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Title: Chewing on the trees: constraints and adaptation in the evolution of the primate mandible

Authors: Carlo Meloro¹, Nilton Carlos Cáceres², Francesco Carotenuto³, Jonas Sponchiado⁴, Geruza Leal Melo⁵, Federico Passaro³, Pasquale Raia³

¹ Research Centre in Evolutionary Anthropology and Palaeoecology, School of Natural Sciences and Psychology, Liverpool John Moores University, James Parsons Building, Byrom Street, Liverpool L3 3AF, United Kingdom

² Laboratory of Ecology and Biogeography, Department of Biology, CCNE, Federal University of Santa Maria, Santa Maria, RS, 97110-970, Brazil.

³Dipartimento di Scienze della Terra, Università degli Studi di Napoli

'Federico II', L.go San Marcellino 10, 80138, Napoli, Italy.

⁴Programa de Pós-Graduação em Biodiversidade Animal, Department of Biology, CCNE, Federal

University of Santa Maria, Santa Maria, RS, 97110-970, Brazil.

⁵Programa de Pós-Graduação em Ecologia e Conservação, CCBS, Federal University of Mato Grosso do Sul, Cx.P. 549, Campo Grande, MS, 79.070-900, Brazil.

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E-mails: Carlo Meloro - C.meloro@ljmu.ac.uk (corresponding author), Nilton Carlos Cáceres - niltoncaceres@gmail.com, Francesco Carotenuto - f.carotenuto@ymail.com, Jonas Sponchiado - jsponchiado@yahoo.com.br, Geruza Leal Melo - geruzalm@yahoo.com.br , Federico Passaro - federico.passaro@unina.it, Pasquale Raia - pasquale.raia@libero.it

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ABSTRACT

Chewing on different food types is a demanding biological function. The classic assumption in studying the shape of feeding apparatuses is that animals are what they eat, meaning that adaptation to different food items accounts for most of their interspecific variation. Yet, a growing body of evidence points against this concept. We use the primate mandible as a model structure to investigate the complex interplay between shape, size, diet and phylogeny. We find a weak but significant impact of diet on mandible shape variation in primates as a whole but not in anthropoids and catarrhines as tested in isolation. These clades mainly exhibit allometric shape changes which are unrelated to diet. Diet is an important factor in the diversification of strepsirrhines and platyrrhines and a phylogenetic signal is detected in all primate clades. Peaks in morphological disparity occur during the Oligocene (between 37 and 25 Ma) supporting the notion that an adaptive radiation characterized the evolution of South American monkeys. In all primate clades, the evolution of mandible size is faster than its shape pointing to a strong effect of allometry on ecomorphological diversification in this group.

Keywords: Geometric morphometrics, morphological disparity, diet, allometry, macroevolution

Data archived in the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.8jq98>

The evolution of the mammalian mandible epitomizes one of the major biological paradigms: on the one side, different mandibular forms adapt to different masticatory functions (hence food types), on the other side, developmental and biomechanical constraints limit the possible range of shape transformations from one species to its descendant. Although “mandible” is in fact synonym for chewing (from the latin *mandere* = to chew), no straightforward link occurs between mandible shape and diet in a broad range of mammals (cf. Turnbull 1970; Raia et al. 2010; Meloro and O’Higgins 2011) and multiple factors need to be considered simultaneously in order to understand mandible shape evolution at the macroevolutionary scale.

We use living primates as a model group to investigate mandibular shape variation in relation to size (= allometry), diet and phylogeny. Primates are an ecologically diverse group that emerged between 71.42- 62.8 Million years ago (Springer et al. 2012). Living primates range in size from less than 100 grams (the mouse lemur) to more than 200 kg (the male gorilla) (Fleagle 2013). The primate tree splits in two major clades: the Strepsirrhini (inclusive of lemurs, galagos and pottos) and Haplorhini (tarsiers plus New and Old World monkeys and apes/humans). Primates colonized tropical and subtropical biomes in both the New and the Old world, including Madagascar (Fleagle and Reed 1996; Harcourt et al. 2002; Yoder and Yang 2004; Poux et al. 2005; Schrago 2007; Springer et al. 2012) and peaked in taxonomic diversity during the Miocene warm climatic optimum (Springer et al. 2012). Although restricted to a limited number of habitats and climatic ranges, primates were

capable of invading different feeding niches including insectivory, gumnivory, frugivory and folivory (Nunn and Van Schuck 2002) which is generally reflected in their functional morphology (Wood 1994).

A broad range of studies focused on primate mandible and its link to functional adaptation to different food types (for a review see Ross et al. 2012). However, we still lack a comprehensive analysis of the broad ecomorphological diversity in this group, how it evolved, and how tight the link between morphology and function is in their feeding activity. Interspecific allometry appears to be one of the major factors influencing mandibular morphology, masticatory muscle arrangements and chewing cycles. It is thus conceivable that a strong interplay between mandibular size and dietary adaptations takes place (Highlander 1979, 1985; Highlander et al. 2005; Ross et al. 2009). Still, mandible shape in primates is also a significant source of taxonomic information (Bouvier 1986; Raveloson et al. 2005; Schmittbuhl et al. 2007), suggesting that phylogenetic effects may override pure feeding adaptation in explaining shape variation among the primate mandibles to some extent.

We expect a strong interplay among mandibular size, diet and phylogeny to take place in primates. Such interplay is evident in a number of studies pertaining to mammalian mandibles (Meloro et al. 2008; Raia et al. 2010; Monteiro and Nogueira 2011) and primate skulls (Fleagle et al. 2010; Perez et al. 2011; Bennet and Goswami 2012; Baab et al. 2014). We further address the question of how mandible shape in different primate subclades evolved, and how functional and phylogenetic constraints interact with each other during these clades' histories. Accordingly, we used clade-level analyses and disparity through time (Harmon et al. 2003) to clarify the impact of allometry, diet and phylogeny at different macroevolutionary scales.

Materials and methods

MORPHOMETRIC ANALYSIS

We collected digital photographs for 648 mandibles belonging to 143 different species of extant primates, including wild caught adult individuals only. Specimens belong to collections from Museu Paraense Emílio Goeldi (MPEG, Brazil), Museu de Zoologia da Universidade de São Paulo (MZUSP, Brazil), and Museum National d'Histoire Naturelle de Paris (MNHN, France) and they were selected in order to maintain a comparable number of males ($n = 331$) and females ($n = 285$) per species whenever possible (see Table. S1). Eighteen landmarks were digitally placed on each photograph in order to describe the main mandibular features: the thickness (height) of the corpus, the relative positioning of the teeth, and the shape of the ramus (Fig. 1).

Two dimensional landmark coordinates were analysed with the Generalised Procrustes algorithm (Rohlf and Slice 1990) to remove the effect of size and sample positioning via scaling, translation and rotation. The new set of coordinates (= Procrustes) were generated for the whole sample and then averaged for each species. Although sexual dimorphism clearly occurs in the skull of Primates (Cardini and Elton 2008), we did not expect it to influence macroevolutionary analyses based on species averages. Indeed, we obtained almost identical results on separate samples of averaged males ($n = 121$) and females ($n = 121$).

Averaged Procrustes coordinates were subsequently analysed using principal component analysis (PCA) to identify major components of interspecific variation. Each species was categorised according to its taxonomy – suborder, family, Fleagle et al. (2010) – and feeding ecology (insectivores, gummivores, frugivores, and folivores, Nunn and van Schaik 2002). We used MANOVA to test for differences in PCA scores among primate suborders, and among diet categories. Due to the sample size limitation, we performed

MANOVA first using the full set of 36 PC scores, and then on different PC subsets selected after excluding the axes that explained less than 5% of variance singularly. This procedure optimised degrees of freedom especially when group size was small in relation to number of PC variables (see Meloro and O'Higgins 2011). Multivariate regression was applied to detect interspecific allometry, with size (= natural log transformed centroid size, Dryden and Mardia 1998) taken as independent, and Procrustes coordinates as dependent variables. We used software of the tps series (<http://life.bio.sunysb.edu/morph/>) and NTSYS 2.21q for geometric morphometrics and MANOVA analyses.

COMPARATIVE METHODS

Shared ancestry is likely to influence interspecific shape variation, implying that phenotypic changes are not independent from phylogeny. To account for this, we first constructed a phylogenetic tree inclusive of the 143 analysed taxa based on Springer et al. (2012). Diet categories were mapped into the phylogeny using squared change parsimony in order to identify major dietary shifts within and between primate clades (Maddison 1991). Similarly, squared change parsimony was employed to reconstruct and visualise ancestral values for mandible shape (cf. Meloro and Jones 2012) and size. By comparing nodal reconstructions (=Heritable Taxonomic Unit, HTU) for all the traits of interest, we aim to provide a first empirical evidence on how mandible size and shape changed through the evolutionary time.

We then tested the strength and significance of phylogenetic signal in size and shape data using the K statistics. Recently Adams (2014) introduced a multivariate generalisation of K that we applied here as a direct measurement for the tendency, in closely related species, to display similar trait values due to their common ancestry. K is here used as a measure of phylogenetic conservatism for size and shape traits in order to provide a direct comparison between the two: $K >$ or close to 1 approximates Brownian motion of character evolution and

is indicative of high phylogenetic conservatism, while K closer to 0 supports no phylogenetic signal in the data. Significance of observed K values was tested by randomising the trait values across the phylogeny (Blomberg et al. 2002).

After checking for phylogenetic signal, Phylogenetic Generalised Least Square (PGLS) regressions (Rohlf 2001, 2006) were applied to introduce the phylogenetic covariance matrix as the error term in the regression of shape versus size (interspecific allometry), and versus dietary categories.

Disparity through time plots (Harmon et al. 2003) were generated to test the hypothesis that mandibular size and shape evolved under the same selective regime in Primates as a whole (cf. Meloro and Raia 2010; Meloro and Jones 2012). These plots were computed by calculating the average disparity of the subclades in existence at time t versus the tree total disparity, where t is the distance from the root of each node in the tree, repeated over all of the tree nodes starting from the root (Harmon et al. 2003). When the average subclade disparity is high, the subclades overlap morphologically. Conversely, when disparity is partitioned among clades, the average relative disparity is small and the subclades are morphologically distinct. The area differences between the observed disparity curves and the one generated by simulation under the Brownian motion model of evolution indicate whether the trait (here either size or shape of the mandible) varies among subclades more or less than expected under the Brownian motion model (Slater et al. 2010).

Due to the different zoogeographic and evolutionary history of the major Primates subclades (Springer et al. 2012), we hypothesize that mandibular size and shape might exhibit different degrees of interspecific variation in different subclades. Consequently, all the analyses were repeated on nested datasets (Anthropoids, $n = 114$; Strepsirrhini $n = 28$; Catarrhini, $n = 82$; Platyrrhini, $n = 32$).

Squared change parsimony analyses for diet (coded as an unordered, categorical variable) and natural log centroid size were performed using Mesquite 2.75 (Maddison and Maddison 2011) while to generate mandible shape configuration at each node we employed tpsTree vs. 1.21 (Rohlf 2007). Phylogenetic Generalised Least Squares analyses were performed using NTSYS while the R packages Geiger (Harmon et al. 2008) and Geomorph (Adams and Otárola Castillo 2013) were used for the comparative analyses.

All the comparative data inclusive of shape coordinates, PC scores, and phylogenetic trees are available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.8jq98>.

Results

The mandible shape space identified by the first two PCs allows discriminating between both large (suborders) and small (families) primate taxonomic groups (Fig. 2). PC1 (56.29% of variance explained) separates Strepsirrhini and *Tarsius* (positive scores) from Platyrrhini (negative scores) being heavily loaded on the relative depth of mandibular corpus and ramus. Strong deformation along this axis also relates to changes in the position of the gonial angle and of the coronoid. The second PC (13.33%) partially separates New from Old World monkeys and describes shape changes in corpus thickness, posterior molar area and gonial angle. The human mandible clusters within other hominids, while Cercopithecidae and Hylobatidae share positive scores on PC1 and PC2 (Fig. 1). MANOVA indicates that significant differences in mandible shape occur between suborders ($F = 32.16$; $p < 0.0001$) and families ($F = 9.675$, $p < 0.0001$).

The impact of size on mandible shape is large and significant (explaining 83.47% of the variance, Table 1). Allometry occurs also when subclades are analysed separately, showing a greater impact in Platyrrhini than in other groups (Table 1). There is a significant association between diet and mandible shape, with Strepsirrhini and Platyrrhini showing the

highest values of variance explained by feeding habits (Table 1). The interaction between diet and size is also present in all cases except for strepsirrhines and catarrhines (Table 1).

Mapping diet into the phylogenetic tree shows that strepsirrhines and platyrrhines have the highest dietary variation (Fig. 3). Strong dietary segregation among clades occurs within Catarrhini with the split between folivore Colobinae and frugivore Cercopithecinae (Fig. 3).

Mandibular size appears to be mostly conserved within strepsirrhines that tend to exhibit always low values at the basal nodes (Fig. 3 and Fig. S1). Within haplorhines, the *Tarsius* branch shows the lowest mandibular centroid size value while a trend towards size increase occurs from the basal node of Anthropoidea towards the terminal nodes of Hominidae (with the gorilla having the highest centroid size value). Shape changes reconstructed at the deep nodes of the primate tree are not particularly dramatic when accompanied by dietary shifts (Fig. 3). Conversely, major shape deformations occur at more terminal nodes. Basal to the Platyrrhini we note a particular enlargement of the gonial angle and mandibular corpus depth while the estimated shape of Lemuridae node shows a similar expansion not followed by increase in corpus depth. The ancestral shape of Hominidae mandible also presents deformation in the posterior region. The condyle and coronoid area are enlarged, and the corpus becomes deep behind the canine region (which will eventually permit the development of the chin in humans).

Phylogenetic signal is significant for both size and shape traits. In all cases the K statistic exhibits higher values for centroid size (Table 2). Platyrrhini have the strongest signal in both traits.

PGLS results corroborate only to some extent previous analyses. The impact of allometry is still significant in all cases, while the association between diet and mandible shape holds only in Primates as a whole, and in Strepsirrhini and Platyrrhini analysed separately (Table 1). The interaction between diet and size is valid for Primates as a whole, but within nested subsets it is significant only in Platyrrhini (Table 1).

Patterns of disparity through time support a larger ‘between clade’ diversification in mandibular size rather than in shape (area differences between size and shape curve always positive, Fig. 4, Fig. S2). However, the rate of evolution in both traits varies dramatically in different groups. The pattern observed for Primates as a whole (which shows a clear peak in disparity at relative time 0.4-0.6 (i.e. between 37 and 25 Ma, Fig. 4d) is not replicated by all nested subsets. Anthropoids and Strepsirrhini similarly show a peak around the Paleogene/Neogene boundary (at c.ca 25 Ma for Anthroidea, and at 32 Ma for Strepsirrhini, both corresponding to relative time 0.4 on Fig. 4a and d) while for Catarrhini there is a relatively rapid decline in disparity that becomes even more extreme in Platyrrhini. South American monkeys clearly diversified much faster in mandibular size and shape than any other group. This is confirmed by the comparison of observed disparity through time with Brownian motion simulations: P values are always non-significant indicating no departure from Brownian motion in all clades except for Platyrrhini (both in size and shape) and Anthroidea (shape only) (Fig. S2).

Discussion

Mandibular shape variation at interspecific scale has been generally interpreted as the result of a compromise between the constraints imposed by phylogenetic history and masticatory function (Caumul and Polly 2005; Meloro et al. 2008; Raia et al. 2010). Primates are no exception among mammals since they primarily exhibit a phylogenetic signal in mandibular morphology, which is secondarily influenced by adaptations to different diets. Indeed, our PCA of mandible shape (Fig. 2) clearly shows that major primate clades occupy distinct portions of the morphospace. Additionally, a significant phylogenetic signal (K) is always detected in both mandibular shape and size (Table 1). This agrees well with the notion that mandibular morphology is relevant to primate systematics (Bouvier 1986; Raveloson et al. 2005; Schmittbuhl et al. 2007) and it does not differ substantially from the cranium, which also exhibits significant phylogenetic signal at all taxonomic scales (see Fleagle et al. 2010 for Primates as a whole, Perez et al. 2011 for Platyrrhini and Bennet and Goswami 2013 for Haplorrhini). The similarity in phylogenetic signal between the cranium and the mandible is most probably driven by their unique functional integration (Cardini and Elton 2008).

However, we also note minor, but non-trivial, differences. For instance, the human mandible clusters with those of other hominids and Catarrhini (Fig. 2), while the cranium does not (Fleagle et al. 2010). Since our data are two-dimensional while the cranial studies are based on 3D landmarks it might be possible that our pattern is due to differences in morphological quantification. Yet, Cardini (2014) recently observed consistency of results between 2D and 3D mandibular datasets of marmots, providing a good reason to believe that 3 dimensional data of mandibular size and shape might not result in a substantially different interspecific pattern. Phylogenetic signals are also reported differently in studies on cranial shape thus making direct comparisons not feasible.

Kamilar and Cooper (2012) provided K values for a multitude of physiological and behavioural primate traits: we note similarities between mandibular size and other morphological traits such as relative brain size, whose K is generally higher than 1 (Table 2). This suggests that closely related species tend to be more similar in mandibular size and relative brain size than in mandible shape. Adams (2014) argues that K_{multiv} is highly appropriate for high dimensional data and it could be comparable with its univariate equivalent. Since shape can vary into many more directions than size it could be possible that what we detected in this primate dataset is a common phenomenon in geometric morphometrics datasets. The evolutionary processes underpinned by our K values seem also consistent to Brownian motion model for both size and shape (cf. Fig. 3 and Fig. S2) and we note that the high values of K in Platyrrhini relates to their relatively quick ecomorphological radiation. That is to say that K higher than 1 relates (in our case) to strong phylogenetic structuring, hence rapid and stable niche diversification that provides little opportunities for evolutionary convergence (cf. Meloro and Raia 2010 on carnivoran lower carnassial angular height).

The phylogenetic signal does not obscure the intimate relationship between mandible size and shape so that PGLS confirms allometry to occur strongly in all cases (Table 1). Daegling and McGraw (2011) explained the influence of allometry on mandibular corpus shape in Old World monkeys as a consequence of the increasing functional demands related to the need for longer chewing cycles and tougher diets (Ravosa 2000) over the evolutionary history of that clade. We detected significant interaction between size and diet (as broadly classified by us) in primates as a whole and in platyrrhines. Yet, this does not imply size is linked to feeding adaptations all the times. In Catarrhini, diet has little to no impact on mandibular size and shape (when phylogeny is accounted for). In Strepsirrhini we similarly found no significant interaction between diet and mandibular size (cf. Ravosa 1991). The

case of catarrhines is instructive since there is a neat phylogenetic separation between frugivores and folivores with few exceptions (Fig. 3). This explains why PGLS fails to detect a relationship between diet and mandibular morphology. Two distinct lines of adaptation from frugivory to folivory are currently recognised in Catarrhini: 1. the size increase that is apparent in Hominidae (Taylor 2006); 2. the foregut fermentation strategy of Colobinae (Sailer et al. 1985). Allometry within Hominidae provided explanation for the lack of direct functional link between mandibular shape and diet (Taylor 2002) while our dietary quantification might not reveal the subtle trend within colobines that shows thin mandibular corpus but more robust profile posteriorly in relation to seed predation and strong bite forces especially for the African species (Koyabu and Endo 2009).

The complexity of diet quantification that should include types of food, time spent chewing, food material properties has been recently reiterated by Ross et al. (2012) that suggests a multiple approach to identify dietary adaption in the mandible of primates. A more detailed dietary quantification might possibly alter the pattern we present here for Anthropoidea and catarrhines, although what we found is supported by previous observations on functional morphology of primate mandible: clades-specific adaptations to different diet categories might obscure the direct link between function and morphology in between species (Ross et al. 2012).

We identify apparent trends of association between diet and mandible shape within other groups such as strepsirrhines and platyrrhines. On the one hand, previous approaches on strepsirrhines argued for a strong adaptive association between skull shape and diet (Viguier 2004). Baab et al. (2014) recently evidenced significant association between skull shape and typical diet. More interestingly, they identified a line of lemur diversification not along allometric axes (i.e. finding no strong interplay between skull size and species ecology) that is also consistent with what we find for the mandible (see Table 1).

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On the other hand, New World monkeys offer a striking contrast with this general pattern. Both size and diet have a strong influence on mandibular shape morphology in Platyrrhini, thus confirming previous findings hinting at size evolution as a “line of least evolutionary resistance” (Marroig and Cheverud 2005, 2010) preferentially taken to provide diversification. Tehrune (2011, 2013) also identified a clear link between the shape of temporomandibular joint and diet in Platyrrhini, still in agreement with our generalisations. Overall, our data suggest that the effect of dietary functional adaptation on mandibular shape variation is not detectable in Old World monkey when phylogeny is accounted for, but present in lemurs, bushbabies and pottos, and also associated to size diversification in New World monkeys. One reason these clades have such different evolutionary dynamics in mandibular shape evolution is their idiosyncratic histories.

Disparity through time plots provide even stronger support to the idea that New World monkeys mandible shape evolution is unique: this is the only example clearly departing from a Brownian motion expectation. In this group, an adaptive radiation (cf. Slater et al. 2010) in both mandibular size and shape, with rapid differentiation more ‘between’ than ‘within’ subclades is clear. The same does not hold true for Strepsirrhini, whose coevolution with the significantly larger Catarrhini favoured a slow, non-size related, ecomorphological diversification. Lemurs are most probably responsible for the association between shape and diet in this group's mandibles, since the long isolation the lemur clade experienced in Madagascar during the last forty million years might have favoured the development of diverse morphologies once they escaped competition from larger relatives. It is no coincidence that fossil lemurs include a spectacular diversity of shapes and sizes, including some of the smallest, and of the largest as well, primates ever (Jungers et al. 2002). In this regard, it is tempting to suggest that a study like the present conducted on a complete

phylogeny of lemurs (that is inclusive of fossil forms) would reveal a pattern of adaptive radiation much alike what we found for New World monkeys.

The timing of mandibular size and shape differentiation seems to be consistent among clades and supports a burst in primate evolutionary morphology during the early Oligocene.

Springer et al. (2012) identified the Miocene as the ‘optimum’ period for primate taxonomic diversification due to its warm climatic condition. Our analyses support major patterns of morphological differentiation to occur slightly earlier. The Eocene-Oligocene boundary is marked by a dramatic climatic global cooling event that coincides with the disappearance of many early primate groups (Omomyidae and Adapidae) thus possibly providing opportunity for new groups to evolve and invade multiple niches in the aftermath, such as the Haplorrhini (Soligo 2006; Schrago 2007).

In conclusion, the paradigm that mandible reflects dietary adaptations to some extent still holds in Primates as a whole and in specific groups like Strepsirrhini and Platyrrhini. Evidences from apes and colobines (Smith 1983; Ravosa 2000; Taylor 2002, 2006) in this respect provide interesting perspectives as to explain why this pattern is not universal: 1. dietary categorisations are reductive and do not take into account food material properties; 2. the chewing mechanism is flexible across primate species but it is also biomechanically constrained by a leverage system that needs to avoid joint distraction (Spencer 1999); 3. adaptations to the same diet might occur differently between clades due to size-related biomechanical constraint and distinct tempo and mode of evolution.

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LITERATURE CITED

Adams, D. C. 2014. A generalized K statistic for estimating phylogenetic signal from shape and other high-dimensional multivariate data. *Syst. Biol.* 63:685–697.

Adams, D. C., and E. Otárola-Castillo. 2013. geomorph: an R package for the collection and analysis of geometric morphometric shape data. *Method. Ecol. Evol.* 4:393–399.

Atchley, W. R., and B. K. Hall. 1991. A model for development and evolution of complex morphological structures. *Biol. Rev.* 66:101–157.

Baab, K. L., J. M. Perry, F. J. Rohlf, and W. L. Jungers. 2014. Phylogenetic, ecological, and allometric correlates of cranial shape in Malagasy Lemuriforms. *Evolution* 68:1450–1468.

Bennett, C. V., and A. Goswami. 2012. Morphometric analysis of cranial shape in fossil and recent Euprimates. *Anat. Res. Int.* Article ID 478903, 7 pages.

Blomberg, S. P., Garland, T., and A. R. Ives 2003. Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution* 57:717–745.

Bouvier, M. 1986. Biomechanical scaling of mandibular dimensions in New World monkeys. *Int. J. Primatol.* 7:551–567.

Cardini, A. (2014). Missing the third dimension in geometric morphometrics: how to assess if 2D images really are a good proxy for 3D structures?. *Hystrix, the Italian Journal of Mammalogy*, 25(2).

Cardini, A., and S. Elton. 2008. Does the skull carry a phylogenetic signal? Evolution and modularity in the guenons. *Biol. J. Linn. Soc.* 93:813–834.

Caumul, R., and P.D. Polly. 2005. Phylogenetic and environmental components of morphological variation: skull, mandible, and molar shape in marmots (*Marmota*, Rodentia). *Evolution* 59: 2460-2472.

Daegling, D. J., and W. S. McGraw. 2001. Feeding, diet, and jaw form in West African *Colobus* and *Procolobus*. *Int. J. Primatol.* 22:1033–1055.

Desdevises, Y., P. Legendre, L. Azouzi, and S. Morand. 2003. Quantifying phylogenetically structured environmental variation. *Evolution* 57:2647–2652.

Dryden, I. L., and K. V. Mardia, eds. 1998. *Statistical shape analysis*. Vol. 4. John Wiley & Sons, New York, NY.

Fleagle, J. G. 2013. *Primate Adaptation and Evolution*. 3rd Edn. Academic Press, New York, NY.

Fleagle, J. G., and K. E. Reed. 1996. Comparing primate communities: a multivariate approach. *J. Hum. Evol.* 30:489–510.

Fleagle, J. G., C. C. Gilbert, and A. L. Baden. 2010. Primate cranial diversity. *Amer. J. Phys. Anthropol.* 142:565–578.

Harcourt, A. H., S. A. Coppeto, and S. A. Parks. 2002. Rarity, specialization and extinction in primates. *J. Biogeogr.* 29:445–456.

Harmon, L. J., J. A. Schulte, A. Larson, and J. B. Losos. 2003. Tempo and mode of evolutionary radiation in iguanian lizards. *Science* 301:961–964.

Harmon, L. J., J. T. Weir, C. D. Brock, R. E. Glor, and W. Challenger. 2008. GEIGER: investigating evolutionary radiations. *Bioinformatics* 24:129–131.

Hylander, W. L. 1979. The functional significance of primate mandibular form. *J. Morphol.* 160:223–240.

Hylander, W. L. 1985. Mandibular function and biomechanical stress and scaling. *Amer. Zool.* 25:315–330.

Hylander, W. L., C. E. Wall, C. J. Vinyard, C. Ross, M. R. Ravosa, S. H. Williams, and K. R. Johnson. 2005. Temporalis function in anthropoids and strepsirrhines: an EMG study. *Amer. J. Phys. Anthropol.* 128:35–56.

Jungers, W. L., Godfrey, L. R., Simons, E. L., Wunderlich, R. E., Richmond, B. G., and P. Chatrath. 2002. *Ecomorphology and behavior of giant extinct lemurs from Madagascar*. Pp. 371–411 in J.M. Plavcan, R. F. Kay, W. L. Jungers, and C. P. van Schaik, eds. *Reconstructing behavior in the primate fossil record*. Springer, New York, NY.

Kamilar, J. M., & Cooper, N. (2013). Phylogenetic signal in primate behaviour, ecology and life history. *Phil. Trans. R. Soc. B* 368(1618):20120341.

Koyabu, D. B., & Endo, H. (2009). Craniofacial variation and dietary adaptations of African colobines. *Journal of human evolution*, 56(6), 525–536.

Maddison, W. P. and D.R. Maddison. 2011. Mesquite: a modular system for evolutionary analysis. Version 2.75 <http://mesquiteproject.org>

Maddison, W.P. 1991. Squared-change parsimony reconstructions of ancestral states for continuous-valued characters on a phylogenetic tree. *Syst. Zool.* 40: 304–314.

Marroig, G., and J. M. Cheverud. 2005. Size as a line of least evolutionary resistance: diet and adaptive morphological radiation in New World monkeys. *Evolution* 59:1128–1142.

Marroig, G., and J. M. Cheverud. 2010. Size as a line of least resistance II: Direct selection on size or correlated response due to constraints? *Evolution* 64:1470–1488.

Meloro, C., and M. E. H. Jones. 2012. Tooth and cranial disparity in the fossil relatives of *Sphenodon* (Rhynchocephalia) dispute the persistent ‘living fossil’ label. *J. Evol. Biol.* 25:2194–2209.

Meloro, C., and P. O’Higgins. 2011. Ecological adaptations of mandibular form in Fissiped Carnivora. *J. Mammal. Evol.* 18:185–200.

Meloro, C., and P. Raia. 2010. Cats and dogs down the tree: the tempo and mode of evolution in the lower carnassial of fossil and living Carnivora. *Evol. Biol.* 37:177–186.

Meloro, C., P. Raia, P. Piras, C. Barbera, and P. O’Higgins. 2008. The shape of the mandibular corpus in large fissiped carnivores: allometry, function and phylogeny. *Zool. J. Linn. Soc.* 154:832–845.

Monteiro, L. R., and M. R. Nogueira. 2011. Evolutionary patterns and processes in the radiation of phyllostomid bats. *BMC Evol. Biol.* 11:137.

Nunn, C. L., and C. P. van Schaik. 2002. A comparative approach to reconstructing the socioecology of extinct primates. Pp. 159–215 in J.M. Plavcan, R. F. Kay, W. L. Jungers, and C. P. van Schaik, eds. *Reconstructing behavior in the primate fossil record*. Springer, New York, NY.

Oksanen, J., F. G. Blanchet, R. Kindt, M. J. Oksanen, and M. Suggests. 2013. *Vegan: Community ecology package*. <http://vegan.r-forge.r-project.org/>

- Perez, S. I., J. Klaczko, G. Rocatti, and S. F. dos Reis. 2011 Patterns of cranial shape diversification during the phylogenetic branching process of New World monkeys (Primates: Platyrrhini). *J. Evol. Biol.* 24:1826–1835.
- Poux, C., P. Chevret, D. Huchon, W. W. de Jong, and E. J. Douzery. 2006. Arrival and diversification of caviomorph rodents and platyrrhine primates in South America. *Syst. Biol.* 55:228–244.
- Raia, P., F. Carotenuto, C. Meloro, P. Piras, and D. Pushkina. 2010. The shape of contention: adaptation, history, and contingency in ungulate mandibles. *Evolution* 64:1489–1503.
- Raveloson, H., J. M. Le Minor, Y. Rumpler, and M. Schmittbuhl. 2005. Shape of the lateral mandibular outline in Lemuridae: a quantitative analysis of variability using elliptical Fourier analysis. *Folia Primatol.* 76:245–261.
- Ravosa, M. J. 1991. Structural allometry of the mandibular corpus and symphysis in prosimian primates. *J. Hum. Evol.* 20:3–20.
- Ravosa, M. J. 2000. Size and scaling in the mandible of living and extinct apes. *Folia Primatol.* 71:305–322.
- Rohlf, F. J. 2001. Comparative methods for the analysis of continuous variables: geometric interpretations. *Evolution* 55:2143–2160.
- Rohlf, F. J. 2006. A comment on phylogenetic correction. *Evolution* 60:1509–1515.
- Rohlf, F. D., and D. Slice. 1990. Extensions of the Procrustes Method for the Optimal Superimposition of Landmarks. *Syst. Biol.* 39:40–59.

Ross, C. F., and D. A. Reed, R. L. Washington, A. Eckhardt, F. Anapol, and N. Shahnoor. 2009. Scaling of chew cycle duration in primates. *Amer. J. Phys. Anthropol.* 138:30–44.

Ross, C. F., J. Iriarte-Diaz, and C. L. Nunn. 2012. Innovative approaches to the relationship between diet and mandibular morphology in primates. *Int. J. Primatol.* 33:632–660.

Sailer, L. D., Gaulin, S. J., Boster, J. S., & Kurland, J. A. (1985). Measuring the relationship between dietary quality and body size in primates. *Primates*, 26(1), 14–27.

Schmittbuhl, M., J. Rieger, J. M. Le Minor, A. Schaaf, and F. Guy. 2007. Variations of the mandibular shape in extant hominoids: generic, specific, and subspecific quantification using elliptical Fourier analysis in lateral view. *Amer. J. Phys. Anthropol.* 132:119–131.

Schrago, C. G. 2007. On the time scale of New World primate diversification. *Am. J. Phys. Anthropol.* 132:344–354.

Slater, G. J., S. A. Price, F. Santini, and M. E. Alfaro. 2010 Diversity versus disparity and the radiation of modern cetaceans. *Proc. R. Soc. B* 277:3097–3104.

Smith, R. J. 1983. The mandibular corpus of female primates: taxonomic, dietary, and allometric correlates of interspecific variations in size and shape. *Amer. J. Phys. Anthropol.* 61:315–330.

Soligo, C. 2006. Correlates of body mass evolution in primates. *Amer. J. Phys. Anthropol.* 130:283–293.

Spencer, M. A. 1999. Constraints on masticatory system evolution in anthropoid primates. *Amer. J. Phys. Anthropol.* 108:483–506.

- Springer, M. S., R. W. Meredith, J. Gatesy, C. Emerling, J. Park, D. L. Rabosky, T. Stadler, C. Steiner, O. Ryder, J. E. Janečka, C. Fisher, W. J. Murphy. 2012. Macroevolutionary dynamics and historical biogeography of primate diversification inferred from a species supermatrix. *PLoS One* 7:e49521.
- Taylor, A. B. 2002. Masticatory form and function in the African apes. *Amer. J. Phys. Anthropol.* 117:133–156.
- Taylor, A. B. 2006. Diet and mandibular morphology in African apes. *Int. J. Primatol.* 27:181–201.
- Terhune, C. E. 2011. Dietary correlates of temporomandibular joint morphology in New World primates. *J. Hum. Evol.* 61:583–596.
- Terhune, C. E. 2013. Dietary correlates of temporomandibular joint morphology in the great apes. *Amer. J. Phys. Anthropol.* 150:260–272.
- Turnbull, W. D. 1970. Mammalian masticatory apparatus. *Fieldiana Geol.* 18:149–356.
- Viguiier, B. 2004. Functional adaptations in the craniofacial morphology of Malagasy primates: shape variations associated with gummivory in the family Cheirogaleidae. *Ann. Anatomy*, 186:495–501.
- Wood, C. 1994. The correspondence between diet and masticatory morphology in a range of extant primates. *Z. Morph. Anthropol.* 80:19–50.
- Yoder, A. D., and Z. Yang. 2004. Divergence dates for Malagasy lemurs estimated from multiple gene loci: geological and evolutionary context. *Mol. Ecol.* 13:757–773.

Figure 1. The position of eighteen anatomical landmarks on a mandible of *Papio cynocephalus*. Scale bar is 8 cm. Landmarks records: 1 – anterior tip of the canine alveolus, 2 – posterior tip of canine alveolus, 3 – contact point between premolar and molar row taken at the alveolus, 4 – contact point between m1 and m2 at the alveolar margin, 5 – contact point between m2 and m3 at the alveolar margin, 6 – posterior tip of m3 at the alveolar margin, 7 – most superior tip of the coronoid process, 8 – lower tip taken on the curvature between coronoid and condyle, 9 – 10: anterior and posterior tip of mandibular condyle in lateral view, 11 – 14– vertical projections of landmark 6 – 2 obtained with lines perpendicular to the 3 – 6 line, 16 – 17 – 18 superior, medial and inferior tip of the gonial angle.

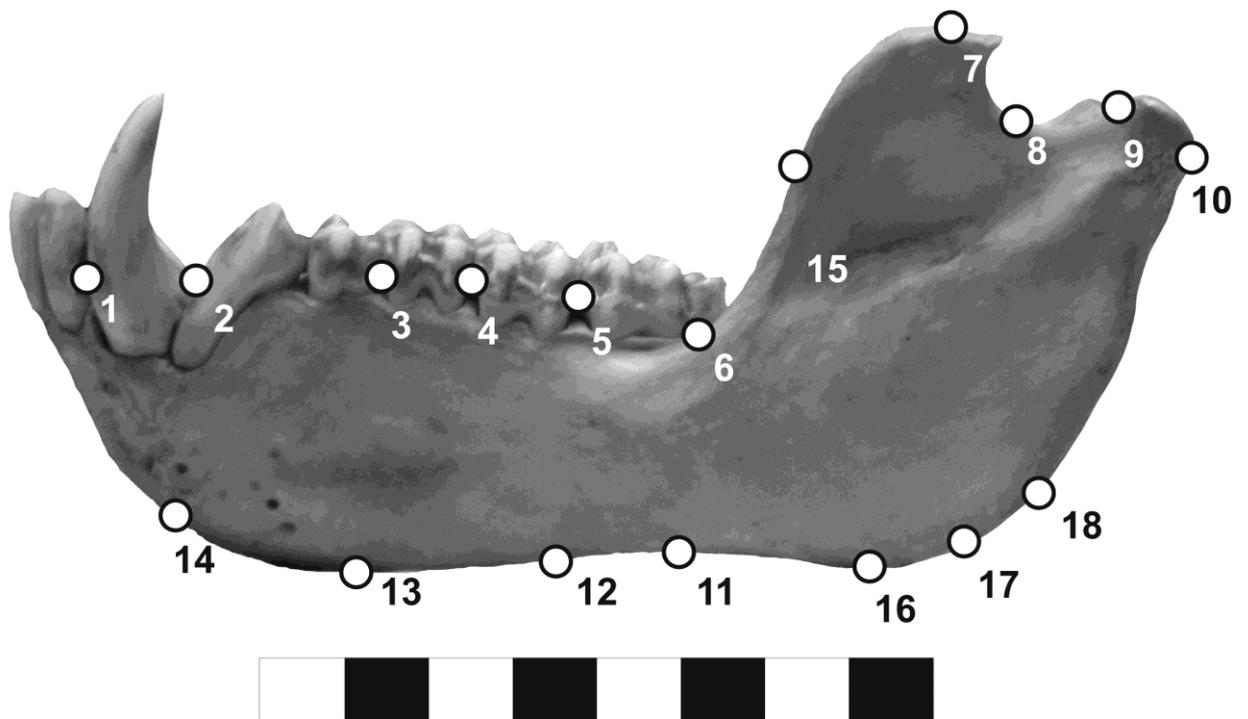


Figure 2. Mandibular morphospace identified for 143 species of Primates by the first two Principal component axes. Each species is represented by a circle colour coded according to taxonomic affiliation. Light steel blue = Hominidae, Black = Cercopithecaidae, Grey = Hylobatidae, Aqua = Pitheciidae, Blue = Cebidae, Dark blue = Atelidae, Brown = Indriidae, Lime = Lorisidae, Dark green = *Tarsius*, Red = Lemuridae, Magenta = Cheirogaleidae, Dark violet = *Daubentonia*. Transformation grids visualize shape deformations relative to the mean at the positive and negative extremes of principal component axes.

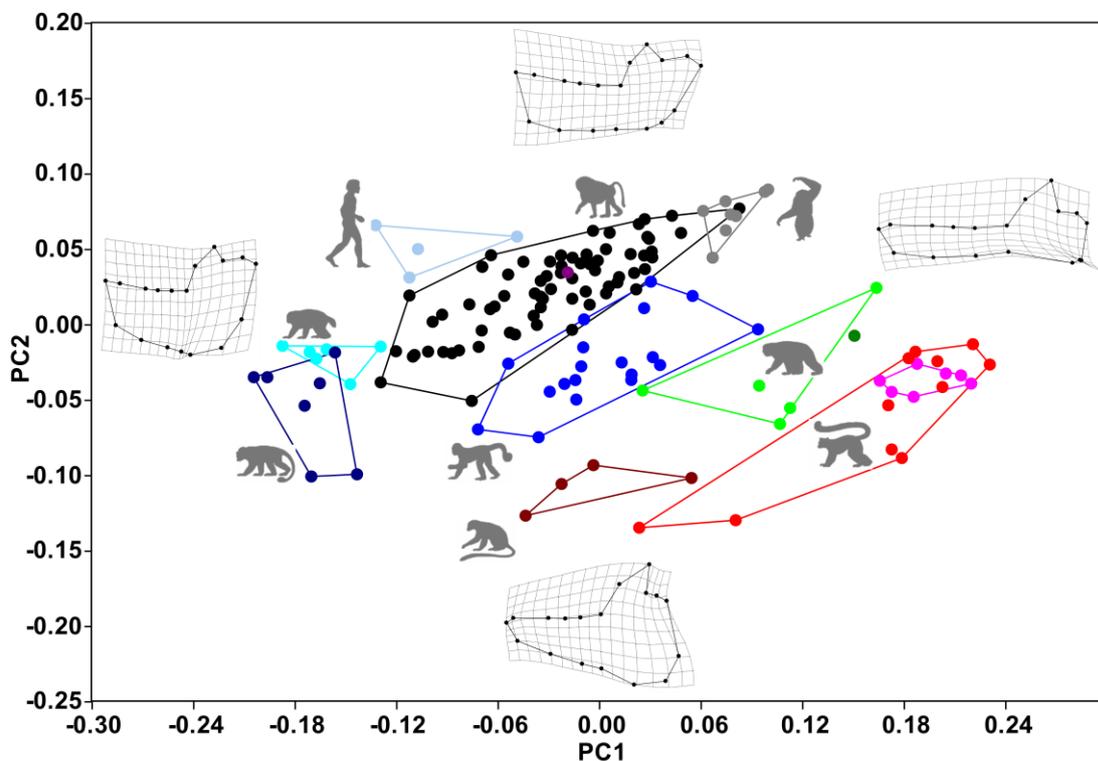


Figure 3. Squared change parsimony reconstruction for diet categorisation, mandible size and shape. Diet categories are mapped in colour within the branches of the primate phylogeny. Mandible size (in grey scale) and shape are shown only at the nodes.

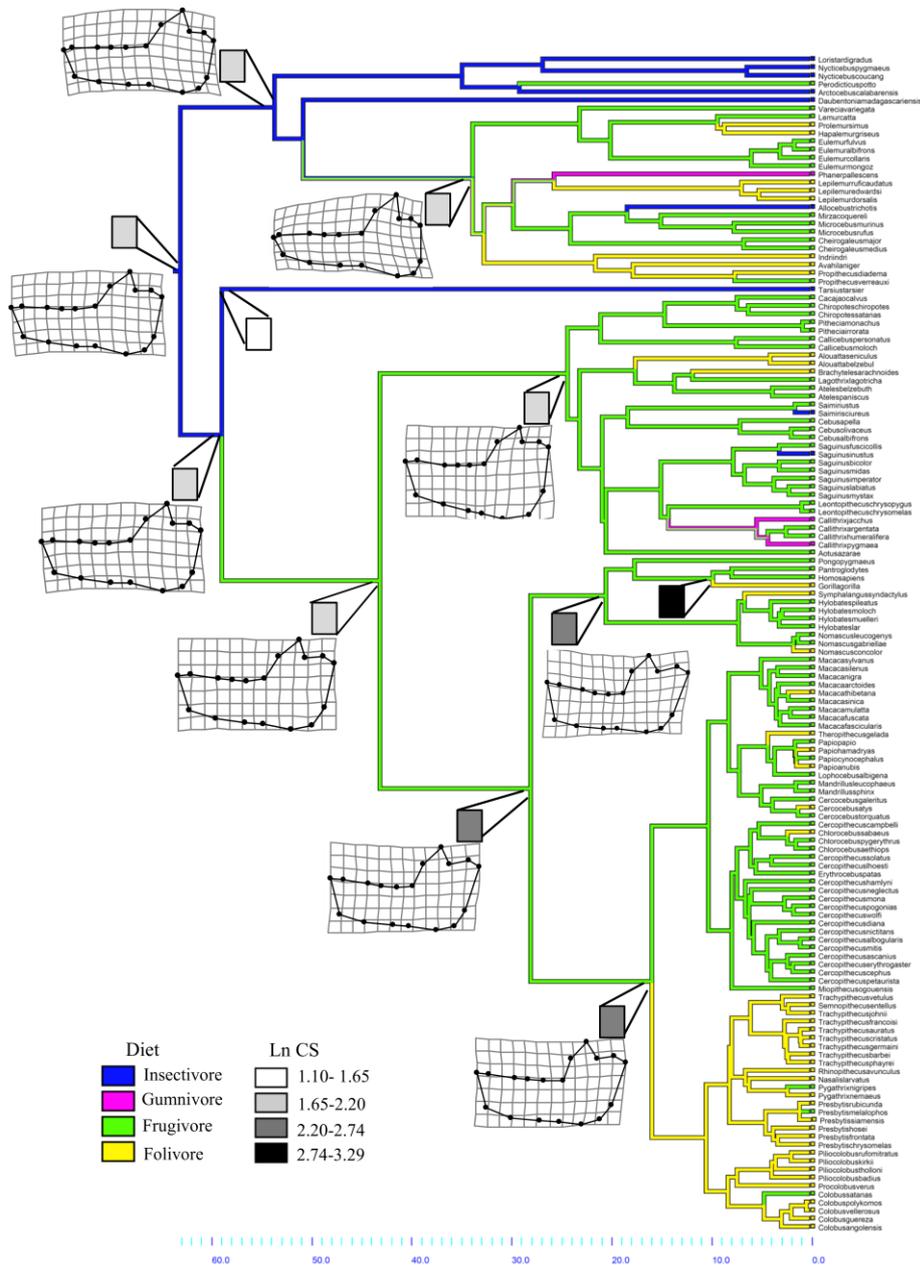


Figure 4. Disparity through time plots for mandible size (black line) and shape (grey line) in (a) all Anthropoidea, b) Catarrhini, c) Platyrrhini, d) Strepsirrhini, e) all Primates.

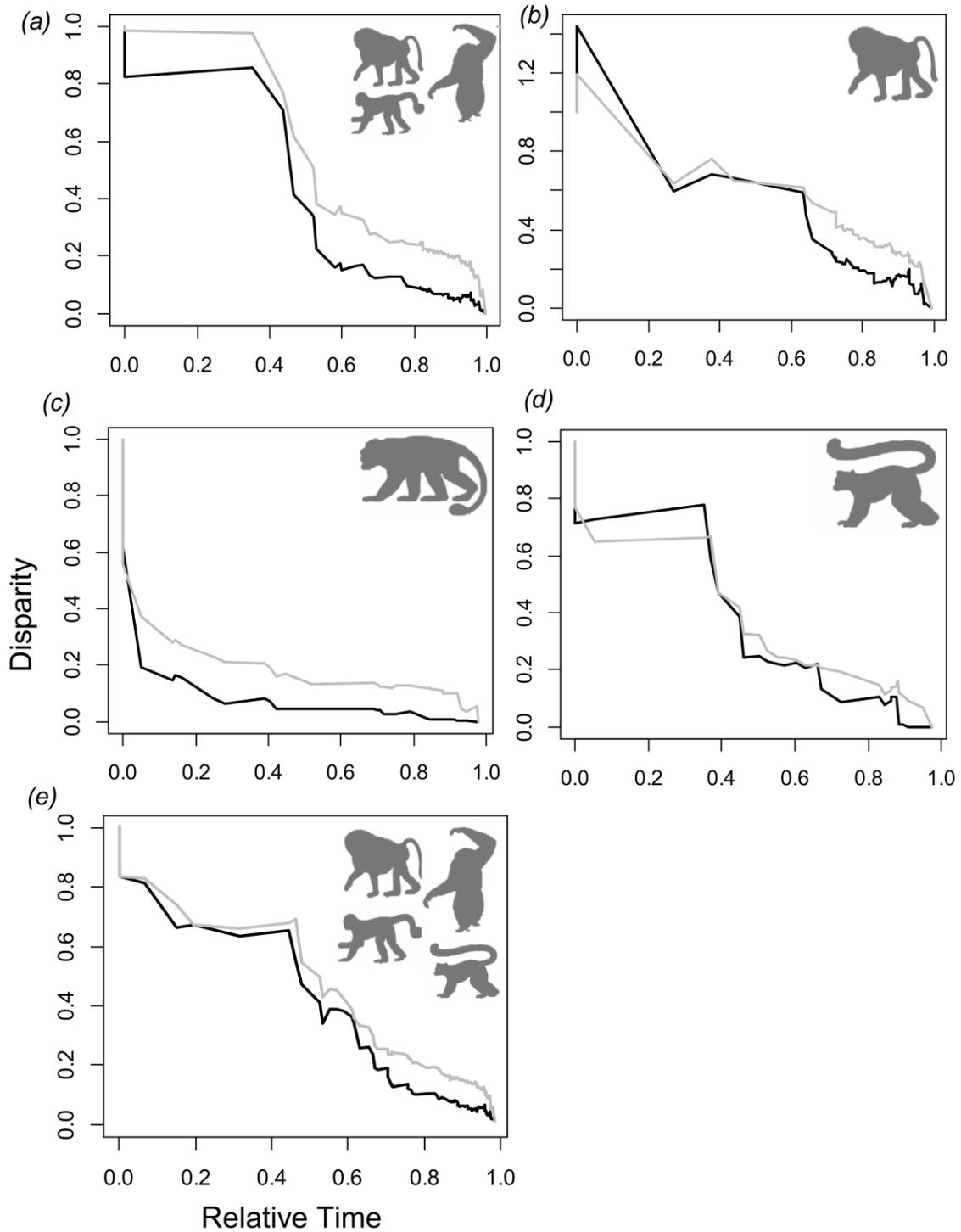


Table 1. Summary statistics for multivariate regressions computed to test the influence of size and diet on mandible shape. Shape variables were represented by 36 Principal Component axes scores unless specified by symbols (* = only 9 PC cores, ~ = only 5 PCs, ^ = only 10 PCs).

Clade		Size vs Shape					Diet vs Shape					Diet vs Size				
		% Var	Fs	df ₁	df ₂	p	% Var	Fs	df ₁	df ₂	p	R ²	Fs	df ₁	df ₂	p
Primates	tips	83.47	12.076	32	110	< 0.001	10.35	3.978	96	324.2	< 0.001	0.278	17.832	3	139	< 0.001
	PGLS		1.419	64	220	0.0337		1.553	96	324.2	0.003		4.792	3	139	0.003
Anthropoidea	tips*	11.25	43.803	9	104	< 0.001	8.72	4.416	27	298.5	< 0.001	0.252	12.362	3	110	< 0.001
	PGLS*		10.234	9	104	< 0.001		1.08	27	298.5	0.363		2.208	3	110	0.091
Strepsirrhini	tips~	14.1	23.929	5	22	< 0.001	32	7.038	10	42	< 0.001	0.162	2.415	2	25	0.110
	PGLS~		4.354	5	22	0.007		2.438	10	42	0.022		1.517	2	25	0.239
Catarrhini	tips^	8.48	21.128	10	71	< 0.001	12.66	4.233	10	71	< 0.001	0.003	0.263	1	80	0.610
	PGLS^		9.67	10	71	< 0.001		0.965	10	71	0.481		2.096	1	80	0.152
Platyrrhini	tips~	48.64	35.207	5	26	< 0.001	30.34	6.166	15	66.7	< 0.001	0.482	8.674	3	28	0.000
	PGLS~		6.102	5	26	< 0.001		1.847	15	66.7	0.046		4.009	3	28	0.017

Table 2. Summary statistics for the K statistics computed for mandibular size and shape. K measures phylogenetic signal in the data so that K close to or bigger than 1 support a Brownian motion evolution mode, while K close to 0 relates to non-significant phylogenetic signal.

	Shape		Size	
	K_{multiv}	p	K	p
Primates	0.503	< 0.0001	1.104	< 0.0001
Strepsirrhini	1.024	< 0.0001	1.212	< 0.0001
Anthropoidea	0.431	< 0.0001	0.916	< 0.0001
Plathyrrhini	1.216	< 0.0001	2.819	< 0.0001
Catarrhini	0.419	< 0.0001	0.853	< 0.0001