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Article

Mandibular shape and diet in extant primates: a 3D geometric morphometric analysis

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With 9 figures and 3 tables

Abstract: Establishing a link between mandibular morphology and diet in extant primates has long been a goal in biological anthropology because it should provide important insight into the diets of extinct primates, including fossil hominins. To date, efforts to explore this question have produced mixed results, largely perhaps due to a reliance on the use of 2D morphological data. Here, we report a study where we investigated whether 3D shape data would provide a clearer picture. We used geometric morphometrics to analyse 3D mandibular shape variation in a sample of > 200 primate specimens, representing individuals from 27 species and five families. Two sets of analyses investigated i) whether there was a relationship between mandibular shape and four standard dietary categories and ii) whether there was a relationship between mandibular shape and a well-known index of diet quality. We found an association between mandibular shape and the dietary categories when we employed raw Procrustes coordinates and allometry-free residuals, but the relationship was weak to non-existent when the effects of phylogeny were taken into account. We found no relationship between shape and the diet quality index, no matter whether the data were raw, corrected for the effects of allometry, corrected for the effects of phylogeny, or corrected for the effects of both allometry and phylogeny. Taken together, the results of the two sets of analyses suggest that there is a weak relationship between 3D mandibular shape and diet in extant primates. Allometry and phylogeny appear to be more important influences on the 3D shape of extant primate mandibles than is diet. We conclude from this that 3D analysis of mandibular shape is unlikely to further illuminate the diets of extinct primates, and research efforts should, therefore, be directed elsewhere.

Keywords: Mandible; diet; extant primates; Diet Quality Index; allometry; phylogeny; 3D geometric morphometrics

1 Introduction

Identifying a link between mandibular morphology and diet in extant primates has been a goal in biological anthropology for several decades (e.g., Bouvier & Hylander 1981; Anapol & Lee 1994; Marroig & Cheverud 2005, 2010; Marcé-Nogué et al. 2017). The main reason for this is that establishing such a link should, in theory, shed additional light on the diets of extinct primates, including fossil hominins (Teaford & Ungar 2000; Lucas et al. 2008; Marcé-Nogué et al. 2020). Unfortunately, however, the task has proven difficult. Although it seems intuitive that the size and shape of an animal's jaw should reflect its diet, the results of studies carried out to date have produced mixed results.

Several studies have found support for a relationship between mandibular morphology and diet by comparing the mandibles of extant primates that rely on hard and tough foods with those that eat soft foods. Bouvier & Hylander's (1981, 1982) analyses, for example, indicated that rhesus macaques (*Macaca mulatta*) raised on hard food items develop mandibles with deeper corpora and thicker cortical bone than conspecifics raised on soft food. Similarly, in an analysis of the craniofacial morphology of five species of African colobine monkeys, Koyabu & Endo (2009) found that species that are heavily reliant on seeds have mandibles with wider bigonial breadths, shorter post-canine tooth rows, and medio-laterally narrower dental batteries than species that are more reliant on leaves.

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However, the results of other studies indicate no clear or consistent relationship between mandibular morphology and diet among extant primates. For instance, while a relationship between a relatively deep mandibular corpus and folivory has been identified in Afro-Eurasian monkeys (Hylander 1979; Bouvier 1986; Ravosa 1990, 1996) and strepsirrhines (Ravosa 1991), in platyrrhines a relatively deep mandibular corpus has been found to be associated with a heavy reliance on seeds (Kay et al. 2004; Ross et al. 2012). In another example, Meloro et al. (2015) identified shape traits that were attributable to diet in bush babies, lemurs, pottos, and American monkeys, but not in Afro-Eurasian monkeys.

A number of potential reasons can be postulated as to why it has proven difficult to identify a link between mandibular morphology and diet in extant primates. First, several non-dietary factors have been found to influence masticatory biomechanics, including canine size, developmental constraints, and allometry (Lucas 1981; Smith 1983, 1984; Daegling & McGraw 2001; Daegling & Grine 2006). Second, there is evidence that phylogeny influences mandibular shape in primates (Raveloson et al. 2005; Meloro et al. 2015; Miarisoa et al. 2023). Third, it has been argued that the dietary data normally used in work on the relationship between mandibular morphology and diet in primates are inadequate because they do not account for the mechanical properties of food (Ross et al. 2012). Fourth, several researchers have proposed that mandibular morphology may be more closely linked to feeding behaviour, such as time spent feeding than food type (Taylor et al. 2008; McGraw & Daegling 2012; Vogel et al. 2014; Ross & Iriarte-Diaz 2019). Lastly, a link may have proven difficult to identify due to the limitations of the type of morphological data used in most studies published to date – namely, two-dimensional data (e.g., Bouvier & Hylander 1981; Taylor 2002, 2006a, 2006b; Daegling & McGraw 2007; Meloro et al. 2015).

The study reported here focused on the last of these possibilities and investigated the relationship between three-dimensional (3D) mandibular shape and diet in a sample of extant primates. The study was inspired by recent work that found a relationship between the 3D shape of the mandible and diet in two groups of non-primate mammals, bears (van Heteren & Figueirido 2019) and mice (Kono et al. 2017). To our knowledge, our study is the most comprehensive 3D analysis of mandible shape and diet in primates carried out to date. A few studies have used 3D data to investigate the relationship between mandibular shape and diet in primates, but the studies in question were more limited in scope as they focused on a single region of the mandible (Terhune et al. 2011, 2015; Terhune 2013) or a single genus (Burrows & Smith 2005; Pitirri et al. 2020; Laird et al. 2020).

In our study, we used a suite of techniques called geometric morphometrics (GM), which allows shape variation to be investigated within a well-understood statistical framework that yields easily interpreted numerical and visual results (Slice 2007). The sample was taxonomically diverse; 27 species and five families of primates were represented among 214 individuals. Because previous studies have found that allometry and phylogeny both influence mandibular shape variation in primates, we ran analyses with and without correcting for the effects of each. In an effort to address the problem of not properly capturing the mechanical properties of food raised by Ross et al. (2012), we included dietary information by i) assigning the species to standard dietary categories and ii) deploying Fish & Lockwood's (2003) Diet Quality Index (DQI).

2 Material and methods

2.1 Sample and data preparation

Our sample included mandibles of 214 individuals, comprising 27 species and five families. The specimens are curated at the Natural History Museum in London, UK, and the Powell-Cotton Museum in Birchington-on-Sea, Kent, UK. Only adult males were included in the sample to avoid the confounding effects of ontogeny and sexual dimorphism. Adult status was determined based on third molar eruption, whilst sex was determined with the aid of the museums' catalogues.

Forty landmarks were used to capture mandibular shape (Fig. 1; Supplementary Material Table 1). According to Bookstein's (1997) scheme, four of the landmarks were type I landmarks and 36 were type II. A RevWare MicroScribe 3D G2X digitising arm was used to record the x,y,z coordinates of the landmarks. Data collection was carried out by a single observer (JO). Intra-observer error was assessed by repeating landmark acquisition three times on a human, guenon, and baboon mandible. The repeated landmark configurations were superimposed using Generalized Procrustes Analysis and obtain pairwise Procrustes distances for the repeated configurations. The smallest distance between the three species was over three times larger than the largest difference between repeated measurements of each mandible. This implies that the intra-observer error in the data is unlikely to influence the interpretation of the results (Neubauer et al. 2009, 2010).

Once the landmark data had been collected, they were subjected to Generalized Procrustes Analysis (GPA), which removes translational, rotational, and scale effects from landmark data (Slice 2007). The Procrustes coordinates yielded by the GPA were used in subsequent analyses.

2.2 Analyses

After completing the GPA, we ran two sets of analyses. One focused on the association between mandibular shape and dietary categories, the other examined the relationship between mandibular shape and the DQI. Previously we explained that there is evidence that allometry influences masticatory biomechanics (Smith 1983; Ravosa 1991; Daegling & Grine 2006) and that phylogeny impacts man-

Fig. 1. Location of landmarks used in the study to capture the 3D shape of the mandibles.

dibular shape variation in primates (Raveloson et al. 2005; Meloro et al. 2015). With this in mind, we ran analyses of raw data, analyses in which we corrected for allometry, analyses in which we corrected for phylogeny, and analyses in which we corrected for both allometry and phylogeny. This systematic approach enabled us to illuminate the effects of controlling for allometry and phylogeny separately and together.

2.2.1 Mandibular shape vs dietary categories

The initial step in the investigation of whether there is an association between mandibular shape and dietary categories was to assign each specimen to a dietary category. To do this, we employed the dietary categories and assignment criteria utilised by Plavcan & van Schaik (1992). As such, the dietary categories we used were 1) frugivores, 2) folivore/frugivores, 3) frugivore/folivores, and 4) frugivore/insectivores. If fruit accounted for ≥ 85% of a species' diet, it was assigned to the frugivores category. A species was assigned to the frugivore/folivores category if ≤ 85% of its diet consists of fruit and ≥ 15% is non-fruit plant materials. Conversely, if ≤ 85% of a species' diet consists of non-fruit plant materials and ≥ 15% is fruit, it was assigned to the folivore/frugivores category. If fruit accounts for ≤ 75% of a species' diet and insects account for ≥ 25%, the species was assigned to the frugivore/insectivores category. Published information was used to assign the specimens to the dietary categories. The assignments and supporting references are shown in Supplementary Material Table 2.

Having assigned the specimens to dietary categories, we investigated the relationship between mandibular shape and dietary categories with the Procrustes coordinates in their raw state, i.e., as they emerge from the GPA. The suite of analyses we carried out are commonly used in GM-based comparative anatomical studies (e.g., Harvati & Weaver 2006; Mitteroecker et al. 2013). We began by subjecting the coordinates to canonical variates analysis (CVA). We then ran a principal component analysis (PCA) on the raw coordinates, followed by a noise reduction procedure devised by Baylac & Frieß (2005). In this procedure, PCs are sequentially added to a discriminant function analysis (DFA) until the cross-validation percentage (CVP) begins to drop; the PCs that contribute positively to the CVP are retained for further analysis. Thereafter, we subjected the retained PCs to MANOVA to assess whether the shapes of the mandibles of the four dietary categories are significantly different.

After completing the analyses of the raw Procrustes coordinates, we assessed the relationship between mandibular shape and dietary categories while controlling for the effects of allometry. In this analysis, we used Ordinary Least Squares (OLS) regression to regress the Procrustes coordinates onto log centroid size and generate allometry-free residuals (Monteiro 1999). We then subjected the residuals to the same suite of analyses to which we subjected the raw Procrustes coordinates.

Upon completion of the analyses of the allometry-free residuals, we evaluated the association between mandibular shape and dietary categories while controlling for phylogeny. To do this, we first created a consensus phylogenetic tree of the 27 species with the aid of the 10kTrees Project website (Arnold et al. 2010). We then mapped the raw Procrustes coordinates onto the phylogenetic tree with squared-change parsimony and generated a set of independent contrasts (Klingenberg & Marugán-Lobón 2013). Thereafter, we subjected the independent contrasts to the same suite of analyses to which we subjected the raw Procrustes coordinates and allometry-free residuals.

The last step in this part of the study was to assess the relationship between mandibular shape and dietary categories while controlling for the effects of both allometry and phylogeny. To do this, we repeated the last set of analyses but with allometry-free residuals rather than raw Procrustes coordinates. As before, the allometry-free residuals were generated by carrying out an OLS regression in which the species' raw Procrustes coordinates were regressed on their log centroid sizes.

The CVAs and OLS regressions were carried out in MorphoJ (Klingenberg 2011), the PCAs in Morphologika (O'Higgins & Jones 2006), and the DFAs in R (R Core Team 2020). SPSS (IBM SPSS Inc. 2020) was used to conduct the MANOVAs. We utilised the 'map onto phylogeny' routine of MorphoJ (Klingenberg 2011) to generate the independent contrasts.

2.2.2 Mandibular shape vs the DQI

To investigate the relationship between mandibular shape and dietary quality, we employed Fish and Lockwood's (2003) DQI. This index was adapted from Sailer et al.'s (1985) dietary quality equation, which was designed to capture the relative contribution of the major types of food to a primate's diet. A species' DQI value is calculated with the following equation:

$$\mathrm{DQI} = 0.33\mathrm{L} + 0.67\mathrm{F} + \mathrm{M}$$

where L is the percentage of time spent foraging for leaves and structural parts of plants (e.g., stems, pith, bark); F is the percentage of time spent foraging for fruit and other reproductive parts including nectar; and M is the percentage of time spent foraging for animal prey (including both vertebrates and invertebrates). The coefficients 0.33 and 0.67 are weightings designed to capture the lower nutrient quality and ease of digestion of leaves and fruit relative to animal products. DQI values were obtained from published literature. We were unable to locate DQI values for 10 of the species, so the sample size for this set of analyses was reduced to 17 (DQI values for the species in question are listed in Table S1, along with the supporting sources).

We carried out four analyses to evaluate the relationship between mandibular shape and the DQI. In the first, we did not control for the effects of allometry or phylogeny. We calculated the Procrustes coordinates of the average shape of each of the 17 species, and then used OLS regression to evaluate the strength of the relationship between the species' Procrustes coordinates and DQI values. We assessed the significance of the relationship with a permutation test (Anderson & Robinson 2001). In this test, the species were randomly reassigned DQI values and a new regression analysis was carried out. This was repeated until 1,000 permuted datasets had been analysed. The original r^2 value was then compared to the distribution of the r^2 values yielded by the permuted datasets.

In the second analysis, we controlled for the effects of allometry but not the effects of phylogeny. Following Mitteroecker et al. (2013), we regressed the species' average Procrustes coordinates on their log centroid sizes to obtain allometry-free residuals. We then regressed the allometry-free residuals on the DQI values. Thereafter, the significance of the relationship was assessed with the permutation test employed in the last analysis.

In the third analysis, we controlled for the effects of phylogeny but not the effects of allometry. In this analysis, we used phylogenetic generalised least squares (PGLS) regression to assess the significance of the relationship between the species' average Procrustes coordinates and their DQI values. The phylogenetic tree used in the PGLS regression was created with the aid of the 10kTrees Project website (https://10ktrees.nunn-lab.org/).

In the fourth and final analysis that dealt with the relationship between mandibular shape and DQI, we controlled for the effects of both allometry and phylogeny. To begin with, we carried out an OLS regression of the species' average Procrustes coordinates and log centroid sizes to generate

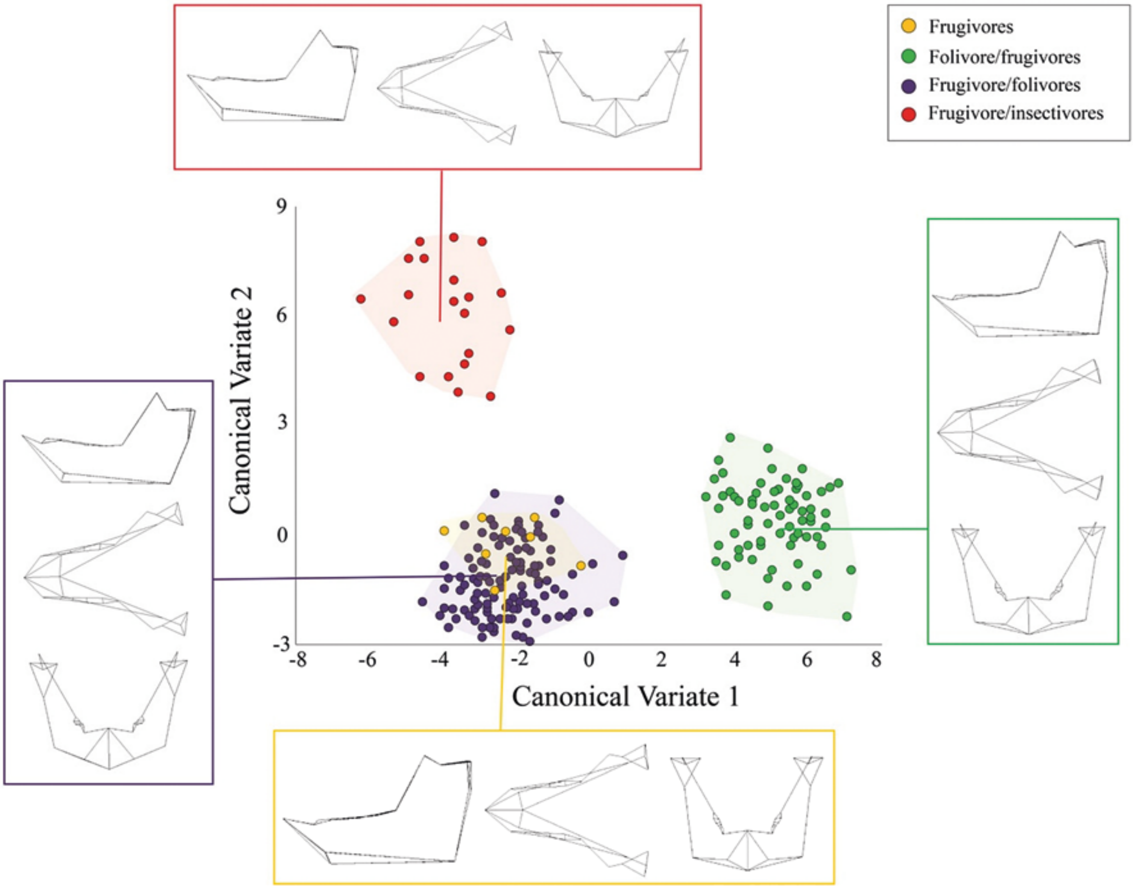

Fig. 2. Scatterplot showing the two CVs yielded by the raw data, with specimens assigned to their dietary categories. The wireframes depict the mean shapes of the four dietary categories.

allometry-free residuals. We then used PGLS regression to assess the significance of the relationship between the size-free residuals and the species' DQI values. The phylogenetic tree utilised in the PGLS regression was the same as the one employed in the last analysis.

The OLS regressions and the permutation tests were performed in MorphoJ (Klingenberg et al. 2011). The PGLS regressions were carried out with the procD.pgls function in the R software environment (R Core Team 2020).

3 Results

3.1 Mandibular shape *vs* dietary categories

3.1.1 Analyses of raw Procrustes coordinates

The CVA of the raw Procrustes coordinates yielded two CVs. CV1 accounted for 66% of the total variance and CV2 for 23%.

When the two CVs were plotted against each other, three groups were discernible (Fig. 2). The first comprised the folivore/frugivores, which scored high on CV1 but low on CV2. The second group consisted of the frugivores/insectivores. These scored low on CV1 but high on CV2. The third group was formed by the frugivores and the frugivore/folivores. These scored low on both CV1 and CV2.

Seventy-one PCs were retained from the PCA of the raw Procrustes coordinates. Collectively, these PCs accounted for 100% of the total variance. There were no obvious differences relating to dietary category on PC1 (27% of total variance), PC2 (23% of total variance), or PC3 (10% of total variance). However, differences were discernible on PC4 (8% of total variance) when PC4 was plotted against PC3 (Fig. 3). Most of the folivore/frugivores were positioned towards the positive end of the PC, while most of the frugivore/folivores were located towards its negative end. The frugivores and frugivore/insectivores fell in the zone of overlap between the folivore/frugivores and the frugivore/folivores.

The overall MANOVA performed on the PCs derived from the raw Procrustes coordinates was significant (λ 0.014, F = 6.166, $p < 0.0001$) and so were all the pairwise comparisons (Table 1). This indicates that the four dietary categories are distinguishable even though the frugivore specimens and the frugivore/folivore specimens overlapped in the CVA and PCA plots.

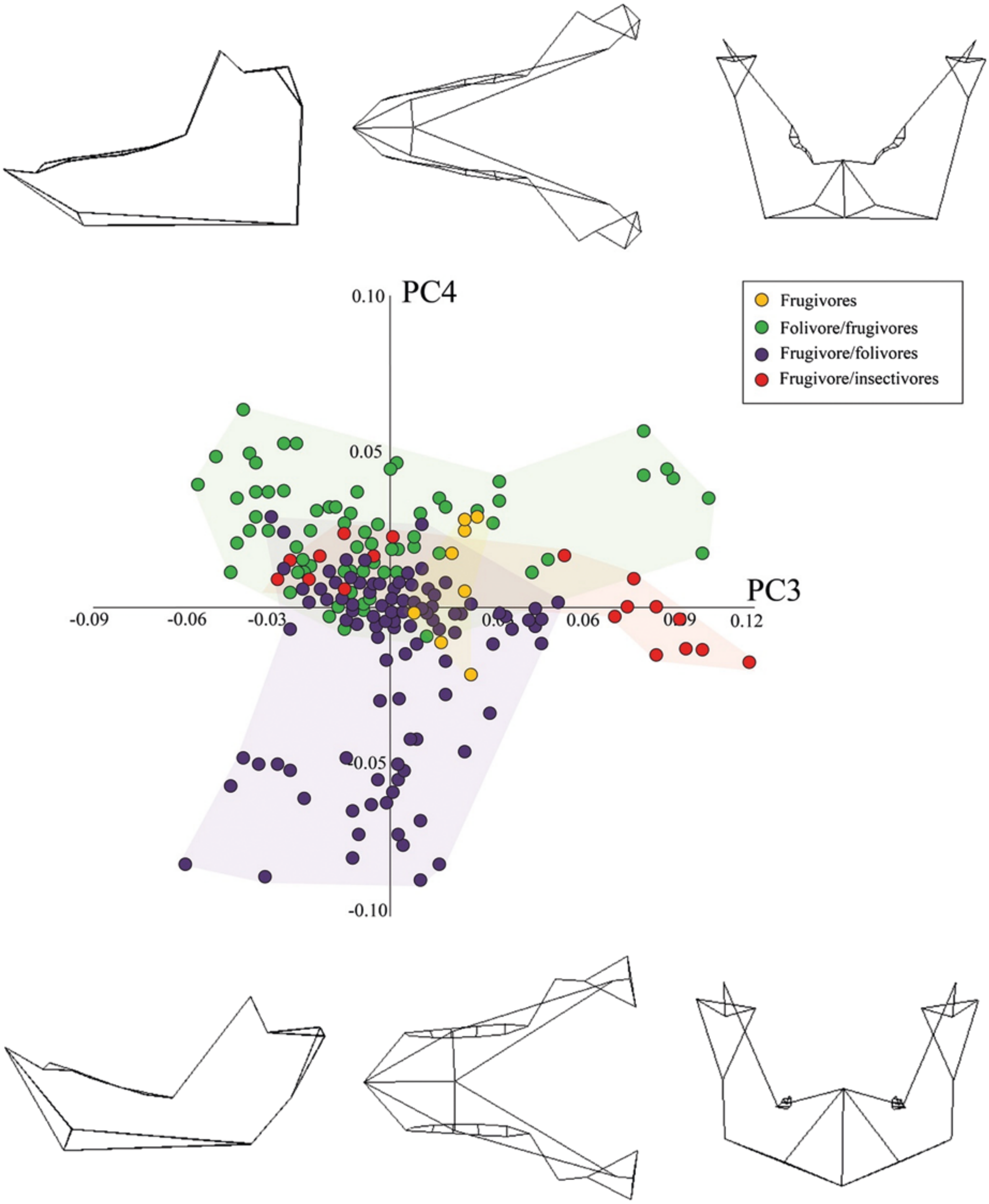

Fig. 3. Scatterplot showing PC3 and PC4 derived from the raw data, with specimens assigned to their dietary categories. The wireframes depict the shape associated with positive and negative extreme of PC4.

3.1.2 Analyses with allometric correction but not phylogenetic correction

The CVA of the allometry-free residuals yielded two CVs. One accounted for 78% of the total variance, the other for 14%.

Differences among the dietary categories were apparent when the two CVs were plotted against each other in Fig. 4. On CV1, the frugivore/insectivores plotted negatively, the folivore/frugivores plot positively, and the frugivore/folivores and frugivores were located in an intermediate position. On CV2, the frugivore/insectivores, folivore/frugivores, and frugivore/folivores overlapped on the positive end, while frugivores separated from the other categories by plotting

Table 1. MANOVA results for pair-wise comparisons between dietary categories using raw data. *p*-values are FDR-corrected (Benjamini & Hochberg 2000).

	Frugivore/folivores	Folivore/frugivores	Frugivore/insectivores
Folivore/frugivores	λ 0.125 F = 11.260 *p* = 0.04*	–	–
Frugivore/insectivores	λ 0.0137 F = 5.499 *p* = 0.04*	λ 0.020 F = 11.029 *p* = 0.042*	–
Frugivores	λ 0.218 F = 2.268 *p* = 0.042*	λ 0.004 F = 2.306 *p* = 0.013*	λ 0.040 F = 8.345 *p* = 0.011*

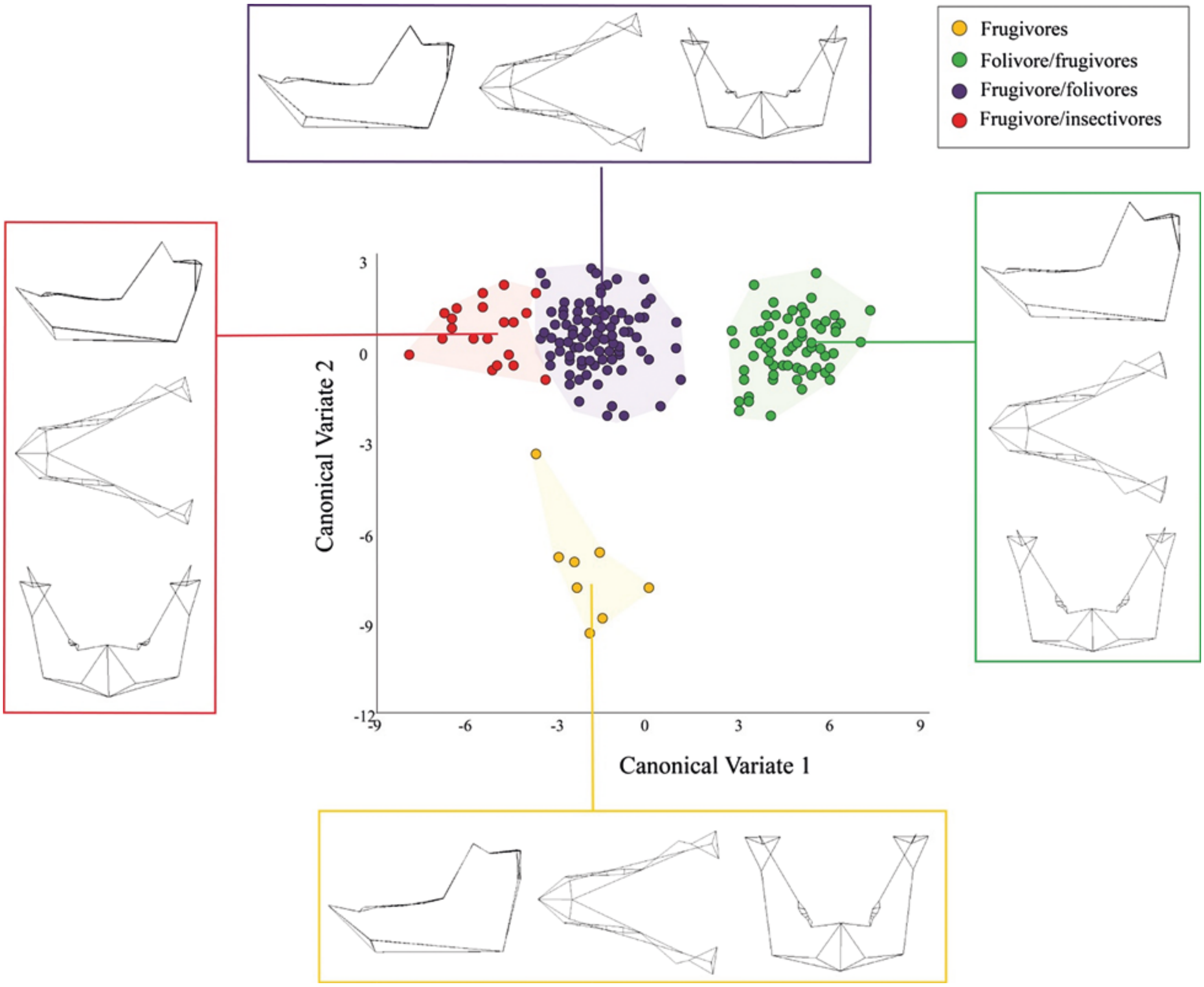

Fig. 4. Scatterplot of the two CVAs derived from the allometry-free residuals, with specimens assigned to their dietary categories. The wireframes depict the mean shapes of the four dietary categories.

more negatively. Thus, in contrast to the situation with the raw data, there was little overlap among the four dietary categories, including between the frugivores and frugivore/folivores. The wireframes depict the mean shape of each group.

Forty-three PCs were retained from the PCA of the allometry-free residuals. Together, these PCs accounted for 98% of the total variance. There were no obvious differences relating to the dietary categories on PC1 (28% of total variance). However, when PC2 (19% of total variance) was plotted against PC3 (11% of total variance), differences could be discerned (Fig. 5). While the frugivores and frugivore/folivores overlapped completely on both PCs, the two groups

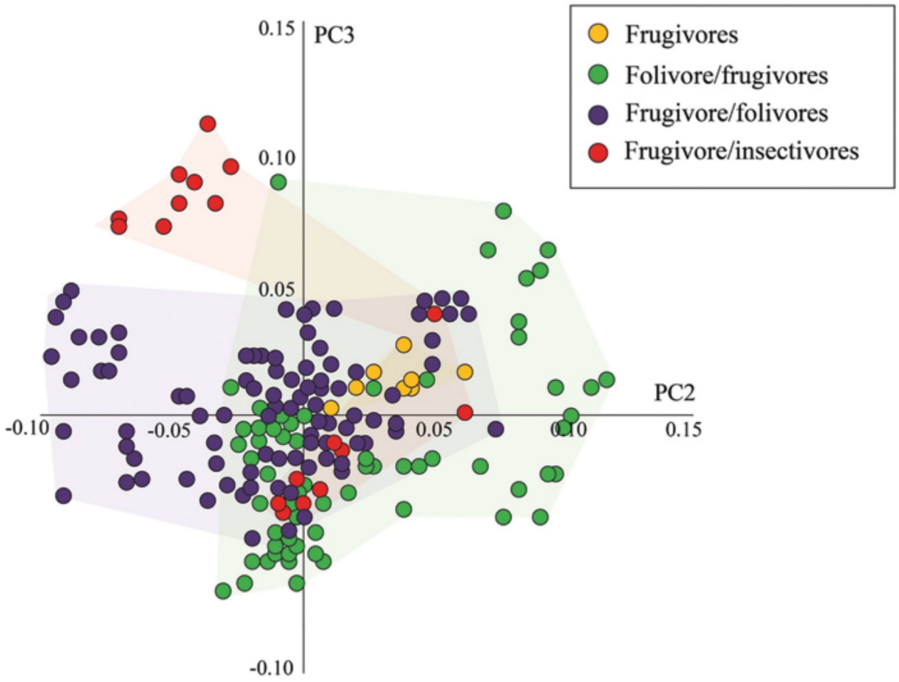

Fig. 5. Scatterplot showing PC2 and PC3 derived from the allometry-free residuals, with specimens coloured by dietary category.

Table 2. MANOVA results for pair-wise comparisons between dietary categories using the allometrically corrected data. *p*-values are FDR-corrected (Benjamini & Hochberg 2000).

	Frugivore/folivores	Folivore/frugivores	Frugivore/insectivores
Folivore/frugivores	ƛ 0.275 F = 21.746 *p* = 0.002*	–	–
Frugivore/insectivores	ƛ 0.191 F = 6.514 *p* = 0.002*	ƛ 0.239 F = 10.654 *p* = 0.002*	–
Frugivores	ƛ 0.403 F = 7.554 *p* = 0.002*	ƛ 0.226 F = 9.442 *p* = 0.002*	ƛ 0.027 F = 12.458 *p* = 0.002*

tended to score more negatively on PC2 than did the folivore/frugivores. In addition, the frugivore/insectivore specimens formed two subgroups. One nine-specimen subgroup plotted negatively on PC2 and positively on PC3 and therefore occupied the upper left quadrant of the plot by itself. The second nine-specimen subgroup plotted more positively on PC2 and more negatively on PC3, and consequently overlapped with the folivore/frugivores, frugivore/folivores, and frugivores.

The overall MANOVA performed on the PCs derived from the allometry-free residuals was significant (ƛ 0.162, F = 7.999, $p < 0.001$), as were all the pairwise comparisons (Table 2). Thus, there are differences among the average shapes of the four dietary categories.

3.1.3 Analyses with phylogenetic correction but not allometric correction

The CVA of the phylogenetically corrected data yielded three CVs. CV1 accounted for 81% of the total variance, CV2 for 12%, and CV3 for 7%. There was no interpretable pattern of variance on CV3. However, the dietary categories separated on CV1 when CV1 was plotted against CV2 (Fig. 6). Specifically, the folivore/frugivores plotted the most negatively on CV1, while the other three categories grouped close together on the positive end, with frugivores and frugivore/insectivores scoring the most positively.

The PCA of the phylogenetically-controlled data yielded 20 CVP PCs, which accounted for 99% of the total shape

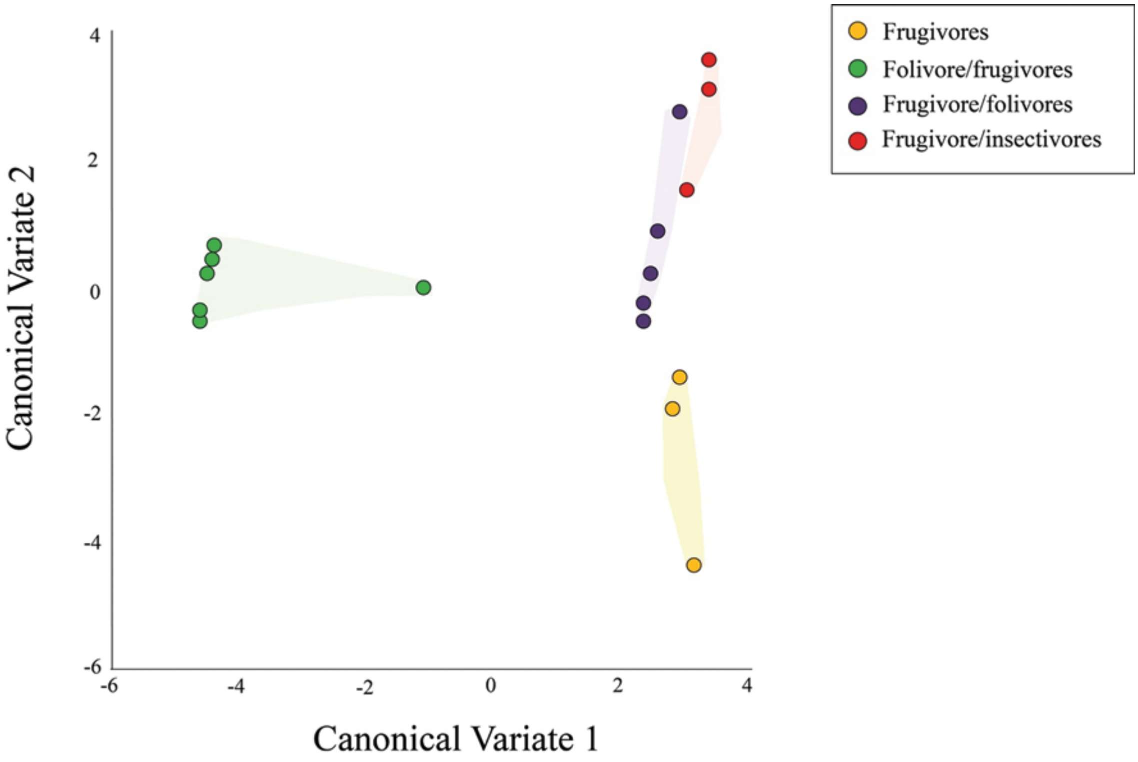

Fig. 6. CVA scatterplot depicting CV1 and CV2 derived from the phylogenetically controlled data.

variance. When PC1 was plotted against PC2 (Fig. 7), the only interpretable variance was that the frugivore/insectivores scored more negatively on both PCs than all other species, except one frugivore species. The other categories overlapped with one another on both PCs.

The overall MANOVA performed on the PCs derived from the phylogenetically controlled data was not significant ($p = 0.085$).

3.1.4 Analyses with both allometric correction and phylogenetic correction

The CVA of the raw Procrustes coordinates yielded three CVs. CV1 accounted for 79% of the total variance, CV2 for 13%, and CV3 for 7%.

There was no interpretable pattern in variance on CV3, but when CV1 and CV2 were compared, the four dietary categories separated on CV1 (Fig. 8). Specifically, the folivore/frugivores plotted most positively, while frugivores and frugivore/folivores overlapped and plotted most negatively. The frugivore/insectivores plotted between the frugivore/folivores and the folivore/frugivores on CV1.

The PCA yielded 20 CVP PCs, which accounted for 99% of the total shape variance. The only PC that yielded a readily interpretable pattern was PC1. As Fig. 9 shows, on this PC, the frugivore/insectivores tended to plot negatively, the frugivore/folivores tended to plot positively, and the frugivores and folivore/frugivores fell between the two other groups.

The overall MANOVA performed on the PCs from the allometrically- and phylogenetically corrected data was significant (λ 0.003, $F = 2.739$, $p = 0.006$). However, in contrast, to the previous two sets of MANOVAs, only two of the six pairwise comparisons were significant (Table 3). These were the frugivore/insectivores vs folivore/frugivore comparison, and the frugivores vs folivore/frugivores one.

3.2 Mandibular shape *vs* the DQI

3.2.1 Analysis of raw Procrustes coordinates

There was a positive linear relationship between the raw Procrustes coordinates and the DQI values when they were plotted against each other. However, the OLS regression indicated that, while the relationship was close to being statistically significant, it did not reach the cut-off ($r^2 = 0.87$, $p = 0.061$).

3.2.2 Analysis with allometric correction but not phylogenetic correction

When allometry-free residuals were plotted against DQI, there was a positive relationship between the variables, but the OLS regression indicated that it was not significant ($r^2 = 0.90$, $p = 0.162$).

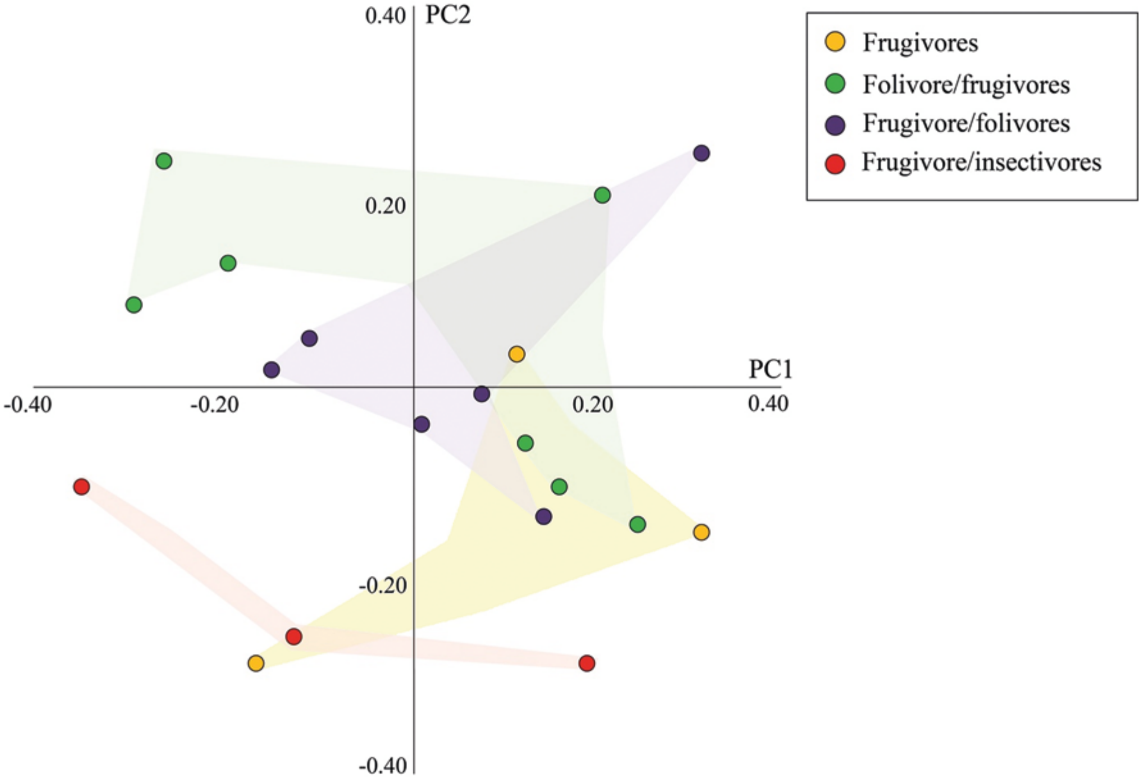

Fig. 7. PCA scatterplot depicting the shape variance of phylogenetically controlled residuals when PC1 is plotted against PC2.

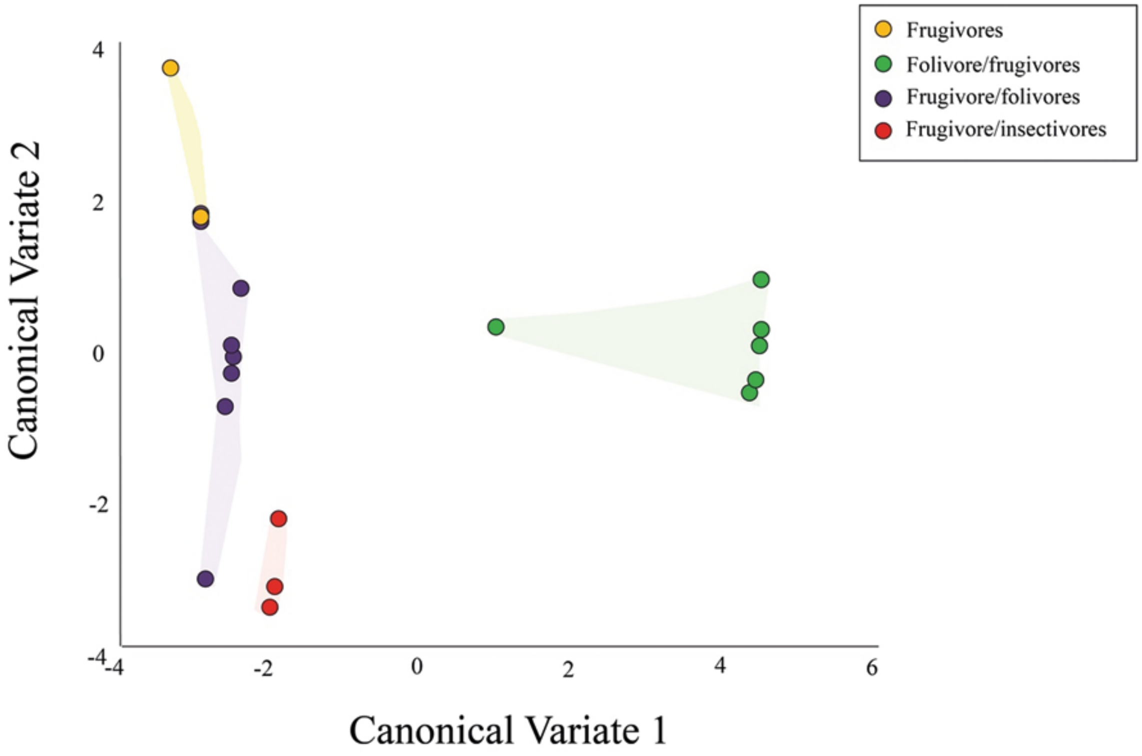

Fig. 8. CVA scatterplot depicting the CV1 and CV2 derived from the allometrically and phylogenetically controlled data.

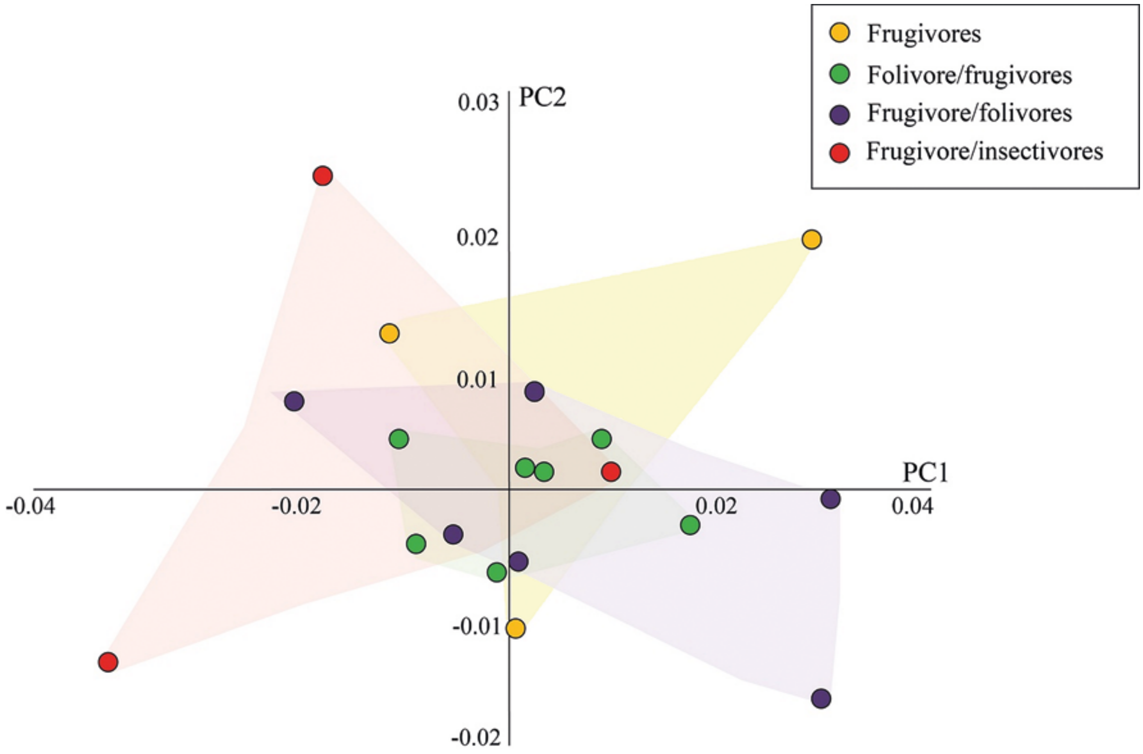

Fig. 9. PCA scatterplot depicting the shape variance of allometry and phylogenetically controlled residuals when PC1 is plotted against PC2.

Table 3. MANOVA results for pair-wise comparisons between dietary categories when allometry is minimized and phylogeny is controlled for in the data. *p*-values are FDR-corrected (Benjamini & Hochberg 2000).

	Folivore/frugivores	Frugivore/folivores	Frugivore/insectivores
Frugivore/folivores	λ 0.095 F = 4.061 *p* = 0.094	–	–
Frugivore/insectivores	λ 0.001 F = 435.289 *p* = 0.003*	λ 0.173 F = 1.438 *p* = 0.636	–
Frugivores	λ 0.001 F = 2978.048 *p* = 0.003*	λ 0.424 F = 603 *p* = 0.877	λ 0.488 F = 0.263 *p* = 0.877

3.2.3 Analysis with phylogenetic correction but not allometric correction

The PGLS regression of the raw Procrustes coordinates and the DQI data yielded a non-significant p-value ($p = 0.194$).

3.2.4 Analysis with both allometric correction and phylogenetic correction

The PGLS regression of the allometry-free residuals and the DQI data also yielded a non-significant p-value ($p = 0.732$).

4 Discussion

In the study reported here, we investigated whether there is a relationship between 3D mandibular shape and diet in 214 extant primate individuals from 27 species and five families. We carried out two sets of analyses. In the first, we investigated whether there was a relationship between mandibular shape and four standard dietary categories. We found an association between mandibular shape and the dietary categories when we employ raw Procrustes coordinates and allometry-free residuals, but the relationship was weak to non-existent when the effects of phylogeny were considered. In the second set of analyses, we investigated whether there was a relationship between mandibular shape and diet quality as measured by Fish and Lockwood's (2003) Diet Quality Index (DQI). None of the analyses supported the existence of such a relationship. No matter whether the data were raw, corrected for the effects of allometry, corrected for the effects of phylogeny, or corrected for the effects of both allometry and phylogeny, the regression analysis returned a non-significant p-value. Taken together, the results of the two sets of analyses suggest that there is, at most, a very weak relationship between 3D mandibular shape and diet in extant primates, and that allometry and phylogeny are considerably more important influences on the 3D shape of primate mandibles. Contrary to expectation, the use of 3D methods did not provide better results than 2D methods used in previous studies.

An obvious concern about these results is that the landmarks we used do not adequately capture the mandibular differences among primates. To evaluate this possibility, we used the wireframes in Fig. 4 to identify traits that vary among the dietary categories and then compared those traits to the traits that previous studies have suggested differentiate frugivores, frugivore/folivores, folivore/frugivores, and frugivore/insectivores. The wireframes depict the mean shapes of the four dietary categories.

We found good concordance between the two sets of traits. For example, the wireframes indicated that frugivores and frugivore/folivores tend to have larger, more projecting incisive processes than folivore/frugivores and frugivore/insectivores. A number of previous studies have identified large, projecting incisive processes as a characteristic of frugivorous primates, including Hylander (1975), Wright (2005), and McGraw et al. (2016).

Similarly, the wireframes suggested that folivore/frugivores differ from the other dietary categories in having taller, mediolaterally larger condyles; more upright, dorso-ventrally wider rami; and smaller, less projecting incisive processes. The first of these traits aligns with the findings of Herring & Herring (1974), Ward & Molnar (1980), Hylander (1979, 1985), Bouvier (1986), Ravosa (1990, 1996), Spencer & Demes (1993), and Taylor (2002). These authors all found that tall, mediolaterally large mandibular condyles are among the traits that distinguish primates who consume large amounts of foliage. The second trait – more upright, dorso-ventrally thicker rami – is consistent with the results obtained by Smith (1983) and Ravosa (1990). Smith (1983) found that folivorous primates tend to have dorso-ventrally wider rami than frugivorous ones, while Ravosa (1990) found that folivorous colobines have smaller mandibular angles (and therefore more upright ramii) than frugivorous cercopithecines. That folivore/frugivores tend to have smaller, less projecting incisive processes than frugivores, frugivore/folivores, and frugivore/insectivores is in line with Hylander's (1975) and McGraw et al.'s (2016) findings regarding the differences between folivores and frugivores. These authors' analyses indicated that folivores have smaller incisors and incisor rows than frugivores.

Several traits that distinguish frugivore/insectivores from the other three dietary categories were also discernible in the wireframes. The wireframes suggested that frugivore/insectivores tend to have wider bigonial breadths and shorter, more recumbent rami. The first of these traits may be consistent with Koyabu & Endo (2009)'s results. These authors found that primates who rely on hard food items have wider bigonial breadths than those that subsist on soft food items, which they suggested is connected with the greater bite force needed to process hard foods. Given that the exoskeletons of insects are harder than leaves and fruits, this may explain why frugivore/insectivores tend to have wider bigonial breadths than frugivores, folivore/frugivores, and frugivore/folivores, according to the wireframes.

The fact that several of the dietary category-distinguishing traits identifiable in the wireframes have been highlighted in studies that used different methods suggests that the results of the present study are not a consequence of incorrect landmark selection and, therefore, are informative about the relationship between mandibular shape and diet in extant primates.

Of the various published assessments of the relationship between mandibular morphology and diet in primates, the one that is most similar to our study is Meloro et al. (2015). Like us, these authors examined a large number of primate species, utilised GM methods, and controlled for the effects of allometry and phylogeny. The main difference between their study and ours is that they used 2D data. Meloro et al. (2015) results were strikingly similar to the ones we obtained. Most importantly, they found that once allometry and phylogeny were taken into account, diet only had a weak influence on mandibular shape in the primate order as a whole and no influence when two of the major primate groups (anthropoids and catarrhines) were considered individually. As was the case with our study, Meloro et al. (2015) analyses indicate that allometry and phylogeny are stronger influences on mandibular shape variation in primates than is diet.

To conclude, we initiated the study reported here to evaluate whether 3D shape analysis techniques would identify a clear relationship between mandibular morphology and diet in extant primates in a way 2D morphometric techniques have so far been unable to do satisfactorily. We were optimistic that this would be the case because it is well-established that 3D shape analysis techniques can capture more detailed morphological information than standard morphometric techniques, and because 3D shape analysis techniques have proven useful for identifying diet-related mandibular traits in some other mammalian groups (Kono et al. 2017; Van Heteren & Figueirido 2019). However, the results of our analyses suggest that the failure of previous studies to identify a relationship between mandibular morphology and diet in extant primates was not a consequence of reliance on standard 2D morphometric techniques. Our analyses indicate that the 3D shapes of the mandibles of extant primates are more strongly influenced by allometry and phylogeny than by diet, and that when allometry and phylogeny are controlled for, the impact of diet on mandibular shape is, at best, weak. Thus, our study supports the suggestion that diet is not the primary influence on mandibular morphology in primates (Raveloson et al. 2005; Taylor et al. 2008; Ross et al. 2012; McGraw & Daegling 2012; Vogel et al. 2014; Meloro et al. 2015; Ross & Iriarte-Diaz 2019) and implies that claims about the diets of extinct primates based on mandibular traits should continue to be treated with caution.

Statement of ethics: An ethics statement was not required for this study type, no human or animal subjects were used.

Conflict of interest statement: The authors have no conflicts of interest to declare.

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KD: co-devised study, edited manuscript.
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