multivariate multiple regressions were also conducted.

## RESULTS

### PCA1: Archontan and prosimian taxa (*Lepilemur* homology 2)

Results were similar for the two hypotheses of cusp homology, and therefore detailed discussion is given only for *Lepilemur* homology 2 (for plots using the cusp homology described by Swindler, 2002; see supplemental information 1). The PCA of the non-primate archontan taxa and prosimian species identified five PCs expressing more than five percent of the variance (77.4% cumulatively), with 12 PCs expressing more than one percent of the variance (94.3%

cumulatively, Figure 4.6). Five percent of the variance was used as a cut off for further analysis, because the aims of this investigation focus on factors that have been proposed to be dominant in explaining interspecific variation in molar morphology. Additionally, visual inspection of the plots indicated that PCs explaining lower proportions of the variance were primarily associated with variation separating individual species.

Plots of species on the first three PCs are given in Figure 4.7, and wireframes illustrating the shape transformations on these axes are provided in Figure 4.8. Shape changes along the first five components are described in Table 4.3. The first PC (33.47% of the variance) separates strepsirrhine from non-strepsirrhine taxa (non-primate archontan species and *Tarsius*). Shape changes along this axis are mainly related to the shorter paracristid in the strepsirrhine taxa associated with the loss of the paraconid, with possibly associated shape changes in the entoconid region, as the postcristid is shorter and the entoconid more distally located in most strepsirrhine taxa. The second PC (16.99% of the variance) closely relates to the relief of the tooth and crest lengths, and has an apparently stronger dietary signal with the highest scores seen in taxa assigned to the folivore group. Many insectivorous species also had high PC2 scores, although *Tarsius* is an exception to this generalization. The insectivorous species with scores overlapping the folivore range on the plot of PC1 against PC2 (Figure 4.7B) are *Arctocebus* and *Loris*. *Arctocebus* specializes on soft-bodied, ductile, prey such as caterpillars that require long blades for particle reduction (Strait, 1993b). In that respect, the foods of *Arctocebus* may be similar to leaves in the demands on the molar dentition. The two frugivore/gummivore taxa within the insectivore range are *Euoticus elegantulus* and *Galago alleni*; the molars of these species have been found previously to be difficult to distinguish from those of more insectivorous species (Kay, 1975; Strait, 1993b; Boyer, 2008).

The third PC comprises 11.46% of the variance and, when combined with PC1, creates a complete separation of the distributions of folivorous and insectivorous species. The shape changes along this axis are associated with relative elongation of the mesiodistal axis of the occlusal outline in more folivorous species and steeper angulation of crests in insectivorous species. Frugivores overlap with both folivores and insectivores in the range of scores shown on PC3. With the exception of the two galagids mentioned previously, frugivores can be separated from both folivores and insectivores when PC2 and PC3 are plotted against each other (Figure 4.7 E, F).

The phylogenetic PCA available in the "phytools" package provides fewer options for visualizing the shape changes, but was used to generate variables for the multiple regression. The distribution of species on the first three phylogenetic principal components is illustrated in Figure 4.9. The pPCA shows a lower degree of separation between insectivore and folivores than was observed on the first three components in the non-phylogenetic analysis, primarily because the differences between the dermopterans and other species are not as clearly summarized by the first three axes. However, some separation between insectivores and folivores is still apparent, with only a small region of overlap in PC1. Without the dermopterans, PC1 and PC3 in combination can separate folivores and insectivores. One additional interesting point in the pPCA is the position of *Galago alleni* and *Euoticus elegantulus*. While morphologically similar to the galagids described as having a greater proportion of insectivory in the diet, these two species are no longer creating overlap between the frugivore/gummivore category and the insectivore category on ordinations of PC1/PC3 or PC2/PC3.

### PCA2: Platyrrhine taxa

The PCA of the platyrrhine species identified four PCs expressing more than 5% of the variance (79.9% cumulatively), with 11 PCs expressing more than 1% of the variance (96.8% cumulatively, Fig. 4.10). Species scores on the first two PCs are plotted in Figure 4.11A and B, and wireframe illustrations of shape changes along these axes are illustrated in Figure 4.12. Shape changes along the first four components are summarized in Table 4.3. Only PC1 and PC2 show clear separation of taxa according to dietary grouping; PC3 and PC4 seem to show a greater phylogenetic component, primarily separating distinctive taxa (e.g, *Brachyteles*, *Callimico*) from other species in the analysis, and separating taxa that appeared similar when projected on the previous axes (*Alouatta* from *Brachyteles*, *Callimico* from *Saimiri*).

The first PC (50.67% of the variance) separates species with a dietary specialization towards sclerocarpic seed-predation (the pitheciines; Kinzey, 1992) from species with a greater component of the diet consisting of leaves and insects (e.g., *Alouatta*, *Saimiri*), foods that might be expected to be more tough/ductile. Frugivorous taxa are intermediate. Shape changes along this axis unsurprisingly include greater relative height of the cusps and increased crest lengths in the taxa with high scores, and also changes in the relative spacing of the cusps and the shape of the occlusal outline. The second PC (14.62% of the variance) separates the two most folivorous taxa, *Alouatta* and *Brachyteles*, from the two more insectivorous taxa, *Saimiri* and *Callimico*. Shape differences along this axis include the lengths of longitudinally oriented crests, such as the cristid obliqua and postmetacristid, which are longer in the more folivorous species, and a trigonid that is more vertically implanted, and taller compared to the talonid cusps, in the insectivorous species.

The phylogenetic PCA in platyrrhines, illustrated in Figure 4.13, is relatively similar to non-phylogenetic PCA in the distribution of species on the first component, and the proportion of variance explained, albeit with the direction reversed (lower scores in folivores and insectivores, higher scores in seed predators). One difference is that the more folivorous species (*Brachyteles arachnoides*, *Alouatta* sp.) are separated from insectivores on this axis, with one *Callicebus* species among the frugivores overlapping with the more insectivorous *Saimiri* and *Callicebus*. The degree of overlap between taxonomic groups on the ordination of the first two PCs is also similar to the non-phylogenetic PCA.

**PGLS regressions of PC scores, body mass, diet, and tooth size**

The relationship between tooth size (represented by the Ln of the centroid size) and body mass (Ln cube root of body mass from Tables 4.1 and 4.2) was evaluated, prior to the use of tooth size in further comparisons, using Phylogenetic Generalized Least Squares regression in COMPARE 4.6b (Martins, 2004). These comparisons were made separately for the two analyses, because the landmarks contributing to the estimate of centroid size differed between the two. The regression of tooth size on body mass included all taxa in the platyrrhine analysis, but omitted the dermopteran species for the prosimian/archontan analysis, because details of body mass are not readily available. The results of these comparisons are presented in Table 4.5. Because the cube root of body mass was used, an isometric relationship between tooth size and body mass predicts a slope of 1. Results are also provided for slopes derived from independent contrast, and the ordinary least squares methods that have previously been applied to the analysis of the relationship between tooth size and body mass. In both groups, centroid size is highly correlated with species average body mass, though the slopes for these comparisons differ. The results from platyrrhines support isometric scaling of the postcanine dentition, while in the

prosimian/archontan sample, tooth centroid size shows some degree of negative allometry with body mass.

PGLS regressions of pPC scores on tooth centroid size are presented in Tables 4.6 and 4.7, performed in the R package "caper" (Orme et al., 2012). The first pPC (the dominant component of shape variation) was not correlated with centroid size in either of the analyses. When all taxa are included, only pPC4 from the platyrrhine analysis is significantly correlated with size. If all pPCs explaining more than 5% of the variance are combined, LnCS explains a significant amount of the shape variation in the platyrrhine analysis, but does not reach significance in the analysis of non-primate archontan and prosimian species.

Results of PGLS multiple regressions performed in the R package "caper" are presented in Tables 4.8 and 4.9. In the regressions of individual pPCs on centroid size, no pPCs were correlated with size in the prosimian/archontan sample, and only pPC4 was correlated with size in the platyrrhine sample. When diet is included in the regression model, size remains an insignificant contributing factor to the shape variables in the prosimian/archontan sample. In the platyrrhine sample, size is a significant contributing factor to pPC1 when diet is included, but is only marginally significant in explaining variation in pPC4 (not significant when adjusting for multiple comparisons). In the regression model including multiple predictor (diet and size) and response (pPC1 – pPC5 variables), size did not contribute significantly to the model.

## DISCUSSION

The goals of this analysis were to evaluate the degree to which dietary information can be captured by overall molar shape, specifically in the m/2, and to test for relationships between

molar morphological variation and size in two samples of primates (and non-primate archontans): prosimian/archontans and platyrrhines. In both regular PCAs, discrete or nearly discrete clusters of individual species could be identified based on broad categories of dietary groups. Additionally, within these broad dietary groups, the relative positions of species in 2-dimensional plots are for the most part consistent with dietary variation within that category. For example, species of *Callicebus* and *Aotus* have been described as incorporating a significant proportion of leaves and/or insects into their diet, and they are closer to the more folivorous and insectivorous species on PC1 in the platyrrhine analysis than are other frugivores in the sample. The dietary ecology of both genera is relatively poorly known, in particular with regard to potential seasonal variation. More information on the mechanical demands of the foods consumed may indicate the degree to which their closer resemblance to the more folivorous and insectivorous species represents true adaptive variation. Within the prosimian sample, the omnivores (*Nycticebus*, *Otolemur*, *Mirza*, *Microcebus*) are animals that incorporate fruit/plant exudates and insects into their diet in high proportions, and typically they plot with either frugivores or insectivores or lie intermediate between the two groups.

Complete separation of dietary groups was less apparent in the ordinations from the PCA of prosimian and non-primate archontan species than in the platyrrhine analysis. This may be due to several factors. Firstly, the temporal depth of divergence between species sampled in the former analysis is much greater, and this may lead to a greater proportion of molar shape variation reflecting independent phylogenetic history. Failure to separate dietary groups might also reflect limited knowledge of the diet of some taxa. *Galago alleni* and *Euoticus elegantulus* would likely be "misclassified" as insectivorous based on molar shape alone using landmark methods (although in the plot of PC1 against PC2, these taxa are at least closer to the other

frugivores in the sample than are some other insectivorous galagids and lorisiforms). Notably, this type of misclassification would also occur with crest length measurements or relief when compared to tooth size (Kay, 1975; Strait, 1993a; Boyer, 2008) and seems to accurately reflect molar morphology in these species. More information on the diet of these species, particularly the non-gum component of the diet of *Euoticus* may shed light on its molar adaptations. The dietary classification of *Galago alleni* is also based on limited data.

Turning to the results from the phylogenetic principal components analyses, in the prosimian/archontan sample none of the individual pPCs were correlated with centroid size, and only the fourth pPC in the platyrrhine sample was associated with size (this axis is similar to the PC2 from the prior analysis in the disposition of species). In a multiple regression model that included coding of diet, the pPC with the strongest association with centroid size in the platyrrhine analysis was pPC1, rather than pPC4. In the prosimian/archontan analysis, the dietary factors explained some of the variation along some shape variables, but size did not. In combination, these results suggest that any shape differences between insectivores and folivores are not a result of size-related shape changes in molar morphology, as suggested by Kay (1979), which would instead predict no association of shape and diet when size is incorporated into the model as a predictor. On the basis of these results, confirmed independently in the two samples, there is no strong reason to conclude that any shape differences between insectivores identified by Seligsohn (1977) in his strepsirrhine sample were due to the consequences of dietarily irrelevant, size-related factors.

The similarity of molar adaptations in insectivores and folivores is therefore somewhat open to question. In both prosimians and platyrrhines, differences between insectivores and folivores include greater relative height of the trigonid cusps and more vertical cusps and crests

in insectivores. This pattern argues that the differences could be interpreted as functionally associated with diet. Possible differences between insects and leaves may be located, both in mechanical resistance to fracture, which depends on the arrangement of substances within a food item, in addition to the material properties of the substance (Lucas, 2004), and in the processing needed to access nutrients efficiently in the two classes of food items.

The argument for functional similarity between the molars of folivores and insectivores is predicated upon similarity between chitin and cellulose in requirements for mechanical breakdown and digestion. It also hinges on the assumption that the energetic gain to the animal of processing chitin is similar to the gain from cellulose. Kay and Sheine (1979) estimated that as much as 50% of the energetic content of an insect may be from chitin, but the basis for this statement is not clear. The chitin content of insects is not homogenous across all insect species (Redford and Dorea, 1984). It therefore seems likely that the relative energy available from chitin will also vary, particularly as insect size increases and the ratio of surface area (exoskeleton) to volume decreases. More fundamentally, the degree to which the food needs to be broken down will affect tooth design (Evans and Sanson, 2003). During mastication of plant leaves, rupture of cellulose cell walls is required to access cell contents, in addition to the energetic benefits of cellulose digestion. In consumption of insects, even initial breakage of the exoskeleton will provide some access to the internal contents of the invertebrate through puncturing which has been shown experimentally to substantially increase the availability of nutrients for absorption (Prinz et al. 2003). Puncturing may be most effectively achieved with sharp points rather than blades (Evans and Sanson, 1998). Thus, while mechanical breakdown of chitin to small particles may provide some energetic benefit to the animal (Kay and Sheine, 1979), it is not clear that the benefits of reducing chitin to fine particles are equivalent to the

benefits of masticating cellulose. Extensive mastication of individual bites likely increases total food handling time, and may therefore reduce the time available to the animal for searching for other prey (a consideration that is likely of more salience to insectivores than to folivores given the differences in spatial distribution of their food). The energetic returns of capturing additional prey may exceed any added benefits of digesting chitin; this is supported by observational evidence that the highly faunivorous tarsiers consume their prey after a small number of masticatory cycles (Jablonski and Crompton, 1994).

Leaving aside the question of insectivore and folivore molar differences, how much variation in molar shape appears to be associated with size? In the comparisons of pPCs and centroid size alone, the first pPCs were not correlated with size in either of the analyses. An association with size was found in the platyrrhine sample for a pPC explaining a much smaller proportion of the total variance (pPC4, which explained approximately 7%). When the first five pPCs were considered together, the effect of size was insignificant in the prosimian/archontan sample, and significant in the platyrrhine sample (adjusted $R^2$=0.17), but when diet was included this effect of size disappeared. It seems likely that only a small proportion of the total variation in molar morphology can be ascribed to size related shape changes, independent of associations between size and diet or phylogeny. Interestingly, it also occurred that when diet was included in the predictive model, a PC not previously found to be associated with size showed some predictive contribution from centroid size (pPC1 in the platyrrhine sample). This may indicate that within dietary groups, there is some contribution of size variation to molar shape.

This conclusion contrasts with the analysis of White (2009), which identified a substantial component of variation in molar morphology correlated with size. The present study differs from that of White in the taxonomic breadth among both non-primate archontans and

prosimians (including several smaller-bodied lemuriforms), in the choice of landmarks, and in the three dimensional representation of dental morphology. Thus, the two analyses are not directly comparable. It does seem likely that the use of methods that ignore phylogenetic non-independence of data points may overestimate the impact of size on dental morphology.

The comparison of centroid size and body mass (Table 4.5) was carried out primarily to identify the degree to which results from tooth size would be concordant with other proxies for body mass. These observations of tooth scaling using centroid size are for the most part consistent with previous observations of tooth size using area or linear dimensions that showed isometry or negative allometry of tooth and body size (e.g., Kay, 1975; Gingerich and Smith, 1985; Vinyard and Hanna, 2005; Copes and Schwartz, 2010). The strong negative allometry in the sample containing prosimians contrasts with Vinyard and Hanna's (2005) results for strepsirrhines; they identified instances of negative allometry, but also found that isometry could not be excluded in most cases. Vinyard and Hanna (2005) used independent contrasts in their calculations of slope for molar area against body mass, rather than PGLS, but this is not likely to cause the difference, as independent contrasts results (Table 4.5) were very similar to the PGLS estimate of the slope, and the confidence intervals also excluded isometry. Possibly, the differences are due to the inclusion in the taxonomic sample of the tree shrews and the relatively large-toothed tarsiers, or the use of lower molars rather than upper molars. However, an additional possibility exists that the measure of tooth size alters the perception of scaling relationships. Previous analyses of relative tooth size have predominantly used area or linear measurements, whereas centroid size, the square root of the sum of squared distances between the landmarks and their centroid, might more closely reflect the total volume of the tooth. These possibilities should be addressed in more detail in future work.

# CONCLUSIONS

The results of this study suggest that approaches that capture geometric shape are able to effectively differentiate among dietary categories. The differences observed suggest the possibility of using dental shape to differentiate between primate insectivores and folivores, two dietary categories often described as possessing similar molar morphology as a result of similar functional requirements. Dental shape differences between insectivores and folivores are not necessarily important for paleodietary reconstruction for individual fossil species. Among extant primates there is a gap between the low end of the body mass range for primate folivores and the high end of the body mass range for primate insectivores (Kay and Hylander, 1978). Despite problems associated with the use of tooth size to predict body mass, an extinct primate insectivore is unlikely to be reconstructed as a folivore (and vice versa). However, the use of morphological diversity as a proxy for adaptive or ecological divergence in the fossil record is likely to be more accurate if approaches that separate insectivores and folivores are employed. For such analyses, the question of whether such variation is due to function or absolute size becomes of less concern. The apparently small influence of overall size on dental morphology is also of advantage in the use of dental morphological characters to reconstruct fossil diversity, as diversity in tooth size can always be measured directly, and greater independence between size and shape may therefore increase the availability of information on factors such as phylogenetic history or dietary adaptation.

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*Table 4.1. Prosimian/non-primate archontan sample. Unless otherwise noted, primate body mass data are from Smith and Jungers (1997) and tree shrew body mass data are from Sargis (2000).*

| | Species | *n* | Diet | Body mass (kg) |
|---|---|---|---|---|
| Non-primate Archonta | *Ptilocercus lowii* | 5 | Insectivore | 0.045 |
| | *Dendrogale murina* | 4 | Insectivore | 0.045 |
| | *Tupaia glis* | 3 | Insectivore | 0.152 |
| | *Tupaia montana* | 4 | Insectivore | 0.126 |
| | *Galeopterus variegatus* | 1 | Folivore | *1.21 |
| | *Cynocephalus volans* | 3 | Folivore | **1.75 |
| Primates: Lorisiformes | *Arctocebus calabarensis* | 4 | Insectivore | 0.306 |
| | *Loris tardigradus* | 3 | Insectivore | 0.269 |
| | *Nycticebus coucang* | 3 | Omnivore | 0.823 |
| | *Perodicticus potto* | 3 | Frugivore/Gummivore | 1.21 |
| | *Euoticus elegantulus* | 4 | Frugivore/Gummivore | 0.261 |
| | *Galago alleni* | 3 | Frugivore/Gummivore | 0.269 |
| | *Galago moholi* | 3 | Insectivore | 0.173 |
| | *Galago senegalensis* | 2 | Insectivore | 0.225 |
| | *Galago zanzibaricus* | 1 | Insectivore | 0.137 |
| | *Galagoides demidoff* | 4 | Insectivore | 0.060 |
| | *Otolemur crassicaudatus* | 4 | Omnivore | 1.11 |
| Primates: Lemuriformes | *Avahi laniger* | 4 | Folivore | 1.32 |
| | *Indri indri* | 2 | Folivore | 6.84 |
| | *Propithecus diadema* | 2 | Folivore | 6.26 |
| | *Propithecus verreauxi* | 3 | Folivore | 2.95 |
| | *Cheirogaleus major* | 2 | Frugivore/Gummivore | 0.362 |
| | *Cheirogaleus medius* | 1 | Frugivore/Gummivore | 0.172 |
| | *Microcebus griseorufus* | 6 | Omnivore | ***0.055 |
| | *Mirza coquereli* | 2 | Omnivore | 0.326 |
| | *Phaner furcifer* | 2 | Frugivore/Gummivore | 0.460 |
| | *Lepilemur mustelinus* | 4 | Folivore | 0.777 |
| | *Eulemur fulvus* | 2 | Folivore | ****2.62 |
| | *Eulemur rufus* | 3 | Folivore | 2.25 |
| | *Hapalemur griseus* | 5 | Folivore/Bamboo | 0.670 |
| | *Hapalemur simus* | 2 | Folivore/Bamboo | 1.3 |
| | *Lemur catta* | 4 | Folivore | 2.21 |
| | *Varecia variegata* | 4 | Frugivore/Gummivore | 3.52 |
| Primates: Tarsiiformes | *Tarsius bancanus* | 2 | Insectivore | 0·117 |
| | *Tarsius spectrum* | 4 | Insectivore | 0·108 |
| | *Tarsius syrichta* | 1 | Insectivore | 0·117 |

* *G. variegatus* data from Medway (1978), four individuals, midpoint of reported range 1.108–1.320

** *C. volans,* five captive animals (wild-caught) data from Wischusen et al. (1994).

*** Genin (2008), females in the non-breeding season.

**** Tattersall (1982), species mean.

*Table 4.2. Platyrrhine sample. Body mass data (wild, female) are from Smith and Jungers (1997) unless otherwise noted.*

| | Species | Sample size | Diet | Body mass (kg) |
|---|---|---|---|---|
| Atelidae | *Alouatta palliata* | 7 | Folivore | 5.35 |
| | *Alouatta seniculus* | 9 | Folivore | 5.21 |
| | *Ateles belzebuth* | 7 | Frugivore | 7.85 |
| | *Ateles geoffroyi* | 6 | Frugivore | 7.29 |
| | *Brachyteles arachnoides* | 6 | Folivore | 8.07 |
| | *Lagothrix lagotricha* | 9 | Frugivore | 7.02 |
| Pitheciidae | *Cacajao calvus* | 6 | Seed predator | 2.88 |
| | *Cacajao melanocephalus* | 5 | Seed predator | 2.71 |
| | *Chiropotes albinasus* | 6 | Seed predator | 2.49 |
| | *Chiropotes satanas* | 6 | Seed predator | 2.58 |
| | *Pithecia monachus* | 8 | Seed predator | 2.11 |
| | *Pithecia pithecia* | 7 | Seed predator | 1.58 |
| | *Callicebus donacophilus* | 4 | Frugivore | 0.909 |
| | *Callicebus moloch* | 10 | Frugivore | 0.956 |
| | *Callicebus torquatus* | 6 | Frugivore | 1.21 |
| Cebidae | *Aotus azarae* | 4 | Frugivore | 1.23 |
| | *Aotus nigriceps* | 12 | Frugivore | 1.04 |
| | *Cebus apella* | 9 | Omnivore | 2.52 |
| | *Cebus capucinus* | 7 | Omnivore | 2.54 |
| | *Saimiri boliviensis* | 9 | Insectivore | 0.711 |
| | *Saimiri sciureus* | 7 | Insectivore | 0.662 |
| | *Callimico goeldii* | 5 | Insectivore | 0.355* |

* Data for wild *Callimico* from Encarnación and Heymann (1998)

*Table 4.3. Description of shape changes along the first four PCs from the PCA of the non-primate archontan and prosimian taxa*

| PC | Variance explained | Shape | | Distribution of taxa on each PC |
|---|---|---|---|---|
| | | Low scores | High scores | |
| 1 | 33.47% | Steeper crests, Paracristid long, reaches lingually (species with paraconid present). Entoconid positioned relatively mesially, entoconid notch deep, postmetacristid vertical, postcristid long, lingual cusps taller than buccal, lingual | Short paracristid, more distal entoconid and talonid notch, wider base of molar crown, inclined lingual face of tooth crown (cusps placed centrally relative to base of tooth) | Strepsirrhines score higher on PC1, non-primate archontans and tarsiers lower. |
| 2 | 16.99% | Occlusal outline wider buccolingually, shorter mesiodistally, cusp height is relatively lower, postcristid and postentoconid crests meet close to midline; cristid obliqua contact with trigonid more buccally positioned. | Occlusal outline elongate mesiodistally, taller cusps with deeper notches, relatively taller lingual cusps, more lingual contact of the cristid obliqua, longer postcristid | Folivorous and insectivorous taxa (except *Tarsius*) score more highly on this principal component, frugivorous taxa such as *Varecia* and *Cheirogaleus* lower. Folivorous taxa, for the most part, higher than insectivorous. |
| 3 | 11.46% | Occlusal outline more mesiodistally elongate, talonid relatively larger, longer postcristid | Taller trigonid, more upright postmetacristid and pre-entocristid (steeper crests) more lingual placement of cristid obliqua. | Insectivorous taxa (higher) separated from folivorous taxa (lower) along this axis. Frugivores/gummivores and omnivores overlap with both groups. |
| 4 | 10.05% | Mesial placement of talonid notch, steep pre-entocristid and postmetacristid crests. | Distal position of talonid notch, lower entoconid. | Separates *Lepilemur* (high) from other taxa in analysis, lowest scores in *Cynocephalus*. |
| 5 | 5.41% | Deep talonid notch, taller metaconid, more buccal position of contact between cristid oblique/ trigonid | Short postmetacristid, shallow talonid notch, mesiodistally expanded trigonid | Low scoring taxa include *Lepilemur*, tarsiers, and *Hapalemur*<br>High scoring taxa include tree shrews, cheirogaleids and lorisids. |

*Table 4.4. Description of shape changes along the first four PCs of the PCA of the platyrrhine analysis*

| PC | Variance explained | Shape | | Distribution of taxa on each PC |
|---|---|---|---|---|
| | | Low scores | High scores | |
| 1 | 50.67% | Occlusal outline mesiodistally compressed; large talonid basin relative to trigonid; cristid obliqua contacts trigonid in relatively buccal position; cusps low and positioned around external margins of tooth. | Mesiodistally elongate; trigonid basin mesiodistally longer; cristid obliqua contact more lingually positioned; cusps higher relative to tooth base; notches between cusps deeper. | Separates seed predators/frugivores (low scores) from more insectivorous and folivorous taxa (high scores). |
| 2 | 14.62% | Relatively wide talonid basin; trigonid larger relative to talonid, more mesial entoconid; pre- and postentocristid less steep; shorter postcristid, cristid obliqua, postmetacristid; distal wall of trigonid more vertically inclined. | Postcristid long and reaches further lingually; more distal placement of entoconid; cristid obliqua and postmetacristid longer; deeper talonid notch; distal wall of trigonid sloped | Separates folivorous (high scores) from more insectivorous species (low scores). |
| 3 | 7.64% | Shorter paracristid and protocristid, short postmetacristid and shallow talonid notch | Taller metaconid, deeper talonid notch, longer talonid basin | Taxa scoring highly include *Callimico* and *Brachyteles*, lower scores in *Saimiri* and *Cebus* |
| 4 | 7.01% | Mesiodistally elongated, buccolingually narrower, smaller talonid | Buccolingually wider base, shorter cristid obliqua | High scoring taxa include *Cebus* and *Brachyteles*; lower scores found in *Callimico* and *Alouatta* |

*Table 4.5. Relationship between body mass (Ln cube root) and centroid size (Ln). RMA slopes calculated from the slope and correlation coefficient of slopes under PGLS, Independent Contrasts (IC), and least squares (OLS) regression. All calculated in the program COMPARE 4.6b. RMA slope recalculated from the PGLS slope*

| | n | Regression method | Corr. Coeff. | Slope (COMPARE output) | SE of slope | 95% +/- | Lower limit of slope estimate | Upper limit of slope estimate | RMA slope |
|---|---|---|---|---|---|---|---|---|---|
| Prosimians and tree shrews | 34 | **PGLS** | **0.88** | **0.67** | **0.06** | **0.1176** | **0.5524** | **0.7876** | **0.76** |
| | | IC | 0.86 | 0.69 | 0.07 | 0.1372 | 0.5528 | 0.8272 | 0.80 |
| | | OLS | 0.91 | 0.71 | 0.06 | 0.1176 | 0.5724 | 0.8076 | 0.78 |
| Platyrrhine | 22 | **PGLS** | **0.90** | **0.95** | **0.10** | **0.1960** | **0.7540** | **1.1460** | **1.06** |
| | | IC | 0.83 | 0.94 | 0.14 | 0.2744 | 0.6656 | 1.2144 | 1.13 |
| | | OLS | 0.93 | 0.95 | 0.08 | 0.1568 | 0.7932 | 1.1068 | 0.98 |

*Table 4.6. Prosimian/non-primate archontan (tree shrews and dermopterans) PGLS results for bivariate regression of the first five phylogenetic PCs on species average Ln Centroid Size (n=36)*

| | pPC variance explained | Adj. $R^2$ | Slope | SE of slope | p value |
|---|---|---|---|---|---|
| pPC1 | 24.75% | 0.010 | -0.035 | 0.030 | 0.2716 |
| pPC2 | 19.73% | -0.025 | 0.010 | 0.024 | 0.8515 |
| pPC3 | 11.53% | -0.006 | -0.030 | 0.033 | 0.4622 |
| pPC4 | 9.57% | -0.003 | -0.026 | 0.028 | 0.4195 |
| pPC5 | 5.77% | -0.006 | -0.021 | 0.024 | 0.4569 |
| pPCs 1 - 5 | 71.35% | 0.054 | -0.090 | 0.052 | 0.0637 |

*Table 4.7. Platyrrhine PGLS results for bivariate regression of the first four phylogenetic PCs on species average Ln Centroid Size (n =22)*

| | pPC variance explained | Adj. $R^2$ | Slope | SE of slope | p value |
|---|---|---|---|---|---|
| pPC1 | 48.35% | -0.028 | -0.047 | 0.073 | .6676 |
| pPC2 | 10.45% | -0.003 | 0.018 | 0.019 | .4092 |
| pPC3 | 8.08% | -0.016 | -0.030 | 0.036 | .5235 |
| **pPC4** | **6.97%** | **0.240** | **-0.091** | **0.033** | **0.003** |
| pPC5 | 5.14% | 0.099 | -0.054 | 0.029 | 0.058 |
| **pPCs 1 - 5** | **79.00%** | **0.166** | **-0.231** | **0.102** | **0.016** |

*Table 4.8. Prosimian/non-primate archontan PGLS regressions of each PC on multiple predictor variables of tooth size and categorical variables coding diet as 0/1 for dietary categories*

| Model | Variable | Slope | Standard error of slope | p value |
|---|---|---|---|---|
| PC1 ~ diet + size | Fruit (0/1) | 0.0089 | 0.0351 | 0.8013 |
| | Leaves (0/1) | **-0.1136** | **0.0293** | **0.0005** |
| | Insects (0/1) | 0.0007 | 0.0375 | 0.9857 |
| Adj. $R^2$=-0.4666 | | | | |
| p <0.0001 | LnCS | 0.0421 | 0.0287 | 0.1519 |
| PC2 ~ diet + size | Fruit (0/1) | 0.0264 | 0.0461 | 0.5712 |
| | Leaves (0/1) | 0.0459 | 0.0405 | 0.2655 |
| | Insects (0/1) | 0.0320 | 0.0464 | 0.4948 |
| Adj. $R^2$=-0.0728 | | | | |
| p=0.8406 | LnCS | 0.0037 | 0.0380 | 0.9231 |
| PC3 ~ diet + size | Fruit (0/1) | **-0.1462** | **0.0361** | **0.0003** |
| | Leaves (0/1) | -0.0636 | 0.0282 | 0.0316 |
| | Insects (0/1) | -0.0954 | 0.0384 | 0.0186 |
| Adj. $R^2$=0.3539 | | | | |
| p=0.0007 | LnCS | -0.0453 | 0.0292 | 0.1307 |
| PC4 ~ diet + size | Fruit (0/1) | 0.0438 | 0.0361 | 0.2343 |
| | Leaves (0/1) | -0.0357 | 0.0298 | 0.2400 |
| | Insects (0/1) | 0.0195 | 0.0386 | 0.6166 |
| Adj. $R^2$=0.1781 | | | | |
| p=0.029 | LnCS | 0.0057 | 0.0294 | 0.8478 |
| PC5 ~ diet + size | Fruit (0/1) | -0.0786 | 0.0305 | 0.0151 |
| | Leaves (0/1) | -0.0476 | 0.0221 | 0.0393 |
| | Insects (0/1) | -0.0680 | 0.0320 | 0.0419 |
| Adj. $R^2$=0.1112 | | | | |
| P=0.0927 | LnCS | -0.0346 | 0.0242 | 0.1626 |
| PC1 - 5 ~ diet + size | Fruit (0/1) | -0.1151 | 0.0737 | 0.1284 |
| | Leaves (0/1) | **-0.1786** | **0.0627** | **0.0077** |
| | Insects (0/1) | -0.0842 | 0.0781 | 0.2894 |
| Adj. $R^2$=0.2141 | | | | |
| P=0.0149 | LnCS | -0.0473 | 0.0602 | 0.4375 |

*Table 4.9. Platyrrhine PGLS regressions of each PC on multiple predictor variables of tooth size and categorical variables coding diet as 0/1 for dietary categories*

| Model | Variable | Slope | Standard error of slope | p value |
|---|---|---|---|---|
| PC1 ~ diet + size | Fruit (0/1) | **0.2179** | **0.0221** | **<0.0001** |
| | Seeds (0/1) | **0.3073** | **0.0264** | **<0.0001** |
| | Insects (0/1) | **0.2154** | **0.0294** | **<0.0001** |
| Adj. $R^2$=0.8743 | | | | |
| p<0.0001 | LnCS | **0.1423** | **0.0318** | **0.0003** |
| PC2 ~ diet + size | Fruit (0/1) | 0.0425 | 0.0196 | 0.0445 |
| | Seeds (0/1) | 0.0513 | 0.0196 | 0.0181 |
| | Insects (0/1) | 0.0309 | 0.0240 | 0.2137 |
| Adj. $R^2$=0.2443 | | | | |
| p=0.0569 | LnCS | 0.0452 | 0.0238 | 0.0753 |
| PC3 ~ diet + size | Fruit (0/1) | 0.0541 | 0.0212 | 0.0208 |
| | Seeds (0/1) | **0.0735** | **0.0213** | **0.0030** |
| | Insects (0/1) | **0.1272** | **0.0260** | **0.0001** |
| Adj. $R^2$=-0.591 | | | | |
| p=0.0003 | LnCS | 0.0642 | 0.0259 | 0.0238 |
| PC4 ~ diet + size | Fruit (0/1) | -0.0365 | 0.0219 | 0.1143 |
| | Seeds (0/1) | -0.0576 | 0.0280 | 0.0552 |
| | Insects (0/1) | -0.0019 | 0.0304 | 0.9520 |
| Adj. $R^2$=0.4564 | | | | |
| p=0.0037 | LnCS | -0.0946 | 0.0337 | 0.0122 |
| PC5 ~ diet + size | Fruit (0/1) | -0.0036 | 0.0217 | 0.8689 |
| | Seeds (0/1) | -0.0258 | 0.0337 | 0.4556 |
| | Insects (0/1) | 0.0059 | 0.0344 | 0.8646 |
| Adj. $R^2$=0.0087 | | | | |
| P=0.4232 | LnCS | -0.0500 | 0.0400 | 0.2279 |
| PC1 - 5 ~ diet + size | Fruit (0/1) | **0.2326** | **0.0513** | **0.0003** |
| | Seeds (0/1) | **0.3176** | **0.0750** | **0.0006** |
| | Insects (0/1) | **0.3304** | **0.0777** | **0.0005** |
| Adj. $R^2$=0.6071 | | | | |
| P=0.0002 | LnCS | 0.0469 | 0.0895 | 0.6071 |

**Fig. 4.1.** Nomenclature for cusps and crests, illustrated on *Tarsius* m/2. Nomenclature follows Kay (1977), and Strait (1991). See Supplemental 4 for more details on crest nomenclature.

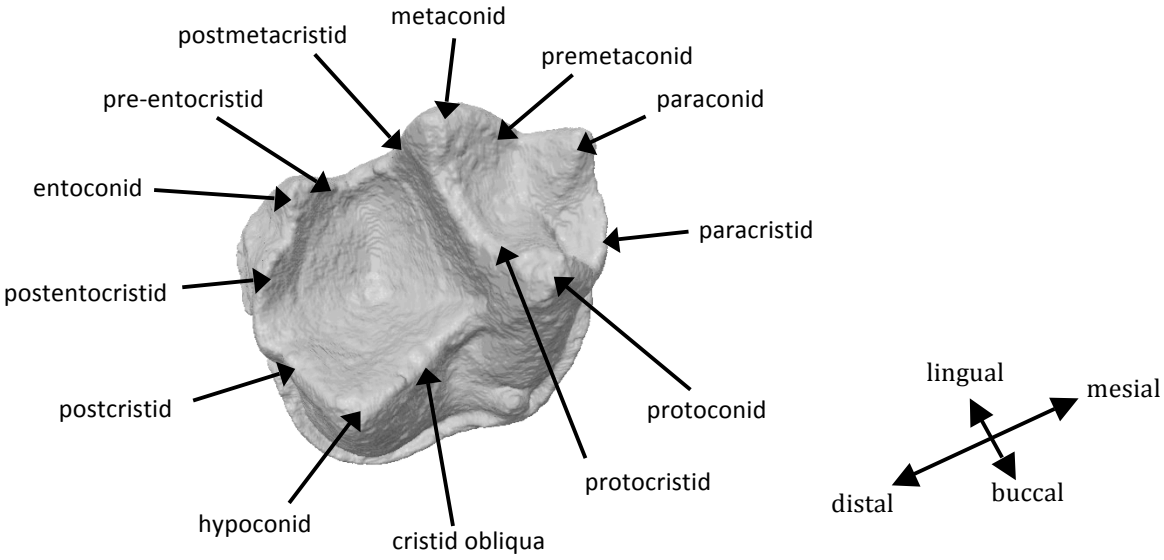
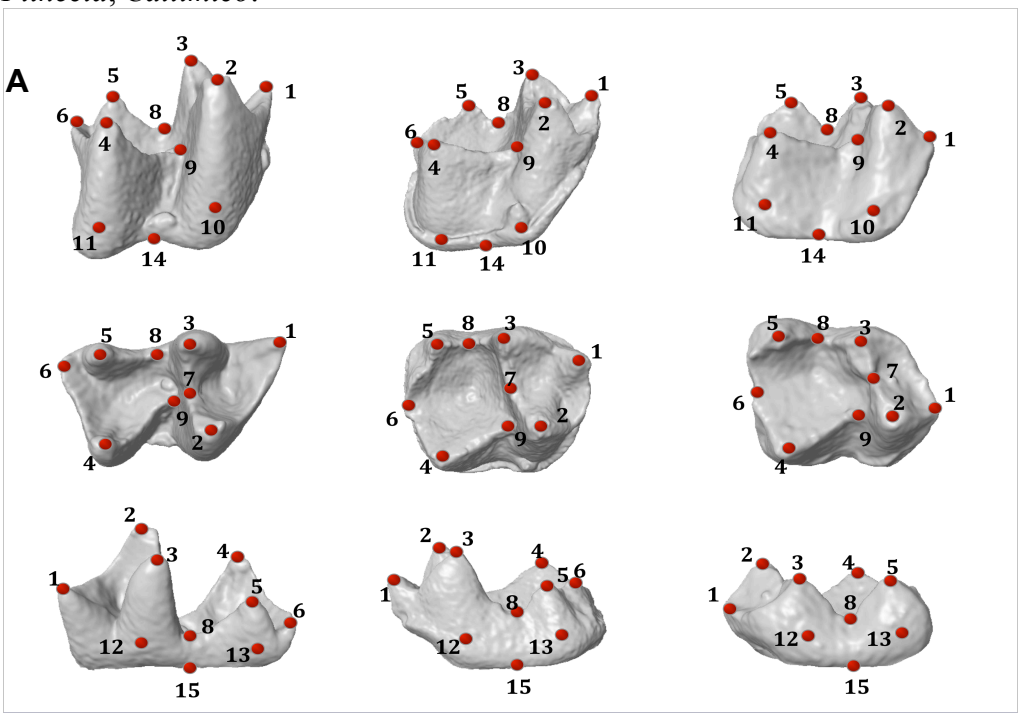


**Fig. 4.2.** Landmarks used for m/2s of archontan and prosimian taxa (**A**) and platyrrhine taxa (**B**). Landmarks are illustrated on three taxa in buccal (top), occlusal (middle), and lingual (bottom) views. (**A**) From left to right, *Tupaia*, *Tarsius*, *Microcebus,* (**B**) From left to right, *Alouatta*, *Pithecia*, *Callimico*.



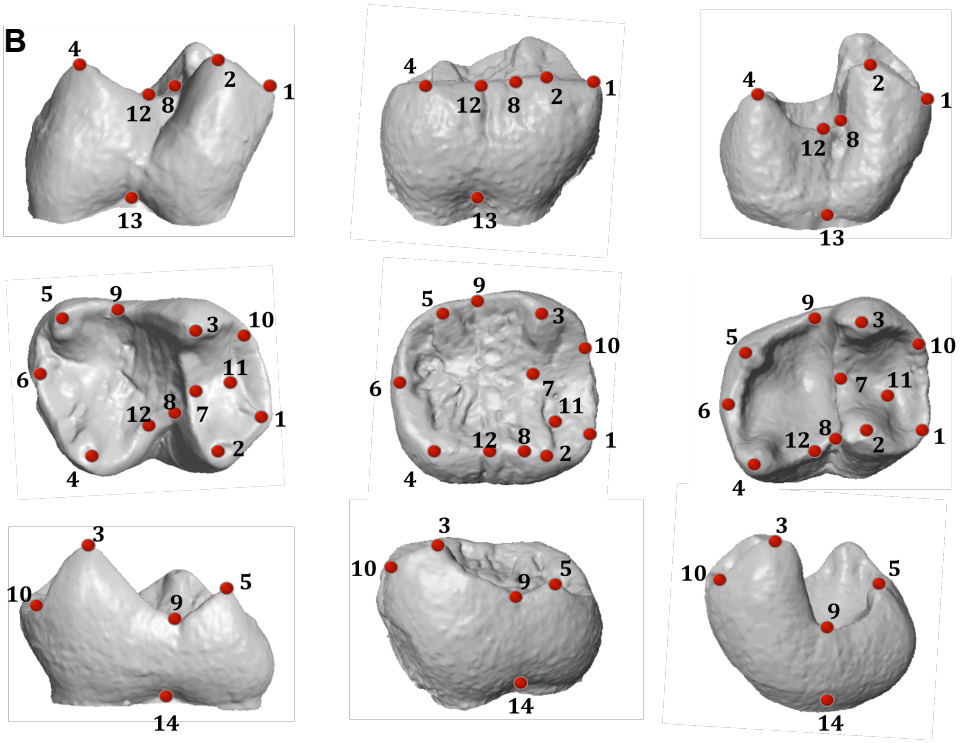



**Fig. 4.3.** (**A**) Occlusal views of m/2 of *Lepilemur* with two possible interpretations of cusp homology. *Lepilemur* homology 1 (Swindler, 2002) is shown on left, *Lepilemur* homology 2 (Schwartz and Tattersall, 1985) is shown on right. (**B**) occlusal view of *Megaladapis* molar with cusps labeled.

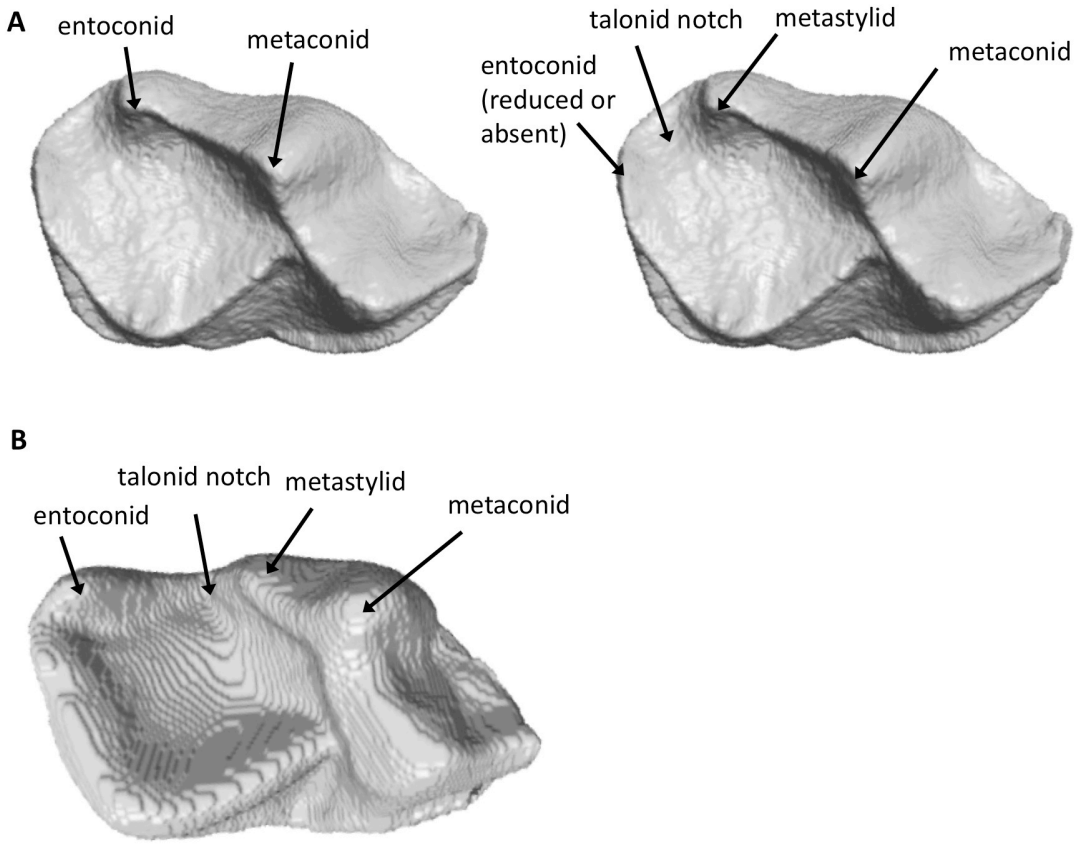


**Fig. 4.4.** Phylogenetic tree used for PGLS regressions of size and shape in prosimian and non-primate archontan sample. Tree is a composite of the 10kTrees Version 3 primate tree, and Roberts et al. (2011) for tree shrew phylogeny with the divergence date for *Tarsius spectrum* from other tarsier species taken from Shekelle et al. (2010) and the divergence date for *Cynocephalus volans* and *Galeopterus variegatus* taken from Janecka et al. (2007). See text for discussion. Scale shows million years before present.

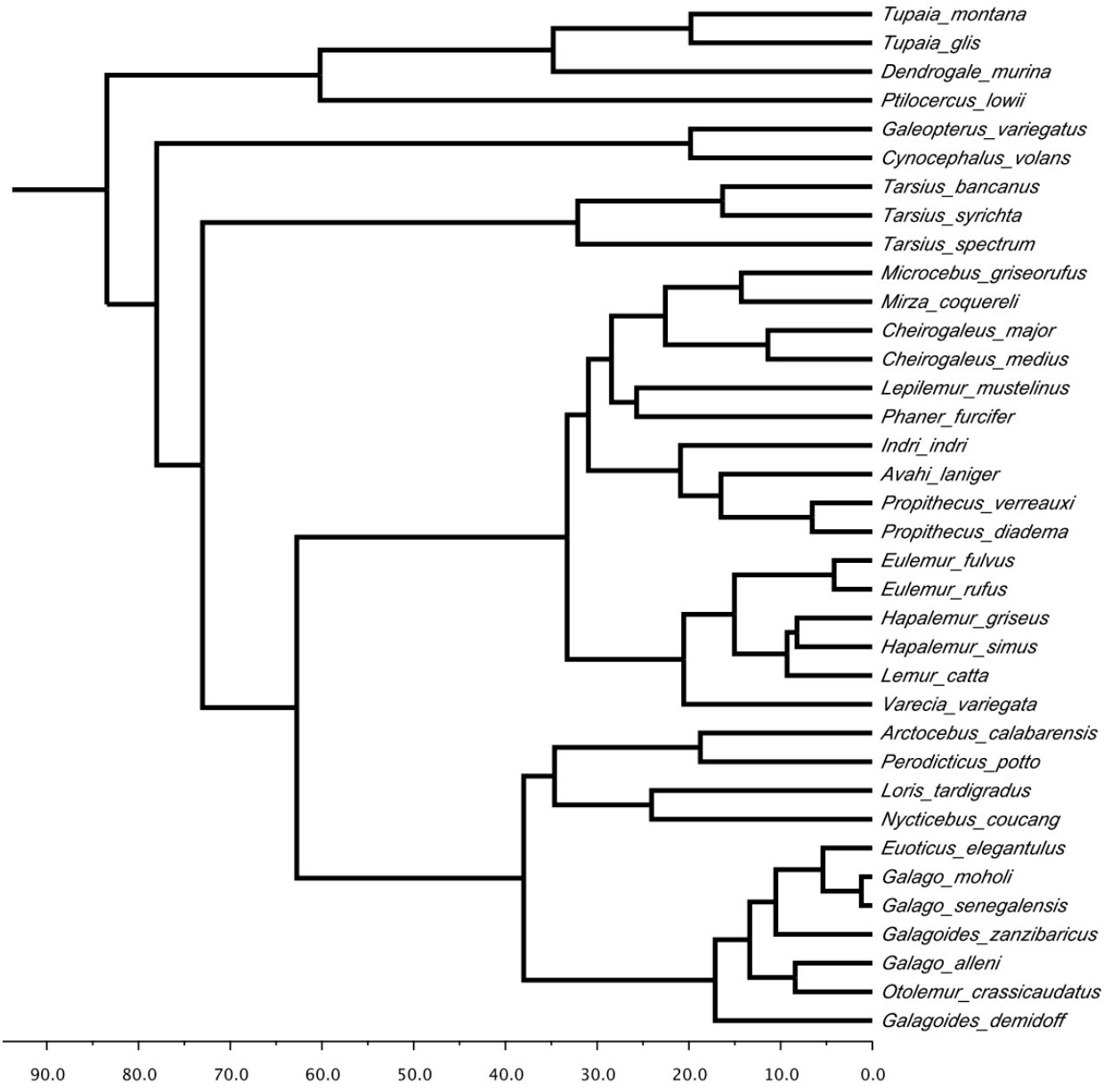


**Fig. 4.5.** Phylogenetic tree used for PGLS regressions of size and shape in platyrrhine sample. Tree is from 10kTrees Version 3 (Arnold et al., 2010). Scale shows million years before present.

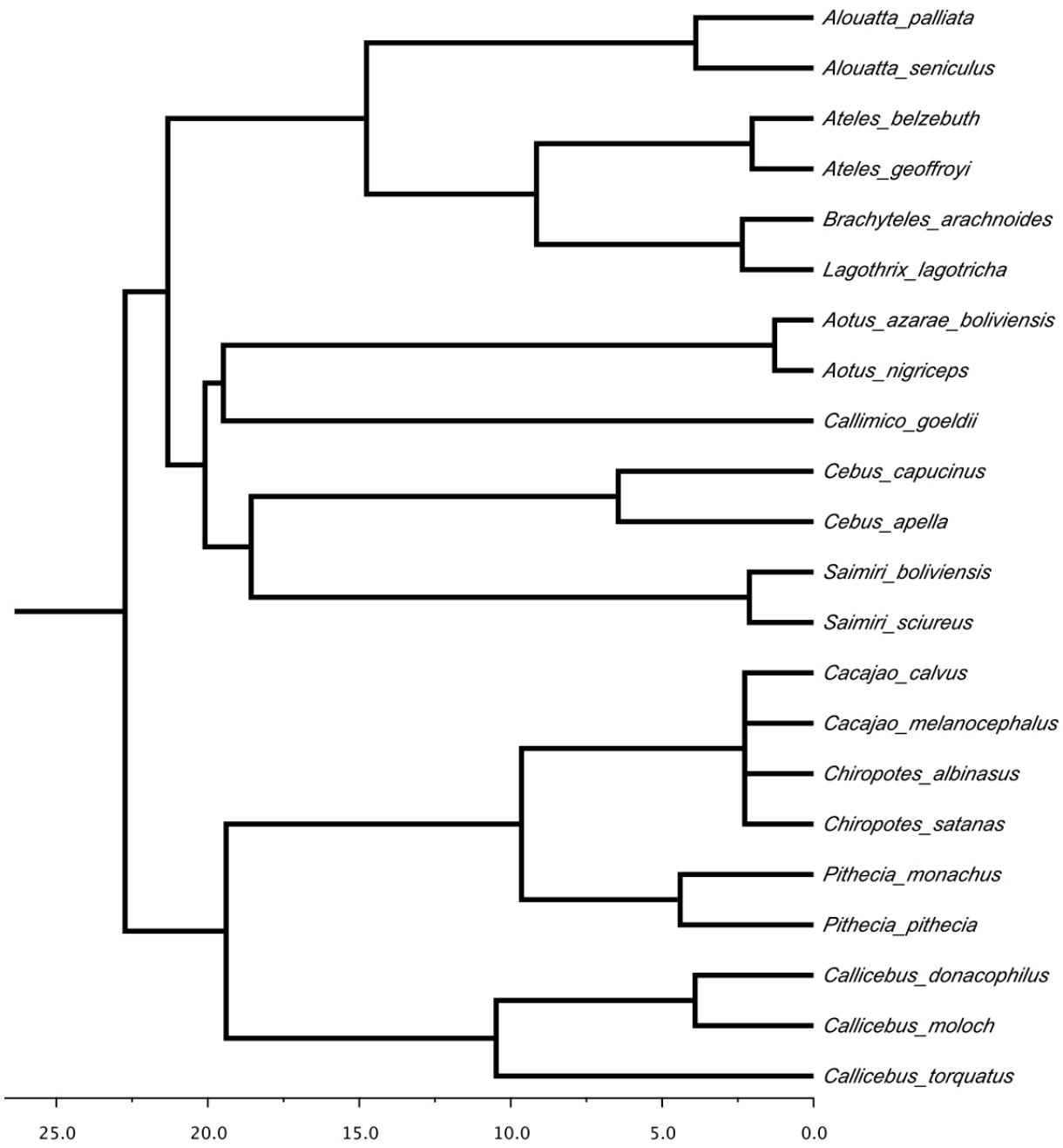


**Fig. 4.6.** Variance explained by individual principal components and cumulative variance explained, for the Archontan/Prosimian PCA (*Lepilemur* homology 2).

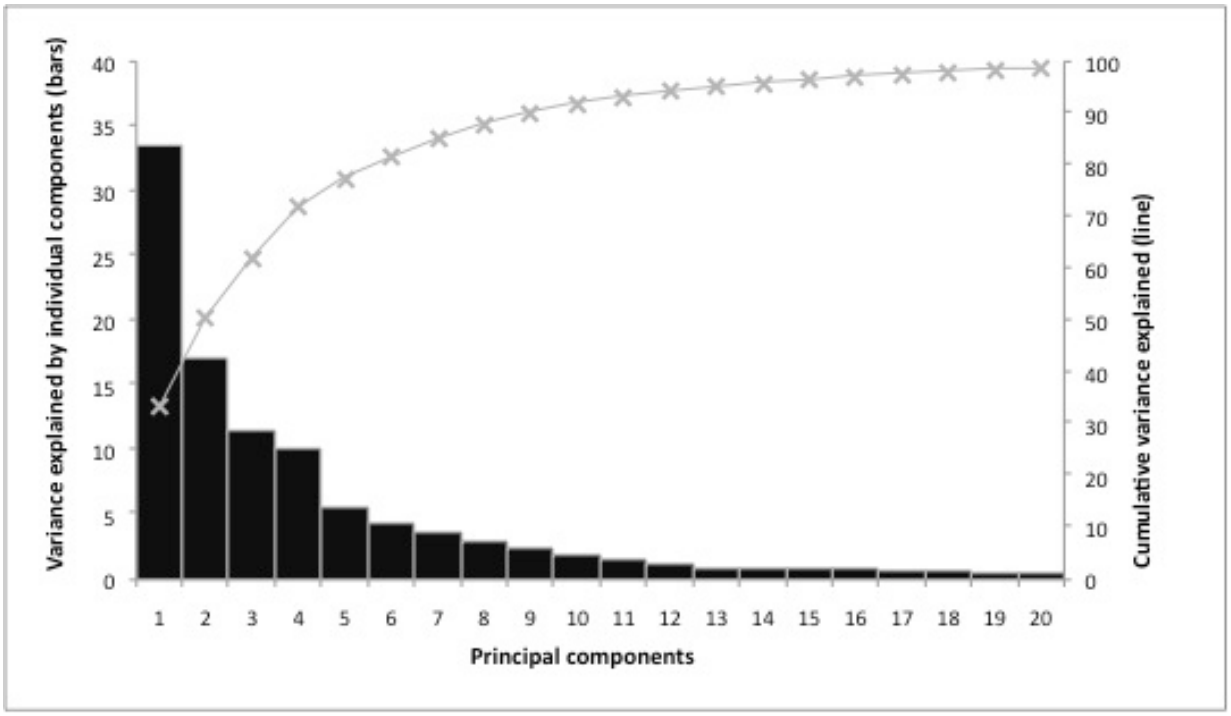
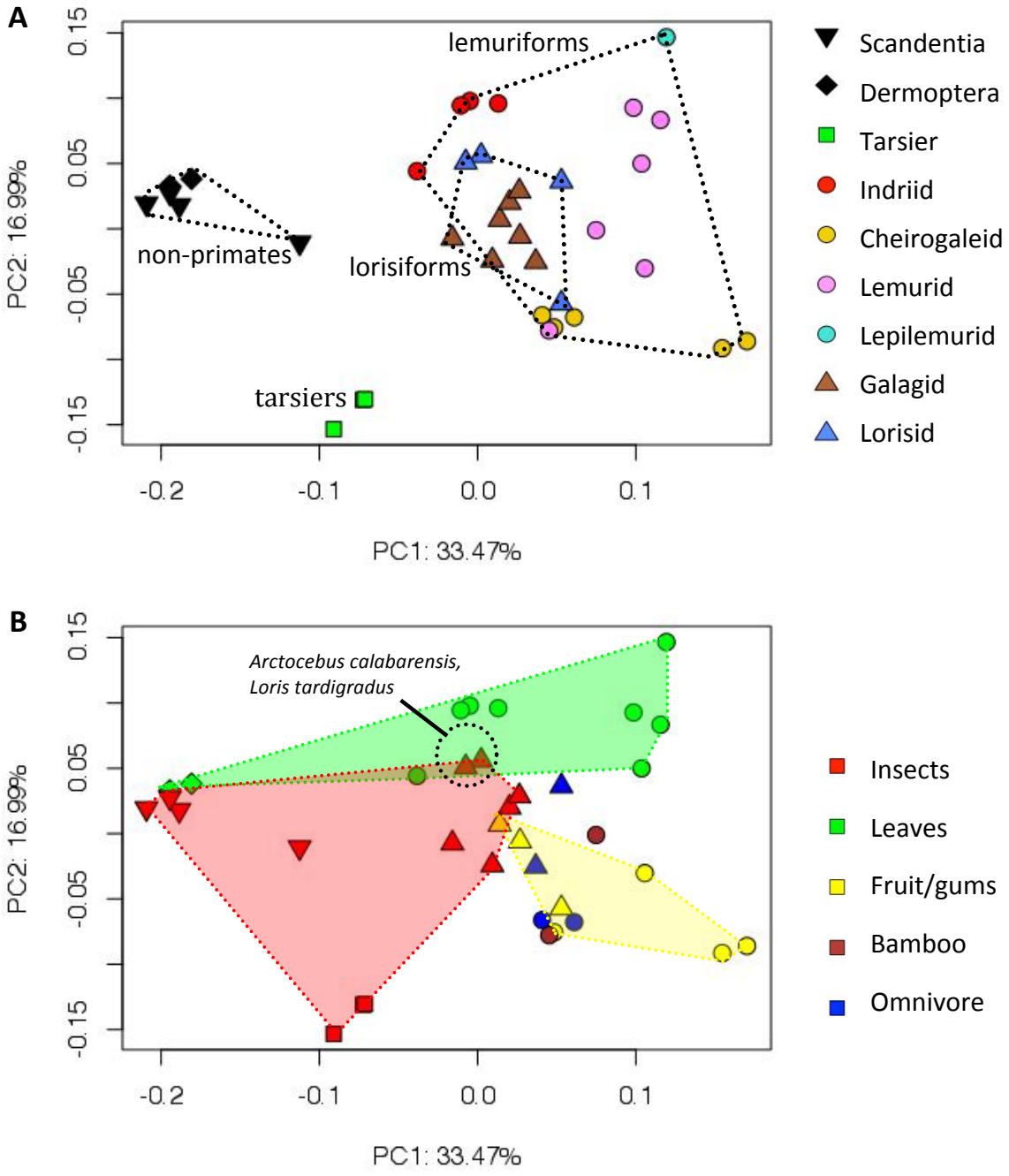
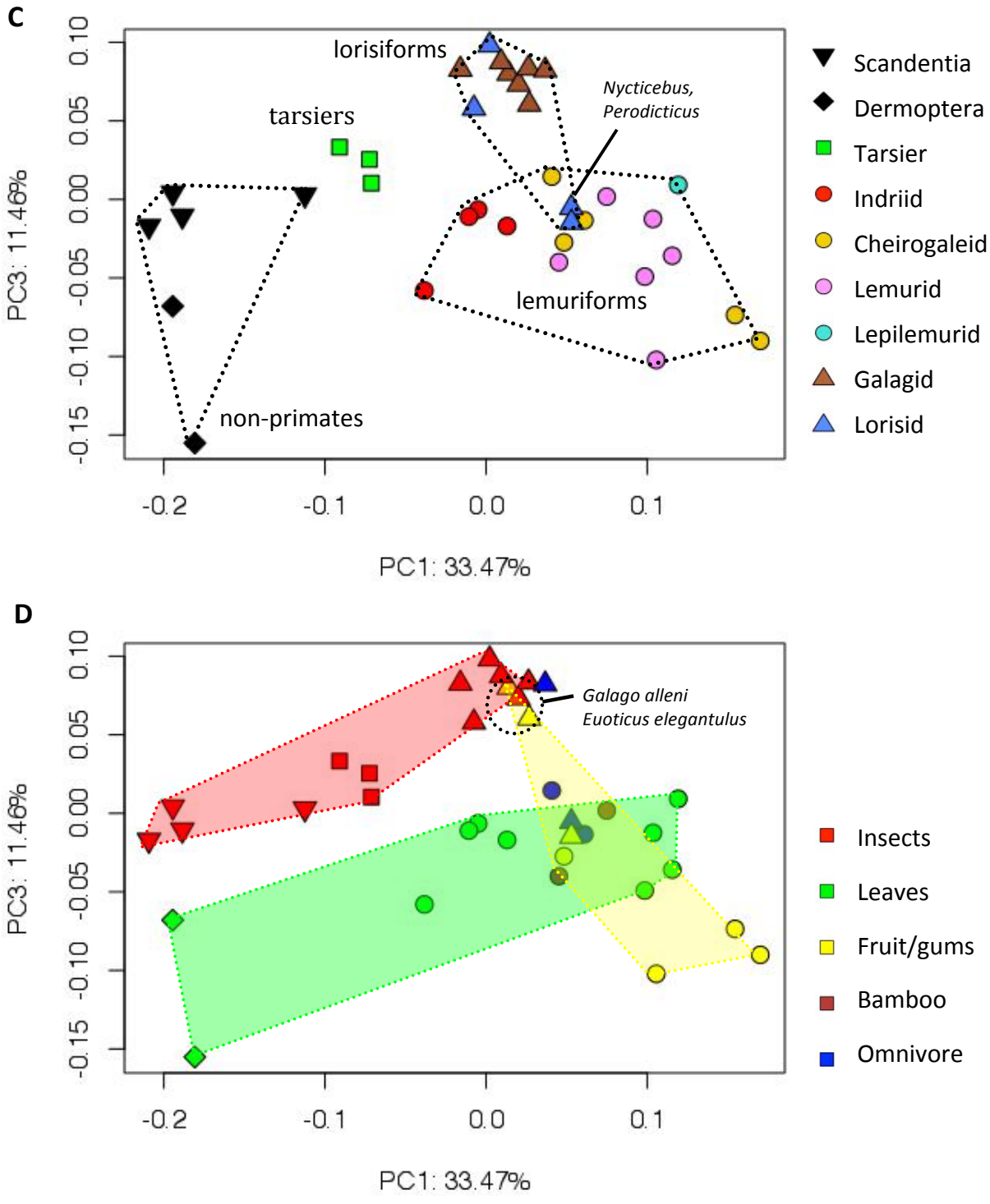
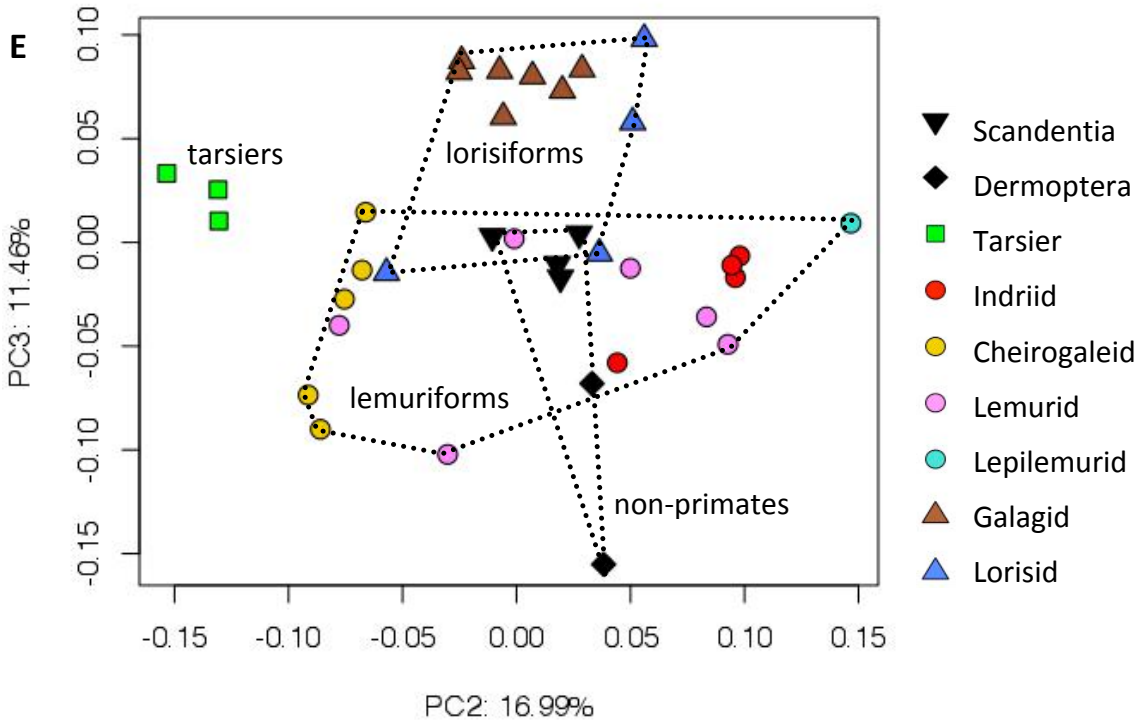


**Fig. 4.7.** Non-primate archontans and prosimian PCA:, with points represented by taxon (**A, C, E**) and by dietary group (**B, D, F**). Markers in the dietary plot retain superfamily identification for marker shape from plot above. A and B show PC1 and PC2, C and D show PC1 and PC3, and E and F show PC2 and PC3.




C
lorisiforms
tarsiers
Nycticebus,
Perodicticus
lemuriforms
non-primates
PC3: 11.46%
PC1: 33.47%
-0.2
-0.1
0.0
0.1
0.10
0.05
0.00
-0.05
-0.10
-0.15
Scandentia
Dermoptera
Tarsier
Indriid
Cheirogaleid
Lemurid
Lepilemurid
Galagid
Lorisid
D
Galago alleni
Euoticus elegantulus
Insects
Leaves
Fruit/gums
Bamboo
Omnivore


E
tarsiers
lorisiforms
lemuriforms
non-primates
PC3: 11.46%
PC2: 16.99%
-0.15
-0.10
-0.05
0.00
0.05
0.10
0.15
Scandentia
Dermoptera
Tarsier
Indriid
Cheirogaleid
Lemurid
Lepilemurid
Galagid
Lorisid

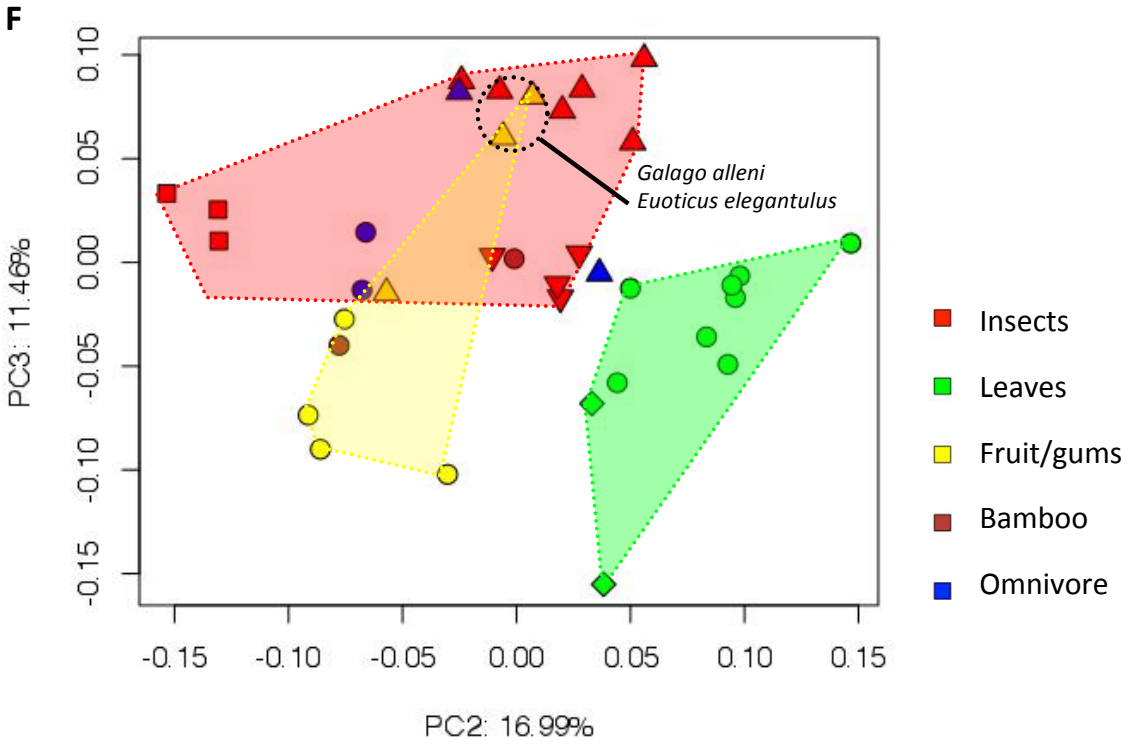

F
Galago alleni
Euoticus elegantulus
PC3: 11.46%
PC2: 16.99%
-0.15
-0.10
-0.05
0.00
0.05
0.10
0.15
Insects
Leaves
Fruit/gums
Bamboo
Omnivore

**Fig. 4.8.** Visualization of the shape changes along the first three principal components in the analysis of non-primate archontan and prosimian taxa. Landmark labels as in Figure 4.2A.

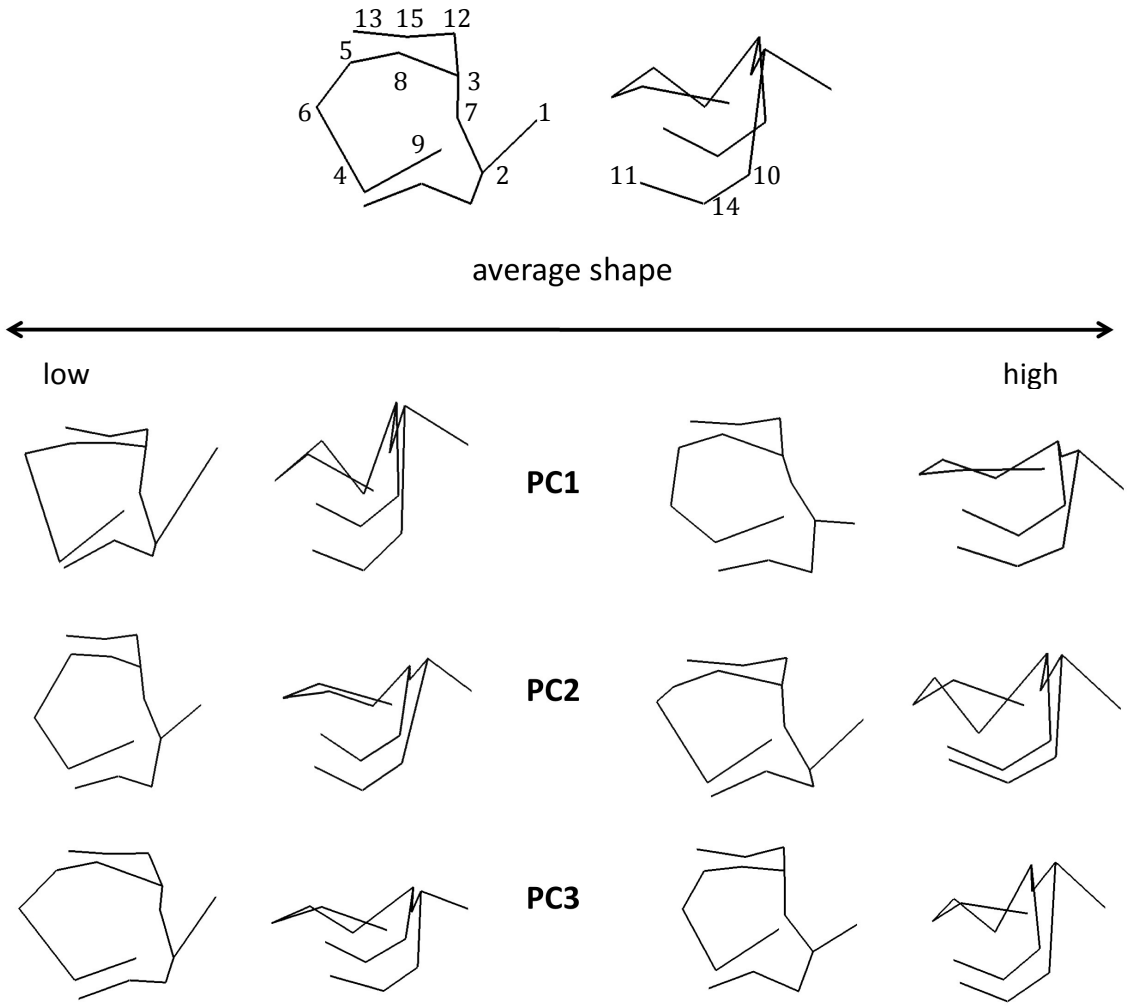
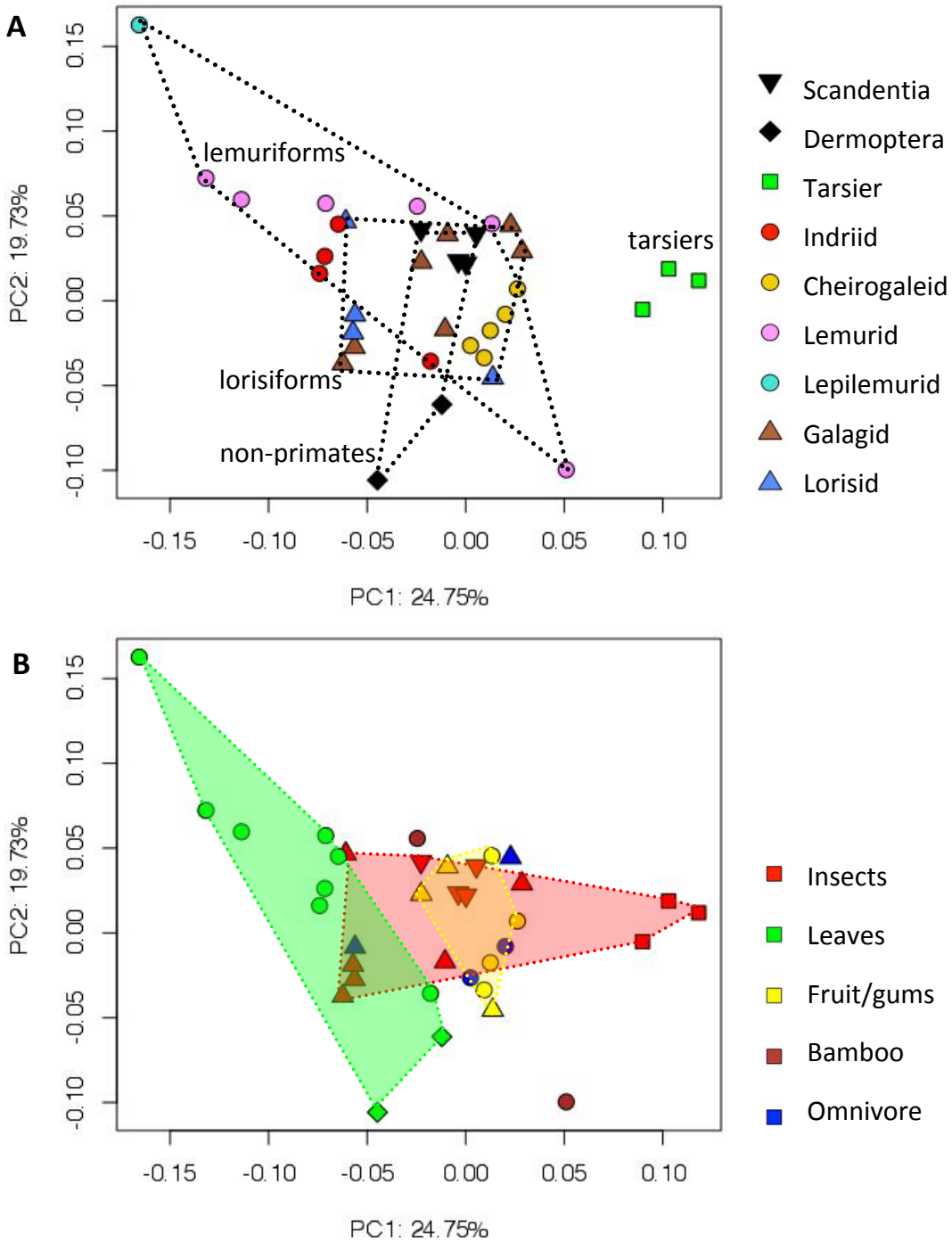
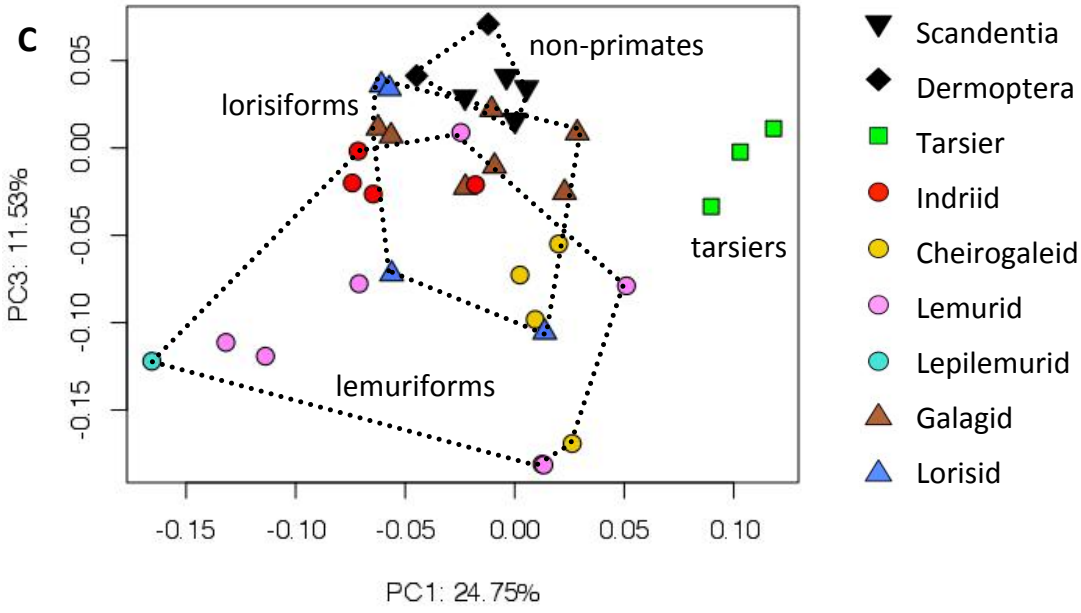
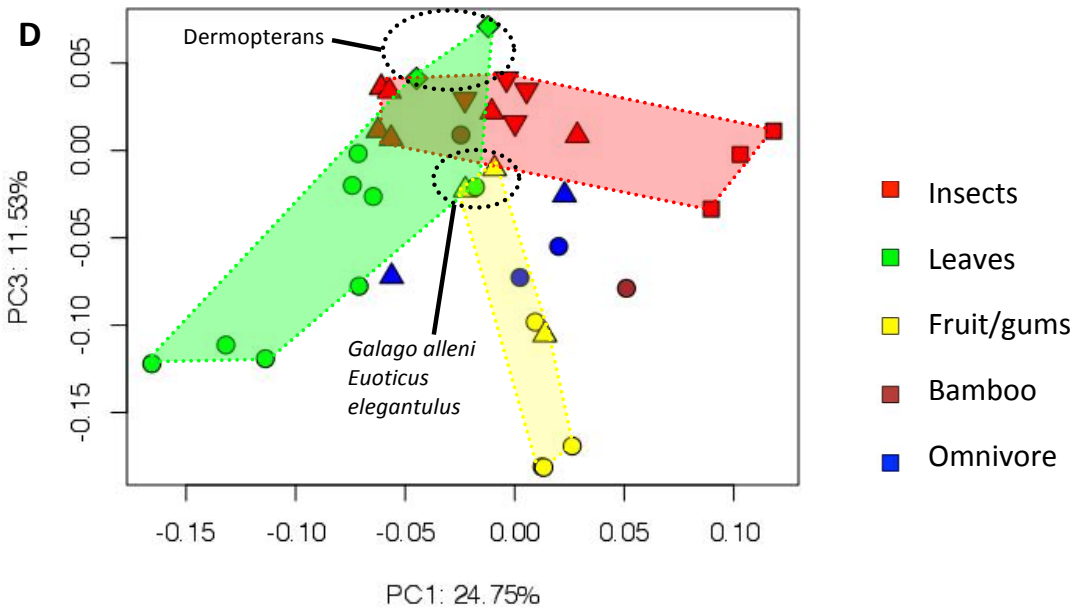
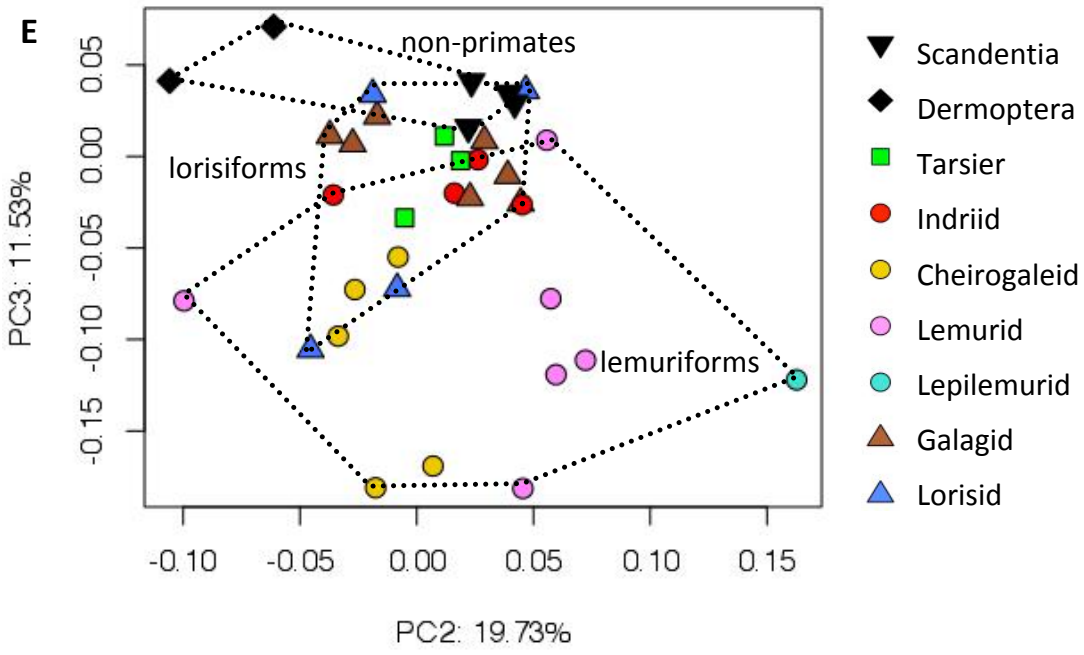


**Fig. 4.9.** Non-primate archontans and prosimian phylogenetic PCA:, with points represented by taxon (**A, C, E**) and by dietary group (**B, D, F**). Markers in the dietary plot retain superfamily identification for marker shape from plot above. A and B show PC1 and PC2, C and D show PC1 and PC3, and E and F show PC2 and PC3.




C
non-primates
lorisiforms
tarsiers
lemuriforms
PC3: 11.53%
PC1: 24.75%
-0.15
-0.10
-0.05
0.00
0.05
0.10
Scandentia
Dermoptera
Tarsier
Indriid
Cheirogaleid
Lemurid
Lepilemurid
Galagid
Lorisid


D
Dermopterans
Galago alleni
Euoticus
elegantulus
PC3: 11.53%
PC1: 24.75%
-0.15
-0.10
-0.05
0.00
0.05
0.10
Insects
Leaves
Fruit/gums
Bamboo
Omnivore


E
non-primates
lorisiforms
lemuriforms
PC3: 11.53%
PC2: 19.73%
-0.15
-0.10
-0.05
0.00
0.05
0.10
0.15
Scandentia
Dermoptera
Tarsier
Indriid
Cheirogaleid
Lemurid
Lepilemurid
Galagid
Lorisid

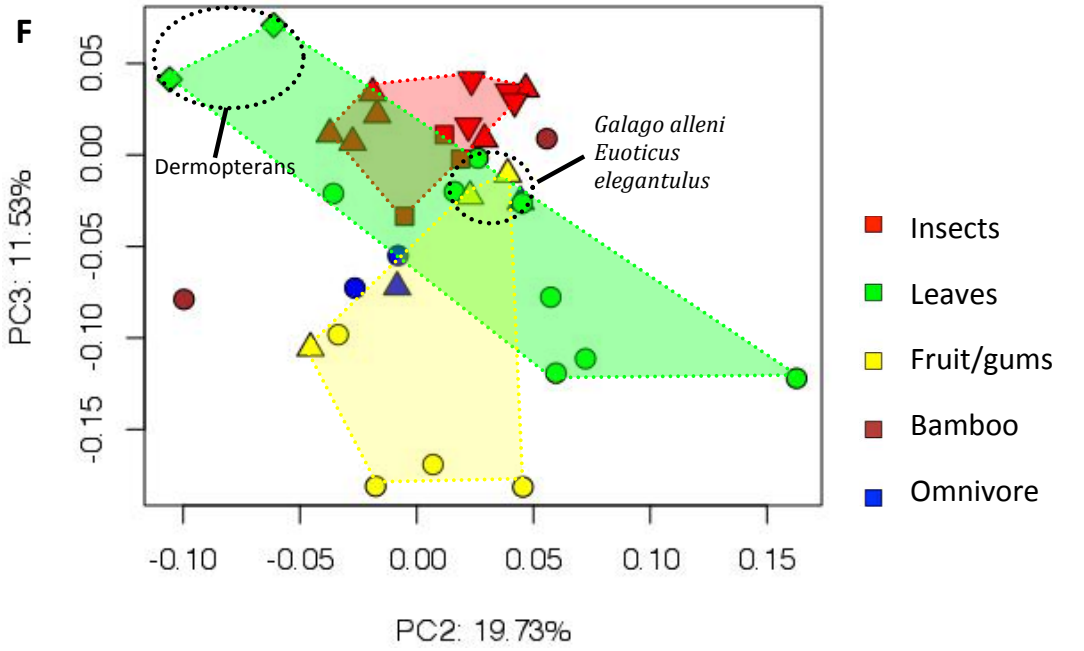

F
Dermopterans
Galago alleni
Euoticus
elegantulus
PC3: 11.53%
PC2: 19.73%
-0.15
-0.10
-0.05
0.00
0.05
0.10
0.15
Insects
Leaves
Fruit/gums
Bamboo
Omnivore

**Fig. 4.10.** Variance explained by individual principal components and cumulative variance explained, for the platyrrhine PCA.

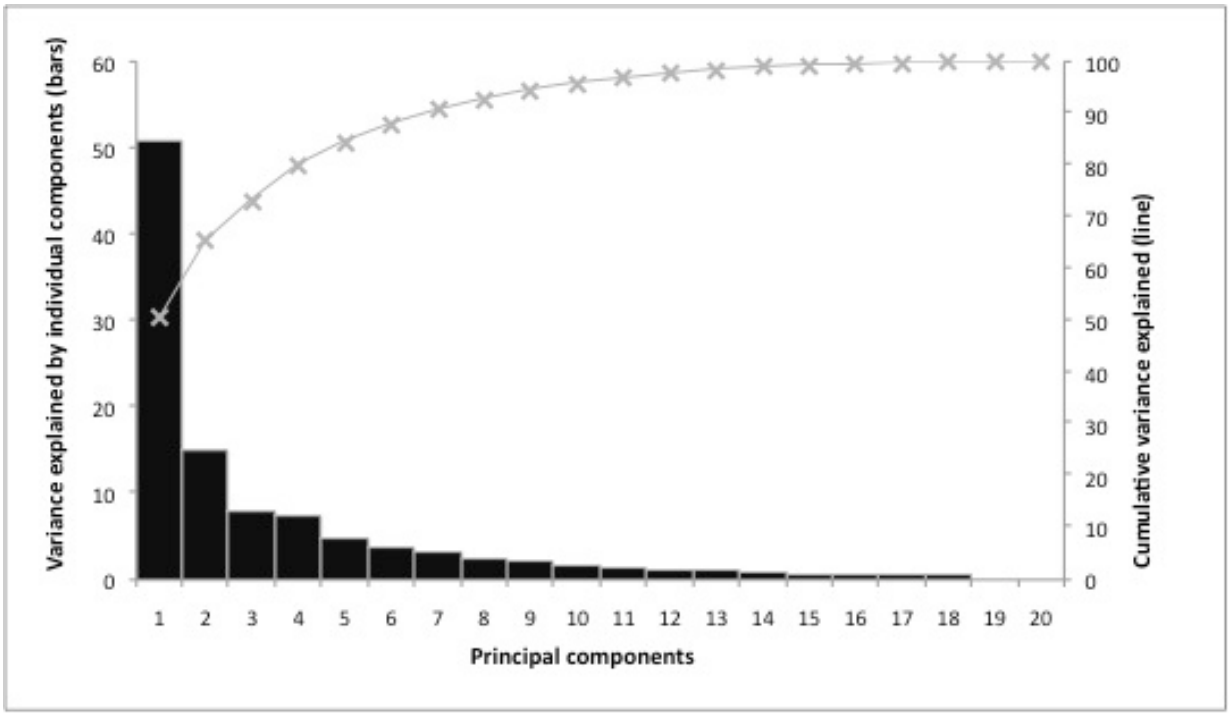


**Fig. 4.11.** Platyrrhine PCA: PC1 and PC2, by (**A**) subfamily and (**B**) diet (dominant food items in diet).

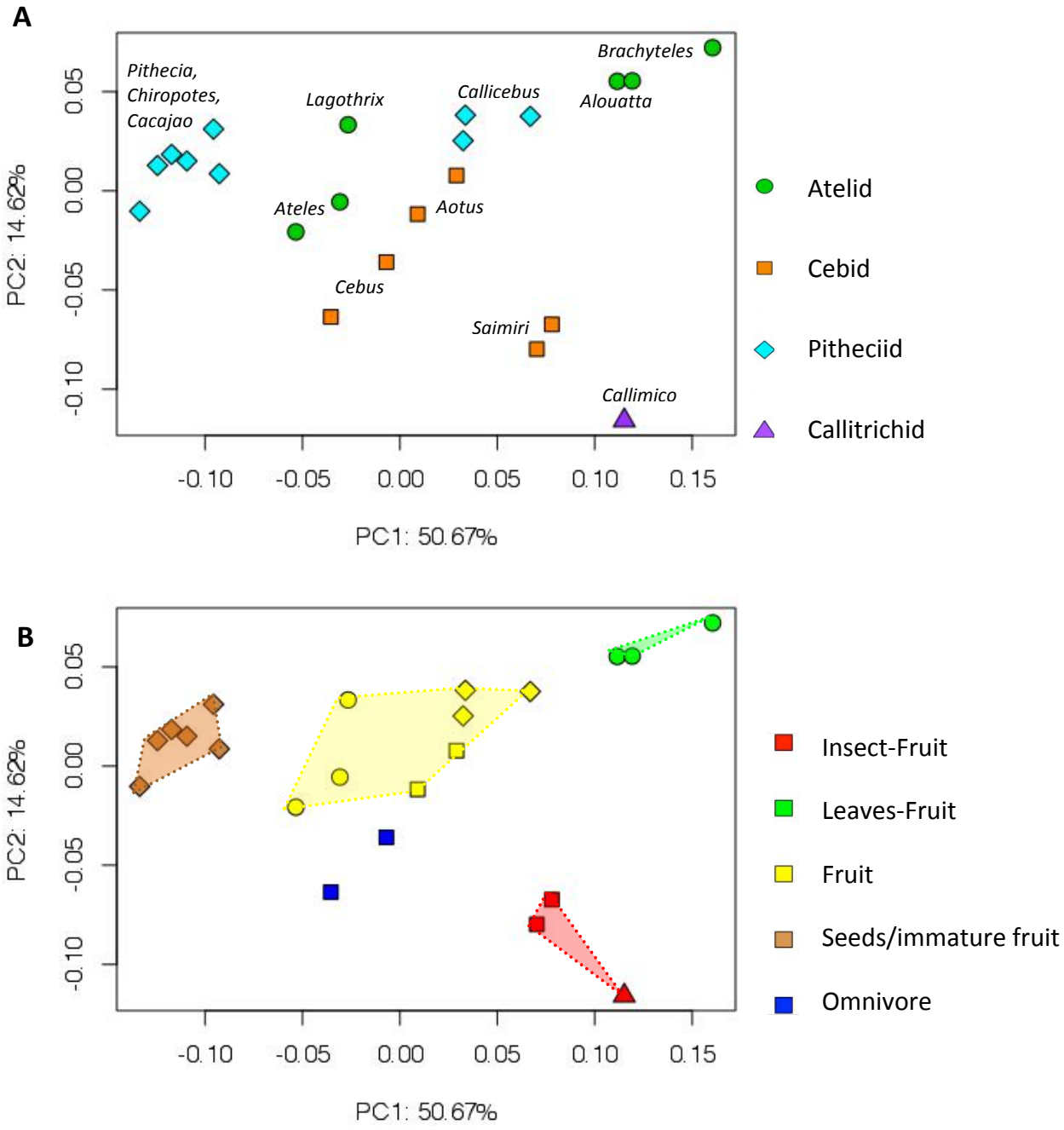


**Fig. 4.12.** Visualization of the shape changes along the first two principal components in the analysis of platyrrhine taxa. Landmark labels as in Figure 4.2B.

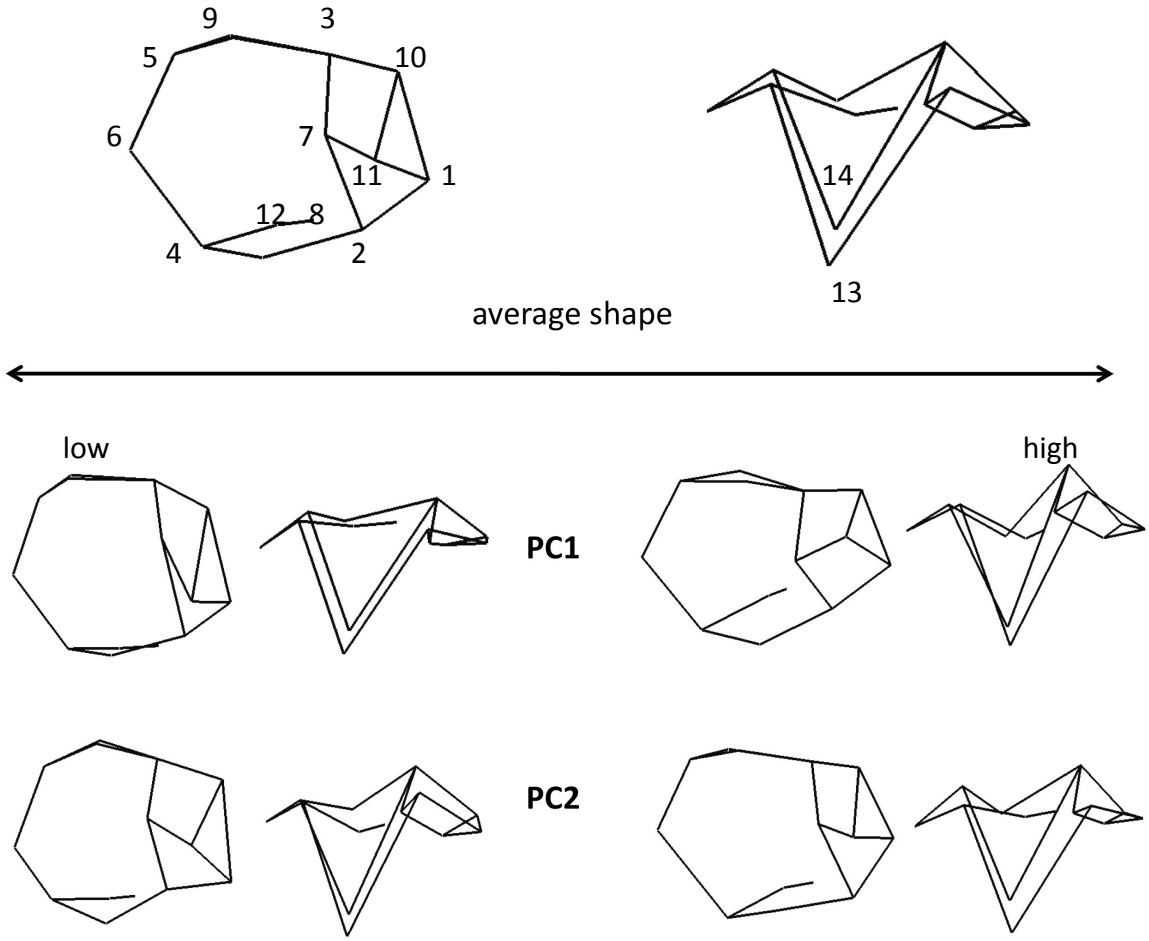
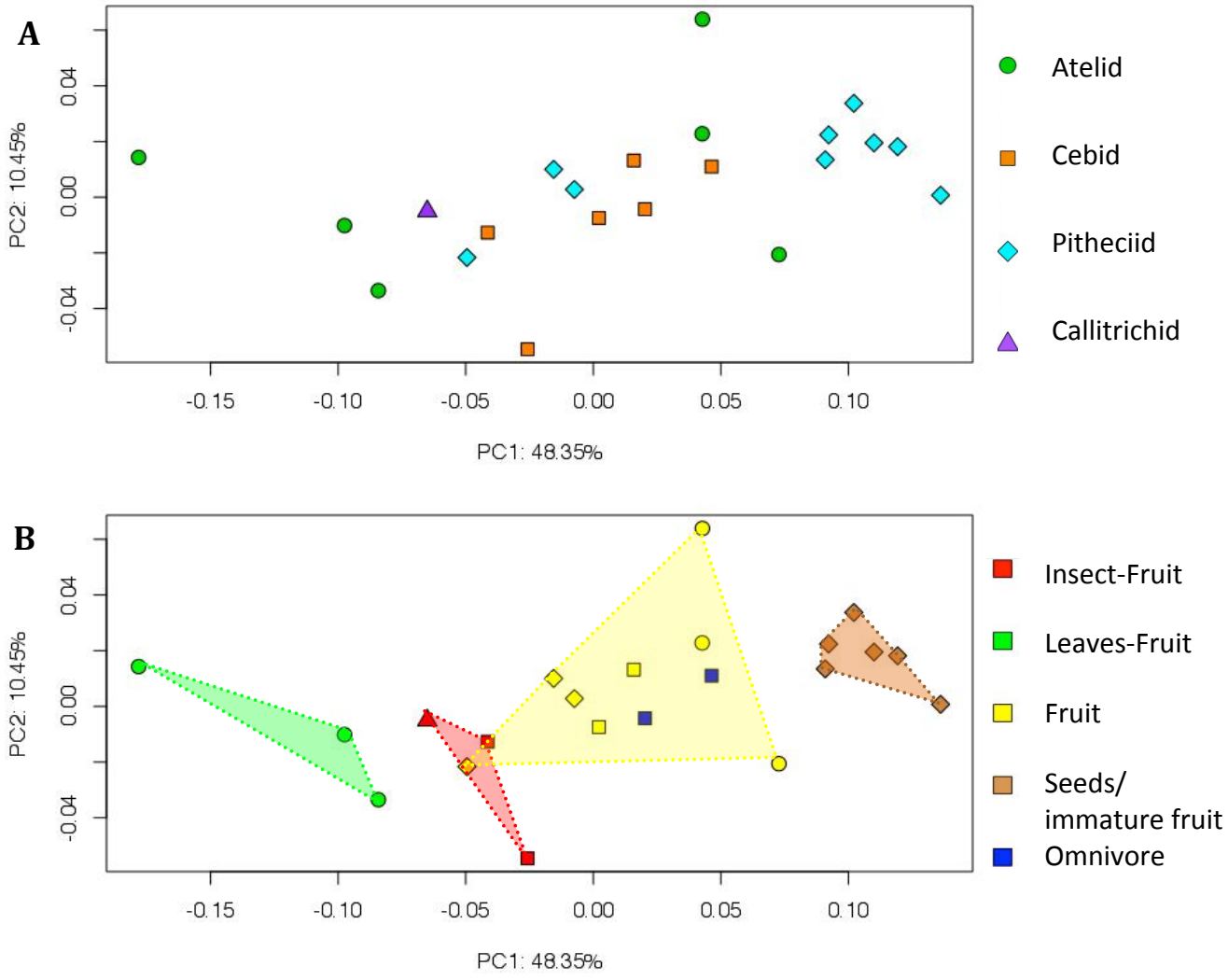
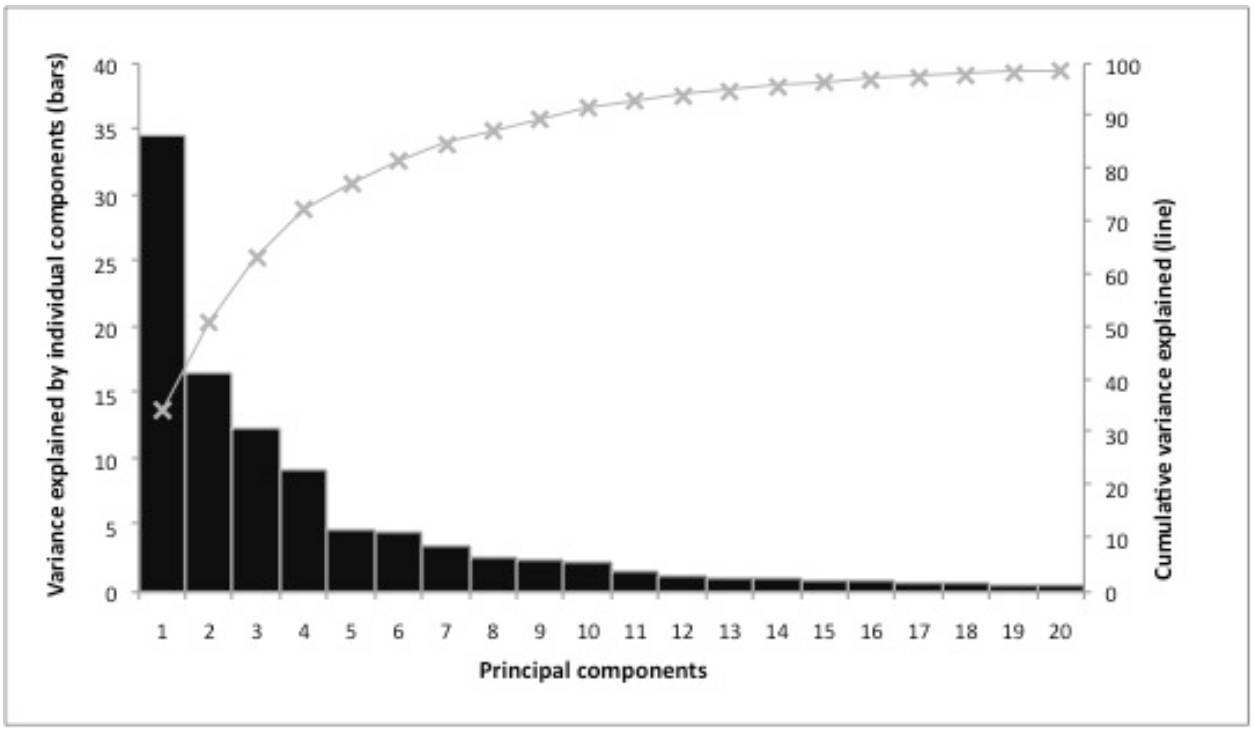


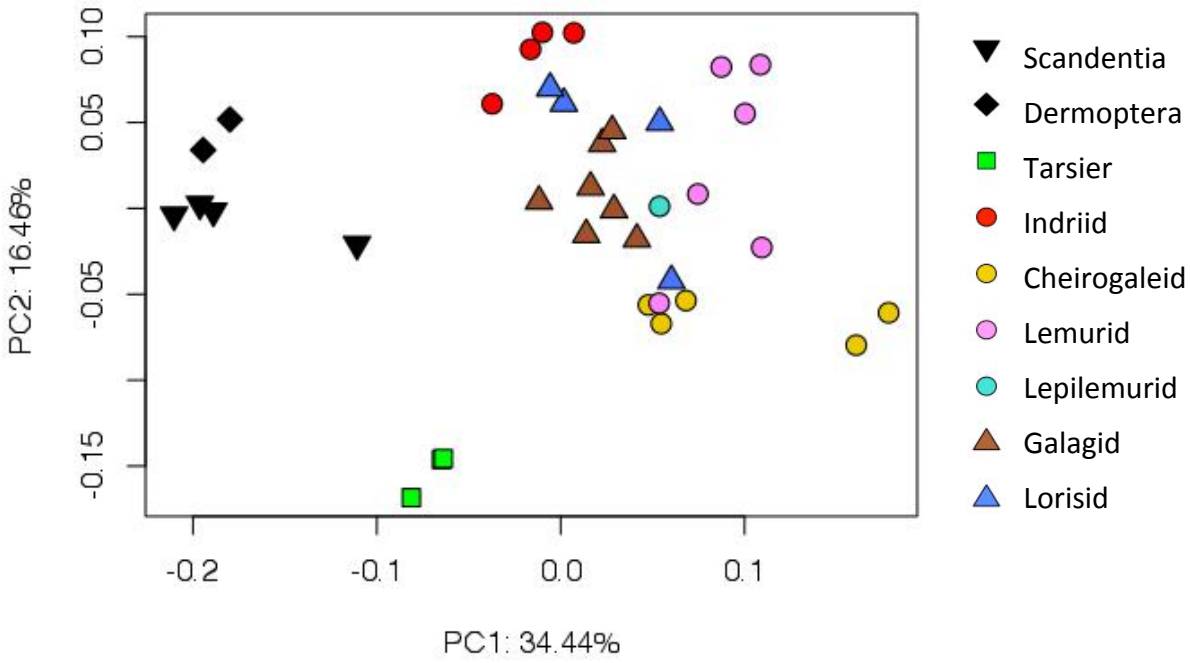
**Fig. 4.13.** Platyrrhine Phylogenetic PCA: PC1 and PC2, by (**A**) subfamily and (**B**) diet (dominant food items in diet).

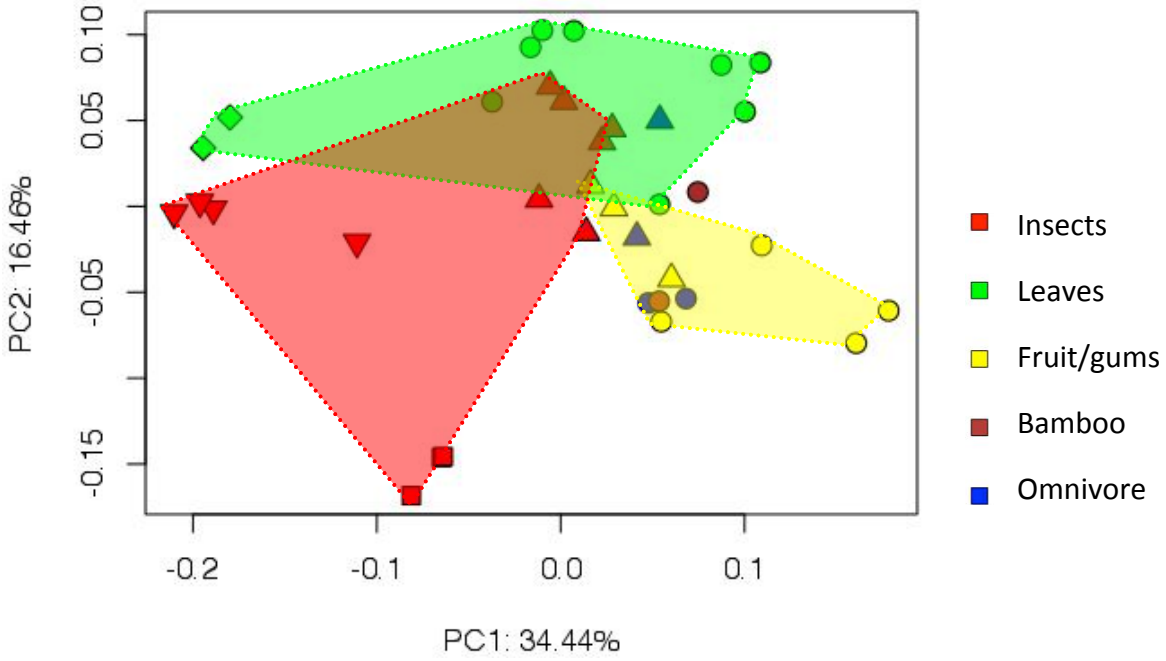


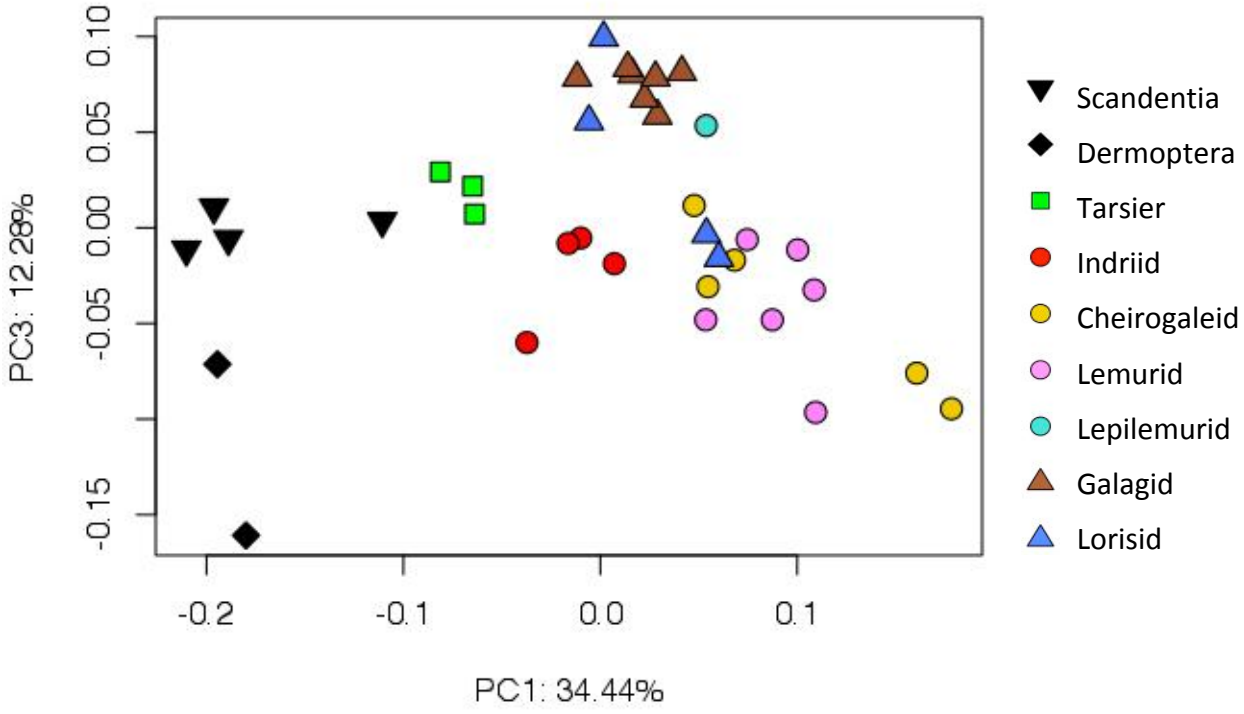
**Supplemental 1:** PCA results for the archontan and prosimian analysis with *Lepilemur* cusp homology following Swindler (2002)

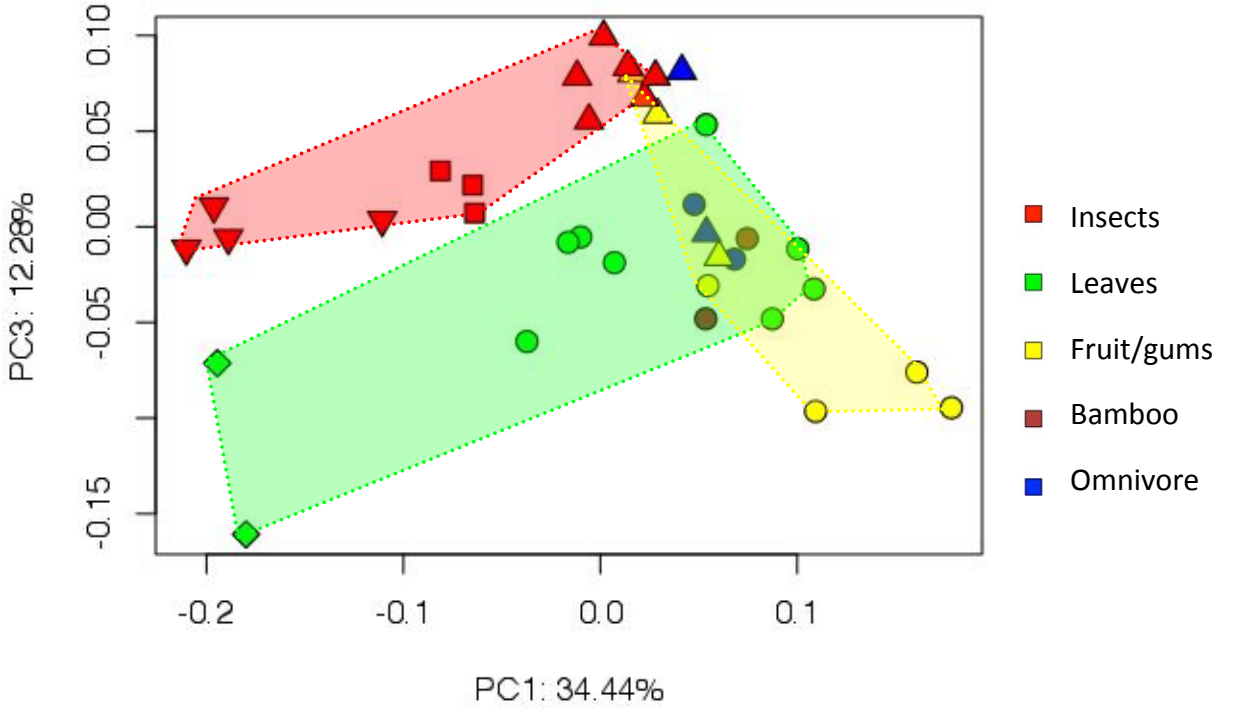
Variance explained by the first 20 principal components from the analysis of prosimian and archontan molar shape



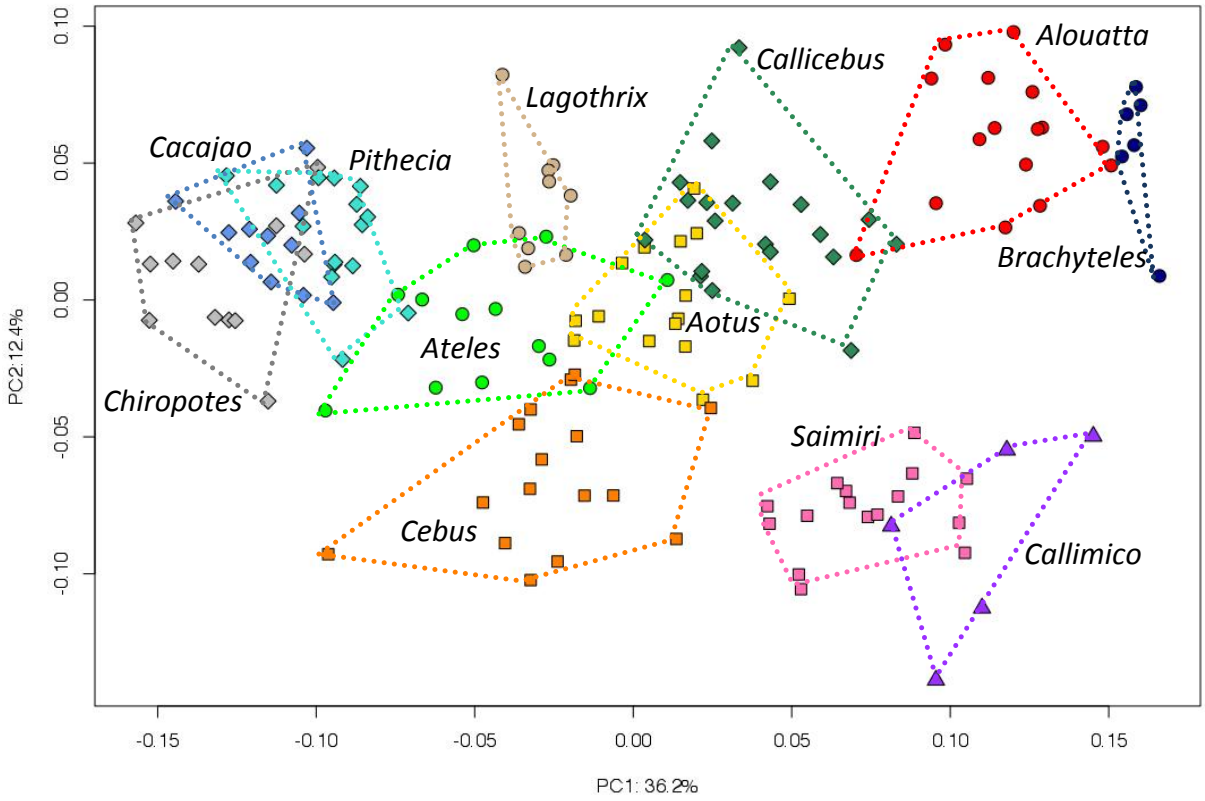

PC2: 16.46%
0.10
0.05
-0.05
-0.15
-0.2
-0.1
0.0
0.1
PC1: 34.44%
Scandentia
Dermoptera
Tarsier
Indriid
Cheirogaleid
Lemurid
Lepilemurid
Galagid
Lorisid


PC2: 16.46%
0.10
0.05
-0.05
-0.15
-0.2
-0.1
0.0
0.1
PC1: 34.44%
Insects
Leaves
Fruit/gums
Bamboo
Omnivore


PC3: 12.28%
0.10
0.05
0.00
-0.05
-0.15
-0.2
-0.1
0.0
0.1
PC1: 34.44%
Scandentia
Dermoptera
Tarsier
Indriid
Cheirogaleid
Lemurid
Lepilemurid
Galagid
Lorisid


PC3: 12.28%
0.10
0.05
0.00
-0.05
-0.15
-0.2
-0.1
0.0
0.1
PC1: 34.44%
Insects
Leaves
Fruit/gums
Bamboo
Omnivore

**Supplemental 2:** PCA results for analyses of all individuals - platyrrhines



**Supplemental 3:** Nexus files used in analyses

## Archonta

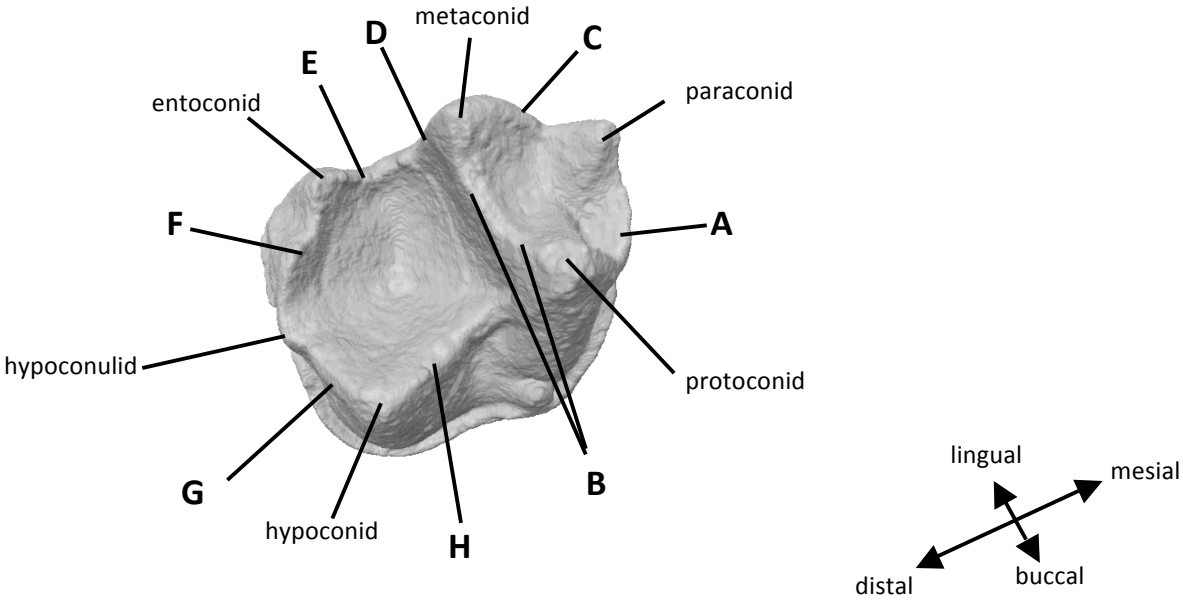
#NEXUS
[created by the 10kTree Website - http://10kTrees.fas.harvard.edu; modified to include non-primate archontan taxa]
BEGIN TREES;
translate
1 Avahi_laniger,
2 Cheirogaleus_major,
3 Cheirogaleus_medius,
4 Eulemur_fulvus,
5 Eulemur_rufus,
6 Hapalemur_griseus,
7 Hapalemur_simus,
8 Indri_indri,
9 Lemur_catta,
10 Lepilemur_mustelinus,
11 Microcebus_griseorufus,
12 Mirza_coquereli,
13 Phaner_furcifer,
14 Propithecus_diadema,
15 Propithecus_verreauxi,
16 Varecia_variegata,
17 Arctocebus_calabarensis,
18 Loris_tardigradus,
19 Nycticebus_coucang,
20 Perodicticus_potto,
21 Euoticus_elegantulus,
22 Galago_alleni,
23 Galago_moholi,
24 Galago_senegalensis,
25 Galagoides_demidoff,
26 Galagoides_zanzibaricus,
27 Otolemur_crassicaudatus,
28 Tarsius_bancanus,
29 Tarsius_syrichta,
30 Tupaia_montana,
31 Tupaia_glis,
32 Dendrogale_murina,
33 Ptilocercus_lowii,
34 Galeopterus_variegatus,
35 Cynocephalus_volans,
36 Tarsius_spectrum;
tree consensus_36species
=((((30:19.76,31:19.76):15.01,32:34.77):25.42,33:60.19):23.24,((((28:16.31,29:16.31):15.79,36:32.10):40.90,((((((11:14.27,12:14.27):8.29,(2:11.39,3:11.39):11.18):5.87,(10:25.69,13:25.69):2.741):2.52,(8:20.91,(1:16.50,(15:6.56,14:6.56):9.95):4.41):10.04):2.32,(((4:4.15,5:4.15):10.87,((6:8.20,7:8.20):1.08,9:9.28):5.74):5.52,16:20.54):12.72):29.47,(((17:18.73,20:18.73):15.90,(18:24.06,19:24.06):10.58):3.36,((((21:5.38,(23:1.19,24:1.19):4.19):5.14,26:10.53):2.84,(22:8.41,27:8.41):4.96):3.77,25:17.13):20.87):24.74):10.27):5.0,(34:19.80,35:19.80):58.20):5.43);
END;

## Platyrrhines

#NEXUS
[created by the 10kTree Website - http://10kTrees.fas.harvard.edu, modified to include *Chiropotes albinasus*, *Pithecia irrorata* used as a proxy for *P. monachus*]
BEGIN TREES;
translate
1 Alouatta_palliata,
2 Alouatta_seniculus,
3 Ateles_belzebuth,
4 Ateles_geoffroyi,
5 Brachyteles_arachnoides,
6 Lagothrix_lagotricha,
7 Aotus_azarae_boliviensis,
8 Aotus_nigriceps,
9 Callimico_goeldii,
10 Cebus_apella,
11 Cebus_capucinus,
12 Saimiri_boliviensis,
13 Saimiri_sciureus,
14 Cacajao_calvus,
15 Cacajao_melanocephalus,
16 Callicebus_donacophilus,
17 Callicebus_moloch,
18 Callicebus_torquatus,
19 Chiropotes_satanas,
20 Pithecia_monachus,
21 Pithecia_pithecia,
22 Chiropotes_albinasus;
tree consensus_22species =
((((1:3.888217,2:3.888216):10.872024,((3:2.029549,4:2.029548):7.117843,(5:2.353770,6:2.353770):6.793621):5.612849):6.561060,(((7:1.285874,8:1.285874):18.201648,9:19.487521):0.605006,((11:6.449384,10:6.449384):12.120521,(12:2.120959,13:2.120959):16.448946):1.522623):1.228773):1.411478,((((14:2.274028,15:2.274028):0,(22:2.274028,19:2.274028):0):7.368851,(20:4.404566,21:4.404566):5.238313):9.753209,((16:3.913001,17:3.913001):6.567518,18:10.480520):8.915568):3.336691);
END;

**Supplemental 4:** Crest terminology

Nomenclature for cusps, illustrated on *Tarsius* m/2, remains relatively stable across different authors. Variation in crest nomenclature listed in table below.



Variation in dental nomenclature for crests of lower molars. Terms used in this dissertation in bold.

| Crest | Van Valen 1966 | Hershkovitz 1971; 1981 | Kay 1977 | Szalay and Delson 1979 | Strait 1991 |
|---|---|---|---|---|---|
| **A** | paralophid | I' paracristid | **crest 2: paracristid** | paralophid | **paracristid** |
| **B** | protolophid | II'+II'' epicristid (linguad and buccad) | **crest 1: protocristid** | protocristid | **protocristid** |
| **C** | metacristid | III protolophid | **premetacristid** | -- | -- |
| **D** | -- | V' mesial pre-entocristid | **crest 5: postmetacristid** | postmetaconid cristid | **postmetacristid** |
| **E** | entocristid | V'' distal section of pre-entocristid | **crest 6 (1st part): pre-entocristid** | pre-entoconid cristid | **pre-entocristid** |
| **F** | } postcristid | VI distocristid* | **crest 6 (2nd part): post-entocristid** | } postcristid | **post-entocristid** |
| **G** | | I'' postmetacristid | crest 4: hypocristid | | **postcristid** |
| **H** | crista obliqua | I''' premetacristid section of centrocristid | crest 3: oblique cristid | **cristid obliqua** | **cristid obliqua** |

* An alternate "pathway" between the entoconid and the hypoconulid is shown in Hershkovitz's illustration (1971: Figure 17), and labeled as VIII'+VIII''- the postentocristid

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## Chapter 5. Geometric morphometric analysis of molar shape and morphological disparity in plesiadapoid plesiadapiforms

*ABSTRACT: Molar morphology has played a central role in hypotheses regarding primate evolutionary origins. Here an exploratory analysis of molar shape is presented using a sample composed of extant prosimian genera, plesiadapiforms, extant non-primate archontans, Eocene euprimates, and a possible fossil euarchontan,* Leptacodon*. The shape space created allows morphological diversification in molar shape in North American plesiadapoids to be placed in a comparative context.*

*Fifteen landmarks were placed on microCT scan surface renderings of lower second molars. Data were subjected to generalized Procrustes analysis, followed by principal components (PC) analysis to identify factors summarizing shape variation. PC1 and 2 account for over 50% of the sample variance. PC1 is associated with variation in the presence/size of the paraconid, mesiodistal length, and talonid proportions; PC1 separates strepsirrhines and* Adapis*, with positive scores on this axis, from other taxa. PC2 is associated with crest development and relief of the tooth, and also proportions of the trigonid basin.* Leptacodon *and* Purgatorius *differ from most other fossil taxa and* Tarsius *on PC2, and approach or overlap the distribution of extant archontans (dermopterans and scandentians) on the first three PC axes. Later occurring plesiadapiforms score lower on PC2 and overlap with tarsiers,* Teilhardina*,* Cantius*, and* Donrussellia*.*

*Analyses of morphological disparity indicate that over the course of the Paleocene sufficient diversity in molar morphology was accumulated such that plesiadapiforms achieved levels of molar disparity comparable to those of extant groups such as strepsirrhines. In the Plesiadapoidea, even though taxonomic diversity in this sample was highest in the early Tiffanian, measurements of morphological disparity were higher in the late Tiffanian, indicating that morphological disparity is capturing variation not present in counts of taxa, and therefore may have potential to add information to analyses of ecological changes in this group.*

Plesiadapiforms are a group of small to medium sized mammals known primarily from the Paleocene and Eocene of North America and Europe, with some reports of additional species occurring in Asia (Beard and Wang, 1995) and Africa (Tabuce et al., 2004). Morphological (primarily dental) similarities to early primates resulted in inclusion of plesiadapiforms within primates in the older paleontological literature (e.g., Simpson, 1935). In more recent studies, plesiadapiforms are not usually included within crown primates, but have received much attention as a possible stem group from which euprimates (Bloch et al., 2007) or other archontan taxa such as dermopterans[4] (Kay et al., 1990; Beard, 1993) may have derived (but see Godinot, 2007). Most authors concur in at least including plesiadapiforms within archontan mammals and, as such, they are the largest group of fossil archontans, and the earliest representatives.

The phylogenetic relationships of archontan mammals have been much debated, both for the relative positions of the extant representatives (primates, dermopterans, and scandentians) and for the placement of plesiadapiforms relative to these groups. The most recent analyses of extant archontans using molecular data indicate that Dermoptera is the sister taxon to primates, with tree shrews as the first branch from the archontan common ancestor (Janecka et al., 2007; Roberts et al., 2011). The placement of plesiadapiforms within this framework is still debated; however, plesiadapiforms are one of the most important groups in the analysis of primate origins, whether they are considered to be the ancestral radiation in which the primate ancestor appeared, or as a sister radiation to the primate or primate/dermopteran clade. In either case their

[4] "Archonta" is used here to refer to extant dermopterans, primates, and tree shrews, and fossil species more closely related to these taxa than to other extant mammalian clades; this definition excludes Chiroptera (bats), which are no longer considered to be close relatives of the remaining archontan mammals; the term "Euarchonta" is also available for the remaining members of Archonta.

morphological similarities to primates inform analysis of the ecological and evolutionary context for primate origins. Examination of plesiadapiform morphology and adaptations can also provide key insights into the morphology and ecological milieu of the earliest archontans, and therefore may be helpful for reconstructing ancestral states and the evolutionary trajectories leading to extant groups.

Within the plesiadapiforms, the superfamily Plesiadapoidea (following the taxonomy of Silcox et al., 2001) provides most of the instances of morphological convergence with primates, and is possibly most closely related to primates (Bloch et al., 2007; Boyer, 2009). The greater part of the species diversity in plesiadapoids is divided between two families, Plesiadapidae and Carpolestidae; a third family, Saxonellidae, is currently known only by the sole genus *Saxonella*, with two species. Outside of these three families, the Asian plesiadapiform *Chronolestes* and a North American early Paleocene species *Pandemonium dis*, may also be basal members of the plesiadapoid radiation (Silcox et al., 2001).

Although the molars are generally similar in the Carpolestidae and Plesiadapidae, the families differ markedly in the morphology of their premolar dentitions. In the Carpolestidae, the lower fourth premolar (p/4) is modified to a greater or lesser extent into a blade of the "plagiaulacoid" type (Simpson, 1933); in some of the more derived species the trigonid cusps of the first lower molar (m/1) form a mesiodistally oriented row that essentially extends the edge of the blade formed by the p/4, and the two teeth have been described as slicing-crushing in food ingestion behaviors (Biknevicius, 1986). A plagiaulacoid complex is also present in saxonellids, but *Saxonella* has a plagiaulacoid p/3, rather than p/4, indicating independent acquisition (Fox, 1991). In the Plesiadapidae, the premolars are less specialized; in most species the premolars have a more typical conical shape with a small talonid. Some later-occurring species of

plesiadapids show reduction in the number of anterior premolars (Gingerich, 1976) or molarized fourth premolars (Boyer et al., 2010).

## Diversification in plesiadapoids

Previous analyses of diversification among plesiadapiforms have focused on the species or generic diversity (taxonomic richness) contained in the group (e.g., Maas et al., 1988; McGee, 1997). These analyses showed that the greatest richness of plesiadapiform species and genera is seen in the first late Paleocene North American Land Mammal "Age" (NALMA), the Tiffanian, though if the duration of the interval is incorporated into estimates, the second part of the late Paleocene, the Clarkforkian, has higher generic richness per million years (Maas et al., 1988). The distribution of diversity among plesiadapiform groups changes through time, with plesiadapoids (defined as plesiadapids, carpolestids, and saxonellids) being most diverse in the Tiffanian. The appearance of rodents in the Clarkforkian NALMA and subsequent competitive exclusion (Maas et al., 1988) have been suggested to be important factors in the decline and disappearance of plesiadapoids (and other non-paromomyoid plesiadapiforms) in North America, but changes in climate may also have contributed (McGee, 1997).

Predictive hypotheses concerning morphological disparity through time within plesiadapoids are difficult to create, in part because variation in morphological disparity in extant groups has not been much investigated in the context of variation with climate, or competitive interactions. If morphological disparity tracks taxonomic diversity in plesiadapoids, rapid increases would be predicted to occur at the boundary between the Torrejonian and Tiffanian, and decreases would be predicted at the Tiffanian/Clarkforkian boundary. However, it is also possible that average intertaxon distances will increase as taxonomic diversity decreases,

depending on the degree to which the total range of occupied morphospace is affected by the removal of species.

### Aims

In this analysis, a geometric morphometric analysis of plesiadapiform molar shape is conducted to investigate the morphospace occupied by extant and extinct archontan mammals. In part, the aims of this study are to evaluate the potential of morphological disparity for analyses of the plesiadapiform and primate fossil record. Two questions are addressed relating to the morphological disparity within plesiadapiform molar morphology: 1) how much variation accumulated within plesiadapiform clades? and 2) what is the nature of the diversification through time among North American plesadapoids?

## METHODS

The sample consisted of 347 specimens from 96 species of extant and fossil archontan mammals. Extant species included dermopterans, tree shrews, and "prosimian" primates (strepsirrhines and tarsiers). Fossil taxa included plesiadapiforms, Eocene euprimates, and one Paleocene genus that has been suggested to be an archontan, the nyctitheriid *Leptacodon* (Hooker, 2001). Even if the latter taxon is not an archontan, it may still be a good model for a relatively primitive therian mammalian molar and has been used as such previously (e.g., Marivaux et al., 2004; Tabuce et al., 2004). *Altanius* was also included in this sample. This taxon was initially described as a euprimate (Dashzeveg and McKenna, 1977) but may also be a plesiadapiform (Rose and Krause, 1984). The plesiadapiform sample does not include microsyopids or micromomyids: the full sample of genera is listed in Table 5.1. The second

mandibular molar was selected for analysis. This tooth has been the frequent focus of investigation for dietary analysis in extant primates (e.g., Kay, 1975), and is available for a large number of fossil primates. MicroCT surface renderings of mandibular second molars were created using methods described by Boyer (2008). Specimens were scanned with a slice thickness of 8–18 microns depending on tooth size (teeth of a similar size were mounted together). Reconstruction of tooth surfaces was completed in the software Amira.

Geometric morphometric methods were used to quantify tooth shape. Landmarks were placed on cusp tips and endpoints of crests (Fig. 5.1) using the software Landmark.exe (IDAV, UC Davis). These landmarks can thus record cusp positions, crest lengths and angular orientations, as well as talonid and trigonid basin size (the areas enclosed by the cusps). Additional landmarks were placed at the base of the crown, capturing information on overall relief of the tooth. The landmarks are defined as: 1) mesial/lingual terminus of paracristid, equivalent to tip of paraconid, when the latter is present; 2) protoconid tip; 3) metaconid tip; 4) hypoconid tip; 5) entoconid tip; 6) distal/lingual terminus of postcristid; 7) notch/lowest point of protocristid; 8) talonid notch (deepest point between metaconid and entoconid); 9) contact of cristid obliqua and trigonid; 10) most buccal point on trigonid; 11) most buccal point on talonid; 12) most lingual point on trigonid; 13) most lingual point on talonid; 14) base of crown on buccal side, where trigonid meets talonid; and 15) base of crown on lingual side, where trigonid meets talonid. Landmarks were subjected to generalized Procrustes analysis to adjust for differences in rotation, translation, and scale. Species average landmark coordinates were calculated in MorphoJ (Klingenberg, 2011).

## Data analysis

A principal components analysis (PCA) on the species average coordinates was performed in Morphologika (O'Higgins and Jones, 1998) to allow a visualization of the differences between species in the sample, and to document the shape changes that separate species in the analysis. The Procrustes distance matrix between pairs of species was created in Morphologika, and these distances were used for the calculation of morphological disparity within the sample. In previous chapters, distances were calculated from PC axes but the Procrustes distance matrix was used here for two reasons. Firstly, the phylogenetic PCA (Revell, 2009) used in previous chapters requires a phylogeny of all species in the analysis. In fossil taxa such a phylogeny must necessarily be created using the morphology of the dentition. As a result, the features used to make the phylogeny would not be independent from the morphological features examined. Secondly, dimension reduction via PCA was conducted in previous chapters as a necessary step to represent multivariate data sets of potentially covarying linear and area measurements as a distance matrix for disparity analysis. Procrustes distance calculation from the landmarks provides a more direct method of estimating morphological distances.

The average and maximum within-group distances were calculated from the Procrustes distance matrix for plesiadapiforms and extant strepsirrhines, and subgroups within them (plesiadapiforms, plesiadapoids, plesiadapids, carpolestids; extant strepsirrhines, lorisiforms, lemuriforms, cheirogaleids, indriids, lemurids, lorisids, galagids). North American plesiadapoid species were divided into four subgroups using time period bins: Torrejonian, Early Tiffanian (Ti1 - Ti3), Late Tiffanian (Ti4 - Ti6), Clarkforkian (Table 5.2). Average and maximum distances were calculated for these time periods. Additionally, the average distance between

pairs composed of carpolestid and plesiadapid species was calculated as an estimate of the diversification between the two clades in molar morphology.

## RESULTS

### Principal components analysis

The PCA of molar shape in plesiadapiforms resulted in five PCs that explained more than 5% of the variance each, and approximately 75% cumulatively (see Table 5.3 for a description of shape changes along the first three PCs). Plots of the first three principal components (PC1: 35.8%, PC2: 16.1%, PC3: 9.6%) are shown in Figure 5.2. The first principal component primarily separates the extant strepsirrhine species (low scores) from the plesiadapiforms, tarsiers, and early Eocene euprimates (high scores). The Eocene euprimates with low scores on this axis are *Afradapis* and the two species of *Adapis*, in which the teeth are similar to extant strepsirrhines in lacking the paraconid. The second principal component primarily separates the extant non-primate archontans and the nyctitheriid *Leptacodon* from the other species in the analysis. Some of the variation on this axis is associated with the relative height of the crown, with species that have higher cusps and more crest development scoring lower. Other morphological variation along this axis is associated with the development of the trigonid basin relative to the talonid. Low scoring species, including extant non-primate archontans, *Leptacodon*, and *Purgatorius* share a relatively well-developed, "open" trigonid with widely spaced cusps. *Eosimias* also shares this morphology to some degree, even relative to *Tarsius*; the latter scores slightly higher on this axis. The third principal component separates the paromomyid plesiadapiforms from the other species in the analysis, and expresses variation in

the relative size and shape of the talonid basin, as well as the mesiodistal dimension of the trigonid. High scores on this axis were associated with greater development of the enamel at the base of the tooth on the buccal side (exodaenodonty); high scores appeared in carpolestids and *Altanius*. *Altanius* also plotted within the range of carpolestid scores on PC1 and close to the carpolestids on PC2. In combination, the first three PCs appear to effectively separate the main families of plesiadapiforms. In the ordination of PC1 and PC2, carpolestids and plesiadapids are for the most part separated by PC2, and paromomyids and palaechthonids are completely separated by PC2; palaecthonids do not overlap with any of the other plesiadapiform groups. In the ordination of PC1 and PC3, carpolestids and plesiadapids again have a small region of overlap with each other, while paromomyids are separated from other plesiadapiforms on PC3. When PC2 and PC3 are plotted against each other (Fig. 5.2c), the four families of plesiadapiform can be seen to form almost completely discrete clusters of points.

**Morphological disparity**

Two measures of morphological disparity were used: 1) the average distances between species, and 2) the maximum distance (range) within a clade of species. These estimates of morphological disparity are illustrated in Figure 5.3 for clades of extant strepsirrhines, and for plesiadapoid plesiadapiforms. Plesiadapiforms included in the sample appear to exhibit a similar range of variation in molar morphology to that displayed by extant strepsirrhines, with the average distance between species being only slightly less, and with the maximum distance being slightly higher. Plesiadapoids as a group were more similar to lorisiforms than to lemuriforms in the amount of within-clade molar disparity. Similarly, the average distances between species within the Plesiadapidae and Carpolestidae were lower than in most extant families examined, with the exception of Galagidae.

In the analyses of morphological distances between species in the four time periods considered here (Fig. 5.4), morphological disparity was highest in the late Tiffanian species, by all three estimates (average distance, maximum distance, and average distance between plesiadapid-carpolestid species pairs). Morphological disparity subsequently declined slightly in the Clarkforkian. In contrast, generic diversity in the sample was highest in the early Tiffanian period. The decline in morphological disparity between the late Tiffanian and the Clarkforkian was sharpest in the range (maximum distance within the sample), which may indicate a contraction of the molar morphospace occupied by plesiadapoids in this time period.

## DISCUSSION

### Archontan dental morphospace

The PCA based on dental landmarks indicated that the landmark method of capturing tooth shape was effective at separating groups of plesiadapiform species by family, with distinct clusters of carpolestids, plesiadapids, paromomyids, and palaechthonids. Morphological resemblances between carpolestids and *Altanius* observed by Rose and Krause (1984) were also apparent from the ordination of species in morphospace, with *Altanius* plotting near or within the carpolestid cluster in the ordinations of the first three PCs illustrated in Figure 5.2.

One surprising aspect of the molar morphospace is the consistency with which dermopteran and treeshrew molars plot in the same region, despite the distinctive nature of dermopteran molar morphology. This was also apparent in the ordination of species in the analysis of extant archontans in the previous chapter. One possible explanation is that the differences between these two groups are not expressed on the three PCs that were examined in

detail here. However, the relative closeness in the morphospaces defined by those PCs may also indicate that some of the ways in which these taxa differ from the other species in the analysis are shared, even though scandentian and dermopteran molar morphology are quite distinct from each other. The relatively close position of *Purgatorius, Leptacodon*, and the extant non-primate archontan cluster may indicate that aspects of their shape are primitive for the molar morphology of archontan mammals. Previously it has been argued that *Purgatorius* has a derived molar morphology that excluded it and, by extrapolation, plesiadapiforms, from possible primate ancestry (Godinot, 2007). It seems that, despite the apparent paraconid reduction in *Purgatorius,* the earliest taxon in the radiation, its molar morphology may be primitive for the group. Possibly, paraconid reduction simply preceded reduction in the other trigonid cusps.

**Level of diversification**

The level of diversification within plesiadapiform molars was gauged by comparisons to extant strepsirrhines and subclades within this group (Fig. 5.3). Plesiadapiform diversity in molar shape was similar to that present in extant strepsirrhines, in both average intertaxon distance and in range. This is interesting because, in terms of time since diversification, the strepsirrhines as a clade have existed for at least 60 my (Steiper and Seiffert, 2012), whereas the radiation of plesiadapiforms took place in a relatively short interval with most plesiadapiform species in the sample occurring during the Paleocene (65.5–55.8 mya, Gradstein et al., 2004). Assuming that the radiation shared a common ancestor in *Purgatorius* or a similar early Paleocene taxon, this would appear to indicate relatively rapid acquisition of morphological disparity in molar morphology, with diversification within plesiadapoids reaching a similar level to that of an extant group with a much deeper evolutionary history (e.g., the lorisiforms). If the molar morphology primarily reflects ecological separation, this might indicate a similar degree of

dietary variation in plesiadapiforms to that seen in extant strepsirrhines, and within plesiadapoids to that seen in lorisiforms.

This conclusion could be questioned on the basis that strepsirrhine diversity has been recently circumscribed by the extinction of the large-bodied subfossil lemurs, several of which possessed morphological particularities in the dentition. Additionally the extant genus *Daubentonia* was excluded from this analysis due to a lack of homologous points for landmark placement. Thus, strepsirrhine disparity in this sample could be viewed as artificially low. However, these points apply primarily to the lemuriform radiation: all available genera were sampled in the lorisiform radiation. Lorisiforms are more conservative in the range of ecological variation and variation in body mass, but have had a considerable time since divergence, and appear somewhat more morphologically conservative relative to plesiadapoid in terms of molar variation. Low disparity in lorisiform might result from a lack of ecological diversification across this lineage but given their relatively poor fossil record, it is also possible that the pattern of diversification and extinction in lorisiforms has resulted in the survival of a subset of species with particular ecological characteristics. As an additional caution, relative to the extant radiations, a greater number of species were sampled within genera in the fossil sample (e.g., *Plesiadapis*), and the degree of diversification in molar morphology may be somewhat underestimated using average distances, because more closely related species will likely have more similar molar morphology.

**Diversification through time**

Morphological diversity was found to be highest in the late Tiffanian (Ti4 and above) by all the metrics used to estimate morphological divergence in the sample (maximum distance, average distance, and average distance between carpolestid and plesiadapid pairs). Generic

diversity in the available sample was highest in the early Tiffanian, indicating that data on morphological disparity in the sample can lead to different conclusions regarding diversification in plesiadapoid radiations than might data on generic richness. The contraction in range associated with the late Tiffanian – Clarkforkian transition is interesting given the hypothesized role of rodents in the extinction of non-paromomyid plesiadapiforms indicated by changes in taxonomic richness and abundance (Maas et al., 1988). Comparisons of morphological disparity in plesiadapoids and rodents might provide an additional test of the competitive exclusion hypothesis. The same could be said of comparisons between plesiadapoids, rodents, and the later-surviving paromomyid plesiadapiforms; it might be predicted that paromomyid disparity would not show a similar pattern of range contraction in the Clarkforkian. It would additionally be predicted that the region of morphospace occupied by early rodents in North America is closer to that of plesiadapoids than to paromomyids.

Some plesiadapiform species were not included in the present sample, such as *Carpomegadon jepseni* (Bloch et al., 2001). For this reason, the morphological disparity was compared to the generic diversity in the sample, rather than to the total generic richness in the time interval. The present sample will be expanded in future analyses to provide more comprehensive sampling. However, Ciampaglio et al. (2001) demonstrated that range and average morphological distances are relatively insensitive to sample size when above 20% of the sample is included, indicating that this pattern may be consistent even with additional species added (however, the estimate of generic diversity may alter).

In addition to expanding the taxonomic sample, expanding the range of tooth positions examined may lead to different results concerning morphological disparity in the plesiadapiform dentition. In particular morphological divergence in the premolar dentition within plesiadapoids,

discussed in the Introduction, might show differences in the pattern or degree of acquisition of morphological disparity. Additionally, alternative methods of quantification for tooth morphology will be explored, including dental topographic methods such as occlusal complexity (Evans et al., 2007) and measurements of the relief of the tooth (Boyer, 2008)

## CONCLUSIONS

Geometric morphometric landmarks appear to capture shape in plesiadapiform molars in a way that is consistent with published descriptions of molar morphology in this clade. Extant non-primate archontans and the early plesiadapiform genus *Purgatorius* seem to share some aspects of their morphology which may indicate that *Purgatorius* (and possibly *Leptacodon*) should be considered relatively representative of the primitive archontan dental morphology. Molar morphology separated later-occurring species along recognized taxonomic boundaries on the first three principal components. The range of variation and average intertaxon distances within plesiadapiforms as a whole, plesiadapoids, and the families Carpolestidae and Plesiadapidae were similar to those found in equivalent taxonomic ranks among extant strepsirrhines, possibly indicating a relatively rapid acquisition of morphological disparity in molar morphology in plesiadapiforms. Morphological disparity peaked later than generic richness in the sample of North American plesiadapoids, possibly indicating that morphological disparity provides insights into changes in biodiversity that are unavailable from taxonomic estimates of biodiversity. Comparisons with morphological disparity in early North American rodents might be interesting in this respect, given their hypothesized role in plesiadapoid extinction via competitive exclusion.

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*Table 5.1. List of genera included in the sample.*

| **Clade** | **Genera** |
|---|---|
| Dermoptera | *Cynocephalus, Galeopterus* |
| Scandentia | *Dendrogale, Tupaia, Ptilocercus* |
| Nyctitheriidae | *Leptacodon sp.* |
| Plesiadapiforms<br>*Incertae sedis*<br>Plesiadapoidea<br>Carpolestidae<br>Plesiadapidae<br>Saxonellidae<br>Paromomyidae<br>Palaechthonidae | <br>*Purgatorius*<br>*Pandemonium, Chronolestes*<br>*Carpodaptes, Carpolestes, Elphidotarsius*<br>*Chiromyoides, Nannodectes, Platychoerops, Plesiadapis, Pronothodectes*<br>*Saxonella*<br>*Acidomomys, Ignacius, Paromomys, Phenacolemur*<br>*Palaechthon, Plesiolestes, Premnoides* |
| **Euprimates**<br>**Fossil**<br>*Incertae sedis*<br>Adapidae<br>Omomyidae<br>Eosimiidae<br>Tarsiidae<br><br>**Extant**<br>Strepsirrhini<br><br><br>Haplorrhini | <br><br>*Altanius* (?Plesiadapiform)<br>*Adapis, Afradapis, Cantius, Caenopithecus, Donrussellia*<br>*Microchoerus, Teilhardina, Uintanius*<br>*Eosimias*<br>*Tarsius*<br><br><br>*Cheirogaleus, Microcebus, Mirza, Phaner, Avahi, Indri, Propithecus, Eulemur, Hapalemur, Lemur, Varecia, Euoticus, Galago, Galagoides, Otolemur, Arctocebus, Loris, Nycticebus, Perodicticus*<br>*Tarsius* |

*Table 5.2. Plesiadapoid species from North American sites. Range information in Gingerich, 1976; Bloch et al., 2001; Fox 1990, 1991; Secord et al., 2006.*

| **North American land mammal age** | **Species** |
|---|---|
| Torrejonian | (*Pandemonium dis* – not included) |
| | *Elphidotarsius florencae* |
| | *Pronothodectes matthewi* |
| | *Pronothodectes jepi* |
| Early Tiffanian | *Elphidotarsius russelli* |
| Ti1 – Ti3 | *Elphidotarsius wightoni* |
| | *Carpodaptes hazelae* |
| | *Nannodectes intermedius* |
| | *Nannodectes gazini* |
| | *Nannodectes simpsoni* |
| | *Plesiadapis praecursor* |
| | *Plesiadapis anceps* |
| | *Plesiadapis rex* |
| | *Pronothodectes gaoi* |
| | *Saxonella naylori* |
| Late Tiffanian | *Chiromyoides sp.* (locality UM SC-243) |
| Ti4- Ti6 | *Plesiadapis churchilli* |
| | *Plesiadapis simonsi* |
| | *Plesiadapis gingerichi* |
| | *Plesiadapis fodinatus* |
| | *Carpodaptes aulacodon* |
| | *Carpodaptes stonleyi* |
| | *Carpolestes dubius* |
| Clarkforkian | *Carpolestes nigridens* |
| | *Carpolestes simpsoni* |
| | *Plesiadapis cookei* |
| | *Plesiadapis dubius* |

*Table 5.3. Summary of the first three principal components.*

| | **Variance explained** | **Cumulative variance** | **Shape changes** | |
|---|---|---|---|---|
| | | | **Low** | **High** |
| PC1 | 35.75% | 35.75% | More buccal/mesial position of the end of paracristid (loss of paraconid); more distal entoconid; longer posthypoconid crest; mesiodistally longer; trigonid cusps close to talonid cusps in height | More lingual/distal position of the end of paracristid (presence of paraconid); buccolingually wider; trigonid elevated relative to the talonid; mesial entoconid; shorter posthypoconid crest |
| PC2 | 16.09% | 51.85% | High relief; steeply angled crests; trigonid basin close to equal in size with talonid basin (open trigonid); longer tooth | Low relief, crests oriented in line with occlusal plane; larger talonid basin; wider tooth |
| PC3 | 9.64% | 61.48% | Compressed trigonid; elongate talonid basin; deep talonid notch | Broader tooth; base of tooth lower on buccal side (exodaenodonty); talonid basin wide as it is long; shallow talonid notch |

**Fig. 5.1.** Landmarks used in the study illustrated on a left mandibular second molar of *Nannodectes intermedius* in lingual, occlusal, and buccal views. See text for verbal description of numbered landmarks.

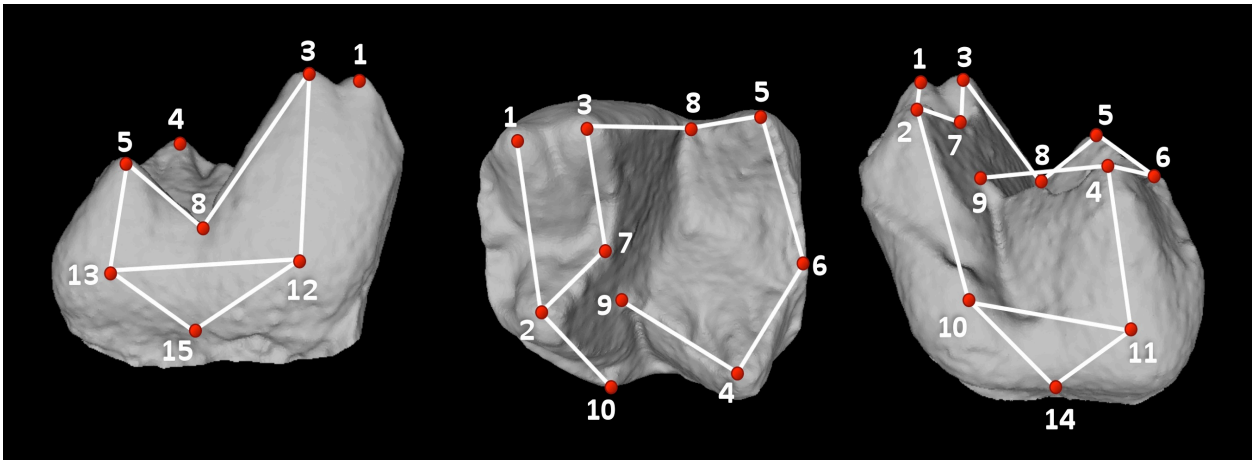
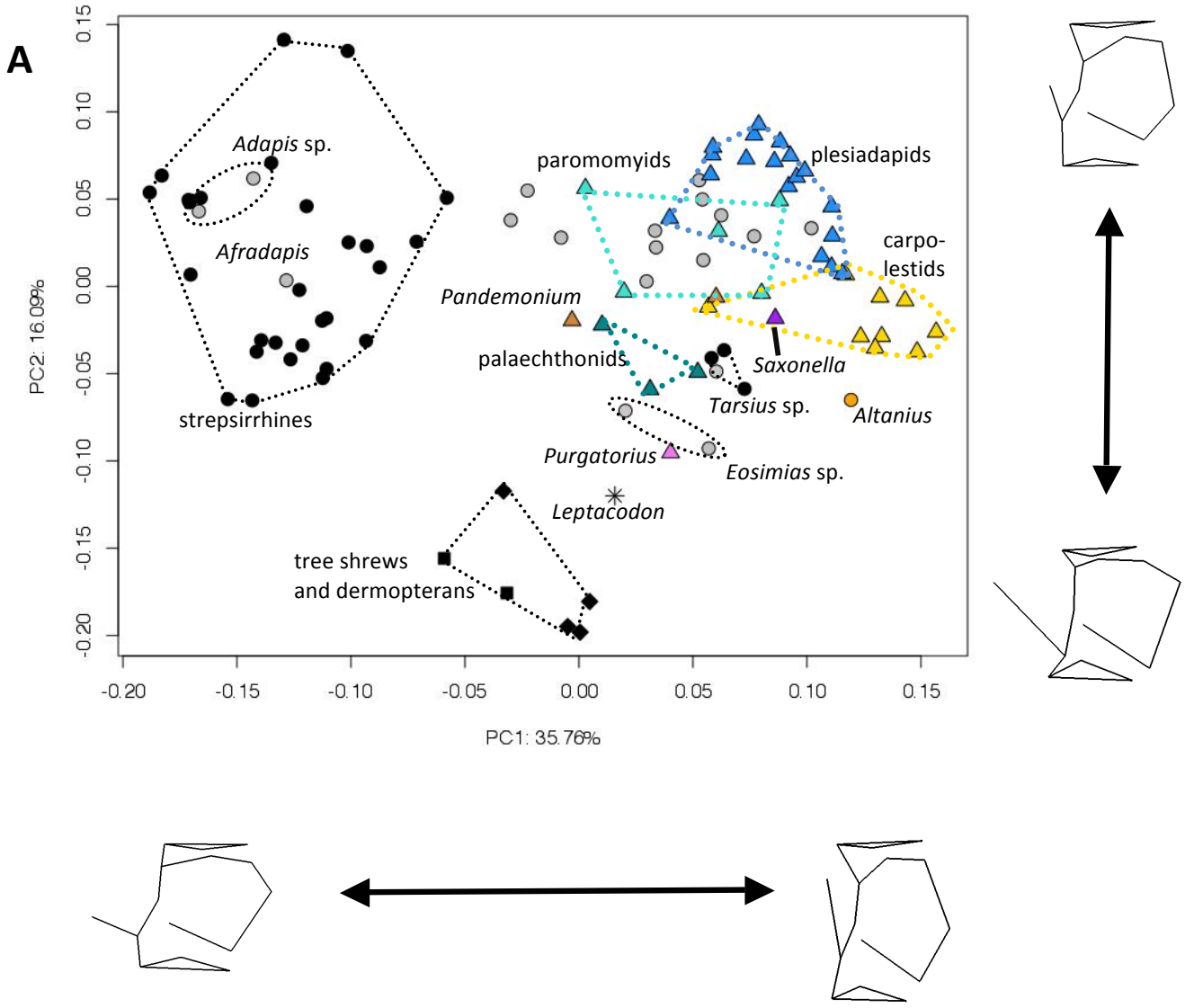
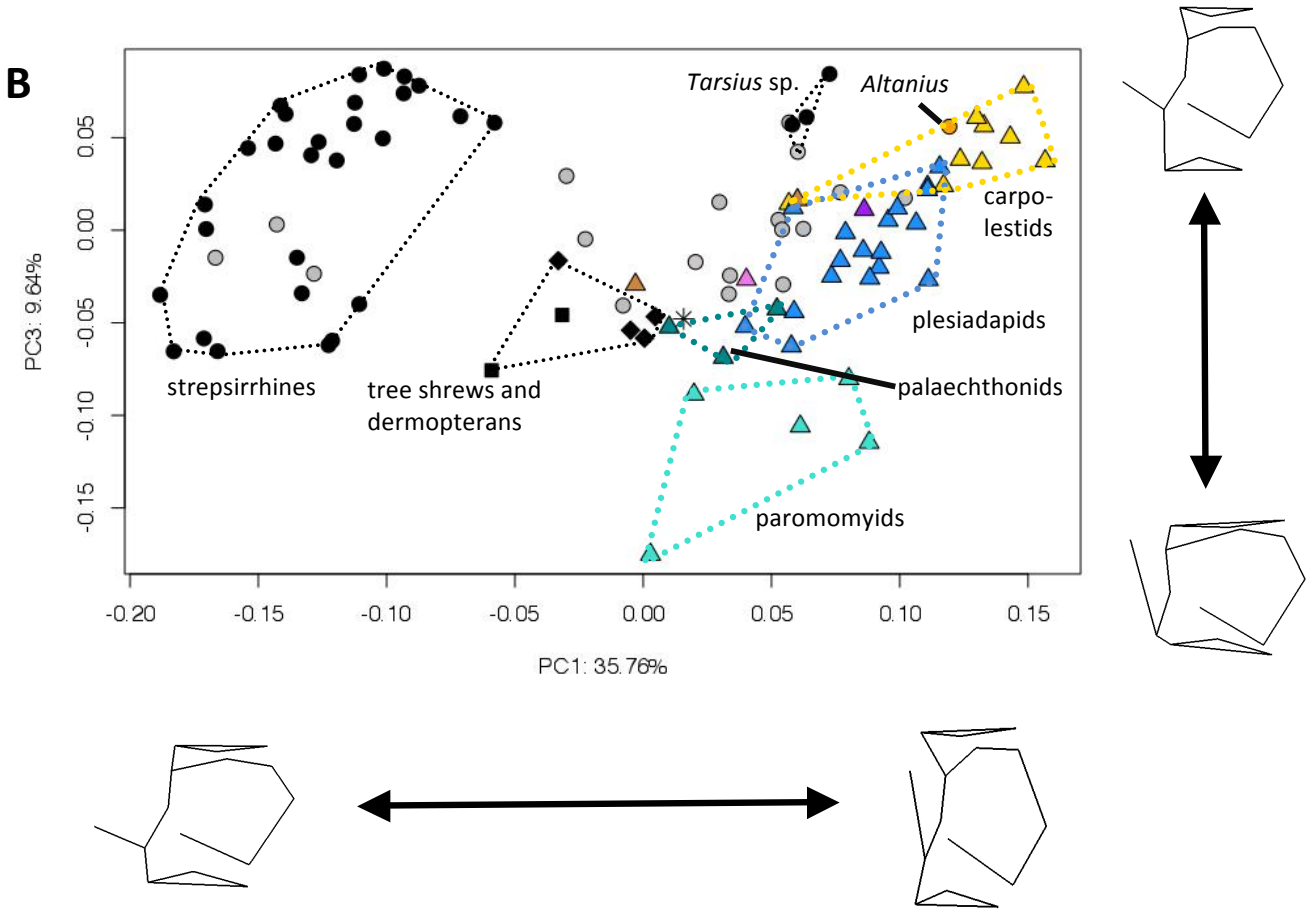


**Fig. 5.2.** Scatterplots from principal components analysis**. A)** Principal component 1 and 2, **B)** Principal components 1 and 3, and **C)** Principal components 2 and 3. Black fill indicates extant species, whereas grey indicates fossil euprimates. Symbols: circles – euprimates (or ?euprimates), triangles - plesiadapiforms, squares - dermopterans, diamonds – tree shrews, star – *Leptacodon*. Families and specific genera discussed in the text are highlighted in color: plesiadapids in blue, carpolestids in yellow, paromomyids in turquoise, palaecothonids in teal, *Saxonella* in purple, *Purgatorius* in pink, *Pandemonium* in brown, *Altanius* in orange.




B
Tarsius sp.
Altanius
carpo-
lestids
plesiadapids
palaechthonids
paromomyids
strepsirrhines
tree shrews and
dermopterans
PC3: 9.64%
PC1: 35.76%
0.05
0.00
-0.05
-0.10
-0.15
-0.20
-0.15
-0.10
-0.05
0.00
0.05
0.10
0.15

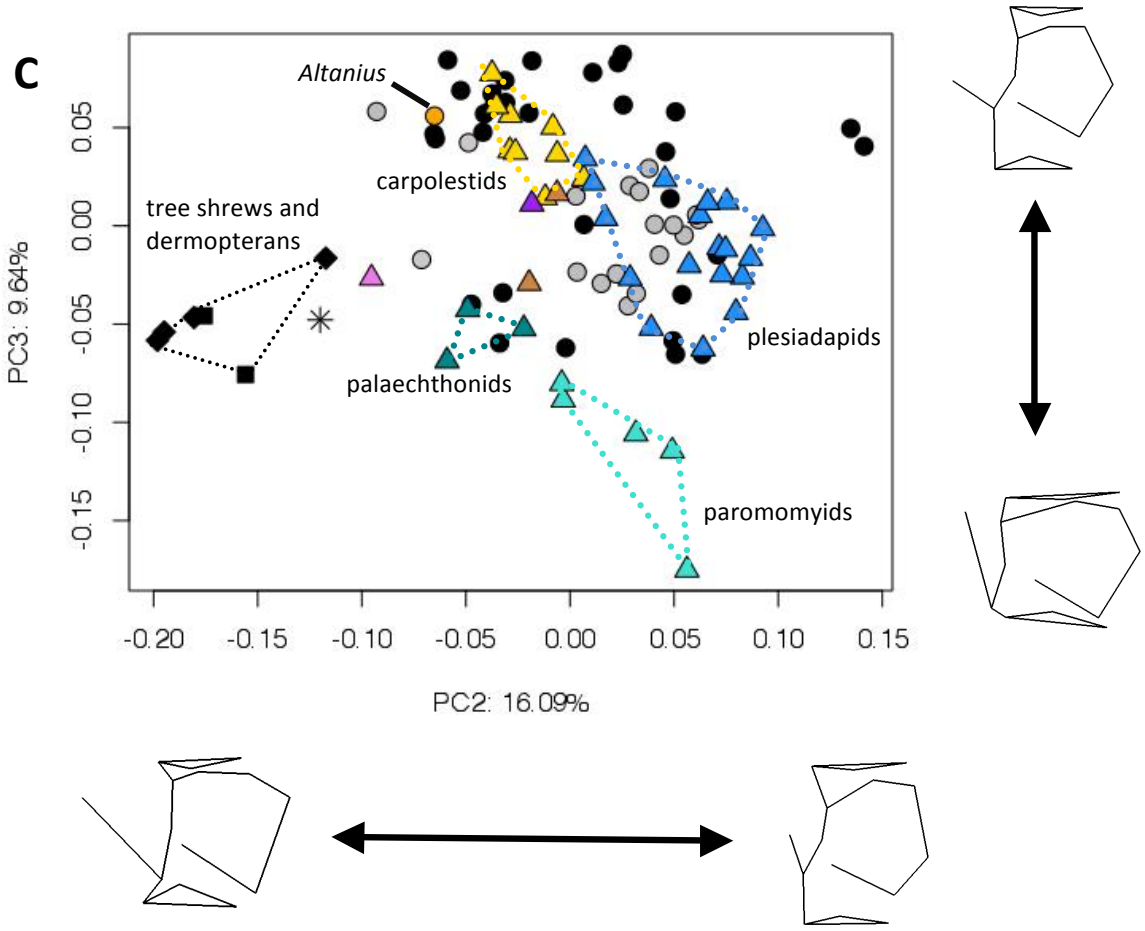

C
Altanius
carpolestids
tree shrews and
dermopterans
plesiadapids
palaechthonids
paromomyids
PC3: 9.64%
0.05
0.00
-0.05
-0.10
-0.15
-0.20
-0.15
-0.10
-0.05
0.00
0.05
0.10
0.15
PC2: 16.09%

**Fig. 5.3.** Average (blue) and maximum (red) Procrustes distances between species in clades included in the analysis

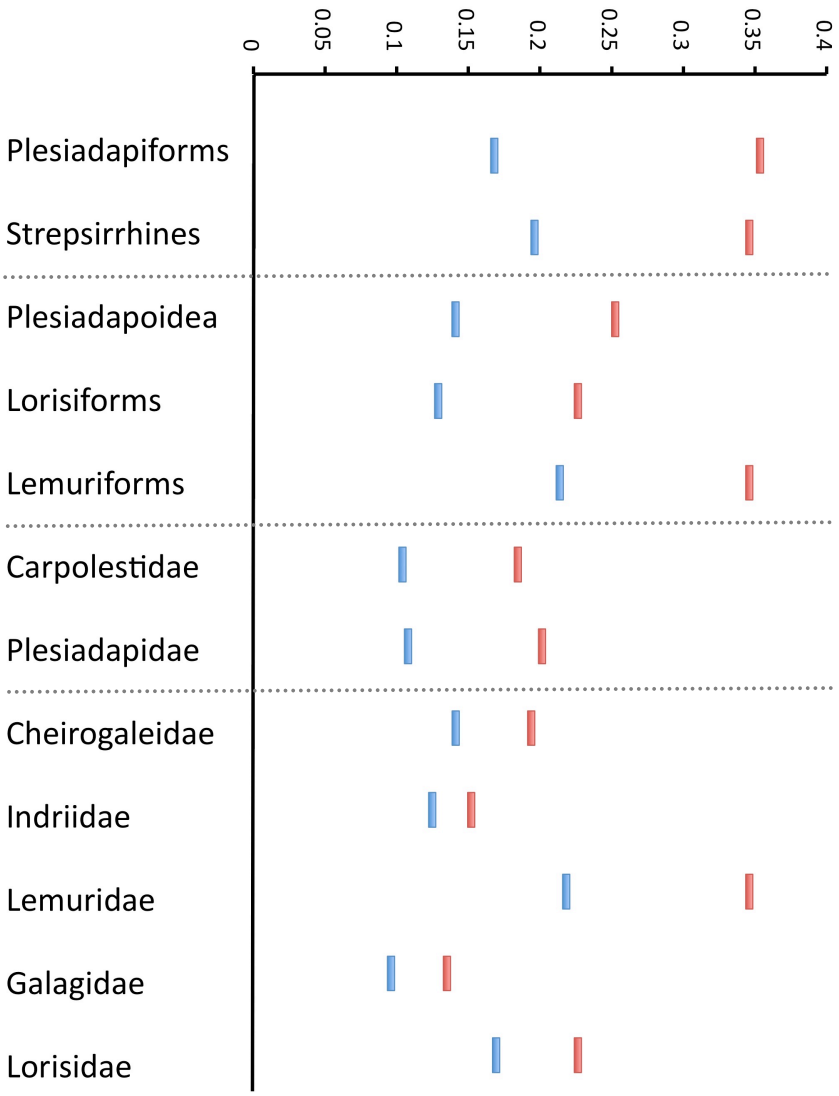
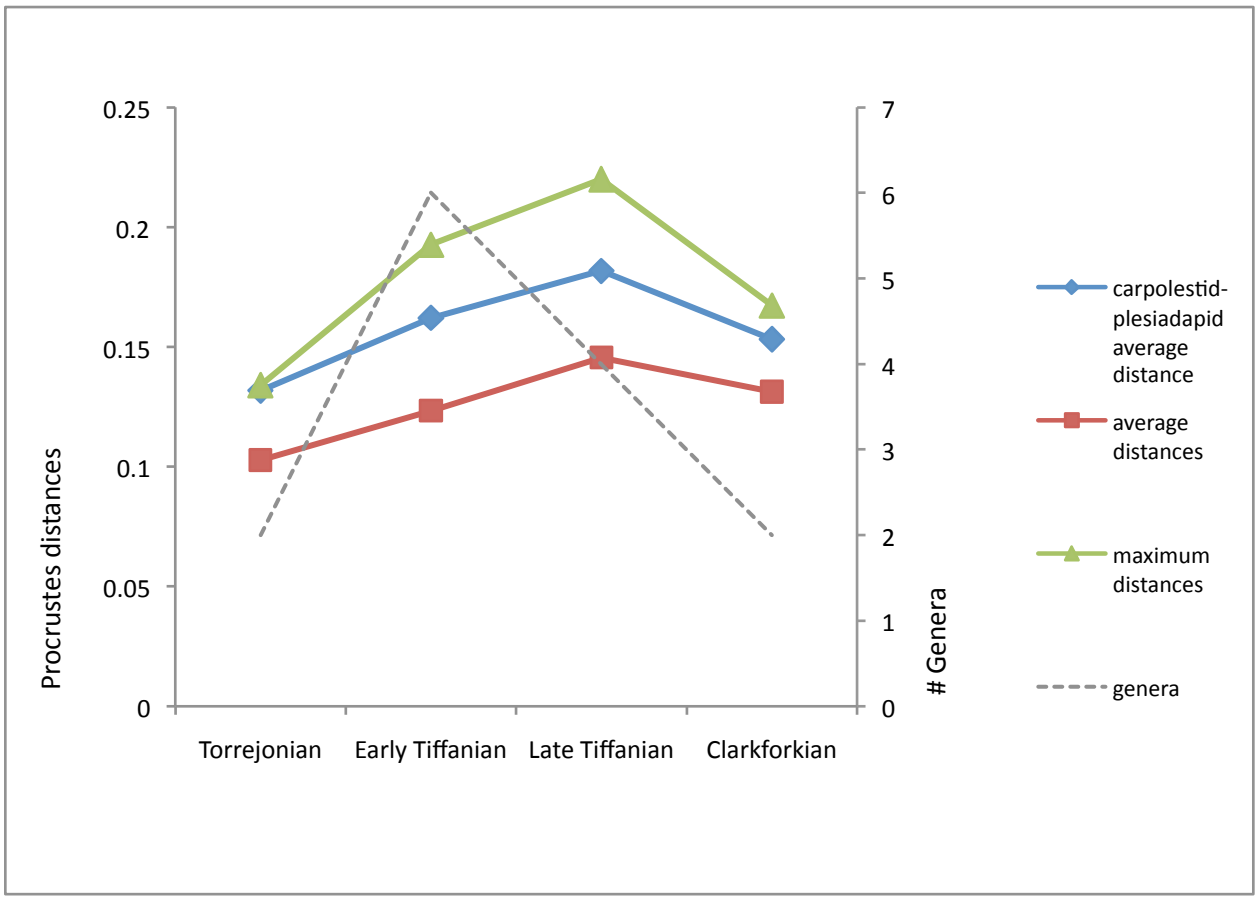


**Fig. 5.4.** Disparity through time in molar morphology of North American plesiadapoids in this sample, compared to the number of genera included in the sample for each stage.



## Chapter 6. Summary and future directions

The goals of this dissertation were to investigate the potential and limitations for the application of morphological disparity to understanding macroevolutionary processes in primates and other mammals, particularly in the fossil record where morphological information may be very limited. In fossil organisms, any association between morphological disparity, defined as the range of form exhibited within a group of taxa, and adaptive or ecological diversity, the range of ecological roles performed by an animal, must be inferred and cannot be tested directly. Additionally, given that only a small portion of an organism's anatomy is likely to be available for morphological comparisons between a large number of species, quantification of morphological disparity for comparisons across multiple taxa is likely to be limited. In mammals, analyses of morphological disparity have been limited to the dentition (e.g., Jernvall et al., 1996; Wesley-Hunt, 2005; Wilson et al., 2012). In the first three data chapters presented here, extant radiations of strepsirrhines and platyrrhines were used to test some of the assumptions that may be present when inferring evolutionary patterns from the distribution and extent of morphological disparity in the fossil record. In the final data chapter, plesiadapoid plesiadapiforms provided an example radiation in which to investigate morphological disparity in molar shape.

### Ecological variation and morphological disparity

In a review of the topic of morphological disparity, Foote (1997) highlighted the need for comparisons of ecological and morphological disparity to justify the use of morphological disparity as a proxy for ecological or adaptive diversity in fossil radiations. This work is

necessary to evaluate questions concerning factors influencing diversification in those clades. For example, a recent analysis of multituberculate dental complexity indicated that morphological diversification within this clade appeared to be associated with angiosperm appearance and diversification and preceded the Cretaceous-Paleogene boundary associated with the mass extinction of non-avian dinosaurs (Wilson et al., 2012). In this case, the morphological disparity was measured as the coefficient of variation in the occlusal patch count, which has been associated with dietary differences (Evans et al., 2007). However, Bunn et al. (2011) found that within strepsirrhine primates folivores and insectivores have similar OPCR measurements. Therefore, variability in OPCR may not map precisely onto dietary variability.

In Chapter 2, morphological distances calculated from measurements of the cranium, mandible, and molar were found to be correlated with distances derived from ecological variables in both radiations examined, strepsirrhines and platyrrhines. However, despite this observation, it was also apparent that species could be close together in morphospace but divergent ecologically, indicating that ecological diversity may not be adequately captured by morphological variation. Additional comparisons of ecological and morphological disparity were conducted using methods devised to examine the distribution of morphological disparity in extant taxa, the "disparity through time" (DTT) method devised by Harmon et al. (2003) and the method to identify clades with unusual levels of morphological disparity devised by Losos and Miles (2002). Results of the DTT analysis showed some similarity between patterns in the distribution of ecological and morphological disparity along the phylogeny, particularly when contrasting the two primate clades analyzed, but also showed some instances in which the distribution of morphological disparity did not match the pattern from ecological variation. Additionally, clades identified as unusually diverse differed between the two datasets, indicating

that it may be problematic to infer unusual levels of adaptive or ecological disparity from the level of morphological disparity within a clade.

If levels of morphological disparity are not directly indicative of amounts of ecological disparity within a clade, can morphological variability be used as an appropriate proxy for adaptive variation in extant or fossil groups? Certainly the results presented here suggest that caution may be needed in making this inference. However, while ecological distances were sometimes high while morphological distances were closer (presumably instances in which ecological diversification occurred without morphological differentiation, at least in the variables measured), the reverse was not so frequently the case, i.e., morphological distances rarely appeared to be high among ecologically similar species. If this is generally true, morphological disparity may act as a conservative estimate of ecological variability. Additional analyses including a wider range of both ecological and morphological variables, and comparisons of other taxa may be necessary to answer this question comprehensively.

**Morphological disparity from different regions**

In Chapter 3, similar comparisons to those made in the previous chapter between ecological and morphological distances were instead made amongst morphological distances from the skull, mandible, and second mandibular molar, the latter regions being those more likely to be preserved in the fossil record. Morphological disparity in molar shape does not necessarily represent morphological disparity in other regions, either in the analysis of disparity through time or for amounts of morphological disparity within primate clades.

The observation that morphological disparity in one region may not show a similar phylogenetic structure to morphological disparity in other regions could argue against the

conclusion of Harmon et al. (2003) that the timing of cladogenesis relative to clade origin is closely linked to the phylogenetic structure of morphological disparity in those clades (specifically, that early cladogenesis is linked to greater partitioning of morphospace among subclades). If the pattern of cladogenesis is a driving factor governing the distribution of morphological disparity among branches of a phylogenetic tree, consistent patterns would be predicted from different regions.

One interesting observation that can be made through comparisons of the regional DTT curves with those from the previous chapter is that the contour of the DTT plot for molar morphology in strepsirrhines (Chapter 3, Fig. 10) shares some similarities with that for dietary disparity in Chapter 2 (Chapter 2, Fig. 8) that were not evident when the morphological disparity measurement was calculated from measurements of the three regions. Specifically, the pattern from the ecological analysis of a distinct steep decline in average subclade disparity at 0.6 of the "time since clade origin" is present in the molar disparity curve, but not those from other regions. This may indicate that the distribution of disparity among subclades in the molar morphospace is more directly comparable to that in the ecospace defined by dietary variables and activity pattern. This could be further tested by comparing the morphological disparity matrices for different regions to the ecological disparity individually. Additionally, cheirogaleid strepsirrhines were identified as unusually diverse in molar shape, and in ecology, but not in other comparisons. These observations provide some evidence that examining molar shape alone may actually improve the fit with ecological variation.

**Macroevolutionary analyses using disparity estimates**

In Chapters 2 and 3 of this dissertation, methods that have been developed to analyze morphological disparity in extant organisms were applied to primates in order to make comparisons that might inform the use of morphological disparity in the analysis of the primate fossil record. The focus here was on comparisons of results from different datasets (ecological vs. morphological disparity, morphological disparity from different regions) rather than on the methods themselves. However, some reflection on the utility of such methods in examining evolutionary questions may be warranted.

The "disparity through time" analysis developed by Harmon et al. (2003) might appear to be comparable to the analyses of temporal shifts in morphological disparity in fossil groups pioneered by Foote's body of work (e.g., Foote, 1991), and followed in subsequent paleontological analyses (e.g., Jernvall et al., 1996; Wilson et al., 2012). However, rather than providing an estimate of disparity at time points in the past, the method developed by Harmon et al. (2003) is more accurately viewed as investigating the phylogenetic structure underlying the distribution of morphological disparity in extant species. The temporal perspective is provided by the dates of divergence points in the phylogeny of the extant representatives of the radiation; these divergence points create the subclades which are then compared relative to disparity levels in all species (for a fuller description of this methodology see Chapter 2).

As a method of visualizing the structure of morphological disparity among subclades in the analysis, and comparing this distribution to that produced under a null evolutionary model (Brownian motion), the approach developed by Harmon et al. (2003) may still be of considerable interest. For example, it might be possible to use the level of similarity between an observed disparity curve and that predicted under the Brownian motion simulations to create an estimate

of phylogenetic signal in a multivariate data set. Measures of phylogenetic signal used for individual variables in phylogenetic regressions, such as Pagel's λ (Pagel, 1999) or Blomberg's K (Blomberg et al., 2003), can also be viewed as estimates of the degree to which the variance in a trait fits that expected under a Brownian motion evolutionary model (Freckleton et al., 2002; Blomberg et al., 2003). By comparing the distribution of species in a multivariate space with that expected under a Brownian motion evolutionary model, the measurement of the difference between the simulation and the observed disparity curves could perhaps also be viewed as indicative of the degree of phylogenetic signal in the multivariate dataset. This might be appropriate where an estimate of phylogenetic signal is desired, but variation of interest cannot be summarized in a single metric.

Chapters 2 and 3 use an additional macroevolutionary method developed by Losos and Miles (2002) as a way of identifying groups possessing unusual levels of morphological disparity. The goal of their analysis was to test a hypothesis that a clade has undergone adaptive radiation, under the premise that such clades would possess unusually high morphological disparity relative to other clades of a similar age. The interpretation of high morphological disparity as indicative of an adaptive radiation may be questioned on the basis of the results of this dissertation. For example, in Chapter 2, ecological and morphological disparity were not found to be unusually high in the same families, despite correlations between ecological and morphological distances in both clades studied. Additionally, in Chapter 3, the morphological region studied was shown to affect the interpretation of relative disparity

This statistical methodology has potential application to other avenues of investigation, when comparisons of the amount of morphological variation within a sample are of interest. The group under investigation could be species in a clade (as here), or a geographic location, or even

individuals in a species, with possible implications for applying quantitative methods to alpha taxonomy. Randomization and bootstrapping have been used previously to investigate whether variation in a sample is greater than expected (e.g., Lockwood et al., 1996). These analyses are univariate in nature, using the coefficient of variation for a single variable as the measure of disparity. The conclusions may therefore be questioned given that fossil taxa are generally described based on unique properties of their morphology (shape), rather than their size. One potential application of the method developed by Losos and Miles (2002) would be to use randomization and bootstrapping methodology to investigate whether shape variation within a proposed fossil group exceeds that expected for individuals at a similar taxonomic rank in extant organisms.

**Geometric morphometric analysis of molar shape**

The relationship between morphological shape, function, and other factors such as body size or phylogenetic history, may influence both the degree of ecological and morphological covariation, and the degree to which morphological disparity in one region is representative of morphological disparity in other regions. A strong effect of body size and/or phylogenetic history on shape would be expected to increase the degree to which morphological disparity in different regions is similar, because these factors are shared across the whole organism. However, in Chapter Three, molar disparity in platyrrhines and strepsirrhines was found to be only weakly related, if at all, to disparity in the mandible and skull. Chapter Four used 3D geometric morphometric analysis, a method only recently applied to dental shape, to assess the relative contribution of diet and size to dental morphology, using statistical methods that incorporate consideration of phylogenetic analysis. In contrast to some previous reports, it appears that

somatic size is not a strong contributing factor to dental morphology in the two extant primate groups examined. Additionally, two dietary groups previously described as sharing many aspects of their molar shape, folivores and insectivores, have geometric differences in the arrangement of crests and cusps that may distinguish them.

Morphological separation between the molars of insectivores and folivores is not necessary for investigating the dietary adaptation of extinct primates, because insectivores and folivores are also markedly separated by body size. However, the apparent differences identified in tooth shape have implications for the use of dental morphological distances to represent ecological variation in fossil mammalian radiations, and for more detailed understanding of the way in which primates mechanically process food items. Detailed investigation of the fracture properties of a range of insects and leaves consumed by primates would be beneficial. Additionally. observational data on mastication in highly faunivorous primates should be collected and compared with those of folivorous primates, particularly small bodied folivores such as *Avahi* and *Lepilemur* to gauge the level of similarity in masticatory processing. Additional experimental data regarding the release of nutrients from leaf and insect food items under different amounts or types of mechanical processing, similar to the methods used by Prinz et al. (2003), would provide necessary further data on the dental adaptations of primates.

**Geometric morphometric analysis of plesiadapiform molars**

Geometric morphometric landmarks captured shape in plesiadapiform molars in a way that is relatively consistent with published descriptions of molar variation in the group. Molar shape separated species by recognized taxonomic groups. Compared to extant strepsirrhines and strepsirrhine subclades, plesiadapiform species from the Paleocene and Eocene appeared to

occupy a similar volume of morphospace, indicated by the average and maximum molar morphological distances. This could be indicative of relatively rapid acquisition of morphological disparity in molar morphology, similar to that described for other fossil radiations (Foote, 1997). Additionally, if disparity in plesiadapiform molar shape is indicative of dietary variability, it might be surmised that the species display a similar range of dietary variation to that seen in extant strepsirrhines. Given the sample included here, morphological disparity in North American plesiadapoids peaked later than generic richness, which confirms a disjunction between taxonomic richness and morphological disparity, but does not necessarily fit the pattern predicted by a classic adaptive radiation scenario in which maximum diversity is acquired early in a clade's history.

**Future directions in morphological disparity**

Possible avenues of future research related directly to the analyses presented here have been discussed in the context of the individual chapters where appropriate. In some respects the aims of the dissertation pertained more directly to the practice of morphological disparity studies, using primates as an example radiation. It is to be hoped that macroevolutionary analyses using morphological disparity might benefit from a consideration of, for example, the observation that morphological and ecological disparity are not necessarily directly analogous, and that conclusions concerning morphological diversification might be dependent on the region examined.

One avenue that could be usefully explored, and that would lend necessary context to the consideration of morphological disparity in fossil radiations, is the relationship between biodiversity and geographic factors such as altitude, latitude or climate. The spatial distribution

of biodiversity has been investigated in order to discern the mechanisms underlying extant patterns of biodiversity (e.g., Ceballos and Ehrlich, 2006). These analyses have focused on taxonomic richness, with less attention paid to other aspects of biodiversity, including morphological disparity. Roy et al. (2001) found that geographic patterning of morphological disparity in gastropods was not well matched with taxonomic richness estimates and that identification of regions as holding high or low diversity might differ, but did not investigate whether there was any structure to the distribution of morphological disparity related to climate or latitude. Harcourt and Schreier (2009) investigated geographic patterning of diversity in body mass in primates and found that the range of body mass in primate communities declined further from the equator. It would be of interest to investigate whether this pattern is also found in variation in other morphological traits, and morphological distances between species. To establish whether general rules apply to morphological disparity within groups, such as have been established for taxonomic diversity, a range of mammalian groups should be examined. Primates are an ideal group for directly comparing ecological and morphological data, given the wealth of detailed investigation on both. However, as predominantly tropical mammals, primates might be less suitable to examining biogeographic trends in morphological disparity than other mammalian groups with a wider geographic distribution, such as rodents, carnivorans, or artiodactyls.

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## APPENDIX 1

## Primate diets

### Non-primate Archontan and Prosimian diets

| Species | Dietary description | Classification | References |
|---|---|---|---|
| *Tupaia glis* and *T. montana* | Primarily insectivorous, fruit also consumed. Some evidence from stomach contents of leaves and shoots. Other 20 – 60% of scats contain some fruit remains, Orthoptera, Coeloptera and ants also common in scat. Frugivory is seasonal/ facultative. *Tupaia* species vary in which insects they consume. Some species also exploit nectar | Insectivore | Butler, 1980; Emmons, 2000; Wiens et al., 2008 |
| *Dendrogale murina* | Very little data; possibly more insectivorous than other species | Insectivore | Observations cited by Emmons, 2000; Timmins et al., 2003 |
| *Ptilocercus lowii* | Consumes insects, some fruit, and nectar (including fermented nectar) | Insectivore | Emmons, 2000; Wiens et al., 2008 |
| *Cynocephalus volans* and *Galeopterus variegatus* | Leaves, primarily young leaves form main component of the diet. *G. variegatus* also observed feeding on fruit, shoots, and flowers | Folivore | Lim, 2007; Wischusen and Richmond, 1998 |
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| *Tarsius bancanus* | Strictly faunivorous – primarily hard carapaced insects such as orthopterans, beetles, but also moths, small vertebrates, spiders | Insectivore | Jablonski and Crompton,1994; Niemitz, 1979 |
| *Tarsius syrichta* | Limited data –appears similar to other tarsier species | Insectivore | Dagosto et al., 2003 |
| *Tarsius spectrum* | Faunivorous – specialized to insects (few if any small vertebrates) | Insectivore | Gursky, 2000, 2007; MacKinnon and MacKinnon, 1980 |
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| *Microcebus griseorufus* | Fruit/gum feeding takes a large proportion of the feeding time, fruit higher in a wet year/season, gum higher in a dry year/season. Insects also consumed. | Omnivore | Bohr et al., 2011; Genin, 2008; Rasoazanabary, 2004 |
| *Mirza coquereli* | Large amount of time spent on Homopteran secretions (honeydew), also consumes gums, insects, small vertebrates, eggs, flowers, fruits | Omnivore | Hladik, 1979; Hladik et al., 1980; Pages, 1980 |
| *Cheirogaleus major* | Predominantly fruit, flower nectar Young leaf buds may be consumed | Frugivore/ Gummivore | Wright and Martin, 1995 |

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| *Cheirogaleus medius* | Mostly plant based diet – primarily fruit some flowers may be used for nectar. Invertebrates present in fecal matter in small amounts, contribute on average 20% of feeding observations (may be overestimate) | Frugivore/ Gummivore | Fietz and Ganzhorn, 1999; Hladik et al., 1980 |
| *Phaner furcifer* | Highly specialized on gum, complemented with flowers nectar and animal food- some invertebrate prey but more insect secretions (honeydew). | Frugivore/ Gummivore | Charles-Dominique and Petter, 1980; Hladik et al., 1980; Petter et al., 1975; Schulke, 2003 |
| *Avahi laniger (*includes *A. occidentalis)* | Predominantly folivorous –feeds on leaves exclusively in some seasons. Mostly young/ higher quality foliage (mature leaves also consumed). Also consumes flower and leaf buds. | Folivore | Faulkner and Lehman, 2006; Harcourt, 1991; Thalmann, 2001 |
| *Indri indri* | Foliage – particularly young leaves, leaf buds and shoots- is the largest part of the diet, fruit may be consumed in high proportions seasonally at some sites, flowers are also eaten | Folivore | Britt et al., 2002; Pollock 1977; Powzyk and Mowry, 2003 |
| *Propithecus diadema (*including *P. d. edwardsi* and *P. d. diadema)* | Proportion of diet composed of leaves is approximately equal to that comprised by fruits and seeds. Seed predation has been reported, may be specific to particular sites or seasons, but is substantial when reported | Folivore | Hemingway 1995, 1998; Irwin 2006; Meyers and Wright 1993; Powzyk 1997; Powzyk and Mowry 2003 |
| *Propithecus verreauxi* | High proportion of the diet consists of leaves – mature and young. Includes flowers and fruit. Seasonal variation in the degree of frugivory – may be high in wet season. | Folivore | Norscia et al., 2006; Richards, 1978; Simmen et al., 2003 |
| *Lepilemur mustelinus leucopus* | Diet almost entirely leaves; leaf and flower buds and flowers also consumed. | Folivore | Nash, 1998 |
| *Hapalemur griseus* | Specialized bamboo feeder; primarily feeds on giant bamboo, supplemented with other bamboo species and grasses. Plant parts are the bamboo leaf bases, petioles and branch shoots. Also includes some proportions of non-bamboo foliage and fruit (higher at some sites- disturbed). *H. g. alaotrensis* replaces bamboo with other large monocotyledons; reeds, papyrus | Bamboo | Grassi 2006; Mutschler et al., 1998; Tan, 1999 |
| *Hapalemur simus* | Specialized bamboo feeder – almost completely dependent on bamboo and grasses, only small amounts of other | Bamboo | Tan, 1999 |

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| | foods consumed. Consumes both mature and immature bamboo leaves, bamboo sheets and the inner bamboo pith. | | |
| *Eulemur fulvus* | Approximately 70% of the diet is fruit (predominantly ripe fruit, some unripe also consumed). Leaves are the second greatest component of the diet, flowers are also eaten | Frugivore/ Folivore | Negre et al., 2006; Rasmussen, 1999 |
| *Eulemur rufus* | Diet consists primarily of fruit, up to a quarter leaves, flowers also consumed. Leaf eating varies widely between months and sites – reported up to 89% in the dry season. Some insects also consumed. | Frugivore/ Folivore | Donati et al., 1999; Overdorff, 1993; Sussman, 1972, 1977 |
| *Lemur catta* | Two primary sources of food are leaves and fruit; folivory equal or slightly dominant to frugivory. Flowers are the third largest food type exploited. Proportions of fruit and leaves vary at different sites and seasons –fruit higher in wet season. | Folivore | Rasamimanana and Rafidinarivo, 1993; Sussman, 1972, 1977; Soma, 2006 |
| *Varecia variegata* | Fruit specialist, approximately 75%, also consumes nectar and small amounts of leaves | Frugivore | Britt, 2000; Morland, 1991; Ratsimbazafy, 2006 |
| *Perodicticus potto* | Primarily frugivorous, some insects and gums also consumed. | Frugivore/ Gummivore | Charles-Dominique, 1977; Oates, 1984 |
| *Arctocebus calabarensis* | Primarily faunivorous – small proportion of fruit also consumed | Insectivore | Charles-Dominique 1977 |
| *Loris tardigradus (L. t. lydekkerianus sub sp.)* | Highly faunivorous – very small plant component of the diet mainly gum | Insectivore | Nekaris 2005; Nekaris and Jayewardene, 2003; Nekaris and Rasmussen, 2003 |
| *Nycticebus coucang* | Insects up to 50% of diet (Huynh), fruit also a substantial component of the diet. Also consumes molluscs and small vertebrates. Some populations exploit plant exudates including nectar, phloem sap, gums | Omnivore | Huynh, 1998; Wiens, 2002; Wiens et al., 2006 |
| *Galago alleni* | Fruit dominant in the diet, also consumes some insects | Frugivore/ Gummivore | Charles-Dominique, 1977 |
| *Galago demidoff* | Primarily insectivorous, also consumes some fruit and gum | Insectivore | Cansdale, 1946; Charles-Dominique, 1977 |
| *Galago moholi* | Highly insectivorous, includes some acacia gum, not seen to include fruits | Insectivore | Bearder and Martin, 1980; Harcourt and Bearder, 1989 |
| *Galago senegalensis* | Highly insectivorous, gum consumed in high quantities in dry season | Insectivore | Crompton 1984; Harcourt, 1986 |
| *Galago gallarum* | Insectivorous, some gum consumed. | Insectivore | Butynski and de Jong, 2004 |

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| | No fruit feeding observed, but limited data | | |
| *Galago zanzibaricus* | Primarily insectivorous – also consumes fruits, but gum feeding has not been observed | Insectivore | Harcourt and Bearder, 1989; Harcourt and Nash, 1986 |
| *Euoticus elegantulus* | Primarily gums, some insects and fruit also in stomach contents | Frugivore/ Gummivore | Charles-Dominique, 1977 |
| *Otolemur crassicaudatus* | Diet consists of gum, fruit and insects. Gum may exceed fruits in the diet as a carbohydrate source at some seasons/ locations, is a key component of the diet at some sites. Diet described as approximately half insects at some sites. | Omnivore | Charles-Dominique and Bearder, 1979; Clark, 1985; Crompton, 1984; Harcourt, 1986; Masters et al., 1988 |

## Platyrrhine species diets

| Species | Dietary description | Classification | References |
|---|---|---|---|
| *Alouatta palliata* | Leaves contribute approximately 50% of the annual feeding time but up to 90% in some seasons and sites, young leaves preferred. Fruit consumed in higher proportions in months when new leaf consumption is lower | Folivore | Chapman, 1988; Estrada et al., 1999; Glander, 1978; Guillen, 2003; Milton, 1980; Smith 1977; Tomblin and Cranford, 1994;Williams-Estrada and Coates-Estrada, 1994; Stoner 1996; |
| *Alouatta seniculus* | Leaves (especially young leaves) form a large part of the diet in some months, 30 -60% of the feeding observations. Fruits also consumed. | Folivore | Gaulin and Gaulin, 1982; Julliot and Sabatier, 1993; Palacios and Rodriguez, 2001 |
| *Ateles belzebuth* | Fruit forms 80–90% of the diet, some leaves also consumed (up to 10%) | Frugivore | Dew, 2005; Klein and Klein, 1977; Nunes, 1998; Russo et al., 2005; Suarez, 2006 |
| *Ateles geoffroyi* | Fruit forms around 80% of the feeding observations, some flowers also consumed, leaves around 20% of the total but a high proportion in some months. | Frugivore | Chapman, 1988; Gonzalez-Zamora et al., 2009; Russo et al., 2005 |
| *Brachyteles arachnoides* | Fruit and leaves form the major components of the diet, folivory ranging from 20% - 67% of the annual diet, up to 80% in some samples, flowers also consumed | Folivore | Carvalho et al., 2004; Milton, 1984; Strier, 1991; Talebi et al., 2005 |
| *Lagothrix lagotricha* | Fruit forms majority of the diet. Leaves form between 10 – 20% of the feeding observations (maybe up to 50% in some periods and sites), flowers and seeds are also consumed; faunivory may also be substantial at some sites (arthropds, small vertebrates) | Frugivore | Defler and Defler, 1996; Dew, 2005; Di Fiore, 2004; Peres, 1994; Stevenson et al., 1994 |
| *Aotus azarae* | Diet is comprised of fruit and varying proportions of leaves; nectar and flowers also form a substantial component of the diet | Frugivore | Fernandez-Duque, 2007; Wright, 1985 |
| *Aotus nigriceps* | Primarily frugivorous, also consumes nectar in large amounts in some months, flowers, shoots, leaves and animal prey also consumed | Frugivore | Hladik et al., 1971;Wright 1981, 1985, 1989, 1994 |
| *Cebus apella* | Insect foraging is a substantial portion of the time budget, fruit diet can include high proportions of seeds in dry season/semi-deciduous forests, other plant items include petioles, legume pods, pith, flowers, bamboo | Omnivore | Brown and Zunino, 1990; Galetti and Pedroni, 1994, Gunst et al., 2008; Janson, 1985; Terborgh, 1983; Wright, 2005 |

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| | shoots | | |
| *Cebus capucinus* | Animal food comprises around 20% of diet (includes small vertebrates and invertebrates). Fruit is the larger component of the diet, flowers and shoots may also be included in small proportions. Relative amounts of insects and fruit can vary between sites and groups. | Omnivore | Chapman, 1987; Chapman and Fedigan, 1990; Freese and Oppenheimer, 1981; Rose, 1994, 1997; Tomblin and Cranford, 1994 |
| *Saimiri boliviensis* (as *S. sciureus*, but at Manu, so *S. boliviensis** | Fruit and insects consumed, time foraging for insects 80%, small vertebrates also eaten. Fruits consumed small, berry-like. | Insectivore/ Frugivore | Mitchell et al., 1991; Terborgh, 1983 |
| *Saimiri sciureus* | Fruit and insects consumed, faunivory 40 - 60%, some bamboo shoots also consumed. | Insectivore/ Frugivore | Boinski et al., 2002; Lima and Ferrari, 2002; Mittermeier and van Roosmalen, 1981; Stone, 2007 |
| *Cacajao calvus* | Fruit and seeds form the greater part of the diet, with a large component of feeding time spent on seeds (65% - 75%) | Seed predation | Aquino, 1998; Aquino and Encarnacion, 1999; Ayres, 1989 |
| *Cacajao melanocephalus* | Fruits and seeds form the bulk of the diet with unripe fruit and seeds contributing around 80% of the feeding records. Some seasonal folivory. | Seed predation | Barnett et al., 2005; Boubli, 1999 |
| *Chiropotes albinasus* | Fruit and seeds form the greater part of the diet, possibly less concentration on seeds than in other pitheciine species. | Seed predation | Ayres, 1989 |
| *Chiropotes satanas* | Fruit and seeds form the greater part of the diet, with most feeding time spent on seeds (65% - 75%) | Seed predation | Kinzey and Norconk, 1993; Norconk, 1996; Peetz, 2001; van Roosmalen et al., 1988 |
| *Pithecia monachus* (= *P. "hirsuta"* **) | Fruit and seeds comprise most of the diet, possibly more leaves than in other pitheciines | Seed predation | Happel, 1982; Izawa, 1975; Soini, 1986 |
| *Pithecia pithecia* | Predominantly frugivorous, most of which is seed predation, leaves also included (up to around 10 - 20%), seasonal resource | Seed predation | Kinzey and Norconk, 1993; Norconk, 1996 |
| *Callicebus moloch* | Fruit supplemented with leaves and a small amount of insect material (limited data). Fruit feeding includes some unripe fruit. | Frugivore | Kinzey, 1978, 1981; Terborgh, 1983; Wright, 1985, 1989 |
| *Callicebus torquatus* | Around 60 - 70% of the diet is fruit (including nuts), insects and leaves also consumed, more insects than leaves (limited data). Seeds may also a significant proportion of the diet (27%) at some time periods. | Frugivore | Kinzey, 1977, 1978, 1981; Palacios et al., 1997 |

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| *Callicebus donacophilus* | no data available on wild population | Frugivore (assumed) | n/a |
| *Callimico goeldii* | Diet predominantly fruit and insect based,"most common" foraging for insects, less exudativory than other callitrichids (legume pods), fungi also consumed in high proportions | Insectivore/ Frugivore | Heltne et al., 1981; Pook and Pook, 1981; Porter, 2001, 2007; Rehg, 2003 |
| *Callithrix jacchus penicillata* | Primarily a gummivorous species, insect foraging also substantial, may consume some fruit. | Gummivore | Alonso and Langguth, 1989; Fonseca and Lacher, 1984 |
| *Mico argentata* | Gums are a large component of the diet (60%) supplemented with fruit (36%) and some insectivory | Frugivore/ Gummivore | Veracini, 1997 cited in Correa, 2000; Veracini 2009 |
| *Cebuella pygmaea* | Main sources of food are exudates (around 2/3 of feeding time) and arthropods. Small amounts of fruit may also be eaten. | Gummivore | Ramirez, 1977; Soini 1982, 1993 |
| *Leontopithecus rosalia* | Majority of the food volume is supplied by plant foods – primarily ripe fruits, insect foraging may occupy more of activity budget but fewer feeding records. In some years/ seasons floral nectar may be a significant component of the diet. Exudate feeding has also been described – including active stimulation of gum flow in lianas | Insectivore/ Frugivore | Dietz et al., 1997; Kierulff et al., 2002; Miller and Dietz, 2005, 2006; Peres 1989; Rylands. 1993 |
| *Saguinus fuscicollis* | Diet includes fruit and insects, also includes plant exudates (legume pods and trunk exudates) and nectar. Reported insect feeding is variable but maybe up to 50%. Nectar is a small proportion of annual diet but important source at some time periods. | Insectivore/ Frugivore | Garber, 1988, 1993; Heymann et al., 2000; Knogge and Heymann, 2003; Lopes and Ferrari, 1994; Porter 2001; Rehg 2003 |
| *Saguinus mystax* | Some reports indicate equal contributions of insects and fruit to foraging time budget, while others report a dominance of fruit over prey. Exudates and nectar also included, exudates are mostly from legume pods rather than branch/ trunk gums. | Frugivore | Garber 1988, 1993; Heymann et al., 2000; Knogge and Heymann, 2003 |
| *Saguinus midas* | Predominantly frugivorous, insects only reaching around 10% seasonally, exudates exploited more when fruit availability is low | Frugivore | Oliveira and Ferrari 2000; Veracini, 2000 |
| *Saguinus oedipus* | Consumes fruits, insects, also includes small amount of new leaves or buds. May consume some small vertebrates. Exploits flowers for nectar or possibly | Insectivore/ Frugivore | Neymann, 1977 |

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|---|---|---|---|
| | insects. | | |
| *Saguinus geoffroyi* | Insects and fruits about equal in feeding time (approximately 40% each). Exudate feeding next largest contributor (15%) - mostly from legume pods (no gouging needed) | Insectivore/ Frugivore | Garber, 1984; Garber and Sussman, 1984 |

*Boinski S, Sughrue K, Selvaggi L, Quatorne R, Henry M, Cropp S. 2002. An expanded test of the ecological model of primate social evolution: competitive regimes and female bonding in three species of squirrel monkeys (*Saimiri oerstedii*, *S. bolviensis,* and *S. sciureus*). Behaviour 139:227–261.

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# APPENDIX 2

## Phylogenetic PCA results

This appendix summarizes the phylogenetic principal component analyses (pPCAs) for the analyses in Chapter Three. These pPCAs were conducted on measurements from three regions, the cranium, mandible, and molar, for platyrrhines and strepsirrhines separately, and for a combined sample of both taxonomic groups producing nine total phylogenetic PCAs (indicated by the letters A-I). Additionally, in cranium and mandible pPCAs on the platyrrhine sample (or including platyrrhines), analyses were conducted on samples including male and female species averages separately. Some platyrrhines show marked dimorphism in facial and mandibular shape, and creating a combined sex species average for such taxa is therefore inappropriate. For each pPCA conducted, the breakdown of variance explained by the components retained for analysis is presented, with a summary of the variables with the highest factor loadings on each component (those with loadings greater than |0.5|, or the three variables with the highest loadings). Plots of PC1 vs. PC2 and PC2 vs. PC3 are provided, with a brief discussion of the placement of taxa in these plots. Tables of species scores for each pPCA are also provided. Platyrrhine-only and strepsirrhine-only analyses were used for the comparisons of distances between regions, and in the analysis of "disparity through time", while the pPCA of all species was used for the comparisons of amounts of morphological disparity.

For comparison with previous studies, the cut-off for retaining PCs for the distance calculation was based on the amount of variance explained (95% for the clade specific PCAs, 85% for the PCAs of all taxa) rather than a cut-off threshold determined by the eigenvalues as recommended by some researchers (e.g. the Kaiser criterion of eigenvalues >1, Kaiser, 1960). The level of variance selected (85% or 95%) followed that of the studies developing the methods used (see Chapter 3 for discussion). This should also facilitate comparisons between analyses using pPCAs from different groups of species, or from different regions, as the total amount of variation represented in the distance matrices is held constant. Additionally, some of the pPCAs below have instances in which variables have factor loadings that are in excess of |0.5|, even though the PC itself has an eigenvalue less than one. This seems to indicate that a substantial proportion of the variation in that measurement is associated with a PC, even though the PC itself does not summarize more variance than any one measurement.

### A: Platyrrhines: Cranial PCA in females and males

Males and females were analyzed separately for pPCAs for the cranial variables, for the reasons explained in the text of Chapter Three. The results are summarized in Table A1 and A2, and the relative position of the major taxonomic groups on the first two phylogenetic principal components are shown in Figures A1 and A2. Tables A3 and A4 show the individual species scores on the axes retained for analysis. Results from the cranial analyses of males and females do not differ strongly. The first two axes in both analyses explain 57% of the variance in shape in both analyses. For the pPCA of female crania, seven pPCs were retained, while eight pPCs were necessary to explain 95% of the variance from the pPCA of male crania.

The male and female pPCA of platyrrhine crania are similar in the variables loading on the first component, and the relative position of species on that axis. In both cranial analyses, higher PC1 scores are associated with a relatively deeper face, and greater facial length, while lower PC1 scores are associated with greater biparietal breadth, a relatively greater width at the

postorbital constriction, and relatively larger orbits. The taxa scoring highest on the first component in both analyses are the two *Alouatta* species, and to a lesser extent *Brachyteles*, with the remaining atelids (*Ateles* and *Lagothrix*) more centrally located. The pitheciidae (*Callicebus*, *Cacajao*, *Chiropotes*, *Pithecia*) and *Cebus* are also relatively centrally located in the ordinations of the first two PCs in both analyses. Some of this variation in shape may be related to scaling relationships of brain and eye size through the relative dimensions of the calvarium and orbit. The smallest taxa, Callitrichidae and *Saimiri*, have low scores on PC1; *Aotus*, with its relatively larger orbits, also scores lower on the first axis. However, *Alouatta* scores higher on PC1 than *Brachyteles*, *Lagothrix* and *Ateles,* which are all larger-bodied (Smith and Jungers, 1997). The latter have similar scores on this axis to the much smaller pitheciids and *Cebus*. Thus, variation in shape along the first principal component is not purely a consequence of variation in body size, even though some shape variables loading on these axes might be expected to co-vary with size.

Subsequent principal components differ between the analysis of males and females in the pattern of factor loadings to a greater extent than PC1. PC2 in the analysis of female crania primarily separates Callitrichidae from the other species, and is associated with relative palatal width and width between the zygomatic arches. In males, PC2 also separates callitrichids from other species, but in additional to palatal and bizygomatic width, changes in relative skull length are also associated with this axis. Interestingly, in the projection of the first two axes there is relatively little overlap between the four (or three, if the callitrichids are embedded within the cebids) major phylogenetic groups. This may be due in part to differences in body mass between clades, but this alone would not explain the separation of the pitheciidae from other taxa, as these species fall within the size range of the cebids.

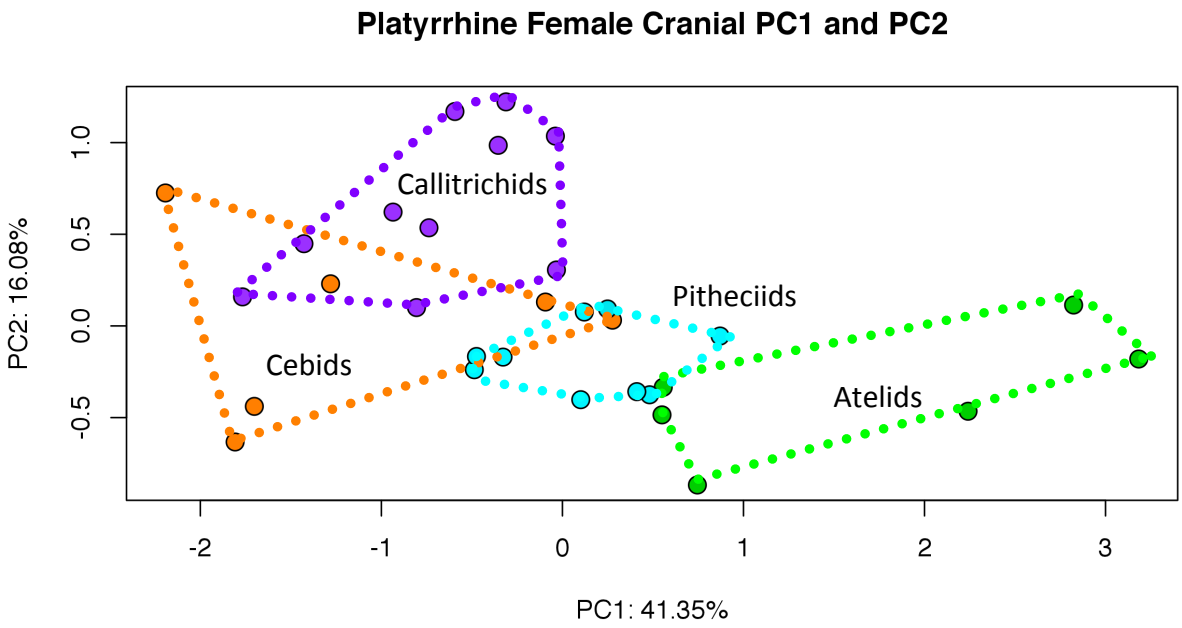
Table A1: Results of cranial pPCA of platyrrhine females.

| PC | % Variance (eigenvalue) | Cumulative Variance | Variables (factor loadings) |
|---|---|---|---|
| PC1 | 41.36 (5.376) | 41.36 | Width of postorbital constriction (-0.92), Biparietal breadth (-0.82), Facial height (0.80), Orbital breadth (-0.79). Zygomatic arch length(0.77), Calvarial length (-0.75) Orbital height (-0.74), Snout length (0.72) |
| PC2 | 16.08 (2.090) | 57.43 | Posterior palatal width (0.77), Anterior palatal width (0.72), Bizygomatic breadth (0.55) |
| PC3 | 11.44 (1.487) | 68.87 | Skull length (-0.73), Calvarial length (-0.57), Orbital height (0.53) |
| PC4 | 9.19 (1.195) | 78.06 | Interorbital breadth (0.72), Bizygomatic breadth (0.43), Anterior palatal width (-0.37), Snout length (-0.37) |
| PC5 | 7.53 (0.979) | 85.59 | Skull length (-0.48), Bizygomatic breadth (-0.48), Snout length (-0.47) |
| PC6 | 6.47 (0.842) | 92.06 | Bizygomatic breadth (0.45), Posterior palatal width (-0.45), Facial height (0.37) |
| PC7 | 3.00 (0.391) | 95.07 | Interorbital breadth (-0.33), Zygomatic arch length (0.28), Anterior palatal width (-0.22) |

Table A2: Results of cranial pPCA of platyrrhine males.

| PC | % Variance (eigenvalue) | Cumulative variance | Variables (factor loadings) |
|---|---|---|---|
| PC1 | 44.65 (5.805) | 44.65 | Width of skull at postorbital constriction (-0.91), Facial height (0.88), Orbital breadth (-0.85), Biparietal breadth (-0.84), Calvarial length (-0.82), Zygomatic arch length (0.81), Snout length (0.79), Orbital height (-0.74) |
| PC2 | 12.46 (1.619) | 57.11 | Posterior palatal width (-0.70), Skull length (0.63), Bizygomatic breadth (-0.38) |
| PC3 | 9.31 (1.211) | 66.42 | Interorbital breadth (0.72), calvarial length (0.39), Anterior palatal width (-0.38) |
| PC4 | 9.08 (1.181) | 75.51 | Anterior palatal width (-0.56), Posterior palatal width (-0.46), Skull length (-0.46) |
| PC5 | 7.79 (1.013) | 83.30 | Bizygomatic arch breadth (-0.78), Anterior palatal width (-0.30), Posterior palatal width (-0.28) |
| PC6 | 5.14 (0.669) | 88.44 | Skull length (-0.42), Snout length (-0.40), Orbital height (-0.34) |
| PC7 | 4.12 (0.536) | 92.56 | Interorbital breadth (0.42), Anterior palatal width (0.33), Biparietal breadth (0.26) |
| PC8 | 2.26 (0.293) | 95.74 | Biparietal breadth (-0.26), Snout length (-0.26), Anterior palatal width (0.24) |

Figure A1. Phylogenetic principal components analysis of platyrrhine crania – females.



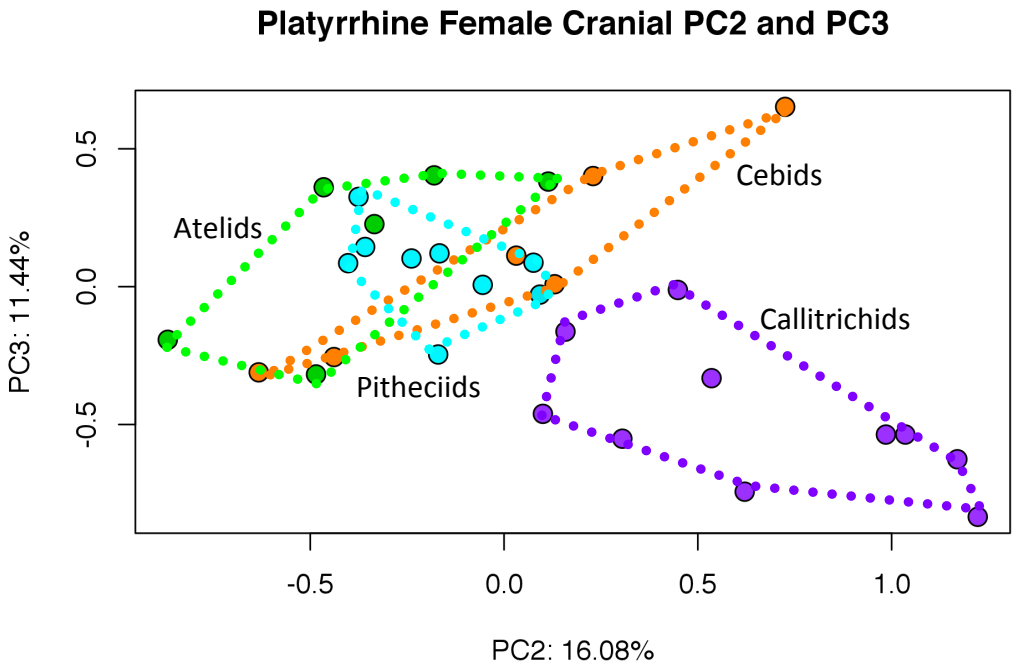
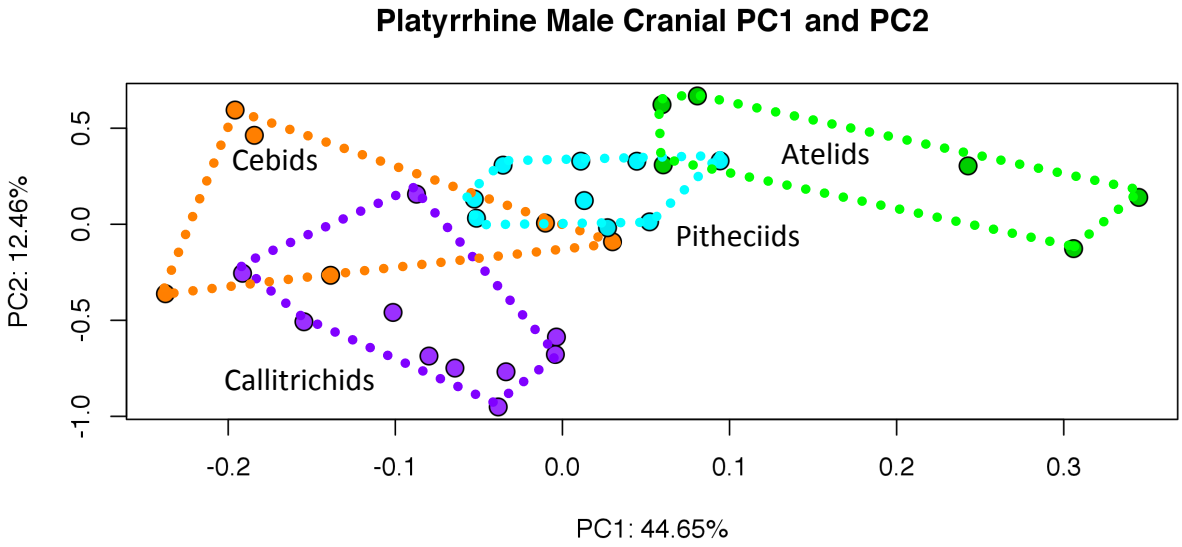



Table A3: Platyrrhine pPC species scores, cranial (female)

| Species | PC1 | PC2 | PC3 | PC4 | PC5 | PC6 | PC7 |
|---|---|---|---|---|---|---|---|
| *Alouatta palliata* | 2.8237 | 0.1140 | 0.3813 | 0.0158 | -0.2569 | 0.0742 | -0.0191 |
| *Alouatta seniculus* | 3.1835 | -0.1804 | 0.4037 | -0.3976 | -0.0922 | -0.1670 | -0.0752 |
| *Ateles belzebuth* | 0.7455 | -0.8677 | -0.1927 | -0.3575 | -0.0202 | -0.2120 | -0.0231 |
| *Ateles geoffroyi* | 0.5501 | -0.4851 | -0.3184 | -0.1948 | -0.1188 | -0.0190 | -0.0436 |
| *Brachyteles arachnoides* | 2.2407 | -0.4654 | 0.3604 | 0.1111 | 0.0921 | 0.0636 | -0.1284 |
| *Lagothrix lagotricha* | 0.5570 | -0.3346 | 0.2268 | -0.3079 | 0.0226 | 0.0374 | -0.1094 |
| *Aotus azarae boliviensis* | -1.2806 | 0.2298 | 0.4012 | 0.0500 | -0.0462 | -0.3323 | 0.0584 |
| *Aotus nigriceps* | -2.1928 | 0.7253 | 0.6521 | 0.0140 | -0.0968 | -0.3244 | 0.0587 |
| *Cebus apella* | 0.2767 | 0.0315 | 0.1126 | -0.3684 | -0.0886 | 0.2670 | 0.1185 |
| *Cebus capucinus* | -0.0938 | 0.1304 | 0.0089 | -0.4022 | -0.0096 | 0.1661 | 0.0387 |
| *Saimiri boliviensis* | -1.8080 | -0.6330 | -0.3108 | -0.4733 | 0.1067 | 0.0528 | 0.0549 |
| *Saimiri sciureus* | -1.7017 | -0.4387 | -0.2553 | -0.4895 | 0.3418 | 0.0324 | -0.0209 |
| *Callimico goeldii* | -1.4278 | 0.4485 | -0.0120 | 0.5917 | 0.1500 | -0.1676 | 0.1142 |
| *Mico argentata* | -0.7372 | 0.5354 | -0.3319 | 0.6553 | 0.2737 | -0.2785 | 0.0305 |
| *Callithrix penicillata* | -0.8060 | 0.1002 | -0.4613 | 0.6979 | -0.1081 | -0.1831 | 0.1310 |
| *Cebuella pygmaea* | -1.7669 | 0.1585 | -0.1630 | 0.6500 | 0.1721 | -0.3087 | 0.0025 |
| *Leontopithecus rosalia* | -0.0331 | 0.3053 | -0.5514 | 0.1982 | 0.3133 | -0.2524 | -0.0207 |
| *Saguinus fuscicollis* | -0.3547 | 0.9852 | -0.5364 | 0.4293 | 0.3908 | -0.0155 | 0.0076 |
| *Saguinus geoffroyi* | -0.3117 | 1.2222 | -0.8348 | 0.5219 | 0.1112 | -0.1020 | -0.1598 |
| *Saguinus midas* | -0.5938 | 1.1696 | -0.6260 | 0.3716 | 0.4542 | -0.0665 | -0.0950 |
| *Saguinus mystax* | -0.0388 | 1.0353 | -0.5364 | 0.0836 | 0.5601 | 0.0734 | -0.0847 |
| *Saguinus oedipus* | -0.9356 | 0.6209 | -0.7437 | 0.6850 | 0.1132 | -0.0718 | -0.2340 |
| *Cacajao calvus* | 0.2493 | 0.0926 | -0.0288 | -0.4970 | -0.4186 | 0.3065 | -0.1321 |
| *Cacajao melanocephalus* | -0.3279 | -0.1700 | -0.2461 | -0.3406 | -0.2689 | 0.4316 | -0.0545 |
| *Callicebus donacophilus* | 0.1013 | -0.4023 | 0.0852 | 0.4351 | -0.0635 | -0.1255 | 0.1567 |
| *Callicebus moloch* | -0.4866 | -0.2388 | 0.1022 | 0.5271 | -0.1535 | -0.1804 | 0.0050 |
| *Callicebus torquatus* | 0.4815 | -0.3755 | 0.3255 | 0.3553 | -0.0377 | -0.1532 | 0.1070 |
| *Chiropotes albinasus* | 0.1208 | 0.0759 | 0.0869 | -0.3062 | -0.2204 | 0.4002 | -0.0593 |
| *Chiropotes satanas* | -0.4748 | -0.1666 | 0.1208 | -0.3195 | -0.1936 | 0.5093 | -0.1340 |
| *Pithecia monachus* | 0.8709 | -0.0550 | 0.0066 | -0.3188 | -0.3444 | 0.3471 | -0.1646 |
| *Pithecia pithecia* | 0.4109 | -0.3584 | 0.1440 | -0.3509 | -0.0752 | 0.4669 | -0.0186 |

Figure A2. Phylogenetic principal components analysis of platyrrhine crania – males.



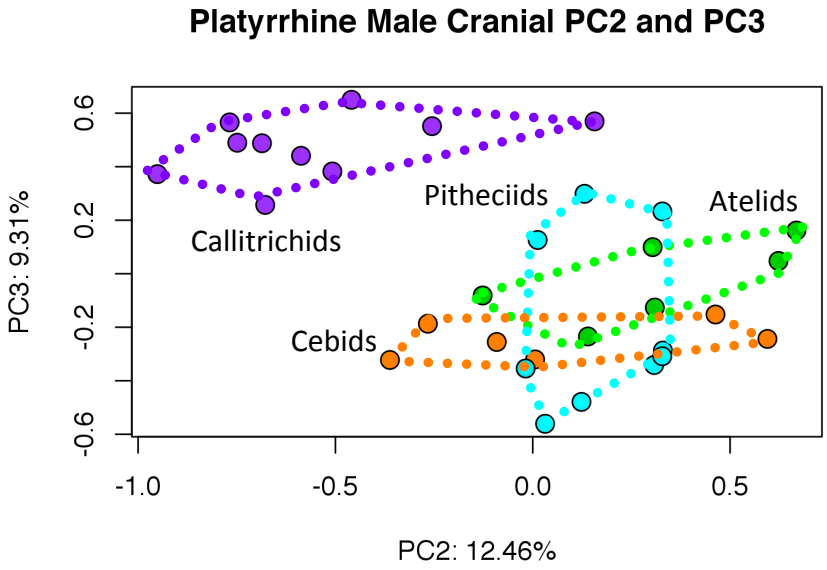



Table A4: Platyrrhine pPC scores, cranial (male)

| | PC1 | PC2 | PC3 | PC4 | PC5 | PC6 | PC7 | PC8 |
|---|---|---|---|---|---|---|---|---|
| *Alouatta palliata* | 2.8446 | -0.1269 | -0.0814 | 0.1748 | 0.0661 | -0.1918 | -0.0595 | -0.0870 |
| *Alouatta seniculus* | 3.6914 | 0.1399 | -0.2345 | -0.1426 | 0.4309 | -0.2429 | -0.1399 | -0.0977 |
| *Ateles belzebuth* | 0.4099 | 0.6681 | 0.1614 | -0.2156 | 0.0976 | 0.0142 | 0.1196 | -0.2290 |
| *Ateles geoffroyi* | 0.1189 | 0.6227 | 0.0477 | 0.1303 | 0.1401 | 0.1504 | -0.0196 | -0.1891 |
| *Brachyteles arachnoides* | 1.6645 | 0.3039 | 0.0993 | 0.3098 | 0.0096 | -0.0160 | 0.2860 | -0.0486 |
| *Lagothrix lagotricha* | 0.6260 | 0.3094 | -0.1263 | 0.0469 | 0.1078 | 0.0082 | 0.1588 | -0.1096 |
| *Aotus azarae boliviensis* | -1.3465 | -0.2657 | -0.1869 | 0.2862 | 0.4962 | -0.2533 | -0.0576 | 0.1753 |
| *Aotus nigriceps* | -2.1133 | -0.3618 | -0.3223 | 0.2889 | 0.4597 | -0.3981 | -0.0914 | 0.1839 |
| *Cebus apella* | 1.0028 | -0.0911 | -0.2550 | 0.1990 | -0.4391 | 0.1947 | -0.1644 | -0.0030 |
| *Cebus capucinus* | 0.3551 | 0.0060 | -0.3202 | -0.1578 | -0.3396 | 0.0582 | -0.1016 | 0.0015 |
| *Saimiri boliviensis* | -1.4479 | 0.5947 | -0.2436 | -0.5193 | -0.2573 | 0.1455 | -0.0245 | 0.0110 |
| *Saimiri sciureus* | -1.7698 | 0.4631 | -0.1523 | -0.5150 | 0.0056 | 0.1531 | 0.0156 | -0.0867 |
| *Callimico goeldii* | -1.1863 | -0.5077 | 0.3822 | 0.0151 | 0.1147 | 0.1599 | -0.2501 | -0.0032 |
| *Mico argentata* | -0.8647 | -0.6861 | 0.4877 | -0.0642 | 0.0369 | 0.0243 | -0.1844 | 0.0357 |
| *Callithrix penicillata* | -0.9180 | 0.1567 | 0.5693 | -0.0143 | 0.0532 | 0.1288 | -0.2328 | 0.0198 |
| *Cebuella pygmaea* | -1.9622 | -0.2552 | 0.5515 | 0.2659 | 0.0040 | -0.0554 | 0.0335 | -0.0361 |
| *Leontopithecus rosalia* | -0.2191 | -0.5871 | 0.4408 | -0.5853 | 0.2495 | 0.1388 | -0.0724 | 0.0882 |
| *Saguinus fuscicollis* | -0.9775 | -0.9511 | 0.3722 | -0.2734 | -0.0915 | 0.1297 | 0.0102 | 0.1444 |
| *Saguinus geoffroyi* | -0.9184 | -0.7680 | 0.5655 | -0.4074 | -0.3946 | -0.0410 | -0.0298 | -0.0489 |
| *Saguinus midas* | -1.1267 | -0.7487 | 0.4896 | -0.5789 | -0.0172 | 0.2079 | 0.0483 | 0.0558 |
| *Saguinus mystax* | -0.5499 | -0.6779 | 0.2571 | -0.5793 | -0.0751 | 0.2705 | 0.0668 | 0.1815 |
| *Saguinus oedipus* | -1.0313 | -0.4591 | 0.6501 | -0.4062 | -0.2840 | -0.0722 | 0.0836 | 0.0325 |
| *Cacajao calvus* | 0.6590 | -0.0180 | -0.3542 | 0.0043 | -0.4195 | -0.1822 | 0.1370 | -0.0666 |
| *Cacajao melanocephalus* | 0.0763 | 0.3077 | -0.3412 | -0.0603 | -0.5168 | -0.1151 | 0.0283 | 0.0232 |
| *Callicebus donacophilus* | -0.3252 | 0.3285 | 0.2327 | 0.5956 | 0.1993 | -0.0259 | -0.2135 | -0.0271 |
| *Callicebus moloch* | -0.6771 | 0.1312 | 0.2987 | 0.4088 | 0.2215 | -0.0328 | -0.0772 | 0.0046 |
| *Callicebus torquatus* | 0.2286 | 0.0125 | 0.1262 | 0.3813 | 0.2873 | 0.0952 | 0.1678 | -0.0104 |
| *Chiropotes albinasus* | 0.4839 | 0.1235 | -0.4789 | 0.0739 | -0.2909 | -0.0655 | 0.1773 | -0.0104 |
| *Chiropotes satanas* | -0.0165 | 0.0314 | -0.5608 | 0.0432 | -0.4146 | -0.0065 | 0.2821 | -0.0498 |
| *Pithecia monachus* | 0.7459 | 0.3299 | -0.2871 | -0.1336 | -0.4171 | -0.1942 | 0.2213 | 0.0466 |
| *Pithecia pithecia* | 0.8311 | 0.3283 | -0.3084 | 0.0582 | -0.3923 | 0.0170 | 0.1769 | 0.0130 |

**B. Platyrrhines: Mandible PCA in females and males**

As in the cranial analyses above, the results for the pPCA using the female species averages are presented first (Table B1 and Figure B1), and the pPCA of male species averages second (Table B2 and Figure B2). In both analyses, nine principal components were retained for 95% of the variance. Species scores on the axes retained for analysis are provided in Table B3 for females, and Table B4 for males.

In the female pPCA, *Cebuella* (Callitrichidae) has the lowest scores on PC1 and the three *Callicebus* (Pitheciidae) species have the highest. The other marmosets, *Callithrix* and *Mico* also have lower scores than other callitrichids, the cebids in this region of the plot are the two *Saimiri* species. Among the atelines, the higher scores are in *Brachyteles*, *Alouatta seniculus* and *Ateles geoffroyi*, while among the cebids higher scores on PC1 are seen in *Aotus*. The factor loadings and general pattern of species differences along PC1 are similar in the analyses of males and females, although the two *Alouatta* species and *Brachyteles* show greater differentiation from the other ateline taxa along PC1 in the analysis of males.

PC2 primarily separates all pitheciids (including *Callicebus*) from other taxa in the analysis, except *Aotus nigriceps.* Again the separation of species is more marked in the analysis of males than that of females. Higher scores on this axis are associated with a relatively narrower mandibular ramus, and a deeper and thicker corpus, as well as lower height of the coronoid process. The relative width of the mandibular condyle is also negatively correlated with this axis.

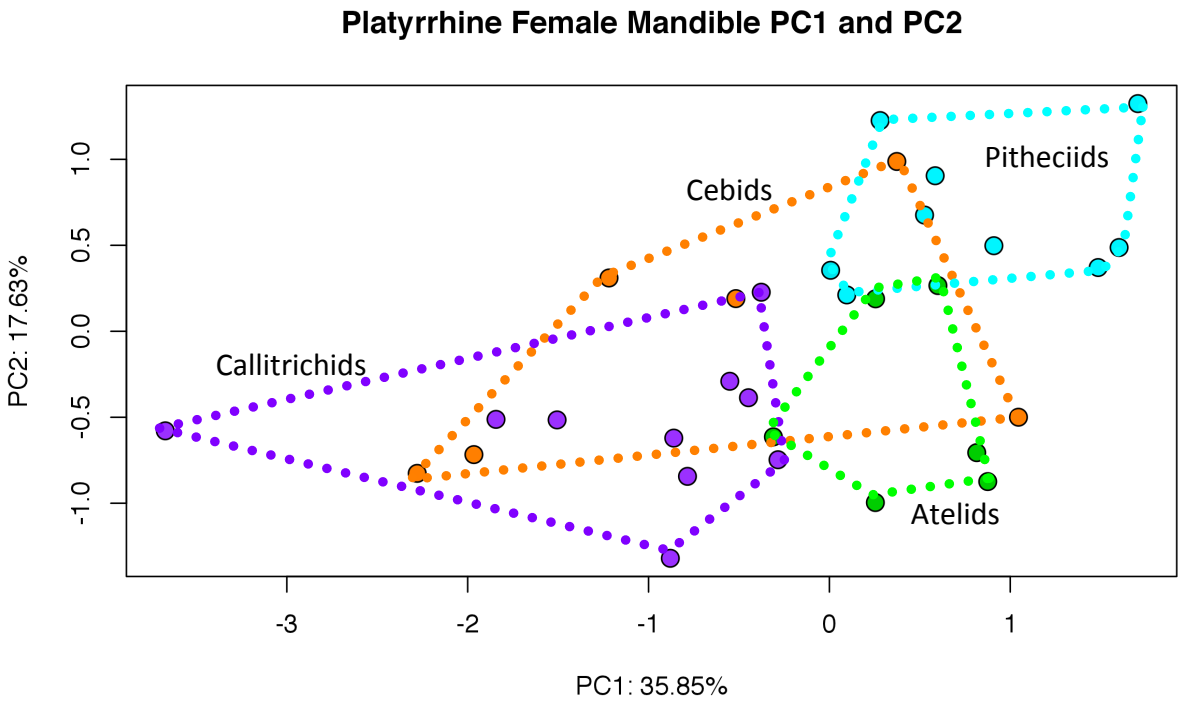
Table B1: Results of mandible pPCA of platyrrhine females.

| PC | % Variance (eigenvalue) | Cumulative variance | Variables (factor loadings) |
|---|---|---|---|
| PC1 | 35.85 (5.377) | 35.85 | Temporalis lever arm (-0.88), Mandible length (-0.86), Ramus height (0.81), Condyle height (0.70), Tooth row length (-0.64), Symphysis height (-0.64), Coronoid process height (0.64), Tooth row width (-0.61) |
| PC2 | 17.63 (2.644) | 53.48 | Ramus breadth (-0.75), Condyle width (-0.66), Corpus height (0.58), Corpus breadth (0.55), Coronoid height (-0.53) |
| PC3 | 13.16 (1.973) | 66.63 | Corpus height (0.67), Corpus breadth (-0.63), Tooth row breadth (-0.60), Tooth row length (-0.52) |
| PC4 | 9.00 (1.351) | 75.64 | Anterior dental width (0.60), Condyle length (-0.41), Coronoid height (0.40) |
| PC5 | 5.97 (0.896) | 81.61 | Condyle height (0.47), Corpus breadth (-0.39), Symphyseal height (0.35) |
| PC6 | 5.51 (0.826) | 87.11 | Condyle length (-0.54), Symphyseal thickness (0.52), Symphyseal height (0.37) |
| PC7 | 4.21 (0.631) | 91.32 | Condyle width (-0.49), Tooth row length (-0.28), Ramus breadth (0.25) |
| PC8 | 2.36 (0.355) | 93.68 | Condyle height (0.28), Condyle length (0.27), Symphysis depth (0.25) |
| PC9 | 2.06 (0.308) | 95.74 | Symphysis height (-0.31), Symphyseal thickness (0.20), Corpus height (0.19) |

Table B2: Results of mandible pPCA of platyrrhine males

| PC | % Variance (eigenvalue) | Cumulative Variance | Variables (factor loadings) |
|---|---|---|---|
| PC1 | 30.77 (4.615) | 30.77 | Temporalis lever arm (-0.79), Ramus height (0.76), Mandible length (-0.76), Condyle height (0.71), Coronoid height (0.66), Tooth row width (-0.66), Tooth row length (-0.60), Symphyseal height (-0.55), Anterior dental width (-0.51) |
| PC2 | 15.71 (2.356) | 46.47 | Ramus breadth (-0.69), Corpus breadth (0.58), Condyle width (-0.56), Corpus height (0.55), |
| PC3 | 12.24 (1.835) | 58.71 | Corpus breadth (-0.54), Tooth row length (-0.54), Corpus height (0.49) |
| PC4 | 11.56 (1.734) | 70.27 | Anterior dental width (0.54), Condyle length (-0.52), Corpus height (0.47) |
| PC5 | 9.27 (1.391) | 79.55 | Symphyseal thickness (0.67), Condyle width (0.45), Symphyseal height (0.42) |
| PC6 | 5.65 (0.848) | 85.20 | Symphyseal height (0.43), Temporalis lever arm (0.37), Condyle height (0.35) |
| PC7 | 4.02 (0.604) | 89.22 | Condyle width (-0.45), Symphyseal height (0.38), Condyle width (-0.35) |
| PC8 | 2.86 (0.429) | 92.08 | Condyle height (-0.40), Condyle length (-0.27), Coronoid height (-0.25) |
| PC9 | 2.46 (0.369) | 94.54 | Symphyseal depth (0.36), Condyle width (-0.34), Corpus breadth (-0.18) |

Figure B1: Phylogenetic principal components analysis of platyrrhine mandible – females.



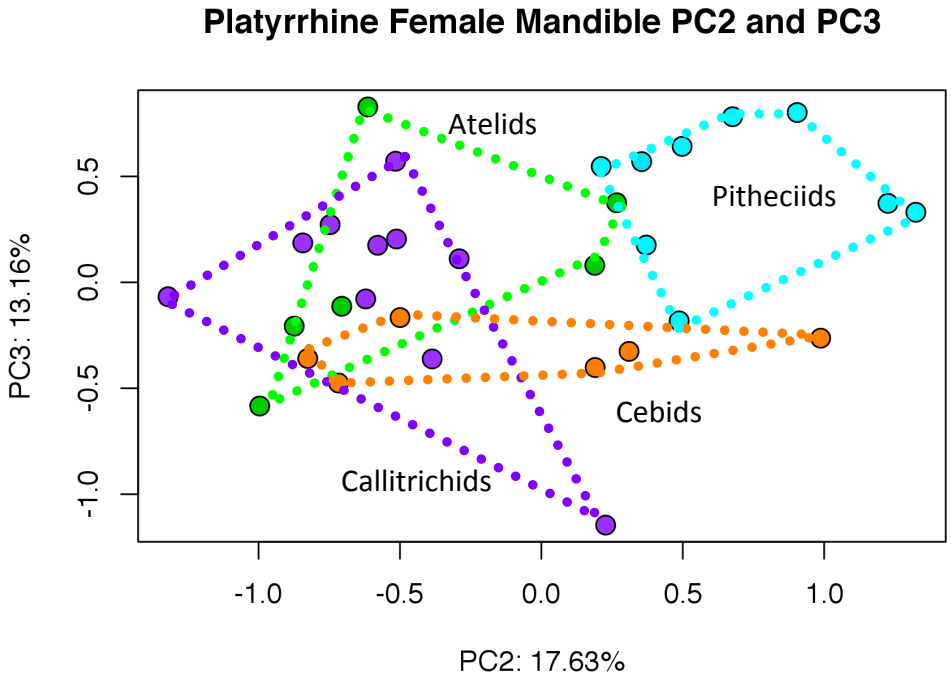
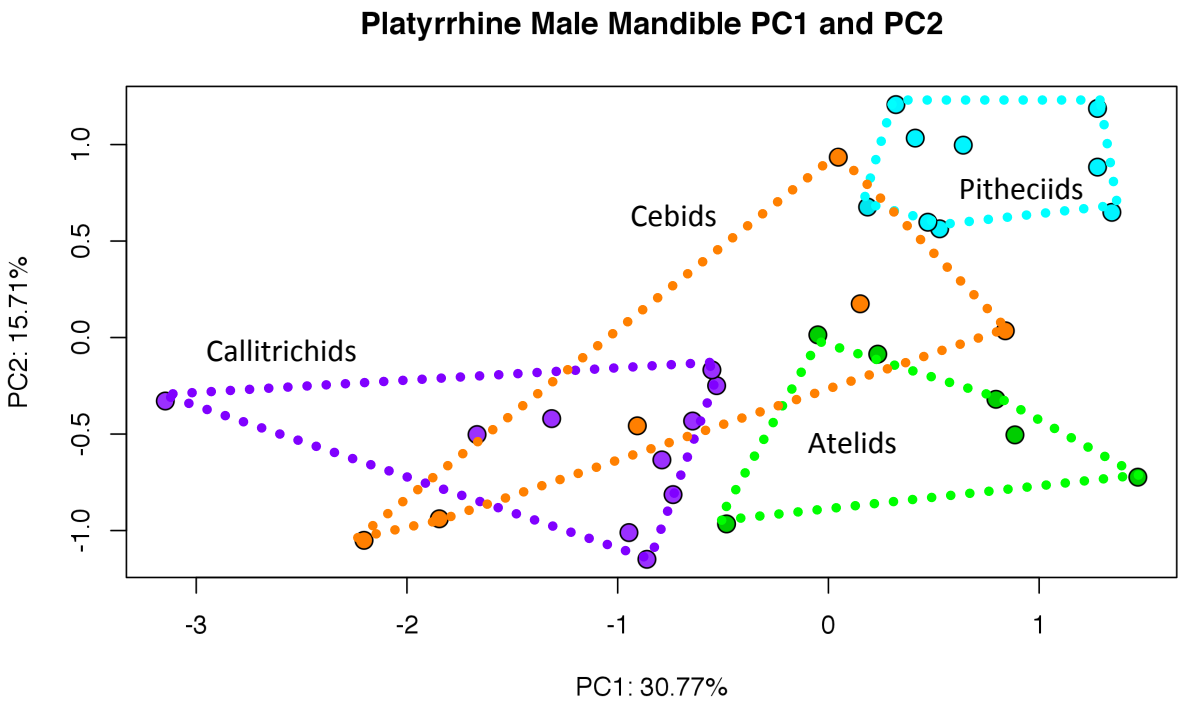



Table B3: Platyrrhine pPC scores, mandible (female)

| | PC1 | PC2 | PC3 | PC4 | PC5 | PC6 | PC7 | PC8 | PC9 |
|---|---|---|---|---|---|---|---|---|---|
| *Alouatta palliata* | 0.2541 | -0.9959 | -0.5836 | -0.5207 | 0.6136 | 0.1131 | -0.1573 | 0.0563 | -0.0124 |
| *Alouatta seniculus* | 0.8147 | -0.7057 | -0.1129 | -0.2070 | 0.4502 | -0.2848 | -0.2850 | 0.0144 | 0.0078 |
| *Ateles belzebuth* | -0.3097 | -0.6138 | 0.8279 | 0.3665 | 0.0268 | -0.0978 | -0.1097 | -0.0690 | 0.0123 |
| *Ateles geoffroyi* | 0.5999 | 0.2660 | 0.3757 | 0.2468 | 0.1055 | -0.0642 | -0.0752 | -0.1217 | -0.0363 |
| *Brachyteles arachnoides* | 0.8755 | -0.8740 | -0.2068 | -0.0803 | 0.0493 | -0.1110 | -0.0405 | -0.0634 | -0.0139 |
| *Lagothrix lagotricha* | 0.2553 | 0.1888 | 0.0805 | -0.0818 | 0.2557 | -0.1187 | -0.0910 | 0.0068 | -0.0382 |
| | | | | | | | | | |
| *Aotus azarae boliviensis* | 1.0455 | -0.4996 | -0.1662 | 0.5258 | 0.0021 | -0.1455 | 0.0612 | 0.0408 | 0.0206 |
| *Aotus nigriceps* | 0.3728 | 0.9876 | -0.2635 | 0.4904 | -0.0828 | -0.1168 | 0.0762 | 0.0640 | 0.0342 |
| *Cebus apella* | -0.5171 | 0.1900 | -0.4019 | -0.2904 | -0.2821 | -0.0759 | 0.0327 | 0.0505 | -0.1345 |
| *Cebus capucinus* | -1.2187 | 0.3101 | -0.3259 | -0.1022 | -0.2574 | -0.0495 | -0.2871 | -0.0306 | -0.1757 |
| *Saimiri boliviensis* | -1.9657 | -0.7171 | -0.4751 | 0.3306 | 0.0183 | 0.0127 | -0.1319 | 0.1691 | 0.0340 |
| *Saimiri sciureus* | -2.2791 | -0.8262 | -0.3593 | 0.5507 | 0.0593 | 0.0242 | 0.0353 | 0.0950 | -0.0164 |
| | | | | | | | | | |
| *Callimico goeldii* | -0.3768 | 0.2273 | -1.1456 | 0.0143 | -0.1352 | -0.0995 | 0.1270 | -0.1001 | -0.0128 |
| *Mico argentata* | -1.5056 | -0.5153 | 0.5716 | -0.4882 | 0.0786 | 0.0107 | 0.3137 | -0.0954 | 0.0139 |
| *Callithrix penicillata* | -1.8435 | -0.5122 | 0.2045 | -0.7998 | 0.0252 | 0.0020 | 0.3379 | -0.1854 | 0.0629 |
| *Cebuella pygmaea* | -3.6720 | -0.5788 | 0.1750 | -0.6380 | 0.0995 | -0.2492 | 0.2527 | -0.1711 | 0.0308 |
| *Leontopithecus rosalia* | -0.4475 | -0.3863 | -0.3615 | 0.0715 | 0.2118 | 0.2253 | 0.1963 | -0.1026 | 0.0169 |
| *Saguinus fuscicollis* | -0.7847 | -0.8436 | 0.1862 | -0.0268 | -0.1046 | 0.0637 | 0.2704 | -0.0678 | -0.0852 |
| *Saguinus geoffroyi* | -0.8605 | -0.6211 | -0.0782 | 0.0668 | -0.1172 | -0.1945 | 0.3437 | 0.0293 | -0.0616 |
| *Saguinus midas* | -0.2840 | -0.7470 | 0.2722 | 0.2374 | -0.0973 | 0.0547 | 0.3271 | -0.0105 | -0.0763 |
| *Saguinus mystax* | -0.5507 | -0.2906 | 0.1112 | 0.3518 | -0.1874 | 0.3579 | 0.2017 | -0.0542 | -0.0749 |
| *Saguinus oedipus* | -0.8796 | -1.3201 | -0.0677 | -0.0990 | -0.1860 | -0.0176 | 0.2091 | 0.0078 | -0.0508 |
| | | | | | | | | | |
| *Cacajao calvus* | 0.0068 | 0.3548 | 0.5698 | -0.1684 | -0.1985 | 0.5411 | -0.0803 | 0.1085 | -0.0426 |
| *Cacajao melanocephalus* | 0.0961 | 0.2116 | 0.5468 | -0.2797 | -0.2501 | 0.2924 | -0.0594 | 0.1648 | -0.0328 |
| *Callicebus donacophilus* | 1.6018 | 0.4872 | -0.1818 | -0.0088 | -0.1098 | -0.2453 | 0.0550 | -0.0356 | 0.1328 |
| *Callicebus moloch* | 1.7054 | 1.3241 | 0.3307 | 0.2724 | 0.0719 | -0.1562 | -0.0457 | -0.0820 | 0.1175 |
| *Callicebus torquatus* | 1.4860 | 0.3708 | 0.1758 | 0.2027 | 0.0680 | -0.0530 | 0.0498 | 0.0138 | 0.1297 |
| *Chiropotes albinasus* | 0.5848 | 0.9047 | 0.8014 | -0.6245 | -0.2528 | 0.4919 | -0.0139 | 0.1349 | -0.0094 |
| *Chiropotes satanas* | 0.5261 | 0.6760 | 0.7816 | -0.6727 | -0.2281 | 0.2697 | -0.1272 | 0.1031 | -0.0624 |
| *Pithecia monachus* | 0.9094 | 0.4977 | 0.6417 | -0.2609 | -0.1023 | 0.0380 | -0.1255 | 0.0463 | -0.0233 |
| *Pithecia pithecia* | 0.2804 | 1.2255 | 0.3729 | -0.0945 | -0.1461 | 0.2671 | -0.2154 | -0.0307 | 0.0474 |

Figure B2: Phylogenetic principal components analysis of platyrrhine mandible – males.



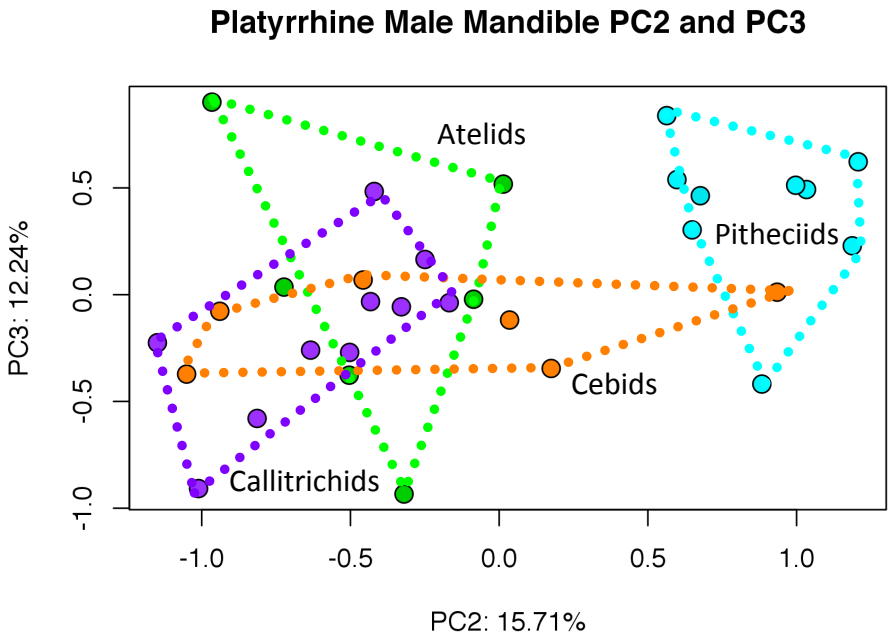



Table B4: Platyrrhine pPC scores, mandible (male)

| | PC1 | PC2 | PC3 | PC4 | PC5 | PC6 | PC7 | PC8 | PC9 |
|---|---|---|---|---|---|---|---|---|---|
| *Alouatta palliata* | 0.7951 | -0.3198 | -0.9336 | -0.3576 | 0.0241 | 0.5477 | 0.0767 | -0.0733 | -0.0102 |
| *Alouatta seniculus* | 1.4683 | -0.7234 | 0.0355 | -0.4945 | -0.4218 | 0.4701 | -0.0253 | -0.1123 | 0.0438 |
| *Ateles belzebuth* | -0.4833 | -0.9657 | 0.9017 | 0.1113 | -0.0484 | 0.1481 | -0.1287 | 0.0589 | -0.0410 |
| *Ateles geoffroyi* | -0.0502 | 0.0140 | 0.5180 | 0.1117 | -0.1979 | 0.0431 | -0.3049 | 0.0604 | -0.0328 |
| *Brachyteles arachnoides* | 0.8852 | -0.5042 | -0.3771 | -0.3016 | 0.0055 | 0.0587 | -0.1003 | 0.1361 | 0.0040 |
| *Lagothrix lagotricha* | 0.2342 | -0.0860 | -0.0214 | -0.2759 | 0.0517 | 0.3232 | -0.0751 | 0.0673 | -0.0418 |
| | | | | | | | | | |
| *Aotus azarae boliviensis* | 0.8395 | 0.0351 | -0.1187 | 0.3951 | -0.1914 | -0.2114 | 0.0498 | 0.0169 | -0.0556 |
| *Aotus nigriceps* | 0.0468 | 0.9346 | 0.0117 | 0.7298 | -0.1757 | -0.1675 | 0.0642 | -0.0137 | -0.0326 |
| *Cebus apella* | 0.1509 | 0.1749 | -0.3456 | -0.7470 | 0.3444 | -0.3002 | 0.1962 | -0.2178 | -0.0090 |
| *Cebus capucinus* | -0.9069 | -0.4573 | 0.0686 | -0.5672 | 0.1835 | -0.2828 | 0.2072 | -0.0319 | -0.1120 |
| *Saimiri boliviensis* | -1.8464 | -0.9392 | -0.0777 | 0.3365 | -0.0680 | -0.2623 | -0.1655 | -0.2431 | -0.0782 |
| *Saimiri sciureus* | -2.2037 | -1.0507 | -0.3720 | 0.3577 | -0.1407 | -0.1867 | 0.0143 | -0.1812 | -0.0575 |
| | | | | | | | | | |
| *Callimico goeldii* | -0.9465 | -1.0105 | -0.9080 | 0.5940 | -0.4526 | -0.0944 | 0.1984 | -0.0697 | 0.0984 |
| *Mico argentata* | -1.3132 | -0.4200 | 0.4834 | -0.5109 | -0.1661 | 0.0301 | 0.2496 | 0.0698 | 0.1625 |
| *Callithrix penicillata* | -1.6674 | -0.5027 | -0.2703 | -0.4530 | -0.1014 | 0.0839 | 0.0955 | 0.0556 | 0.2574 |
| *Cebuella pygmaea* | -3.1468 | -0.3287 | -0.0568 | -1.0045 | -0.4674 | -0.0341 | 0.0017 | 0.1121 | 0.1593 |
| *Leontopithecus rosalia* | -0.7373 | -0.8138 | -0.5796 | 0.4529 | -0.2349 | 0.1139 | 0.1988 | -0.0544 | 0.2239 |
| *Saguinus fuscicollis* | -0.6444 | -0.4325 | -0.0324 | -0.1792 | -0.0698 | -0.1432 | 0.2139 | -0.1068 | 0.0445 |
| *Saguinus geoffroyi* | -0.7902 | -0.6339 | -0.2597 | -0.2397 | -0.2186 | -0.2981 | 0.1191 | -0.1676 | -0.0089 |
| *Saguinus midas* | -0.5304 | -0.2492 | 0.1650 | -0.2451 | -0.0037 | -0.2402 | 0.2988 | -0.0513 | 0.0974 |
| *Saguinus mystax* | -0.5529 | -0.1677 | -0.0376 | -0.0234 | 0.0736 | -0.2059 | 0.2632 | -0.0008 | 0.0135 |
| *Saguinus oedipus* | -0.8612 | -1.1489 | -0.2251 | -0.1559 | 0.0593 | -0.2383 | 0.0536 | -0.1542 | -0.0113 |
| | | | | | | | | | |
| *Cacajao calvus* | 0.1860 | 0.6763 | 0.4633 | -0.1647 | 0.9237 | -0.0759 | -0.2092 | 0.0859 | 0.0104 |
| *Cacajao melanocephalus* | 0.5280 | 0.5635 | 0.8385 | -0.2733 | 0.6435 | 0.0309 | -0.3000 | 0.0510 | 0.0476 |
| *Callicebus donacophilus* | 1.2771 | 0.8832 | -0.4185 | 0.3272 | -0.2260 | 0.0735 | -0.2075 | 0.1858 | -0.0506 |
| *Callicebus moloch* | 1.2769 | 1.1871 | 0.2288 | 0.4239 | -0.2506 | -0.0505 | 0.1179 | 0.1774 | -0.0410 |
| *Callicebus torquatus* | 1.3451 | 0.6489 | 0.3035 | 0.4694 | -0.0713 | 0.1784 | -0.2295 | 0.0851 | -0.0590 |
| *Chiropotes albinasus* | 0.3203 | 1.2070 | 0.6225 | -0.4215 | 0.9024 | 0.0126 | -0.2820 | 0.0505 | 0.0523 |
| *Chiropotes satanas* | 0.4120 | 1.0335 | 0.4924 | -0.5205 | 0.6481 | 0.1245 | -0.1805 | 0.0546 | -0.0498 |
| *Pithecia monachus* | 0.6399 | 0.9969 | 0.5124 | -0.2520 | 0.2996 | -0.0118 | 0.0328 | 0.0832 | -0.0229 |
| *Pithecia pithecia* | 0.4719 | 0.5977 | 0.5389 | 0.2554 | 0.3135 | 0.1181 | -0.1388 | 0.1425 | -0.0390 |

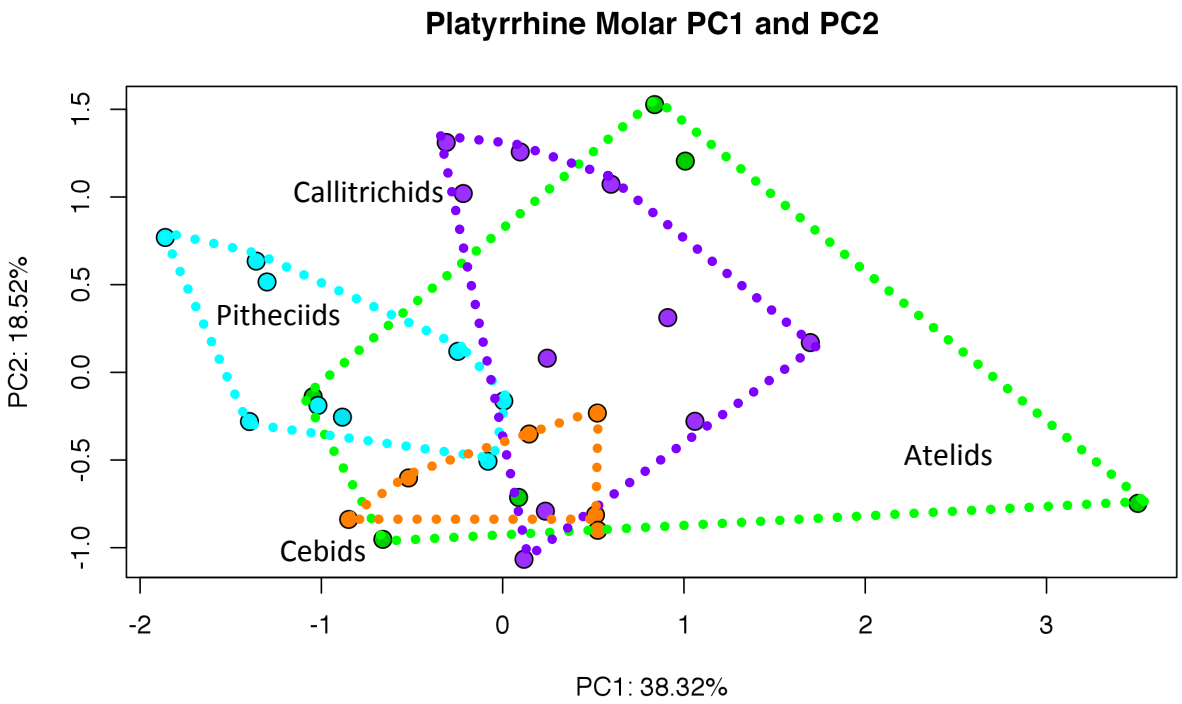
**C. Platyrrhines: Molar PCA**

The phylogenetic PCA of platyrrhine molar shape resulted in eight PCs that summarized 95% of the variance; PC1 and PC2 together express 56.8% of the variance (illustrated in Figure C1). Variables loading on these components are shown in Table C1, with scores for individual species listed in Table C2. In the molar sample, species averages were calculated from combined sex samples, so only one pPCA is presented in this section. Variables with high loadings on PC1 include measurements of the width of the tooth, trigonid height, and talonid height, in addition to the relative lengths of the postmetacristid and the relative area of the talonid basin. *Brachyteles* has the highest score, with a narrow tooth, higher relief, and longer lingual crests while the seed predating pitheciids have the highest scores with wider teeth, lower height of the trigonid, and a greater talonid area. Species of *Cebus* and *Ateles* are close to the pitheciines, while *Callicebus, Aotus*, *Saimiri,* and *Lagothrix* are closer to the callitrichids in the center of the axis. *Alouatta* is also central on PC1, but higher on PC2 than the other non-callitrichid platyrrhines with similar PC1 scores. PC2 is associated with the relative length of the molars, and also with changes in the relative lengths of the posthypoconid crest and the cristid obliqua; this axis separates some callitrichids and *Alouatta* from the other taxa. In combination PC1 and PC2 separate the hard object feeders (pitheciines, *Cebus*) and ripe fruit specialists in the lower left corner from frugivores that have a greater component of insects or leaves in the diet (callitrichids, *Aotus*, *Callicebus*) and more folivorous species (*Alouatta*, *Brachyteles*).

Table C1: Results of molar pPCA of platyrrhines.

| PC | % Variance (eigenvalue) | Cumulative variance | Variables (factor loadings) |
|---|---|---|---|
| PC1 | 38.32 (5.365) | 38.32 | Talonid width (-0.94), Trigonid height (0.90), Trigonid width (-0.90), Postmetacristid length (0.74), Square root occlusal area (-0.73), Talonid height (0.73), Square root talonid area (-0.68), Pre-entoconid length (0.61) |
| PC2 | 18.52 (2.593) | 56.84 | Molar length (0.75), Pre-entoconid length (0.69), Cristid obliqua (0.69) Posthypoconid length (-0.58), Square root occlusal area (0.55) |
| PC3 | 10.77 (1.508) | 67.61 | Postmetacristid length (0.70), Cristid obliqua length (-0.57), Posthypoconid length (-0.48) |
| PC4 | 9.06 (1.268) | 76.67 | Protocristid length (0.71), Square root trigonid area (0.49), Molar length (-0.36), |
| PC5 | 6.84 (0.958) | 83.51 | Protocristid length (-0.51), Posthypoconid length (-0.38), Square root trigonid area (0.34) |
| PC6 | 5.69 (0.796) | 89.20 | Posthypoconid length (-0.56), Square root trigonid area (-0.43), Square root talonid area (0.29) |
| PC7 | 3.64 (0.511) | 92.84 | Talonid height (-0.37), Paracristid length (-0.34), Molar length (0.27) |
| PC8 | 2.96 (0.415) | 95.81 | Postmetacristid length (-0.30), Protocristid length (0.27), Talonid height (0.23) |

Figure C1: Phylogenetic principal components analysis of platyrrhine molars.



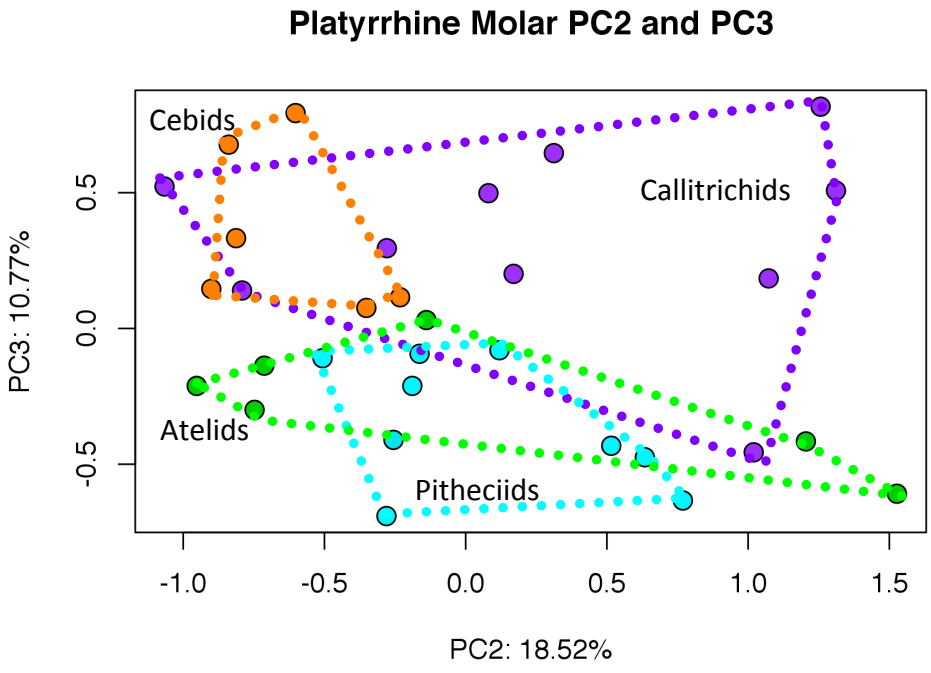



Table C2: Platyrrhine pPC scores, molar

| | PC1 | PC2 | PC3 | PC4 | PC5 | PC6 | PC7 | PC8 |
|---|---|---|---|---|---|---|---|---|
| *Alouatta palliata* | 0.8385 | 1.5268 | -0.6087 | 0.0605 | -0.3059 | -0.0093 | -0.0905 | -0.0145 |
| *Alouatta seniculus* | 1.0074 | 1.2046 | -0.4161 | -0.1434 | -0.4943 | 0.0240 | -0.2795 | -0.0489 |
| *Ateles belzebuth* | -1.0454 | -0.1390 | 0.0309 | -0.1117 | -0.5188 | 0.1051 | 0.0748 | -0.0944 |
| *Ateles geoffroyi* | -0.6609 | -0.9523 | -0.2116 | 0.4406 | -0.1957 | 0.0054 | -0.0174 | -0.2019 |
| *Brachyteles arachnoides* | 3.5037 | -0.7474 | -0.2998 | 0.2905 | -0.4008 | -0.0420 | -0.0503 | 0.0060 |
| *Lagothrix lagotricha* | 0.0880 | -0.7132 | -0.1371 | 0.3327 | -0.2349 | 0.1321 | -0.1372 | 0.0420 |
| | | | | | | | | |
| *Aotus azarae boliviensis* | 0.5223 | -0.2321 | 0.1149 | -0.2153 | -0.0346 | 0.1166 | -0.1525 | -0.0956 |
| *Aotus nigriceps* | 0.1461 | -0.3517 | 0.0755 | 0.2543 | -0.1562 | 0.1474 | -0.2321 | 0.0294 |
| *Cebus apella* | -0.8495 | -0.8389 | 0.6770 | 0.4050 | 0.1974 | -0.3765 | 0.2114 | 0.1009 |
| *Cebus capucinus* | -0.5192 | -0.6022 | 0.7933 | 0.4854 | 0.2240 | -0.3158 | 0.1699 | -0.0939 |
| *Saimiri boliviensis* | 0.5121 | -0.8129 | 0.3326 | -0.0218 | 0.2058 | -0.0834 | -0.1229 | 0.1104 |
| *Saimiri sciureus* | 0.5245 | -0.9006 | 0.1458 | 0.0318 | 0.3851 | 0.0325 | 0.0238 | 0.1817 |
| | | | | | | | | |
| *Callimico goeldii* | 1.6972 | 0.1698 | 0.2012 | 0.6202 | 0.1979 | 0.4037 | 0.1153 | -0.0760 |
| *Mico argentata* | 1.0607 | -0.2791 | 0.2957 | -0.6034 | 0.1844 | 0.2203 | 0.0122 | -0.0794 |
| *Callithrix penicillata* | 0.2357 | -0.7917 | 0.1398 | -0.3145 | -0.0054 | 0.2966 | 0.0070 | -0.1393 |
| *Cebuella pygmaea* | 0.5979 | 1.0727 | 0.1844 | -0.0557 | 0.1875 | 0.4196 | -0.0313 | -0.1115 |
| *Leontopithecus rosalia* | -0.2174 | 1.0198 | -0.4562 | -0.6481 | -0.0288 | 0.3861 | -0.0765 | 0.0899 |
| *Saguinus fuscicollis* | -0.3113 | 1.3110 | 0.5078 | -0.2134 | -0.0477 | -0.2125 | 0.1524 | 0.1611 |
| *Saguinus geoffroyi* | 0.9109 | 0.3121 | 0.6458 | -0.3157 | 0.4388 | 0.0987 | 0.0777 | 0.2132 |
| *Saguinus midas* | 0.0971 | 1.2567 | 0.8169 | 0.3861 | -0.0404 | 0.1649 | 0.2311 | -0.0048 |
| *Saguinus mystax* | 0.2460 | 0.0807 | 0.4983 | -0.1969 | 0.0785 | 0.3663 | 0.1945 | -0.1734 |
| *Saguinus oedipus* | 0.1177 | -1.0661 | 0.5228 | -0.3268 | 0.2298 | 0.0171 | 0.1072 | 0.1819 |
| | | | | | | | | |
| *Cacajao calvus* | -0.8837 | -0.2555 | -0.4104 | 0.0824 | 0.0867 | -0.0483 | -0.0212 | 0.0133 |
| *Cacajao melanocephalus* | -1.0190 | -0.1889 | -0.2116 | -0.1713 | 0.1653 | -0.0273 | -0.0842 | -0.1215 |
| *Callicebus donacophilus* | -0.2474 | 0.1196 | -0.0802 | 0.0125 | -0.2526 | -0.1964 | 0.0383 | 0.0102 |
| *Callicebus moloch* | -0.0809 | -0.5067 | -0.1096 | -0.3710 | 0.0676 | -0.1753 | -0.0319 | 0.0292 |
| *Callicebus torquatus* | 0.0062 | -0.1633 | -0.0933 | -0.2936 | 0.1902 | -0.0854 | -0.1011 | 0.1237 |
| *Chiropotes albinasus* | -1.8609 | 0.7691 | -0.6337 | -0.0647 | 0.2194 | -0.3096 | -0.0356 | -0.1190 |
| *Chiropotes satanas* | -1.3966 | -0.2804 | -0.6910 | -0.1428 | 0.1903 | 0.0401 | 0.0915 | -0.0394 |
| *Pithecia monachus* | -1.2998 | 0.5155 | -0.4321 | -0.0042 | 0.0075 | -0.1771 | 0.1675 | -0.0381 |
| *Pithecia pithecia* | -1.3595 | 0.6344 | -0.4745 | 0.1851 | -0.0849 | 0.0506 | 0.1370 | -0.1066 |

**D. Strepsirrhines: Cranial PCA**

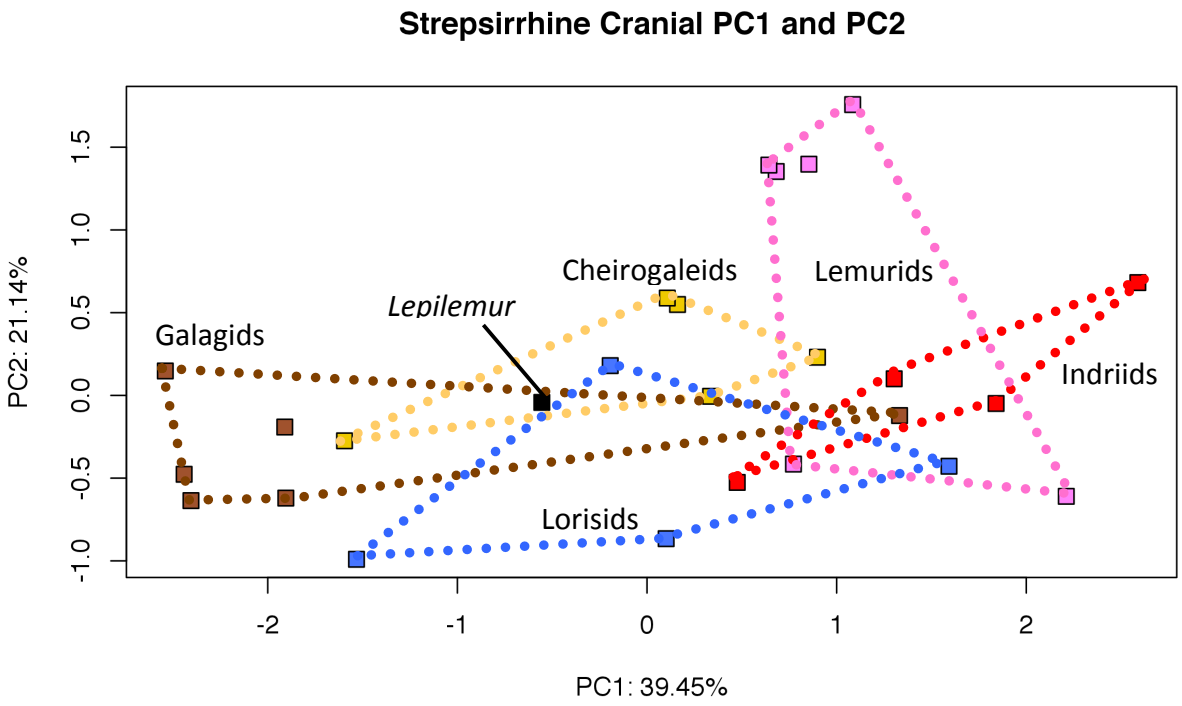
The cranial PCA of strepsirrhine primates resulted in seven PCs that expressed 95% of the variance (Table D1). The ordination of PC1 and PC2 is seen in figure D1. PC scores for individual species are shown in Table D2. The cranial pPCA in strepsirrhines was fairly similar to that for platyrrhines in the variables loading on the first PC; with high factor loadings for orbit size (breadth and height), and calvarial dimensions (length and biparietal diameter, and relative width of the skull at postorbital constriction), in addition to facial height and zygomatic arch length. Taxa with low scores on PC1 included the smaller galagos and lorisids, in addition to the cheirogaleid *Microcebus*, while higher scores were found in the larger bodied lemurids and indriids. The galago that appears to the right on PC1 is *Otolemur*; this species has an unusual degree of postorbital constriction relative to other galagos, longer zygomatic arches, and relatively smaller orbits and cranial vault. Similarly, the largest lorisid, *Perodicticus*, is also positioned to the right of other members of this family. The cheirogaleid with the lowest score on PC1 is the smallest genus, *Microcebus*. The position of these three genera (*Microcebus*, *Perodicticus*, and *Otolemur*) relative to others in the same families are primarily responsible for the overlap between lorisiforms and lemuriforms on the plot of PC1 against PC2.

PC2 separates the lemurids (*Lemur*, *Eulemur*, *Varecia*) with greater facial length from the other taxa, including the closely related *Hapalemur* species. Variables loading on this component include the total skull length and snout length measurements. PC3 and PC2 in combination act to create some separation of the larger-bodied indriidae and lemuridae from the smaller galagids, lorisids, and cheirogaleids, with only the small, nocturnal indriid *Avahi*, and the *Hapalemur* species located in the overlapping region of morphospace. Variables loading onto PC3 include bizygomatic breadth, facial height and palatal width.

Table D1: Results of cranial pPCA in strepsirrhines

| PC | % Variance (eigenvalue) | Cumulative variance | Variables (factor loadings) |
|---|---|---|---|
| PC1 | 39.45 (5.129) | 39.45 | Orbital breadth (-0.90), Orbital height (-0.86), Biparietal breadth (-0.85), Zygomatic arch length (0.78), Width of the skull at postorbital constriction (-0.76), Facial height (0.68), Calvarial length (-0.66), Posterior palatal width (0.56), Anterior palatal width (0.53) |
| PC2 | 21.14 (2.748) | 60.59 | Skull length (0.89), Snout length (0.87), Interorbital breadth (0.62) |
| PC3 | 10.98 (1.427) | 71.57 | Bizygomatic breadth (-0.74), Facial height (0.65), Posterior palatal width (-0.59), |
| PC4 | 9.67 (1.257) | 81.23 | Anterior palatal width (0.62), Interorbital breadth (-0.62), Calvarial length -0.46) |
| PC5 | 5.33 (0.693) | 86.56 | Anterior palatal width (-0.43), Width of the skull at postorbital constriction (0.39), skull length (-0.26) |
| PC6 | 4.93 (0.641) | 91.50 | Bizygomatic breadth (-0.41), Calvarial length (-0.40), Posterior palatal width (0.36) |
| PC7 | 3.24 (0.421) | 94.73 | Calvarial length (-0.33), Posterior palatal width (-0.28), Anterior palatal width (0.26) |

Figure D1: Phylogenetic principal components analysis of strepsirrhine crania.



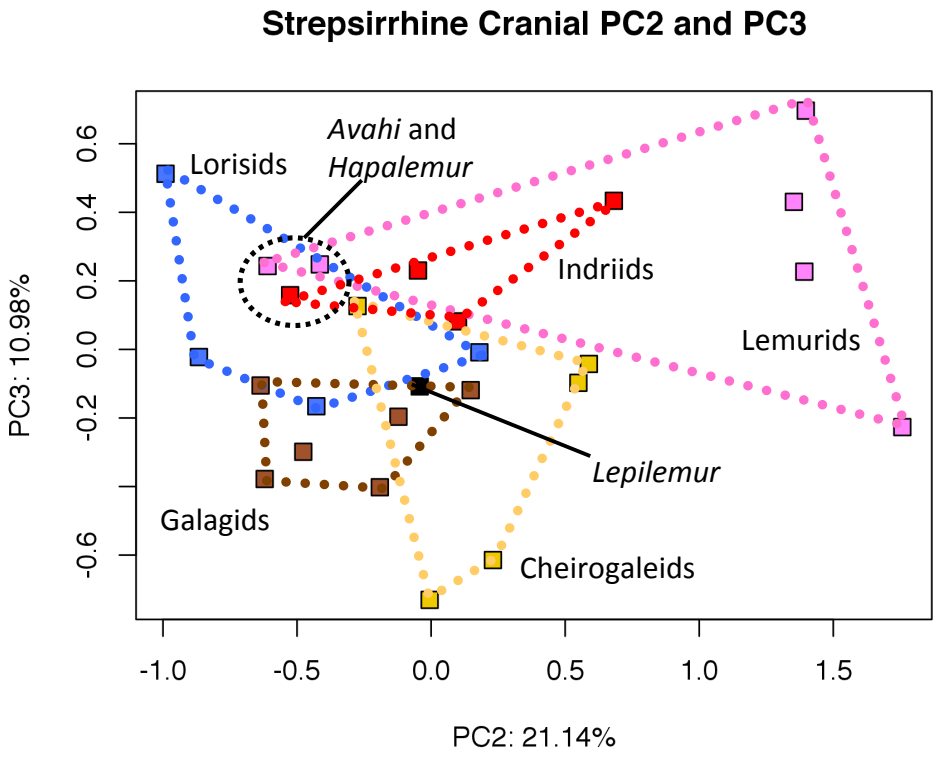



Table D2: Strepsirrhine pPC scores, cranium

| | PC1 | PC2 | PC3 | PC4 | PC5 | PC6 | PC7 |
|---|---|---|---|---|---|---|---|
| *Avahi laniger* | 0.4757 | -0.5258 | 0.1582 | -0.5338 | 0.1675 | 0.0811 | -0.1238 |
| *Indri indri* | 2.5883 | 0.6817 | 0.4336 | -0.4594 | -0.0352 | 0.1439 | -0.1230 |
| *Propithecus diadema* | 1.3034 | 0.1004 | 0.0819 | -0.4886 | 0.3065 | -0.0309 | 0.0956 |
| *Propithecus verreauxi* | 1.8408 | -0.0489 | 0.2302 | -0.3632 | 0.3785 | -0.0185 | -0.0264 |
| | | | | | | | |
| *Cheirogaleus major* | 0.8990 | 0.2306 | -0.6145 | 0.0941 | -0.1145 | 0.2055 | -0.1145 |
| *Cheirogaleus medius* | 0.3353 | -0.0054 | -0.7307 | -0.0387 | -0.1767 | 0.0301 | 0.0105 |
| *Microcebus griseorufus* | -1.5952 | -0.2744 | 0.1265 | 0.2085 | -0.0211 | -0.0218 | 0.1419 |
| *Mirza coquereli* | 0.1608 | 0.5494 | -0.0975 | 0.0689 | -0.0527 | 0.2881 | 0.0549 |
| *Phaner furcifer* | 0.1068 | 0.5884 | -0.0424 | -0.2541 | -0.1712 | 0.0927 | 0.1644 |
| | | | | | | | |
| *Eulemur fulvus* | 0.6812 | 1.3532 | 0.4305 | -0.1611 | -0.0430 | -0.2709 | -0.0304 |
| *Eulemur rufus* | 0.8536 | 1.3974 | 0.6966 | -0.3315 | 0.0621 | -0.2181 | -0.1032 |
| *Hapalemur griseus* | 0.7723 | -0.4151 | 0.2480 | -0.0596 | 0.0905 | -0.3531 | -0.1052 |
| *Hapalemur simus* | 2.2109 | -0.6099 | 0.2432 | -0.5724 | 0.0393 | -0.1626 | -0.0606 |
| *Lemur catta* | 0.6427 | 1.3920 | 0.2268 | -0.3204 | 0.1684 | -0.2402 | 0.0718 |
| *Varecia variegata* | 1.0844 | 1.7575 | -0.2266 | -0.3003 | -0.1033 | -0.2514 | -0.0925 |
| | | | | | | | |
| *Lepilemur mustelinus* | -0.5546 | -0.0424 | -0.1079 | -0.4625 | -0.0006 | -0.3111 | -0.0633 |
| | | | | | | | |
| *Arctocebus calabarensis* | -0.1940 | 0.1800 | -0.0085 | 0.2276 | -0.0502 | -0.0851 | -0.2119 |
| *Loris tardigradus* | -1.5320 | -0.9904 | 0.5124 | 0.6843 | -0.1115 | 0.2162 | 0.0276 |
| *Nycticebus coucang* | 0.1009 | -0.8659 | -0.0222 | 0.6348 | 0.0503 | 0.1090 | 0.1035 |
| *Perodicticus potto* | 1.5925 | -0.4280 | -0.1658 | 0.1109 | 0.2944 | -0.1211 | 0.1908 |
| | | | | | | | |
| *Euoticus elegantulus* | -2.4049 | -0.6359 | -0.1053 | -0.2574 | -0.3144 | 0.1337 | 0.2089 |
| *Galago alleni* | -1.9102 | -0.1912 | -0.4021 | 0.0024 | -0.1080 | 0.1025 | -0.1553 |
| *Galago demidoff* | -2.5402 | 0.1477 | -0.1188 | -0.1119 | 0.0342 | -0.0007 | -0.0794 |
| *Galago gallarum* | -1.9046 | -0.6207 | -0.3780 | -0.1833 | -0.0207 | 0.1709 | 0.1097 |
| *Galago moholi* | -2.4409 | -0.4767 | -0.2987 | -0.0876 | 0.0784 | 0.2436 | 0.1326 |
| *Otolemur crassicaudatus* | 1.3318 | -0.1219 | -0.1964 | 0.2646 | -0.1856 | 0.0137 | 0.0074 |

**E. Strepsirrhine: Mandible PCA**

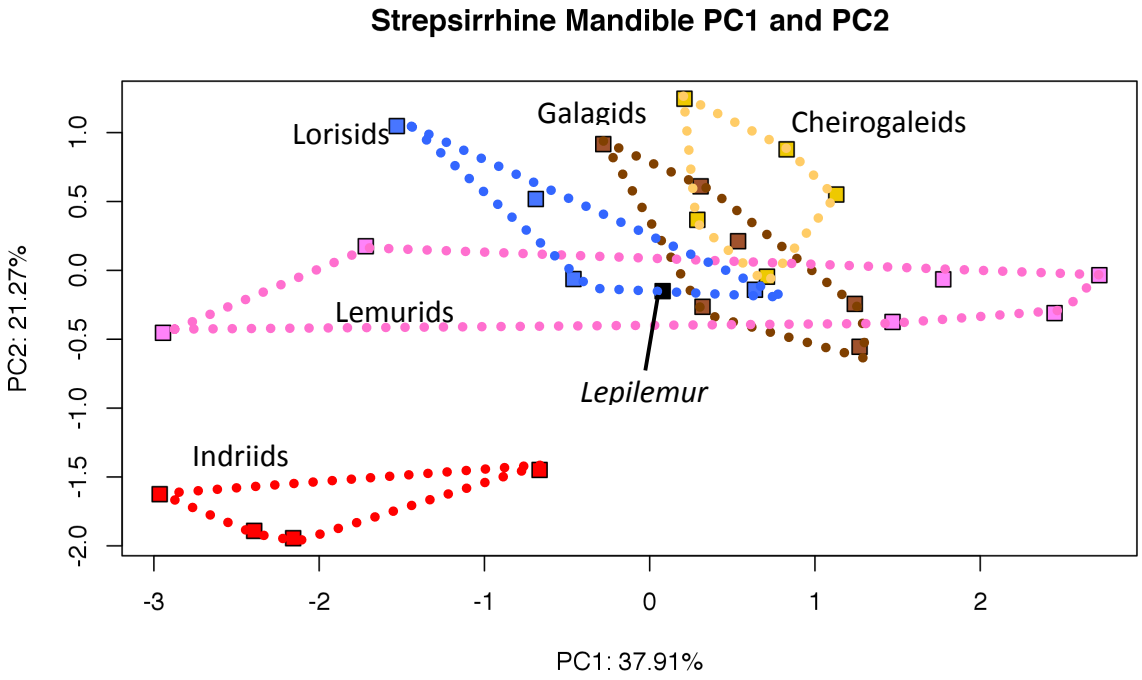
The pPCA of strepsirrhine mandibles created eight PCs that capture 95% of the variance (summarized in table E1); the first two PCs capture 59% of the variation in mandibular shape. Scores for individual species are presented in Table E2, and plots of the first three PCs are presented in Figure E1. PC1 separates indriids and the two *Hapalemur* sp.) in addition to the lorisid *Nycticebus*, with lower scores on this axis, from the other strepsirrhines. The highest scores on PC1 are seen in the remaining lemurids. Variables loading positively on this PC include the relative length of the mandible and tooth row, and anteroposterior breadth of the mandibular ramus, while the thickness of the mandibular corpus, the height of the corpus, and the height of the ramus are negatively correlated with PC1.

PC2 separates the indriids from all other species; variables loading on this axis include the relative height of the condyle and, to a lesser extent, coronoid process above the tooth row, and the symphyseal depth and ramus height. Height of the condyle, coronoid process, and ramus height are negatively correlated with this axis, while symphyseal depth is positively associated. *Phaner* is the highest scoring cheirogaleid on PC2, and the *Euoticus* is the highest scoring galagid, which may indicate that some of the shape changes on this axis may be functionally related the dietary habit of gummivory in these two species, possibly through increased gape associated with lower condyle height (Vinyard et al., 2003). Interestingly the highest scoring lorisid on this axis is *Nycticebus coucang*, which may also have a significant component of gummivory in the diet, including gouging of the substrate (Tan and Drake 2001; Wiens 2002; Nekaris et al., 2010). PC3 further demonstrates the clear differences in mandible morphology of indriids, with separation on this axis associated with symphyseal height and condyle shape.

Table E1: Results of mandible pPCA in strepsirrhines.

| PC | % Variance (eigenvalue) | Cumulative Variance | Variables (factor loadings) |
|---|---|---|---|
| PC1 | 37.91 (5.686) | 37.91 | Mandible length (0.97), Tooth row length (0.87), Mandibular corpus height (-0.80), Ramus breadth (0.70), Mandibular corpus breadth (-0.68), Temporalis lever arm (0.66), Anterior dental width (0.65), Ramus height (-0.64), Symphyseal thickness (0.50) |
| PC2 | 21.27 (3.191) | 59.18 | Condyle height (-0.91), Symphyseal thickness (0.69) Ramus height (-0.61), Ramus breadth (0.56), Condyle width (0.53), Coronoid process height (-0.52) |
| PC3 | 14.68 (2.201) | 73.85 | Symphyseal height (-0.75), Condylar width (0.64), Tooth row width (0.58), Coronoid height (0.53) |
| PC4 | 6.94 (1.041) | 80.79 | Condyle length (-0.63), Anterior dental width (0.45), Corpus height (0.38) |
| PC5 | 5.01 (0.751) | 85.80 | Corpus breadth (-0.39), Condyle head width (0.36), Coronoid height (0.34) |
| PC6 | 3.47 (0.520) | 89.27 | Temporalis lever arm (0.31), Toothrow width (-0.30), Anterior dental width (0.27) |
| PC7 | 3.30 (0.495) | 92.57 | Anterior dental width (-0.40), Temporalis lever arm (0.39), Condyle length (-0.23) |
| PC8 | 2.63 (0.395) | 95.20 | Toothrow width (0.38), Temporalis lever arm (0.27), Coronoid height (-0.24) |

Figure E1: Phylogenetic principal components analysis of strepsirrhine mandibles.



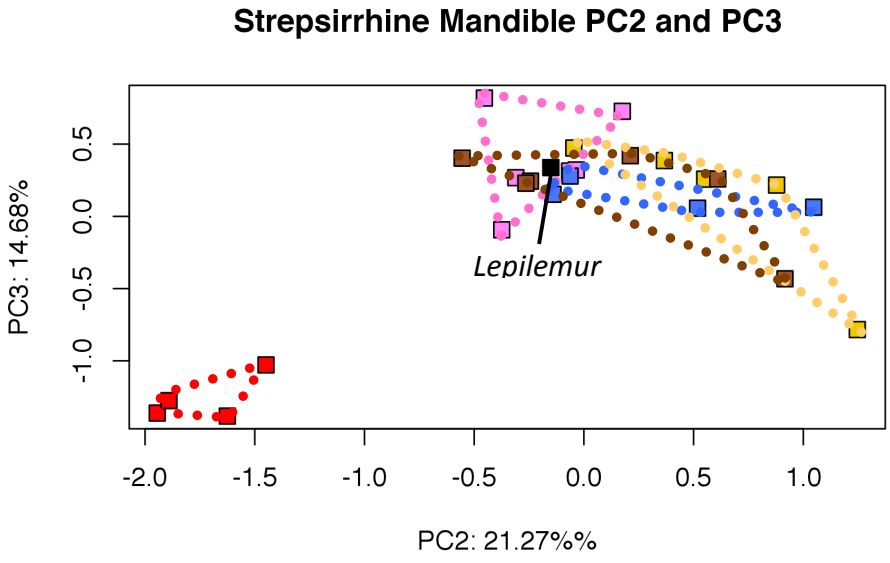



Table E2: Strepsirrhine pPC scores, mandible

| | PC1 | PC2 | PC3 | PC4 | PC5 | PC6 | PC7 | PC8 |
|---|---|---|---|---|---|---|---|---|
| *Avahi laniger* | -2.9649 | -1.6250 | -1.3825 | 0.0510 | 0.1107 | 0.0030 | 0.1717 | 0.0429 |
| *Indri indri* | -0.6661 | -1.4489 | -1.0283 | -0.5627 | 0.0902 | 0.1806 | -0.2312 | 0.0828 |
| *Propithecus diadema* | -2.1573 | -1.9445 | -1.3616 | 0.1040 | 0.2268 | -0.0124 | 0.1047 | 0.0884 |
| *Propithecus verreauxi* | -2.3930 | -1.8912 | -1.2759 | 0.0979 | 0.2753 | 0.0715 | 0.2405 | 0.1496 |
| | | | | | | | | |
| *Cheirogaleus major* | 0.2883 | 0.3670 | 0.3862 | 0.0597 | 0.0052 | -0.0989 | 0.1540 | 0.0172 |
| *Cheirogaleus medius* | 0.8286 | 0.8785 | 0.2167 | 0.1017 | -0.0030 | -0.0650 | 0.2579 | -0.0353 |
| *Microcebus griseorufus* | 0.7096 | -0.0459 | 0.4730 | -0.0391 | 0.0315 | 0.0151 | 0.1965 | -0.0417 |
| *Mirza coquereli* | 1.1290 | 0.5506 | 0.2576 | 0.2406 | -0.0756 | -0.0191 | 0.2634 | 0.0583 |
| *Phaner furcifer* | 0.2105 | 1.2460 | -0.7837 | 0.0639 | -0.1714 | 0.0133 | 0.0941 | 0.1733 |
| | | | | | | | | |
| *Eulemur fulvus* | 1.7763 | -0.0651 | 0.3137 | 0.2678 | -0.1619 | 0.1059 | -0.2101 | -0.0609 |
| *Eulemur rufus* | 2.4499 | -0.3103 | 0.2677 | 0.3555 | 0.0837 | 0.1094 | -0.0882 | -0.0664 |
| *Hapalemur griseus* | -1.7179 | 0.1752 | 0.7273 | -0.0982 | -0.0215 | 0.1878 | 0.1297 | 0.0469 |
| *Hapalemur simus* | -2.9448 | -0.4534 | 0.8188 | 0.4783 | -0.0976 | 0.1608 | -0.1187 | 0.0648 |
| *Lemur catta* | 1.4695 | -0.3745 | -0.0929 | 0.3093 | 0.0817 | 0.2105 | 0.0048 | 0.0525 |
| *Varecia variegata* | 2.7209 | -0.0349 | 0.3212 | 0.2316 | -0.1565 | 0.1191 | -0.1210 | 0.0263 |
| | | | | | | | | |
| *Lepilemur mustelinus* | 0.0784 | -0.1507 | 0.3374 | 0.3505 | -0.0269 | 0.3527 | 0.1804 | 0.0497 |
| | | | | | | | | |
| *Arctocebus calabarensis* | 0.6369 | -0.1408 | 0.1528 | -0.1379 | -0.1498 | -0.0966 | 0.1244 | -0.0296 |
| *Loris tardigradus* | -0.4612 | -0.0628 | 0.2791 | -0.2539 | 0.0119 | -0.1676 | 0.0194 | 0.0134 |
| *Nycticebus coucang* | -1.5301 | 1.0475 | 0.0634 | -0.1350 | 0.0585 | -0.0670 | -0.1956 | -0.0697 |
| *Perodicticus potto* | -0.6891 | 0.5181 | 0.0566 | 0.0168 | 0.4781 | -0.1320 | -0.2258 | -0.1289 |
| | | | | | | | | |
| *Euoticus elegantulus* | -0.2809 | 0.9165 | -0.4321 | -0.0131 | -0.2733 | -0.0188 | -0.0938 | -0.0446 |
| *Galago alleni* | 1.2701 | -0.5549 | 0.4028 | 0.0245 | -0.1805 | -0.0858 | -0.0375 | -0.0349 |
| *Galago demidoff* | 1.2411 | -0.2433 | 0.2436 | -0.0604 | -0.2180 | -0.0293 | -0.0278 | 0.0710 |
| *Galago gallarum* | 0.5349 | 0.2116 | 0.4198 | -0.1434 | -0.0303 | -0.0635 | -0.1282 | 0.0251 |
| *Galago moholi* | 0.3197 | -0.2645 | 0.2294 | -0.1410 | -0.2178 | -0.0569 | -0.0856 | -0.1455 |
| *Otolemur crassicaudatus* | 0.3082 | 0.6100 | 0.2589 | -0.0298 | 0.0677 | -0.0181 | 0.0170 | -0.2215 |

**F. Strepsirrhine: Molar PCA**

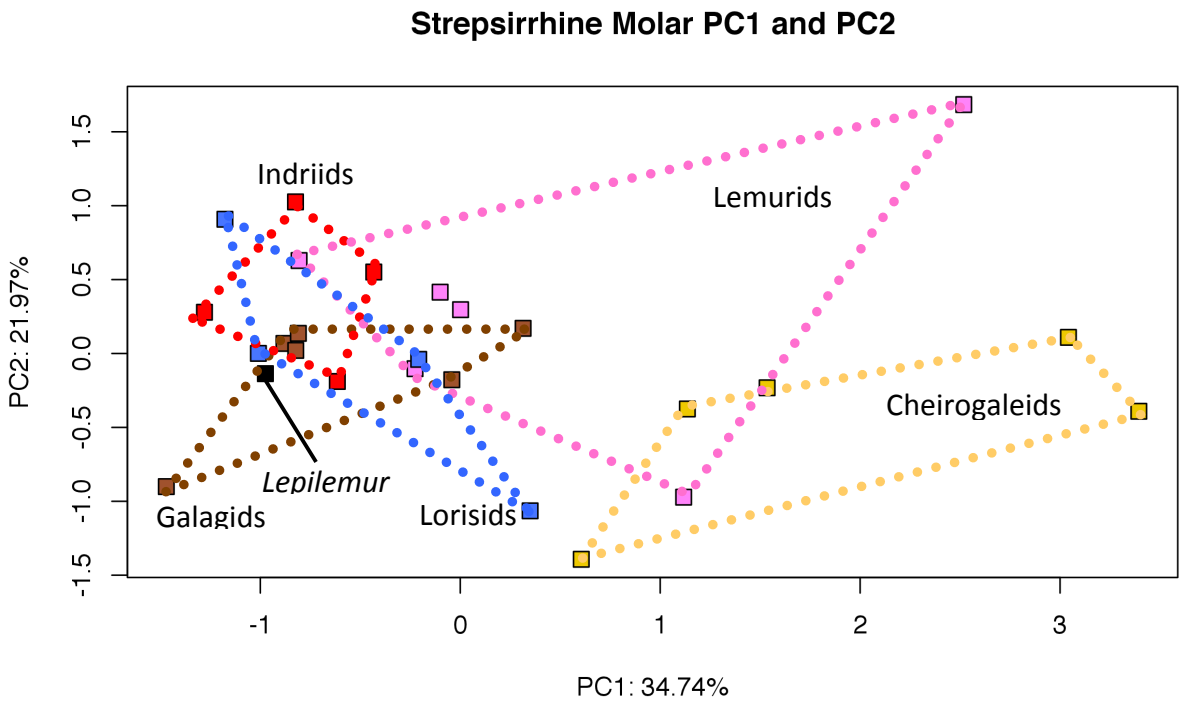
The pPCA of strepsirrhine molar morphology created seven PCs that express 95% of the variance, summarized in Table F1. Species scores on these seven PCs are presented in Table F2. Of these PCs, over 55% of the variance is contained in the first two PCs (Figure F1). The first PC separates species with relatively large occlusal area for the size of the tooth (variables loading on this axis include talonid and trigonid width, occlusal area); species with high scores on PC1 include *Varecia* and *Cheirogaleus*. Lower scores on PC1 are associated with greater crest development, particularly of the lingual crests, as in the more folivorous indriids and more insectivorous lorisids and galagids. Galagids with lower scores on PC1 included *Otolemur crassicaudatus* and *Galago alleni* (although, not the gummivore *Euoticus*), and lorisids with lower scores were *Nycticebus coucang* and *Perodicticus potto*, indicating that at least some of the species with more frugivore/ominivore dietary tendencies scored lower than their more insectivorous relatives. PC2 was also associated with variation in crest lengths, including more buccal crests on both the trigonid (paracristid, buccal section of protocristid) and the talonid (cristid obliqua). This PC axis is also associated with the relative length of the tooth.

The molar shape of *Hapalemur simus* is quite distinct from that of other lemurids, including the congeneric *Hapalemur griseus*. *Hapalemur simus* has high scores on PC1 and low scores on PC2, which reflects a buccolingually broader shape with more limited crest development than in closely related species. This tooth shape may be related to the diet of the species; *Hapalemur simus* and *griseus* both feed on bamboo, but *H. simus* eats a greater proportion of the inner culm pith, requiring breaking open mature bamboo stems (Tan, 1999).

Table F1: Results of molar pPCA in strepsirrhines.

| PC | % Variance (eigenvalue) | Cumulative Variance | Variables (factor loadings) |
|---|---|---|---|
| PC1 | 34.74 (4.864) | 34.74 | Talonid width (0.90), Trigonid width (0.89), Talonid height (-0.86), Square root occlusal area (0.84), Square root talonid area (0.80), Postmetacristid length (-0.62), Pre-entoconid length (-0.52) |
| PC2 | 21.97 (3.076) | 56.72 | Paracristid length (0.80), Protocristid length (0.77), Square root trigonid area (0.69), Cristid obliqua length (0.65), Molar length (0.59) |
| PC3 | 13.33 (1.866) | 70.05 | Trigonid height (0.70), Posthypoconid length (0.67), Pre-entoconid length (-0.48) |
| PC4 | 10.25 (1.435) | 80.29 | Molar length (0.75), Pre-entoconid length (-0.44), Square root trigonid area (-0.43) |
| PC5 | 6.38 (0.894) | 86.67 | Posthypoconid length (0.56), Cristid obliqua length (-0.47), Protocristid length (0.38) |
| PC6 | 5.41 (0.757) | 92.09 | Posthypoconid length (0.45), Square root trigonid area (-0.41), Talonid width (0.30) |
| PC7 | 3.67 (0.514) | 95.76 | Postmetacristid length (0.54), Protocristid length (-0.27), Pre-entoconid length (0.24) |

Figure F1: Phylogenetic principal components analysis of strepsirrhine molars.



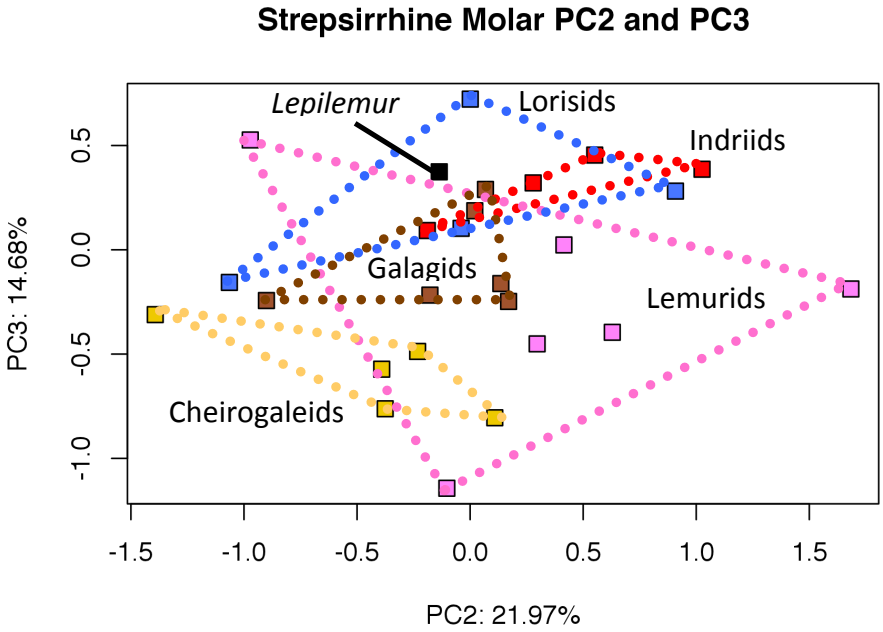



Table F2: Strepsirrhine pPC scores, molar

| | PC1 | PC2 | PC3 | PC4 | PC5 | PC6 | PC7 |
|---|---|---|---|---|---|---|---|
| *Avahi laniger* | -1.2794 | 0.2789 | 0.3208 | -0.2246 | 0.2208 | 0.0205 | 0.1713 |
| *Indri indri* | -0.6149 | -0.1893 | 0.0924 | 0.0172 | 0.3563 | 0.1328 | 0.0827 |
| *Propithecus diadema* | -0.4325 | 0.5511 | 0.4541 | 0.0492 | 0.4461 | 0.0846 | 0.0320 |
| *Propithecus verreauxi* | -0.8241 | 1.0257 | 0.3863 | -0.0021 | 0.1565 | 0.0182 | 0.0296 |
| | | | | | | | |
| *Cheirogaleus major* | 3.0418 | 0.1091 | -0.8053 | 0.4321 | 0.0850 | 0.2526 | 0.2016 |
| *Cheirogaleus medius* | 3.3940 | -0.3910 | -0.5724 | 0.2832 | -0.3561 | 0.3171 | 0.2108 |
| *Microcebus griseorufus* | 1.5347 | -0.2321 | -0.4873 | 0.0029 | -0.1273 | 0.3170 | 0.0009 |
| *Mirza coquereli* | 1.1359 | -0.3755 | -0.7622 | 0.0086 | -0.2527 | 0.1644 | -0.0531 |
| *Phaner furcifer* | 0.6052 | -1.3925 | -0.3108 | 0.0461 | -0.3641 | 0.2380 | -0.0330 |
| | | | | | | | |
| *Eulemur fulvus* | -0.1007 | 0.4149 | 0.0234 | 0.3990 | -0.0715 | -0.0994 | 0.0770 |
| *Eulemur rufus* | 0.0017 | 0.2964 | -0.4510 | 0.4704 | 0.0595 | -0.0188 | 0.0310 |
| *Hapalemur griseus* | -0.2262 | -0.1029 | -1.1433 | -0.3595 | 0.0715 | 0.1625 | 0.1701 |
| *Hapalemur simus* | 1.1173 | -0.9722 | 0.5267 | -0.2351 | 0.1418 | 0.0930 | 0.1739 |
| *Lemur catta* | -0.8062 | 0.6288 | -0.3956 | 0.2665 | -0.0119 | 0.1275 | 0.1578 |
| *Varecia variegata* | 2.5184 | 1.6839 | -0.1877 | 0.8354 | 0.1823 | 0.0350 | 0.0346 |
| | | | | | | | |
| *Lepilemur mustelinus* | -0.9746 | -0.1365 | 0.3738 | 0.8162 | -0.4478 | 0.2129 | 0.3222 |
| | | | | | | | |
| *Arctocebus calabarensis* | -1.1769 | 0.9082 | 0.2815 | -0.1155 | 0.1307 | -0.0329 | -0.1317 |
| *Loris tardigradus* | -1.0096 | 0.0007 | 0.7225 | -0.3382 | 0.4205 | 0.1447 | -0.0968 |
| *Nycticebus coucang* | -0.2078 | -0.0398 | 0.1029 | -0.2751 | 0.1165 | -0.1310 | -0.0926 |
| *Perodicticus potto* | 0.3495 | -1.0646 | -0.1564 | 0.1577 | -0.1276 | -0.3180 | -0.1079 |
| | | | | | | | |
| *Euoticus elegantulus* | -0.8818 | 0.0679 | 0.2895 | -0.3789 | -0.4307 | -0.1363 | -0.1920 |
| *Galago alleni* | 0.3143 | 0.1702 | -0.2476 | -0.2618 | -0.1469 | -0.1683 | -0.0429 |
| *Galago demidoff* | -0.8228 | 0.0208 | 0.1871 | -0.4041 | -0.1633 | -0.1894 | -0.0611 |
| *Galago gallarum* | -1.4702 | -0.9008 | -0.2432 | -0.1726 | -0.1772 | -0.2410 | -0.0810 |
| *Galago moholi* | -0.8098 | 0.1360 | -0.1619 | -0.5999 | -0.2628 | -0.2969 | -0.0451 |
| *Otolemur crassicaudatus* | -0.0422 | -0.1777 | -0.2172 | -0.2823 | -0.0464 | -0.4401 | -0.0924 |

**G. All taxa: Cranial PCA**

Two pPCAs combining platyrrhine and strepsirrhine cranial measurements were created; one used female platyrrhines and the other male platyrrhines. In both pPCAs, 85% of the variance was represented on the first six principal components (Table G1 and G2). Species scores are presented in Tables G3 and G4, and ordinations of taxa on the first three PCs are presented in Figures G1 and G2 .In both analyses the dominant variables loading on the first principal components (37% of the variance in the analysis with females, and 39% of the variance in the analysis with males) were measurements of the relative proportions of the orbital (orbital height and breadth), cranial vault (biparietal breadth and calvarial length) and face (zygomatic arch length and facial height); the relative width of the skull at maximal post-orbital constriction is also likely related to relative cranial vault size and also loads on this component. These variables were shared between the two pPCAs, additionally the measurement of the difference between the total cranial length and the length of the calvarium loaded on PC1 in the analysis using males. In both analyses the highest scoring species on PC1 were *Alouatta* species, with additional high scores seen in *Brachyteles* among the platyrrhines, and *Indri* and *Hapalemur simus* among the strepsirrhines. Other lemurids and indriids also have higher scores on this axis, as do isolated examples of lorisids (*Perodicticus*), galagids (*Otolemur*), and, in the female analysis, cheirogaleids (*Cheirogaleus major*). Lowest scores on this axis are found in the other galagids, *Microcebus*, and *Loris* among the strepsirrhines and *Cebuella*, *Aotus*, and *Saimiri* among the platyrrhines. PC1 therefore appears to have some association with size, as might be expected given allometric variation in brain and eye size, particularly when constellations of closely related species are compared on this axis. However, this is not universal, given that *Alouatta* possessed the highest scores, but is exceeded in body mass by other atelids.

Subsequent PCs also show a similar configuration of species in the analyses using female and male platyrrhines, despite some differences in the variables loading onto these axes. PC2 summarizes variation in cranial length and the difference between cranial and calvarial length, and in both analyses primarily separates lemurids (excepting the bamboo lemurs, *Hapalemur* ) from other species in the analysis. PC3 summarizes some of the variation in palatal width in both analyses and provides some degree of separation between callitrichids and other platyrrhines, and between strepsirrhines and non-callitrichid platyrrhines. Two exceptions to this are the asian lorisids *Loris* and *Nycticebus*, which have much higher scores on PC3 than most other taxa, indicating narrower palates, and in general lemuriform strepsirrhines have lower scores than lorisiforms on this axis.

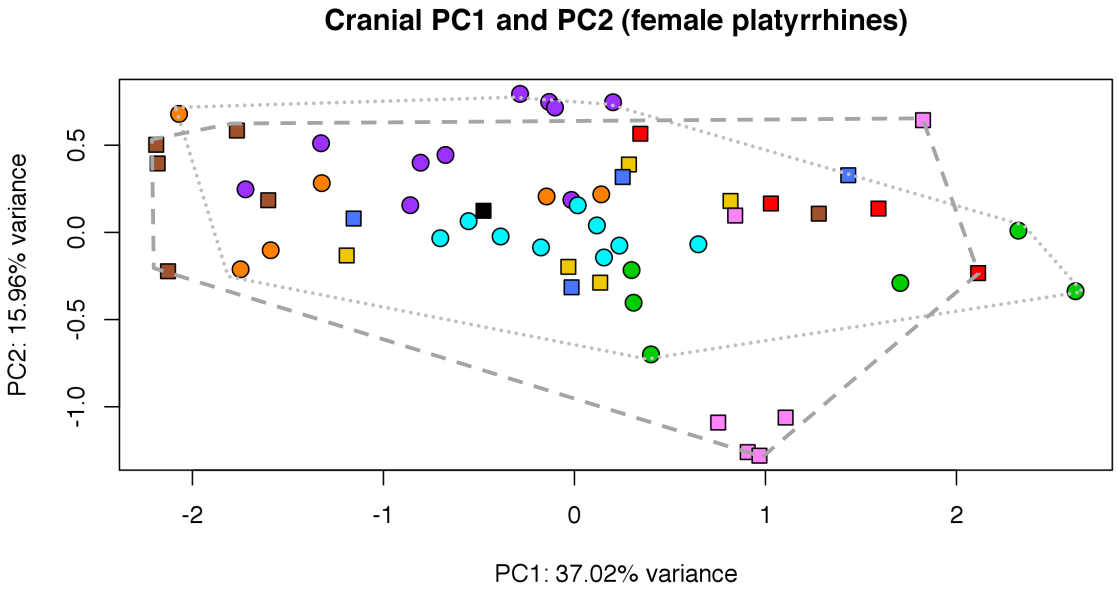
Table G1. Results of cranial pPCA of all taxa together (female platyrrhines).

| PC | % Variance (eigenvalue) | Cumulative Variance | Variables (factor loadings) |
|---|---|---|---|
| PC1 | 37.02 (4.813) | 37.02 | Biparietal breadth (-0.85), Width at postorbital constriction (-0.84), Orbital breadth (-0.83), Orbital height (-0.80), Zygomatic arch length (0.78), Facial height (0.73), Calvarial length (-0.70) |
| PC2 | 15.96 (2.075) | 52.98 | Cranial length (-0.74), Snout length (-0.65), Bizygomatic breadth (0.54) |
| PC3 | 12.94 (1.682) | 65.92 | Posterior palatal width (-0.72), Anterior palatal width (-0.57), Skull length (-0.51) |
| PC4 | 8.75 (1.137) | 74.67 | Snout length (0.52), Calvarial length (-0.48), Orbital height (0.40) |
| PC5 | 7.22 (0.939) | 81.89 | Bizygomatic breadth (0.57), Interorbital breadth (0.52), Anterior palatal width (-0.37) |
| PC6 | 6.11 (0.795) | 88.00 | Interorbital breadth (0.49), Bizygomatic breadth (-0.42), Posterior palatal width (0.32) |

Table G2. Results of cranial pPCA of all taxa together (male platyrrhines).

| PC | % Variance (eigenvalue) | Cumulative Variance | Variables (factor loadings) |
|---|---|---|---|
| PC1 | 38.65 (5.024) | 38.65 | Orbital breadth (-0.86), Biparietal breadth (-0.85), Width at postorbital constriction (-0.83), Orbital height (-0.80), Zygomatic arch length (0.80), Facial height (0.79), Calvarial length (-0.76), Snout length (0.50) |
| PC2 | 14.81 (1.926) | 53.46 | Cranial length (-0.89), Snout length (-0.70), Interorbital breadth (-0.45) |
| PC3 | 12.44 (1.617) | 65.90 | Posterior palatal width (-0.85) Anterior palatal width (-0.64), Facial height (0.41) |
| PC4 | 7.70 (1.001) | 73.60 | Bizygomatic breadth (-0.79), Anterior palatal width (0.33), Interorbital breadth (-0.25) |
| PC5 | 6.76 (0.879) | 80.36 | Calvarial length (0.43), Snout length (-0.41), Interorbital breadth (-0.40) |
| PC6 | 6.27 (0.815) | 86.64 | Anterior palatal width (0.54), Bizygomatic breadth (0.36), Interorbital breadth (-0.34) |

Figure G1. Phylogenetic PCA: Crania of all taxa, with female platyrrhines. Circles = platyrrhines, squares = strepsirrhines. Atelids = green, Callitrichids = purple, Cebids = orange, Pitheciids = turquoise, Cheirogaleids = gold, Indriids = red, Galagids = brown, Lemurids = pink, Lorisids in blue, *Lepilemur* = black.



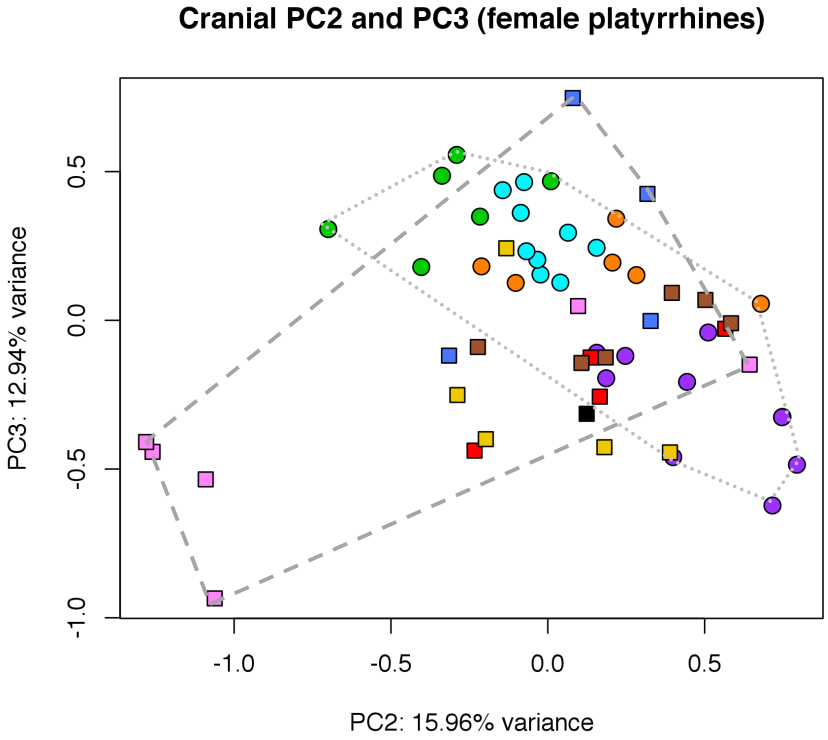
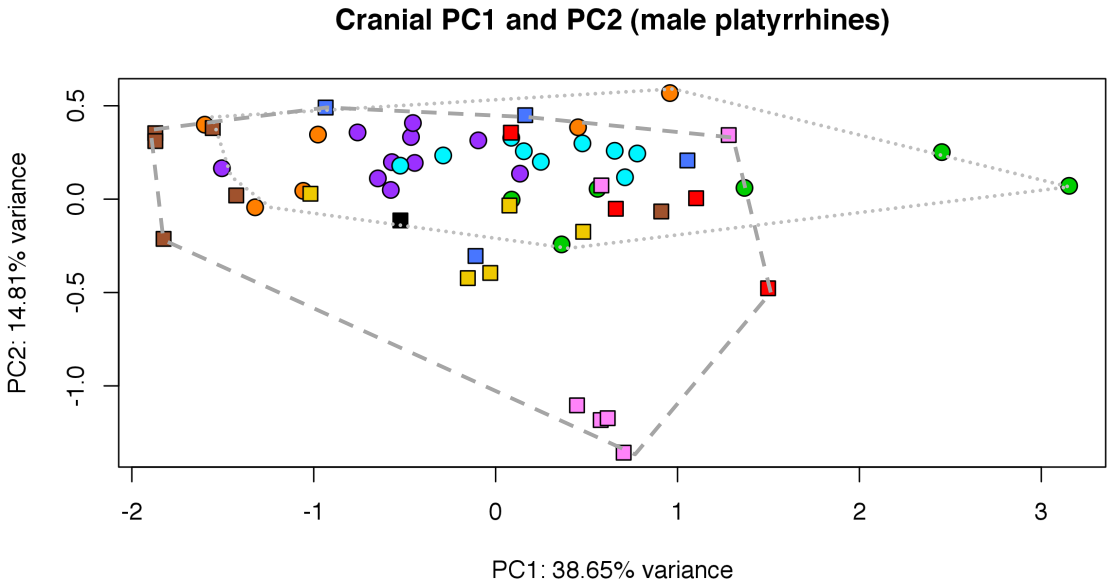



Figure G2. Phylogenetic PCA: Crania of all taxa, with male platyrrhines. Circles = platyrrhines, squares = strepsirrhines. Atelids = green, Callitrichids = purple, Cebids = orange, Pitheciids = turquoise, Cheirogaleids = gold, Indriids = red, Galagids = brown, Lemurids = pink, Lorisids in blue, *Lepilemur* = black.



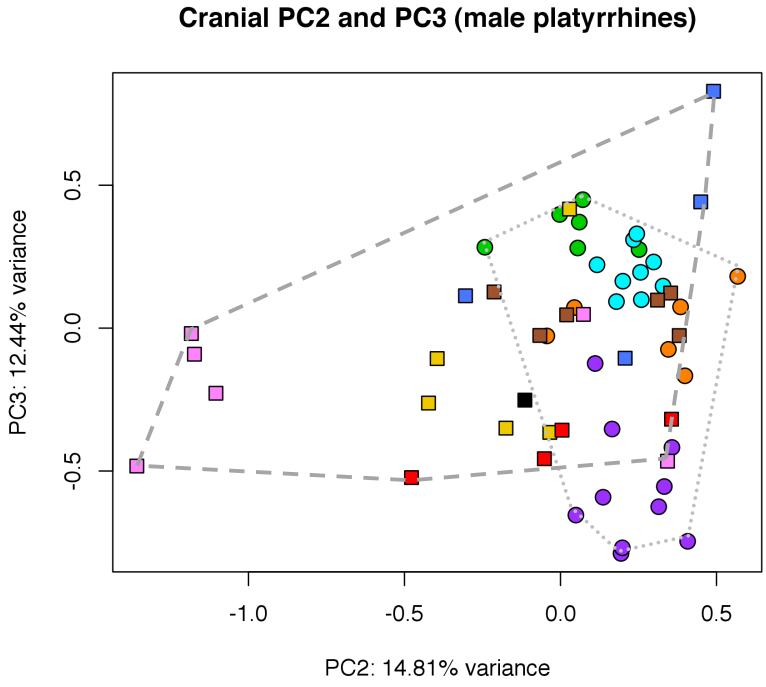



Table G3: All taxa pPC scores, cranium (female platyrrhines)

| | PC1 | PC2 | PC3 | PC4 | PC5 | PC6 |
|---|---|---|---|---|---|---|
| *Alouatta palliata* | 2.3241 | 0.0101 | 0.4676 | -0.0931 | -0.1635 | -0.1239 |
| *Alouatta seniculus* | 2.6233 | -0.3373 | 0.4861 | -0.1060 | -0.4126 | -0.0122 |
| *Ateles belzebuth* | 0.4007 | -0.6997 | 0.3067 | -0.4029 | -0.3763 | -0.1048 |
| *Ateles geoffroyi* | 0.3096 | -0.4033 | 0.1793 | -0.4102 | -0.2610 | -0.2044 |
| *Brachyteles arachnoides* | 1.7061 | -0.2903 | 0.5562 | -0.2927 | -0.1769 | -0.0360 |
| *Lagothrix lagotricha* | 0.2990 | -0.2160 | 0.3487 | -0.3271 | -0.3958 | -0.1054 |
| *Aotus azarae boliviensis* | -1.3229 | 0.2825 | 0.1520 | -0.2398 | -0.3649 | 0.0388 |
| *Aotus nigriceps* | -2.0697 | 0.6794 | 0.0556 | -0.1372 | -0.4241 | 0.0609 |
| *Cebus apella* | 0.1404 | 0.2182 | 0.3417 | -0.3207 | -0.3476 | -0.2884 |
| *Cebus capucinus* | -0.1458 | 0.2061 | 0.1941 | -0.3643 | -0.4092 | -0.2366 |
| *Saimiri boliviensis* | -1.7477 | -0.2116 | 0.1814 | -0.5862 | -0.4515 | -0.2487 |
| *Saimiri sciureus* | -1.5902 | -0.1023 | 0.1258 | -0.6348 | -0.5214 | -0.1645 |
| *Callimico goeldii* | -1.3265 | 0.5114 | -0.0408 | -0.4110 | -0.0460 | -0.0082 |
| *Mico argentata* | -0.6752 | 0.4439 | -0.2071 | -0.4979 | -0.0354 | 0.0266 |
| *Callithrix penicillata* | -0.8594 | 0.1561 | -0.1091 | -0.4262 | 0.1198 | -0.1301 |
| *Cebuella pygmaea* | -1.7220 | 0.2471 | -0.1196 | -0.4554 | -0.0332 | 0.0390 |
| *Leontopithecus rosalia* | -0.0159 | 0.1862 | -0.1948 | -0.5929 | -0.2461 | -0.0419 |
| *Saguinus fuscicollis* | -0.1322 | 0.7480 | -0.3246 | -0.6288 | -0.1514 | -0.0906 |
| *Saguinus geoffroyi* | -0.1017 | 0.7162 | -0.6226 | -0.5102 | -0.0253 | -0.1365 |
| *Saguinus midas* | -0.2847 | 0.7942 | -0.4854 | -0.6450 | -0.2015 | -0.0578 |
| *Saguinus mystax* | 0.2021 | 0.7465 | -0.3258 | -0.6772 | -0.3316 | -0.1001 |
| *Saguinus oedipus* | -0.8053 | 0.3997 | -0.4600 | -0.5614 | 0.0610 | -0.1181 |
| *Cacajao calvus* | 0.1174 | 0.0400 | 0.1270 | -0.2463 | -0.3661 | -0.3684 |
| *Cacajao melanocephalus* | -0.3865 | -0.0234 | 0.1540 | -0.4274 | -0.2776 | -0.4191 |
| *Callicebus donacophilus* | -0.1750 | -0.0862 | 0.3612 | -0.3393 | -0.0168 | -0.0772 |
| *Callicebus moloch* | -0.7022 | -0.0334 | 0.2037 | -0.2890 | 0.0094 | -0.0463 |
| *Callicebus torquatus* | 0.1546 | -0.1438 | 0.4376 | -0.2647 | -0.0838 | -0.0039 |
| *Chiropotes albinasus* | 0.0171 | 0.1555 | 0.2440 | -0.3292 | -0.3123 | -0.3321 |
| *Chiropotes satanas* | -0.5541 | 0.0644 | 0.2946 | -0.3862 | -0.3129 | -0.3602 |
| *Pithecia monachus* | 0.6488 | -0.0682 | 0.2321 | -0.2875 | -0.2898 | -0.3326 |
| *Pithecia pithecia* | 0.2351 | -0.0756 | 0.4647 | -0.4210 | -0.3353 | -0.3200 |
| *Cheirogaleus major* | 0.8172 | 0.1805 | -0.4266 | 0.4305 | 0.0511 | 0.1429 |
| *Cheirogaleus medius* | 0.2853 | 0.3894 | -0.4440 | 0.4301 | 0.1640 | 0.0380 |
| *Microcebus griseorufus* | -1.1923 | -0.1323 | 0.2422 | 0.3223 | 0.1425 | 0.0188 |
| *Mirza coquereli* | 0.1349 | -0.2882 | -0.2511 | 0.2929 | -0.0624 | 0.1760 |
| *Phaner furcifer* | -0.0319 | -0.1976 | -0.3995 | 0.1901 | 0.0324 | 0.1075 |
| *Avahi laniger* | 0.3450 | 0.5657 | -0.0284 | -0.0323 | 0.3693 | 0.3755 |
| *Indri indri* | 2.1132 | -0.2335 | -0.4380 | -0.1211 | 0.0377 | 0.2971 |
| *Propithecus diadema* | 1.0284 | 0.1657 | -0.2566 | -0.1298 | 0.3513 | 0.2567 |
| *Propithecus verreauxi* | 1.5917 | 0.1365 | -0.1250 | -0.1472 | 0.3655 | 0.2918 |

| | | | | | | |
|---|---|---|---|---|---|---|
| *Eulemur fulvus* | 0.9071 | -1.2599 | -0.4421 | 0.0555 | 0.2978 | 0.0575 |
| *Eulemur rufus* | 0.9686 | -1.2805 | -0.4092 | -0.1211 | 0.2719 | 0.1558 |
| *Hapalemur griseus* | 0.8416 | 0.0965 | 0.0480 | 0.0395 | 0.3551 | -0.0168 |
| *Hapalemur simus* | 1.8248 | 0.6434 | -0.1490 | -0.2139 | 0.3221 | 0.1397 |
| *Lemur catta* | 0.7525 | -1.0905 | -0.5348 | -0.0100 | 0.3930 | 0.1369 |
| *Varecia variegata* | 1.1055 | -1.0618 | -0.9348 | 0.2405 | 0.3579 | 0.0999 |
| | | | | | | |
| *Lepilemur mustelinus* | -0.4760 | 0.1239 | -0.3143 | 0.0439 | 0.4176 | 0.0255 |
| | | | | | | |
| *Arctocebus calabarensis* | -0.0150 | -0.3148 | -0.1187 | 0.2148 | 0.0021 | -0.0715 |
| *Loris tardigradus* | -1.1559 | 0.0795 | 0.7473 | 0.2667 | -0.3392 | -0.1159 |
| *Nycticebus coucang* | 0.2525 | 0.3176 | 0.4250 | 0.3648 | -0.0683 | -0.0768 |
| *Perodicticus potto* | 1.4335 | 0.3277 | -0.0022 | 0.1334 | 0.3045 | 0.0248 |
| | | | | | | |
| *Euoticus elegantulus* | -2.1895 | 0.5023 | 0.0685 | 0.3446 | 0.1092 | 0.0790 |
| *Galago alleni* | -1.6031 | 0.1844 | -0.1249 | 0.4601 | 0.1751 | 0.1236 |
| *Galago demidoff* | -2.1276 | -0.2229 | -0.0897 | 0.2588 | 0.1995 | 0.1033 |
| *Galago gallarum* | -1.7670 | 0.5840 | -0.0097 | 0.3191 | 0.1893 | 0.1316 |
| *Galago moholi* | -2.1819 | 0.3953 | 0.0922 | 0.3543 | 0.1740 | 0.2027 |
| *Otolemur crassicaudatus* | 1.2792 | 0.1074 | -0.1434 | 0.3654 | 0.0397 | -0.0317 |

Table G4: All taxa pPC scores, cranium (male platyrrhines)

| | PC1 | PC2 | PC3 | PC4 | PC5 | PC6 |
|---|---|---|---|---|---|---|
| *Alouatta palliata* | 2.4530 | 0.2518 | 0.2750 | 0.1208 | 0.0161 | 0.1337 |
| *Alouatta seniculus* | 3.1530 | 0.0713 | 0.4494 | 0.3297 | -0.1535 | 0.0383 |
| *Ateles belzebuth* | 0.3623 | -0.2424 | 0.2830 | 0.3863 | 0.2547 | 0.1814 |
| *Ateles geoffroyi* | 0.0879 | -0.0026 | 0.3978 | 0.3573 | 0.2833 | 0.1445 |
| *Brachyteles arachnoides* | 1.3682 | 0.0603 | 0.3710 | 0.2126 | 0.2809 | 0.1851 |
| *Lagothrix lagotricha* | 0.5605 | 0.0553 | 0.2804 | 0.3553 | 0.1278 | 0.2003 |
| *Aotus azarae boliviensis* | -0.9767 | 0.3459 | -0.0743 | 0.3956 | -0.0546 | 0.0359 |
| *Aotus nigriceps* | -1.5991 | 0.3988 | -0.1668 | 0.3650 | -0.1771 | 0.0688 |
| *Cebus apella* | 0.9584 | 0.5680 | 0.1810 | 0.1844 | 0.2062 | 0.3916 |
| *Cebus capucinus* | 0.4531 | 0.3848 | 0.0743 | 0.3202 | 0.0835 | 0.4088 |
| *Saimiri boliviensis* | -1.0575 | 0.0445 | 0.0720 | 0.5743 | 0.1756 | 0.4587 |
| *Saimiri sciureus* | -1.3223 | -0.0437 | -0.0273 | 0.6079 | 0.1426 | 0.3299 |
| *Callimico goeldii* | -0.7591 | 0.3572 | -0.4175 | 0.3123 | 0.3214 | 0.0843 |
| *Mico argentata* | -0.4654 | 0.3327 | -0.5543 | 0.2519 | 0.3098 | 0.1013 |
| *Callithrix penicillata* | -0.6475 | 0.1112 | -0.1238 | 0.3315 | 0.4895 | 0.1039 |
| *Cebuella pygmaea* | -1.5050 | 0.1654 | -0.3530 | 0.1745 | 0.4252 | 0.1044 |
| *Leontopithecus rosalia* | 0.1339 | 0.1365 | -0.5917 | 0.5255 | 0.2366 | 0.0995 |
| *Saguinus fuscicollis* | -0.4549 | 0.4076 | -0.7459 | 0.3590 | 0.2984 | 0.2220 |
| *Saguinus geoffroyi* | -0.4448 | 0.1940 | -0.7883 | 0.1637 | 0.3272 | 0.3000 |
| *Saguinus midas* | -0.5704 | 0.1982 | -0.7687 | 0.4795 | 0.3465 | 0.2054 |
| *Saguinus mystax* | -0.0953 | 0.3148 | -0.6249 | 0.5488 | 0.2966 | 0.2841 |
| *Saguinus oedipus* | -0.5765 | 0.0493 | -0.6541 | 0.2462 | 0.4061 | 0.2718 |
| *Cacajao calvus* | 0.6547 | 0.2590 | 0.0997 | 0.1665 | 0.0059 | 0.4404 |
| *Cacajao melanocephalus* | 0.1549 | 0.2566 | 0.1953 | 0.2457 | 0.1084 | 0.5018 |
| *Callicebus donacophilus* | -0.2882 | 0.2340 | 0.3095 | 0.1802 | 0.3446 | 0.0306 |
| *Callicebus moloch* | -0.5245 | 0.1794 | 0.0928 | 0.2512 | 0.3414 | 0.0434 |
| *Callicebus torquatus* | 0.2485 | 0.1998 | 0.1642 | 0.3222 | 0.2855 | 0.0594 |
| *Chiropotes albinasus* | 0.4771 | 0.2986 | 0.2315 | 0.2772 | 0.0057 | 0.4225 |
| *Chiropotes satanas* | 0.0860 | 0.3287 | 0.1471 | 0.2880 | 0.0104 | 0.4968 |
| *Pithecia monachus* | 0.7112 | 0.1171 | 0.2217 | 0.2766 | 0.0952 | 0.4744 |
| *Pithecia pithecia* | 0.7787 | 0.2445 | 0.3300 | 0.2785 | 0.1851 | 0.4435 |
| *Cheirogaleus major* | 0.4814 | -0.1748 | -0.3499 | -0.3105 | -0.3896 | -0.2237 |
| *Cheirogaleus medius* | 0.0760 | -0.0341 | -0.3649 | -0.3934 | -0.3546 | -0.1062 |
| *Microcebus griseorufus* | -1.0183 | 0.0289 | 0.4165 | -0.2370 | -0.1639 | -0.1092 |
| *Mirza coquereli* | -0.0295 | -0.3952 | -0.1065 | -0.1376 | -0.3052 | -0.1819 |
| *Phaner furcifer* | -0.1529 | -0.4229 | -0.2622 | -0.1301 | -0.2050 | -0.0307 |
| *Avahi laniger* | 0.0840 | 0.3559 | -0.3187 | -0.0926 | 0.2369 | -0.3136 |
| *Indri indri* | 1.4980 | -0.4775 | -0.5230 | 0.1259 | 0.1004 | -0.1659 |
| *Propithecus diadema* | 0.6608 | -0.0516 | -0.4569 | -0.0949 | 0.3035 | -0.1371 |
| *Propithecus verreauxi* | 1.1023 | 0.0049 | -0.3570 | -0.0629 | 0.3625 | -0.2239 |

| | PC1 | PC2 | PC3 | PC4 | PC5 | PC6 |
|---|---|---|---|---|---|---|
| *Eulemur fulvus* | 0.5778 | -1.1830 | -0.0190 | -0.1727 | 0.1787 | -0.0550 |
| *Eulemur rufus* | 0.6162 | -1.1731 | -0.0913 | -0.0220 | 0.3260 | -0.0834 |
| *Hapalemur griseus* | 0.5812 | 0.0734 | 0.0480 | -0.1599 | 0.2041 | -0.0513 |
| *Hapalemur simus* | 1.2814 | 0.3430 | -0.4656 | 0.0065 | 0.3365 | -0.0858 |
| *Lemur catta* | 0.4474 | -1.1042 | -0.2279 | -0.2161 | 0.2763 | -0.0621 |
| *Varecia variegata* | 0.7039 | -1.3578 | -0.4826 | -0.3658 | -0.0186 | -0.0597 |
| *Lepilemur mustelinus* | -0.5236 | -0.1141 | -0.2519 | -0.2541 | 0.1765 | -0.0197 |
| *Arctocebus calabarensis* | -0.1105 | -0.3045 | 0.1131 | -0.1337 | -0.1575 | -0.0570 |
| *Loris tardigradus* | -0.9346 | 0.4905 | 0.8287 | 0.0869 | -0.3658 | -0.0804 |
| *Nycticebus coucang* | 0.1626 | 0.4495 | 0.4417 | -0.1619 | -0.3230 | -0.1182 |
| *Perodicticus potto* | 1.0543 | 0.2072 | -0.1053 | -0.2557 | 0.0660 | -0.0845 |
| *Euoticus elegantulus* | -1.8713 | 0.3530 | 0.1228 | -0.2382 | -0.3089 | -0.1002 |
| *Galago alleni* | -1.4261 | 0.0198 | 0.0464 | -0.3606 | -0.3194 | -0.2385 |
| *Galago demidoff* | -1.8255 | -0.2128 | 0.1265 | -0.2666 | -0.0954 | -0.1511 |
| *Galago gallarum* | -1.5553 | 0.3807 | -0.0261 | -0.3034 | -0.2206 | -0.1855 |
| *Galago moholi* | -1.8709 | 0.3110 | 0.0980 | -0.3024 | -0.2324 | -0.2376 |
| *Otolemur crassicaudatus* | 0.9106 | -0.0661 | -0.0257 | -0.2311 | -0.3158 | -0.0987 |

**H. All taxa: Mandible PCA**

Results of the pPCA on the mandible of all species are summarized in Tables H1 and H2, with species scores provided in Tables H3 and H4. Like the cranial pPCA with all species, the mandible pPCA was performed separately using male and female platyrrhine species averages. In the analysis using female platyrrhines six principal components summarized 85% of the variance in the sample, while in the second pPCA using platyrrhine males seven PCs were necessary to pass this threshold (Table H2). As in the previous analysis of cranial measurements, a similar set of variables loaded on to the first principal component, including relative length of the mandible, height and breadth of the mandibular ramus, breadth of the incisor row (anterior mandibular width), distance of the coronoid process from the jaw joint (temporalis lever arm) and length of the postcanine tooth row. However, the sign of loadings in the male analysis was reversed and the axis is therefore inverted in the second PCA (Figures H1 and H2). PC2 shares some of the same variables in both PCAs, specifically the height above the tooth row of the coronoid process and mandibular condyle,and the thickness at the manidbular symphysis. Subsequent PCs show variation in the loading variables between the two analyses.

Principal components 1 and 2 in both analyses provide distinct separation of platyrrhine and strepsirrhines. Overlap between the two groups is primarily due to the position of some indriids (*Indri* and *Propithecus*) and lemurids (*Hapalemur* sp.) falling within the scatter of platyrrhine points, and the position of *Cebuella* with a PC1 score well within the range of the strepsirrhine species. The strepsirrhine region of PC1 is associated with greater length of the mandible, greater ramus breadth, longer postcanine tooth rows, and a greater temporalis lever arm. Indriids and the bamboo lemurs have scores in the platyrrhine range, indicating mandibular proportions that appear more anthropoid like. The lowest scores on PC1 are those of the Pitheciidae (including *Callicebus*), atelidae and *Aotus.* In addition to the distinction on PC1, the strepsirrhines also in general have lower scores on PC2, particularly in the remaining lemurid primates. In both analyses, PC1 and PC2 together separate four species that have either a high proportion of gums in the diet, and/ or are known to gouge for gums (*Euoticus*, *Phaner*, *Nycticebus* and *Cebuella*). This suggests the possibility that this region of shape space is associated with some functional relationship to accessing exudates. Vinyard et al. (2003) found that a lower height of the mandibular condyle is associated with gummivory/ gouging adaptations through increasing capacity for gape, and the association of PC2 and condylar height provides some support for this. However, the need for both PC1 and PC2 to create this space indicates that some of the morphological variables loading on PC1 may also be relevant to distinguishing gummivores.

As mentioned above, PCs beyond PC2 in these analyses are not very obviously similar when compared between the analysis using male platyrrhines and that using females. For example PC3 in the male analysis provides almost total separation of strepsirrhines and platyrrhines, with only indriids overlapping with platyrrhine shape space, a separation that is not seen in PC3 on the female analysis. This does not necessarily indicate that male and females differ markedly in the relative differences between species

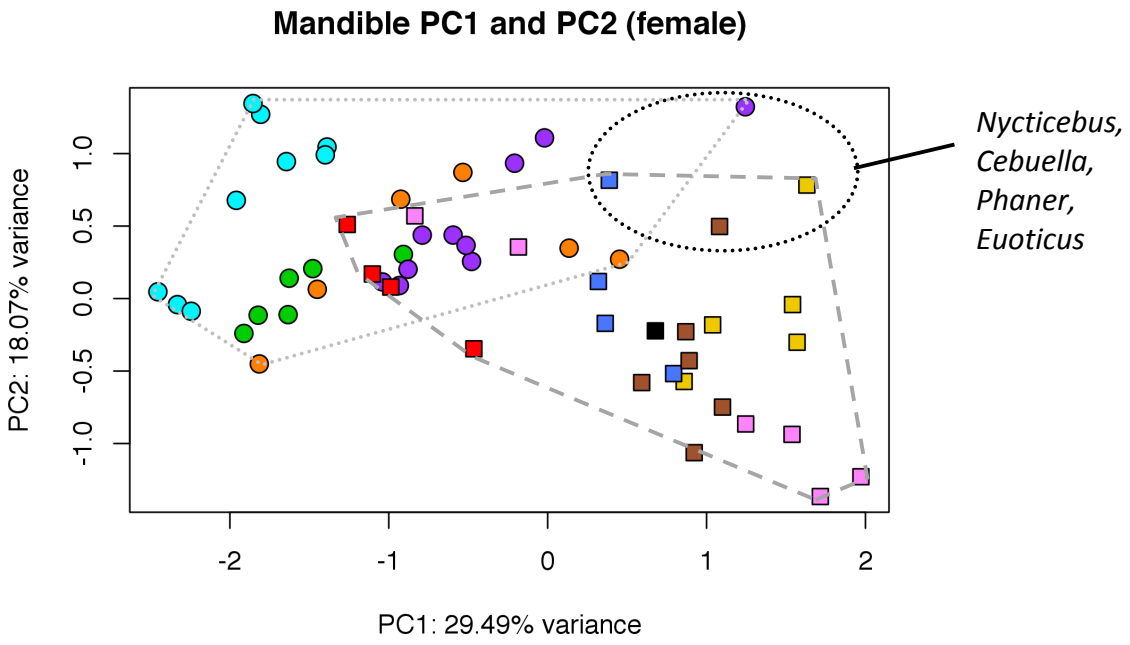
Table H1: Results of mandible pPCA of all taxa together (female platyrrhines).

| PC | % Variance (Eigenvalue) | Cumulative Variance | Variables (factor loadings) |
|---|---|---|---|
| PC1 | 29.49 (4.424) | 29.49 | Mandible length (0.87), Ramus height (-0.82), Temporalis lever arm (0.82), Ramus breadth (0.67), Tooth row length (0.64), Anterior dental width (0.54), Condyle length (0.53) |
| PC2 | 18.07 (2.711) | 47.57 | Coronoid height (-0.82), Condyle height (-0.72), Tooth row length (-0.55), Symphyseal thickness (0.51) |
| PC3 | 12.53 (1.879) | 60.10 | Condyle width (-0.67), Anterior dental width (0.58), Symphyseal thickness (-0.52), Corpus height (0.50) |
| PC4 | 11.61 (1.742) | 71.71 | Corpus breadth (0.77), Tooth row width (0.63), Corpus height (-0.42) |
| PC5 | 7.072 (1.061) | 78.78 | Symphyseal height (-0.72), Condyle height (-0.34), Ramus height (-0.33) |
| PC6 | 6.566 (0.985) | 85.34 | Condyle length (-0.61), Condyle width (0.41), Anterior dental width (0.30) |

Table H2: Results of mandible pPCA of all taxa together (male platyrrhines).

| PC | % Variance (Eigenvalue) | Cumulative Variance | Variables (factor loadings) |
|---|---|---|---|
| PC1 | 26.78 (4.017) | 26.78 | Mandible length (-0.91), Ramus height (0.78), Temporalis lever arm (-0.76), Tooth row length (-0.70), Ramus breadth (-0.60), Anterior dental width (-0.53) |
| PC2 | 19.24 (2.885) | 46.01 | Coronoid height (-0.79), Condyle height (-0.78), Symphyseal thickness (0.65), Corpus breadth (0.60) |
| PC3 | 11.33 (1.700) | 57.35 | Condyle width (0.63), Corpus height (-0.60), Anterior dental width (-0.52) |
| PC4 | 10.54 (1.581) | 67.88 | Ramus breadth (-0.70), Tooth row width (0.66), Anterior dental width (0.39) |
| PC5 | 8.95 (1.343) | 76.84 | Condyle length (0.62), Condyle width (-0.47), Corpus breadth (0.45) |
| PC6 | 6.75 (1.013) | 83.59 | Symphyseal height (-0.68), Ramus height (-0.33), Temporalis lever arm (-0.31) |
| PC7 | 4.11 (0.617) | 87.70 | Condyle width (0.32), Temporalis lever arm (0.31), Corpus breadth (-0.28) |

Figure H1: Phylogenetic PCA: Mandible of all taxa, with female platyrrhines. Circles = platyrrhines, squares = strepsirrhines. Atelids = green, Callitrichids = purple, Cebids = orange, Pitheciids = turquoise, Cheirogaleids = gold, Indriids = red, Galagids = brown, Lemurids = pink, Lorisids in blue, *Lepilemur* = black.



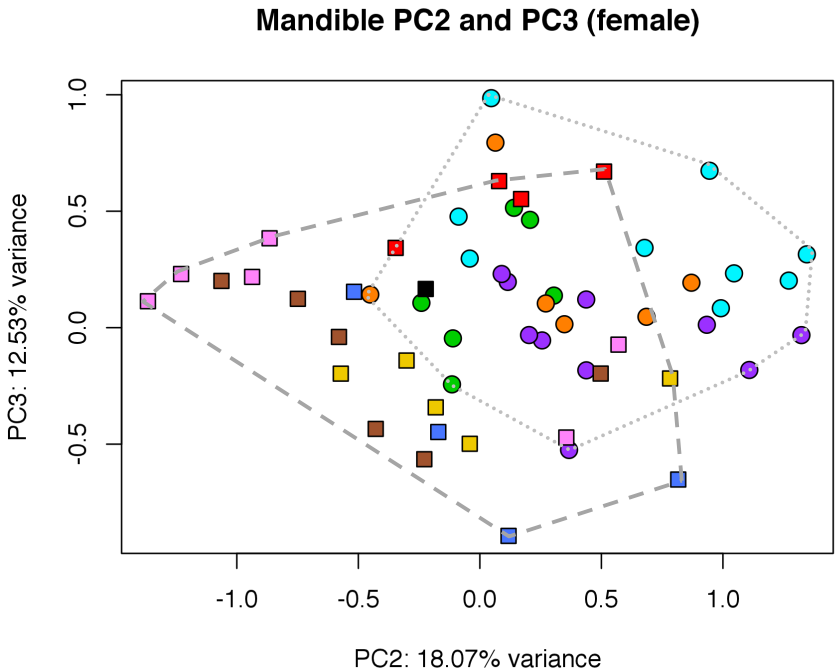
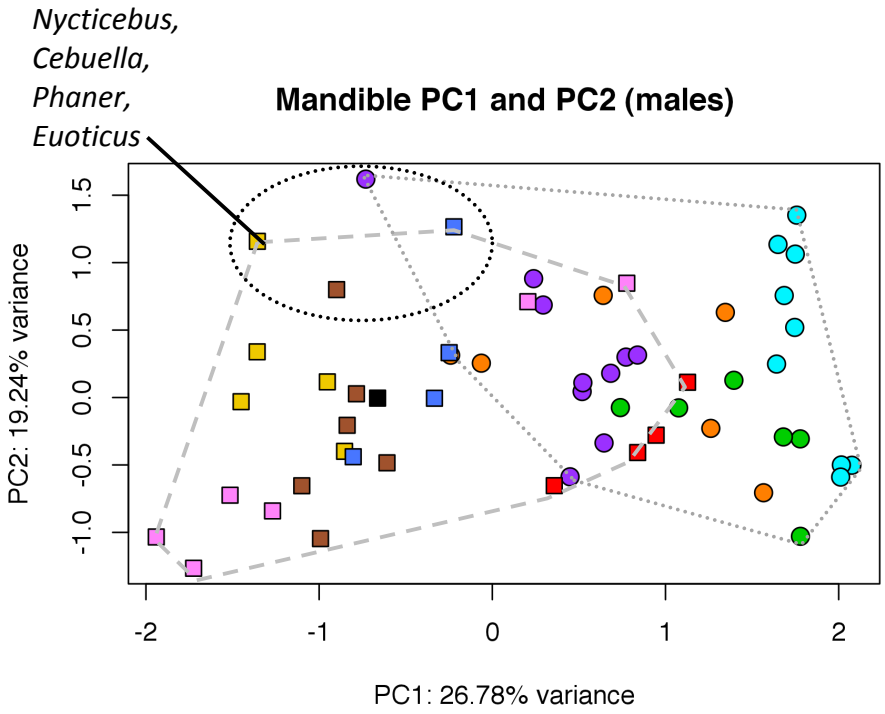



Figure H2: Phylogenetic PCA: Mandibles of all taxa, with male platyrrhines. Circles = platyrrhines, squares = strepsirrhines. Atelids = green, Callitrichids = purple, Cebids = orange, Pitheciids = turquoise, Cheirogaleids = gold, Indriids = red, Galagids = brown, Lemurids = pink, Lorisids in blue, *Lepilemur* = black.



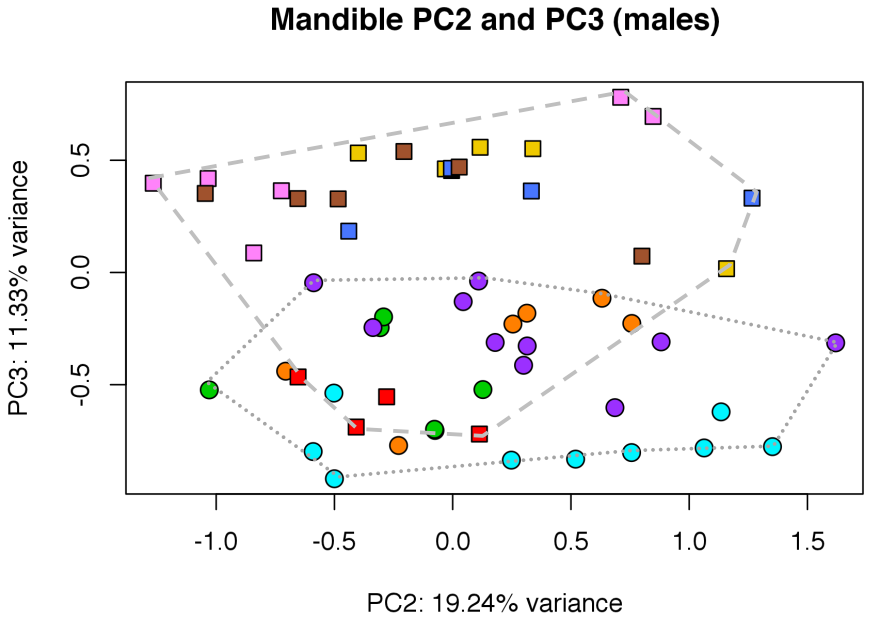



Table H3: All taxa pPC scores, mandible (female platyrrhines)

| | PC1 | PC2 | PC3 | PC4 | PC5 | PC6 |
|---|---|---|---|---|---|---|
| *Alouatta palliata* | -1.6336 | -0.1110 | -0.0459 | -0.3167 | -0.7185 | 0.1826 |
| *Alouatta seniculus* | -1.9117 | -0.2406 | 0.1065 | -0.5763 | -0.3682 | 0.0596 |
| *Ateles belzebuth* | -0.9081 | 0.3045 | 0.1378 | -0.8489 | 0.0858 | 0.3278 |
| *Ateles geoffroyi* | -1.6270 | 0.1404 | 0.5146 | -0.5959 | -0.0103 | 0.2297 |
| *Brachyteles arachnoides* | -1.8221 | -0.1148 | -0.2433 | -0.3625 | -0.1559 | 0.1170 |
| *Lagothrix lagotricha* | -1.4782 | 0.2065 | 0.4629 | -0.4855 | -0.2243 | 0.1435 |
| | | | | | | |
| *Callimico goeldii* | -1.0396 | 0.1147 | 0.1965 | 0.3506 | -0.1601 | -0.0159 |
| *Mico argentata* | -0.2083 | 0.9337 | 0.0125 | -0.6636 | -0.3145 | 0.0547 |
| *Callithrix penicillata* | -0.0199 | 1.1085 | -0.1816 | -0.3636 | -0.4051 | -0.0304 |
| *Cebuella pygmaea* | 1.2441 | 1.3230 | -0.0319 | -0.3390 | -0.4763 | -0.0590 |
| *Leontopithecus rosalia* | -0.9335 | 0.0897 | 0.2305 | -0.1955 | -0.3385 | 0.2565 |
| *Saguinus fuscicollis* | -0.5951 | 0.4380 | -0.1830 | -0.4218 | -0.1477 | 0.1750 |
| *Saguinus geoffroyi* | -0.4789 | 0.2560 | -0.0547 | -0.2844 | -0.0803 | 0.0286 |
| *Saguinus midas* | -0.8789 | 0.2024 | -0.0316 | -0.5375 | -0.0382 | 0.2036 |
| *Saguinus mystax* | -0.7894 | 0.4376 | 0.1210 | -0.3532 | 0.0003 | 0.4094 |
| *Saguinus oedipus* | -0.5138 | 0.3669 | -0.5250 | -0.2703 | -0.1263 | 0.1399 |
| | | | | | | |
| *Aotus azarae boliviensis* | -1.8150 | -0.4509 | 0.1423 | -0.3793 | 0.0863 | 0.1750 |
| *Aotus nigriceps* | -1.4500 | 0.0640 | 0.7944 | -0.1710 | 0.1620 | 0.1469 |
| *Cebus apella* | -0.9245 | 0.6854 | 0.0467 | 0.0087 | -0.0551 | 0.0272 |
| *Cebus capucinus* | -0.5337 | 0.8703 | 0.1930 | -0.0130 | -0.0519 | 0.1715 |
| *Saimiri boliviensis* | 0.1350 | 0.3478 | 0.0148 | -0.0337 | -0.1294 | 0.3680 |
| *Saimiri sciureus* | 0.4526 | 0.2713 | 0.1040 | -0.1258 | -0.1471 | 0.4128 |
| | | | | | | |
| *Cacajao calvus* | -1.3887 | 1.0457 | 0.2332 | -0.5587 | 0.0176 | 0.4700 |
| *Cacajao melanocephalus* | -1.3997 | 0.9915 | 0.0834 | -0.5384 | 0.0641 | 0.3173 |
| *Callicebus donacophilus* | -2.3304 | -0.0417 | 0.2967 | -0.2442 | 0.1351 | -0.0441 |
| *Callicebus moloch* | -2.4530 | 0.0468 | 0.9853 | -0.5847 | 0.1772 | 0.0855 |
| *Callicebus torquatus* | -2.2433 | -0.0876 | 0.4768 | -0.5168 | 0.0833 | 0.1500 |
| *Chiropotes albinasus* | -1.8545 | 1.3453 | 0.3148 | -0.6428 | 0.0461 | 0.2974 |
| *Chiropotes satanas* | -1.8063 | 1.2709 | 0.2021 | -0.6585 | 0.0134 | 0.2066 |
| *Pithecia monachus* | -1.9596 | 0.6775 | 0.3425 | -0.6840 | 0.0699 | 0.1532 |
| *Pithecia pithecia* | -1.6444 | 0.9449 | 0.6737 | -0.4444 | 0.0971 | 0.3097 |
| | | | | | | |
| *Cheirogaleus major* | 1.0382 | -0.1816 | -0.3420 | 0.3640 | 0.1158 | -0.0061 |
| *Cheirogaleus medius* | 1.5411 | -0.0415 | -0.4984 | 0.3045 | 0.1093 | -0.0489 |
| *Microcebus griseorufus* | 0.8588 | -0.5722 | -0.1973 | 0.4126 | 0.1146 | -0.0716 |
| *Mirza coquereli* | 1.5697 | -0.3016 | -0.1410 | 0.3716 | 0.0695 | 0.0413 |
| *Phaner furcifer* | 1.6313 | 0.7827 | -0.2180 | -0.0526 | -0.1016 | -0.2021 |
| | | | | | | |
| *Avahi laniger* | -1.2616 | 0.5109 | 0.6702 | -0.3627 | -0.5398 | 0.0129 |
| *Indri indri* | -0.4645 | -0.3466 | 0.3425 | -0.2696 | -0.4233 | -0.5148 |
| *Propithecus diadema* | -0.9873 | 0.0792 | 0.6292 | -0.3883 | -0.6909 | 0.1105 |
| *Propithecus verreauxi* | -1.1034 | 0.1695 | 0.5522 | -0.3006 | -0.7070 | 0.1148 |

| | PC1 | PC2 | PC3 | PC4 | PC5 | PC6 |
|---|---|---|---|---|---|---|
| *Eulemur fulvus* | 1.5377 | -0.9371 | 0.2179 | 0.3970 | 0.1584 | 0.0697 |
| *Eulemur rufus* | 1.7160 | -1.3656 | 0.1135 | 0.2832 | 0.0744 | 0.2082 |
| *Hapalemur griseus* | -0.1840 | 0.3557 | -0.4716 | 0.7088 | 0.1169 | -0.1051 |
| *Hapalemur simus* | -0.8360 | 0.5703 | -0.0728 | 0.8926 | 0.0392 | 0.4473 |
| *Lemur catta* | 1.2462 | -0.8652 | 0.3837 | 0.1599 | -0.0138 | 0.0858 |
| *Varecia variegata* | 1.9712 | -1.2292 | 0.2303 | 0.4163 | 0.1166 | 0.0370 |
| *Lepilemur mustelinus* | 0.6778 | -0.2227 | 0.1661 | 0.6255 | -0.0489 | 0.1441 |
| *Arctocebus calabarensis* | 0.7928 | -0.5176 | 0.1540 | 0.2147 | 0.1627 | -0.2591 |
| *Loris tardigradus* | 0.3622 | -0.1711 | -0.4479 | 0.2285 | 0.0415 | -0.2360 |
| *Nycticebus coucang* | 0.3877 | 0.8162 | -0.6519 | 0.0826 | 0.3423 | -0.2416 |
| *Perodicticus potto* | 0.3192 | 0.1180 | -0.8939 | -0.1544 | 0.3206 | 0.0420 |
| *Euoticus elegantulus* | 1.0817 | 0.4970 | -0.1970 | 0.0446 | 0.0940 | -0.2238 |
| *Galago alleni* | 0.9221 | -1.0633 | 0.2007 | 0.3721 | 0.1124 | -0.0395 |
| *Galago demidoff* | 1.1002 | -0.7488 | 0.1239 | 0.3629 | 0.0265 | -0.1638 |
| *Galago gallarum* | 0.8903 | -0.4285 | -0.4345 | 0.3174 | 0.1490 | -0.1775 |
| *Galago moholi* | 0.5917 | -0.5797 | -0.0398 | 0.3132 | 0.1159 | -0.1760 |
| *Otolemur crassicaudatus* | 0.8691 | -0.2286 | -0.5648 | 0.1855 | 0.3122 | -0.0994 |

Table H4: All taxa pPC scores, mandible (male platyrrhines)

| | PC1 | PC2 | PC3 | PC4 | PC5 | PC6 | PC7 |
|---|---|---|---|---|---|---|---|
| *Alouatta palliata* | 1.7780 | -0.3067 | -0.2458 | -0.2954 | -0.2073 | -0.5214 | 0.2653 |
| *Alouatta seniculus* | 1.7791 | -1.0292 | -0.5231 | -0.7494 | -0.1328 | -0.3043 | 0.3217 |
| *Ateles belzebuth* | 0.7393 | -0.0748 | -0.7038 | -0.4207 | -0.6969 | 0.0073 | 0.3156 |
| *Ateles geoffroyi* | 1.0758 | -0.0768 | -0.6987 | -0.2156 | -0.3052 | 0.1344 | 0.3639 |
| *Brachyteles arachnoides* | 1.6805 | -0.2923 | -0.1979 | -0.4292 | -0.2423 | -0.0856 | 0.2187 |
| *Lagothrix lagotricha* | 1.3947 | 0.1278 | -0.5218 | -0.3111 | -0.3250 | -0.2140 | 0.3045 |
| *Aotus azarae boliviensis* | 1.5662 | -0.7061 | -0.4397 | -0.0244 | -0.1997 | 0.1648 | 0.1129 |
| *Aotus nigriceps* | 1.2616 | -0.2288 | -0.7708 | 0.3510 | -0.1778 | 0.2075 | 0.1392 |
| *Cebus apella* | 1.3455 | 0.6312 | -0.1147 | -0.3329 | -0.1402 | -0.0109 | -0.0901 |
| *Cebus capucinus* | 0.6402 | 0.7573 | -0.2271 | -0.3647 | -0.3296 | -0.0413 | -0.0280 |
| *Saimiri boliviensis* | -0.0634 | 0.2546 | -0.2297 | 0.0323 | -0.5319 | 0.0571 | 0.1676 |
| *Saimiri sciureus* | -0.2408 | 0.3138 | -0.1813 | 0.0989 | -0.5047 | -0.1116 | 0.1301 |
| *Callimico goeldii* | 0.4489 | -0.5879 | -0.0457 | 0.1867 | -0.2640 | -0.2063 | 0.1401 |
| *Mico argentata* | 0.2936 | 0.6860 | -0.6023 | -0.4633 | -0.2731 | -0.2210 | 0.0933 |
| *Callithrix penicillata* | 0.2386 | 0.8812 | -0.3092 | -0.2703 | -0.2496 | -0.3145 | 0.1584 |
| *Cebuella pygmaea* | -0.7303 | 1.6193 | -0.3135 | -0.4032 | 0.1040 | -0.3113 | 0.2298 |
| *Leontopithecus rosalia* | 0.6451 | -0.3370 | -0.2453 | 0.0692 | -0.3976 | -0.3047 | 0.1779 |
| *Saguinus fuscicollis* | 0.6835 | 0.1796 | -0.3118 | -0.2194 | -0.2666 | -0.1313 | 0.0447 |
| *Saguinus geoffroyi* | 0.5186 | 0.0443 | -0.1299 | -0.2533 | -0.1286 | -0.0472 | 0.0336 |
| *Saguinus midas* | 0.7720 | 0.2998 | -0.4134 | -0.2898 | -0.2627 | -0.0249 | -0.0471 |
| *Saguinus mystax* | 0.8385 | 0.3150 | -0.3273 | -0.0749 | -0.3275 | -0.0377 | 0.0212 |
| *Saguinus oedipus* | 0.5228 | 0.1095 | -0.0380 | -0.2976 | -0.4252 | -0.0939 | 0.0443 |
| *Cacajao calvus* | 1.6495 | 1.1349 | -0.6210 | -0.1441 | -0.6950 | 0.1697 | 0.1268 |
| *Cacajao melanocephalus* | 1.6853 | 0.7563 | -0.8025 | -0.3732 | -0.6039 | 0.1882 | 0.2153 |
| *Callicebus donacophilus* | 2.0761 | -0.5023 | -0.5374 | 0.1259 | 0.0145 | 0.1032 | 0.3515 |
| *Callicebus moloch* | 2.0153 | -0.5000 | -0.9191 | 0.0849 | -0.0414 | 0.2085 | 0.1644 |
| *Callicebus torquatus* | 2.0113 | -0.5899 | -0.7980 | 0.0164 | -0.3112 | 0.1458 | 0.3893 |
| *Chiropotes albinasus* | 1.7580 | 1.3521 | -0.7760 | -0.2229 | -0.5455 | 0.1923 | 0.1777 |
| *Chiropotes satanas* | 1.7492 | 1.0632 | -0.7818 | -0.2974 | -0.4134 | 0.0360 | 0.1942 |
| *Pithecia monachus* | 1.7461 | 0.5197 | -0.8316 | -0.2260 | -0.2758 | 0.1227 | 0.1196 |
| *Pithecia pithecia* | 1.6413 | 0.2481 | -0.8361 | -0.0516 | -0.5326 | 0.1453 | 0.2747 |
| *Cheirogaleus major* | -0.9527 | 0.1159 | 0.5579 | 0.1501 | 0.0815 | 0.1005 | -0.0820 |
| *Cheirogaleus medius* | -1.3577 | 0.3388 | 0.5517 | -0.0372 | 0.0705 | 0.1060 | -0.1912 |
| *Microcebus griseorufus* | -0.8531 | -0.3990 | 0.5321 | 0.1832 | 0.1765 | 0.0620 | -0.1279 |
| *Mirza coquereli* | -1.4506 | -0.0310 | 0.4616 | 0.1974 | 0.0234 | 0.0454 | -0.1411 |
| *Phaner furcifer* | -1.3567 | 1.1579 | 0.0169 | -0.2970 | 0.1741 | -0.1197 | -0.2022 |
| *Avahi laniger* | 1.1274 | 0.1129 | -0.7199 | 0.0061 | -0.0188 | -0.5206 | -0.1572 |
| *Indri indri* | 0.3577 | -0.6536 | -0.4655 | -0.1332 | 0.6459 | -0.4453 | -0.1099 |
| *Propithecus diadema* | 0.8393 | -0.4081 | -0.6886 | 0.0773 | -0.1387 | -0.6012 | -0.1314 |
| *Propithecus verreauxi* | 0.9458 | -0.2793 | -0.5540 | 0.0436 | -0.1626 | -0.6746 | -0.1191 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| *Eulemur fulvus* | -1.5144 | -0.7243 | 0.3641 | 0.4661 | 0.0450 | 0.1150 | -0.1729 |
| *Eulemur rufus* | -1.7246 | -1.2661 | 0.3977 | 0.3693 | -0.1746 | 0.0537 | -0.1671 |
| *Hapalemur griseus* | 0.2051 | 0.7106 | 0.7808 | 0.3285 | 0.2664 | -0.0074 | -0.0430 |
| *Hapalemur simus* | 0.7765 | 0.8473 | 0.6953 | 0.8316 | -0.2772 | -0.0186 | -0.0888 |
| *Lemur catta* | -1.2691 | -0.8410 | 0.0870 | 0.3629 | -0.0548 | -0.0720 | -0.0413 |
| *Varecia variegata* | -1.9405 | -1.0340 | 0.4187 | 0.4017 | 0.0975 | 0.0552 | -0.2133 |
| *Lepilemur mustelinus* | -0.6623 | -0.0047 | 0.4543 | 0.5894 | -0.0243 | -0.1438 | -0.1714 |
| *Arctocebus calabarensis* | -0.8031 | -0.4393 | 0.1841 | 0.1145 | 0.4079 | 0.1010 | -0.0868 |
| *Loris tardigradus* | -0.3340 | -0.0056 | 0.4639 | -0.0168 | 0.3145 | 0.0377 | 0.0118 |
| *Nycticebus coucang* | -0.2218 | 1.2657 | 0.3313 | -0.1617 | 0.2561 | 0.3131 | 0.0853 |
| *Perodicticus potto* | -0.2492 | 0.3325 | 0.3630 | -0.4276 | -0.1777 | 0.3386 | 0.0979 |
| *Euoticus elegantulus* | -0.8991 | 0.8001 | 0.0729 | -0.1341 | 0.2687 | 0.0648 | -0.2084 |
| *Galago alleni* | -0.9920 | -1.0463 | 0.3522 | 0.3306 | 0.2122 | 0.0709 | -0.1614 |
| *Galago demidoff* | -1.1001 | -0.6543 | 0.3292 | 0.2487 | 0.3375 | -0.0164 | -0.1460 |
| *Galago gallarum* | -0.8382 | -0.2061 | 0.5391 | 0.0544 | 0.2867 | 0.1236 | -0.0305 |
| *Galago moholi* | -0.6082 | -0.4843 | 0.3279 | 0.1744 | 0.3388 | 0.0768 | -0.2274 |
| *Otolemur crassicaudatus* | -0.7845 | 0.0276 | 0.4698 | -0.1547 | 0.1264 | 0.2651 | -0.1779 |

**I. All taxa: Molar PCA**

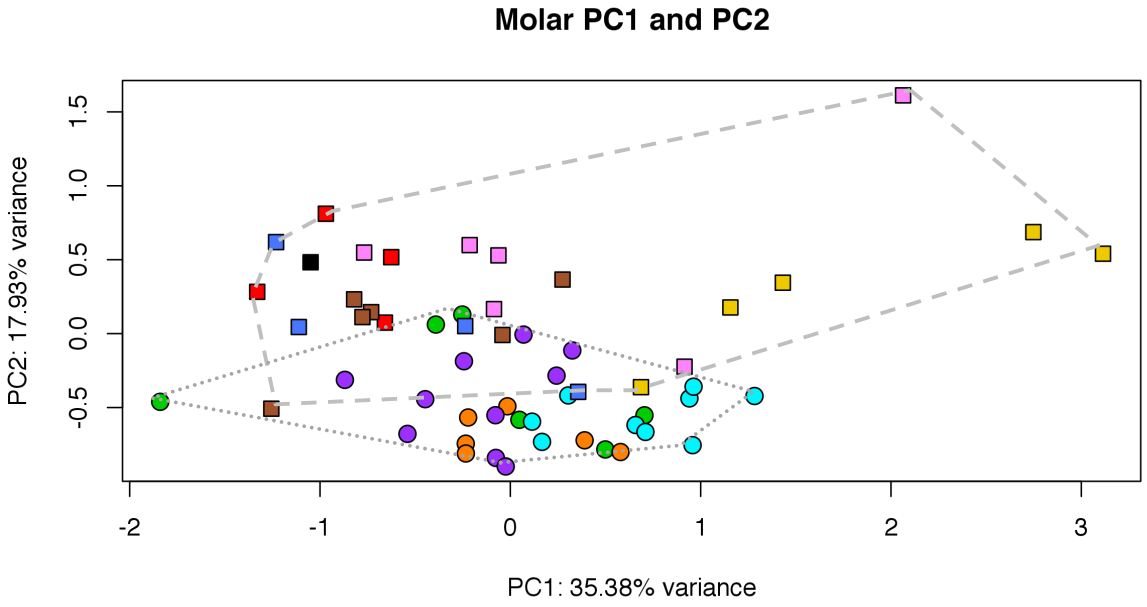
Results of the pPCA on the second molar of all species are summarized in Table I1, with species scores provided in Table I2. The molar pPCA with all species produced six PCs that summarize 85% of the variance in the sample. Only one PCA was performed in this case as dimorphism in dental shape than in would not be expected outside of the canine/ anterior premolar region. PC1 is dominated by variation in the relative buccolingual width of the tooth, and by the relative height of the talonid and trigonid basin, in addition to the relative length of two lingual crests, the postmetacristid and the pre-entoconid crest. The species with the highest scores on PC1 are the two *Cheirogaleus* species and *Varecia*; the highest PC1 scores among the platyrrhines are in the seed-predating pitheciines. The former two genera have some of the lowest relative crown heights among the sample; the use of crown height measurements in calculation of the geometric mean may lead to some exaggeration of the relative size of the width of the tooth. Lower scores on PC1 are associated with more folivorous taxa such as *Brachyteles* and *Alouatta* among the platyrrhines, and the indriids, galagos and more faunivorous lorisids (*Loris* and *Arctocebus*) among the strepsirrhines. These species have teeth that are relatively taller and buccolingually narrower, with a smaller talonid area.

PC2 provides some separation between strepsirrhines and the majority of platyrrhine species; higher scores are associated with greater relative length of the tooth, increased length of the cristid obliqua and paracristid, and a greater area of the trigonid basin. Some callitrichids and the two *Alouatta* species have higher scores on PC2 than other platyrrhines possibly indicating greater relative length of the tooth. Among the strepsirrhines the highest score on PC2 is found in *Varecia*.

Table I1: Results of molar pPCA of all taxa together.

| PC | Variance explained (Eigenvalue) | Cumulative Variance | Variables (factor loadings) |
|---|---|---|---|
| PC1 | 35.38 (4.954) | 35.38 | Talonid width (0.93), Trigonid width (0.90), Square root occlusal area (0.79), Talonid height (-0.78), Trigonid height (-0.74), Square root talonid area (0.72), Postmetacristid length (-0.68), Pre-entoconid length (-0.55) |
| PC2 | 17.93 (2.510) | 53.31 | Molar length (0.69), Cristid obliqua length (0.67), Paracristid length (0.60), Square root trigonid area (0.60), Pre-entoconid length (0.52) |
| PC3 | 10.21 (1.430) | 63.53 | Posthypoconid length (-0.63), Paracristid length (0.42), Trigonid height (-0.40) |
| PC4 | 8.15 (1.141) | 71.68 | Molar length (0.57), Trigonid area (-0.54), Protocristid length (-0.37) |
| PC5 | 7.48 (1.048) | 79.15 | Protocristid length (-0.70), Cristid obliqua length (0.44), Pre-entoconid length (0.40) |
| PC6 | 5.64 (0.790) | 84.80 | Talonid height (-0.45), Posthypoconid length (-0.42). Tigonid height (0.42) |

Figure I1: Phylogenetic PCA: Molar with all taxa. Circles = platyrrhines, squares = strepsirrhines. Atelids = green, Callitrichids = purple, Cebids = orange, Pitheciids = turquoise, Cheirogaleids = gold, Indriids = red, Galagids = brown, Lemurids = pink, Lorisids in blue, *Lepilemur* = black.



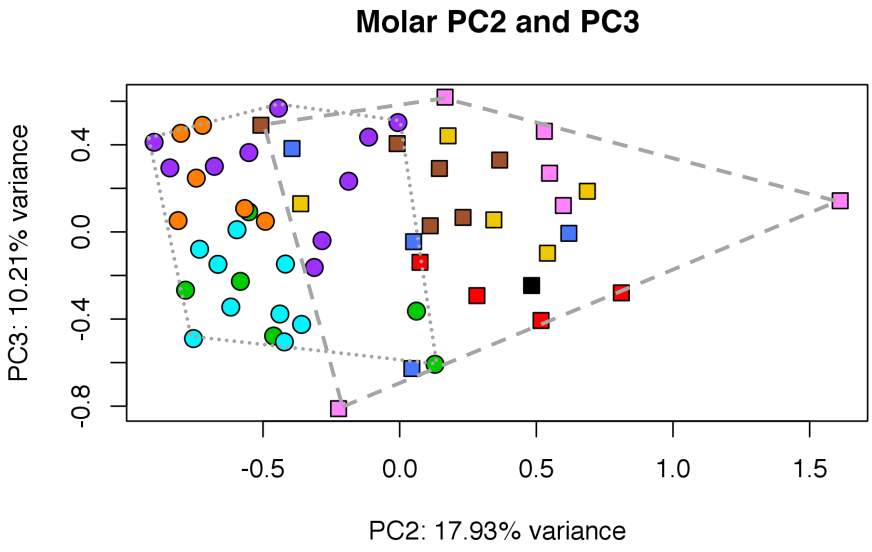



Table I2: All taxa pPC scores, molar

| | PC1 | PC2 | PC3 | PC4 | PC5 | PC6 |
|---|---|---|---|---|---|---|
| *Alouatta palliata* | -0.2524 | 0.1292 | -0.6078 | 0.0007 | 0.0515 | -0.0876 |
| *Alouatta seniculus* | -0.3914 | 0.0614 | -0.3635 | 0.0320 | -0.0255 | -0.2050 |
| *Ateles belzebuth* | 0.7047 | -0.5524 | 0.0927 | -0.0004 | -0.2620 | -0.0443 |
| *Ateles geoffroyi* | 0.4992 | -0.7835 | -0.2673 | -0.2324 | -0.2027 | -0.0259 |
| *Brachyteles arachnoides* | -1.8396 | -0.4612 | -0.4779 | -0.1100 | -0.2665 | -0.0750 |
| *Lagothrix lagotricha* | 0.0476 | -0.5828 | -0.2270 | -0.2787 | -0.2099 | -0.0397 |
| *Aotus azarae boliviensis* | -0.2217 | -0.5672 | 0.1074 | -0.1263 | 0.0795 | 0.0062 |
| *Aotus nigriceps* | -0.0155 | -0.4915 | 0.0490 | -0.2897 | -0.0881 | -0.0419 |
| *Cebus apella* | 0.5790 | -0.8009 | 0.4528 | -0.4161 | -0.1353 | 0.2273 |
| *Cebus capucinus* | 0.3903 | -0.7216 | 0.4895 | -0.4056 | -0.0969 | 0.2848 |
| *Saimiri boliviensis* | -0.2343 | -0.7441 | 0.2470 | -0.3054 | 0.0740 | 0.0642 |
| *Saimiri sciureus* | -0.2336 | -0.8108 | 0.0520 | -0.3213 | 0.1445 | 0.1673 |
| *Callimico goeldii* | -0.8693 | -0.3126 | -0.1631 | -0.2758 | 0.0111 | 0.3975 |
| *Mico argentata* | -0.5405 | -0.6782 | 0.3012 | -0.0213 | 0.2244 | 0.1545 |
| *Callithrix penicillata* | -0.0759 | -0.8407 | 0.2940 | -0.0603 | 0.0462 | 0.0586 |
| *Cebuella pygmaea* | -0.2438 | -0.1866 | 0.2328 | -0.1146 | 0.2902 | 0.1874 |
| *Leontopithecus rosalia* | 0.2427 | -0.2840 | -0.0399 | 0.0748 | 0.3447 | -0.1054 |
| *Saguinus fuscicollis* | 0.3255 | -0.1137 | 0.4354 | -0.1100 | 0.0825 | 0.1060 |
| *Saguinus geoffroyi* | -0.4472 | -0.4434 | 0.5686 | -0.2239 | 0.2890 | 0.2626 |
| *Saguinus midas* | 0.0693 | -0.0063 | 0.5021 | -0.2154 | -0.1129 | 0.4099 |
| *Saguinus mystax* | -0.0783 | -0.5518 | 0.3644 | -0.0439 | 0.0587 | 0.3395 |
| *Saguinus oedipus* | -0.0243 | -0.8986 | 0.4117 | -0.2216 | 0.0328 | 0.1898 |
| *Cacajao calvus* | 0.6578 | -0.6180 | -0.3450 | -0.2263 | 0.0736 | -0.0247 |
| *Cacajao melanocephalus* | 0.7099 | -0.6649 | -0.1487 | -0.1674 | 0.1847 | -0.0011 |
| *Callicebus donacophilus* | 0.3045 | -0.4180 | -0.1475 | -0.1202 | -0.1281 | -0.0302 |
| *Callicebus moloch* | 0.1665 | -0.7322 | -0.0794 | -0.1115 | 0.1096 | -0.0377 |
| *Callicebus torquatus* | 0.1142 | -0.5953 | 0.0103 | -0.1954 | 0.2066 | -0.0395 |
| *Chiropotes albinasus* | 1.2829 | -0.4219 | -0.5049 | -0.1610 | 0.3231 | -0.0920 |
| *Chiropotes satanas* | 0.9576 | -0.7544 | -0.4897 | -0.1129 | 0.2037 | -0.0055 |
| *Pithecia monachus* | 0.9409 | -0.4383 | -0.3770 | -0.1011 | 0.0910 | 0.0238 |
| *Pithecia pithecia* | 0.9626 | -0.3590 | -0.4247 | -0.1080 | 0.0299 | 0.0539 |
| *Cheirogaleus major* | 2.7480 | 0.6866 | 0.1868 | 0.5645 | -0.0423 | -0.2080 |
| *Cheirogaleus medius* | 3.1140 | 0.5407 | -0.0976 | 0.5737 | 0.3331 | -0.0487 |
| *Microcebus griseorufus* | 1.4317 | 0.3445 | 0.0553 | 0.3170 | 0.2697 | -0.2729 |
| *Mirza coquereli* | 1.1562 | 0.1770 | 0.4413 | 0.1993 | 0.2650 | -0.1267 |
| *Phaner furcifer* | 0.6864 | -0.3621 | 0.1295 | 0.3503 | 0.4409 | -0.0118 |
| *Avahi laniger* | -1.3300 | 0.2826 | -0.2925 | -0.0557 | -0.0342 | -0.1476 |
| *Indri indri* | -0.6590 | 0.0744 | -0.1395 | 0.1983 | -0.1024 | -0.2585 |
| *Propithecus diadema* | -0.6258 | 0.5172 | -0.4067 | 0.1534 | -0.2785 | -0.2589 |
| *Propithecus verreauxi* | -0.9692 | 0.8110 | -0.2798 | 0.0370 | -0.1754 | -0.1408 |

| | PC1 | PC2 | PC3 | PC4 | PC5 | PC6 |
|---|---|---|---|---|---|---|
| *Eulemur fulvus* | -0.2137 | 0.5987 | 0.1212 | 0.2918 | -0.1201 | 0.1531 |
| *Eulemur rufus* | -0.0625 | 0.5293 | 0.4622 | 0.3614 | -0.1355 | -0.0099 |
| *Hapalemur griseus* | -0.0858 | 0.1660 | 0.6188 | 0.0072 | 0.3310 | -0.3797 |
| *Hapalemur simus* | 0.9152 | -0.2236 | -0.8115 | 0.2026 | 0.1578 | -0.0602 |
| *Lemur catta* | -0.7681 | 0.5484 | 0.2696 | 0.1676 | -0.1176 | -0.1916 |
| *Varecia variegata* | 2.0636 | 1.6117 | 0.1431 | 0.5444 | -0.6062 | 0.0256 |
| *Lepilemur mustelinus* | -1.0496 | 0.4827 | -0.2461 | 0.6729 | 0.1713 | 0.2655 |
| *Arctocebus calabarensis* | -1.2307 | 0.6190 | -0.0065 | -0.1433 | -0.2357 | -0.1184 |
| *Loris tardigradus* | -1.1114 | 0.0446 | -0.6273 | -0.0667 | -0.1564 | -0.3608 |
| *Nycticebus coucang* | -0.2372 | 0.0509 | -0.0448 | -0.1476 | -0.0830 | -0.0706 |
| *Perodicticus potto* | 0.3567 | -0.3940 | 0.3829 | 0.0675 | -0.0764 | 0.3523 |
| *Euoticus elegantulus* | -0.8207 | 0.2318 | 0.0664 | -0.2320 | 0.2525 | 0.1885 |
| *Galago alleni* | 0.2742 | 0.3658 | 0.3299 | -0.1712 | 0.0621 | 0.1558 |
| *Galago demidoff* | -0.7771 | 0.1118 | 0.0281 | -0.2803 | 0.0736 | 0.1257 |
| *Galago gallarum* | -1.2557 | -0.5077 | 0.4899 | -0.1655 | 0.1074 | 0.1829 |
| *Galago moholi* | -0.7313 | 0.1452 | 0.2913 | -0.4680 | 0.1868 | 0.1779 |
| *Otolemur crassicaudatus* | -0.0414 | -0.0092 | 0.4054 | -0.2972 | -0.0862 | 0.2681 |

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