One Genus or Two? Evaluating Whether Gracile and Robust Capuchin Monkeys are Validly Classified as Separate Genera Based on Craniofacial Shape

Katharine L. Balolia1 · Alexandra Wulff1

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Abstract

Assessments of whether closely related species should be classified into more than one genus have been a longstanding source of controversy in primatology. For example, researchers hold differing opinions about whether cebine species should be classified into one or two genera. In this study, we investigated whether craniofacial shape is a reliable taxonomic indicator among cebines and statistically evaluated whether the magnitude of craniofacial shape differences observed among gracile and robust capuchin species is consistent with a two-genus taxonomic framework. We quantify craniofacial shape using 3D landmark data taken from 72 surface models, representing five cebine species (Cebus albifrons, C. capucinus, C. olivaceus, C. (Sapajus) libidinosus, and C. (S.) macrocephalus). We find that although statistically significant shape differences exist between gracile and robust capuchins in all four craniofacial regions investigated (face and palate, basicranium, calvarium, and frontal region of the calvarium), the magnitude of shape differences between species pairs does not support gracile and robust species being classified into separate genera. The shape of the frontal region of the calvarium and the face and palate show the highest magnitude of shape differences between the gracile and robust capuchin groups, and both regions are good taxonomic predictors, showing correct classification rates of 97% and 96%, respectively. At the species-level, face and palate shape is the only craniofacial measure that consistently shows high correct classification rates among species (84-97% for combined-sex analyses). Our findings suggest that robust capuchin species that are often assigned to Sapajus may be more appropriately considered as Cebus under a single-genus framework for cebines based on craniofacial shape evidence.

Keywords Cebus · Sapajus · Geometric morphometrics · 3D surface scanning · Platyrhine · Taxonomy
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Introduction

Assessments of whether closely related species should be classified into more than one genus have been a longstanding source of controversy in primatology and palaeoanthropology, and multiple criteria have been proposed as the basis for grouping species at the genus level (Wood & Collard, 1997, 1999; Groves, 2001, 2004, 2014; Wood & Lonergan, 2008; Garbino, 2015). Researchers have assigned primate species to genera based on criteria such as divergence time, morphological, behavioural, and ecological characteristics, including whether specimens show phenotypic differences that are associated with different grades, or adaptive zones (Garbino, 2015; Groves, 2001; Wood & Collard, 1997, 1999; Wood & Lonergan, 2008). Among extant and extinct primate species, assigning species to genera is typically undertaken based on a minimum criterion that species subsumed within the proposed genus are monophyletic (Garbino, 2015; Groves, 2001, 2004), and the proponents of this viewpoint maintain that monophyly alone is not a uniquely sufficient basis by which to delineate genera. Furthermore, acceptance of the monophyly criterion is not universal. For example, others argue that genera can be delineated by groups of species that occupy different ecological circumstances or adaptive zones, whether they be monophyletic or paraphyletic (Wood & Collard, 1999).

Overall, researchers disagree about how to delineate primate species by genus. These disagreements are in part reflective of differing views about what a genus-level taxonomic rank should represent and whether it is the unique phenotypes found within a group (apomorphies), or those that unite the group (synapomorphies) that are the most important for classification at this level (Garbino, 2015). Among extinct hominin species, the basis for assigning species to genera becomes even more problematic based on an emphasised reliance on cranial, mandibular, postcranial, and dental evidence in assessing behaviour, evolutionary relationships (including whether groups of taxa are monophyletic), and whether adaptive zones occupied by taxa are distinctive enough to categorise species into more than one genus (Wood & Collard, 1997, 1999; Wood & Lonergan, 2008). As craniodental evidence is the primary basis by which taxonomic rank among fossil hominins is assessed, information about whether hard tissue morphology can validly delineate primate taxa at the species and genus level is likely to afford insights about whether taxonomic assessments among fossil primates, including hominins, are consistent with those among extant primate groups.

During the past decade, researchers have debated whether gracile and robust capuchin monkeys, traditionally assigned to a single genus (*Cebus* Erxleben 1777), may alternatively be considered as two genera, with gracile capuchin species (*C. albifrons*, *C. capucinus*, *C. kaapori*, and *C. olivaceus*) retained under *Cebus*, and the robust capuchin species (*C. apella*, *C. cay*, *C. flavius*, *C. libidinosus*, *C. macrocephalus*, *C. nigritus*, *C. robustus*, *C. xanthosternos*) placed into a second genus (*Sapajus* Kerr, 1792) (Lynch-Alfaro, Boubli, et al., 2012a; Lynch-Alfaro, Silva Jr, & Rylands, 2012b; Silva, 2001). The main arguments for separating these 12 recognised species into two separate genera are based on morphological (including cranial, dental, postcranial, and facial pelage) differences and some.
behavioural differences between the two groups, including those associated with tool use, vocalisations, courtship, and mating behaviours (Lynch-Alfaro, Silva Jr, & Rylands, 2012b). Findings based on molecular data show that each group comprises a well-supported monophyletic clade and are consistent with groupings made based on morphological and behavioural evidence (Lynch-Alfaro, Silva Jr, & Rylands, 2012b; Silva, 2001). Evidence to support the notion that the gracile and robust capuchin groups are monophyletic has been reported through several studies (Lynch-Alfaro, Boublí, et al., 2012a; Martins-Junior et al., 2015, 2018), leading these authors to advocate for genus-level distinctions between gracile and robust capuchins.

Although there are well-reasoned arguments for categorising gracile and robust capuchin species into different genera, including fulfillment of the criterion that all species within each proposed genus are monophyletic (Lynch-Alfaro, Boublí, et al., 2012a; Martins-Junior et al., 2015, 2018), not all researchers agree that the differences between the gracile and robust capuchin clades are sufficient for them to be separated into different genera (Feijó & Langguth, 2013; Rosenberger, 2012; Ruiz-García et al., 2012; Ruiz-García et al., 2016). Arguments that question the validity of capuchin species being separated into two genera are based on genetic evidence. Among these authors, Ruiz-García et al. (2016) have been the most vocal in arguing that categorising gracile and robust capuchin species into different genera (Lynch-Alfaro, Boublí, et al., 2012a) may be premature, as Lynch-Alfaro et al. (2012a, b) sampled too few genes as part of their analyses. Based on a large sample of gracile and robust capuchin monkey individuals, and using mitochondrial genetic data from 4-16 mitochondrial genes, subsequent analyses show that the genetic distances between species pairs representing gracile and robust groups are consistent with those of a single genus when compared with genetic distances observed across other platyrrhine genera (Ruiz-García et al., 2016). Importantly, this comprehensive genetic analysis also showed no monophyly within gracile and robust capuchin groups, further adding to the authors’ argument that these groups should be placed within a single genus, Cebus (Ruiz-García et al., 2016). Other researchers, while showing monophyly for each of the gracile and robust capuchin groups, make no genus-level assertions (Nascimento et al., 2015).

The main proponents of the gracile and robust capuchin monkeys being classified into two genera, Cebus and Sapajus, predominantly base their arguments on morphological differences between the two groups (Lynch-Alfaro, Silva Jr, & Rylands, 2012b; Silva, 2001; Wright et al., 2015). Gracile, or untufted, capuchins are characterised by the absence of a crown tuft and the lack of dark brown eyebrows, sideburns, and a beard relative to robust groups, whose males, and often females, show these traits (Lynch-Alfaro, Silva Jr, & Rylands, 2012b; Silva, 2001). Robust, or tufted, capuchins show more robust craniodental and mandibular traits than do gracile capuchins, including sagittal cresting in males, which these authors interpret as adaptations for processing hard and tough foods (Lynch-Alfaro, Silva Jr, & Rylands, 2012b; Silva, 2001; Wright et al., 2015). Some of these authors further argue that robust and gracile capuchins differ in their body proportions, where robust species show relatively short forelimbs, hands, and feet, relative to gracile capuchins (Lynch-Alfaro, Silva Jr, & Rylands, 2012b; Silva, 2001). Other researchers propose
that the gracile and robust capuchin groups, i.e., *Cebus* and *Sapajus* respectively, are best considered as *Cebus* subgenera (Feijó & Langguth, 2013). Little research has been conducted to quantitatively assess whether genus-level distinctions between *Cebus* and *Sapajus* are warranted based on hard tissue evidence. Research assessing whether there are interspecific cranial differences among two robust capuchin monkey species (*Cebus* (*Sapajus*) *nigritus* and *Cebus* (*Sapajus*) *libidinosus*) shows that statistically significant interspecific and interpopulation craniofacial shape differences exist (Arístide *et al.*, 2014). Beyond this research, quantitative research to understand intergroup and interspecific craniofacial shape differences among gracile and robust capuchin groups has not yet been conducted.

In assessing the validity of revisions to taxonomic nomenclature, while there is an argument for separating capuchin species into separate genera, the necessity for increasing the number of genera among the cebines may be questioned (Rosenberger, 2012). Much of the debate about whether the two capuchin monkey groups should be separated into two distinct genera indeed comes back to questions surrounding the purpose of genus-level classifications, specifically surrounding whether it is a) the unique, derived traits possessed by a group that should be emphasised in making genus-level distinctions, or b) the shared ancestral traits that are important (Garbino, 2015). A genus-level classification system that emphasises shared derived features (apomorphies) is consistent with genus-level distinctions based on adaptive zones (Wood & Collard, 1997, 1999; Wood & Lonergan, 2008). According to this perspective, differences in ecological habitat are likely to be associated with differences in morphological and behavioural adaptations (i.e., unique, derived characteristics) that also form the basis for genus-level classifications. When adopting this approach to genus-level classifications, one would expect morphological differences that are associated with the adaptive zone/ecological habitat of the candidate genus to be apomorphic within each genus, i.e., the apomorphic traits associated with the adaptive zone of the species grouping in question should be defining features of the candidate genus.

While there has been substantial debate about whether cebine species ought to be placed in one or two genera, beyond the work by Silva (2001) and Lynch-Alfaro, Silva Jr, and Rylands (2012b), there is a paucity of research that seeks to address this question based on craniofacial data, using morphometric techniques. Understanding whether craniofacial morphology can diagnose gracile and robust capuchin taxa, and understanding the degree of morphological differences between species pairs among those previously categorised into *Cebus* and *Sapajus*, is likely to afford important insights as to whether classifying the gracile and robust capuchin groups into separate genera based on morphological evidence is a valid endeavour. Using data taken from 3D surface models, we investigated craniofacial shape differences among three gracile capuchin and two robust capuchin species (*C. albifrons*, *C. capucinus*, *C. olivaceus*, *C. (Sapajus) libidinosus*, *C. (Sapajus) macrocephalus*). We first investigated whether *Cebus* and *Sapajus* species show quantifiable craniofacial shape differences at the genus level, and how well these two proposed genera can be distinguished from one another based on four craniofacial measures: face and palate shape, basicranial shape, calvarial shape, and frontal region of the calvarium shape. We conduct these analyses among gracile and robust groups separately to
address whether specific craniofacial regions can reliably diagnose taxa at the species level. We conduct further sex-specific analyses to assess whether sexual dimorphism confounds attempts to discriminate among capuchin taxa using craniofacial morphology. We use the results of these analyses to assess whether the magnitude of craniofacial shape differences between species of different proposed genera exceed those between species of the same genus. Finally, we consider these findings in the context of the taxonomic revisions suggested by Lynch-Alfaro, Silva Jr, and Rylands (2012b) of two distinct genera: *Cebus* and *Sapajus* to assess whether these two proposed genera are valid based on craniofacial shape.

**Methods**

**Sample and 3D Model Acquisition** The sample consists of 72 dentally mature cranial specimens belonging to three gracile capuchin species (*C. albifrons, C. capucinus* and *C. olivaceus*) and two robust capuchin species (*C. (S.) macrocephalus* and *C. (S.) libidinosus*) (Table I). We sampled equal numbers of males and females and obtained sex information from museum records. We obtained 3D surface models for all five taxa using a Creaform Go!Scan 20 or from CT data. We scanned the majority (42) of cranial specimens using a Creaform Go!Scan20 white light scanner and we obtained models for the remaining specimens (30) from CT data, which were converted to surface models. We processed scan data using each scanner’s proprietary software. All 3D models used have a scan resolution of <0.5 mm. Differences in how 3D models were generated are unlikely to have produced substantial measurement error (Balolia & Massey, 2021; Fruciano et al., 2017; Marcy et al., 2018).

**Data Collection**

We obtained morphometric data for all five taxa by taking 3D landmarks from surface models using Stratovan Checkpoint v. 2017.03.03.0771. To ascertain which regions of the craniofacial skeleton are good taxonomic indicators, we selected 3D landmarks on the basis that they sampled four craniofacial regions: the face and palate, the basicranium, the calvarium, and the frontal region of the calvarium. We sampled these four regions because they are hypothesised to distinguish among taxa (Lynch-Alfaro, Silva Jr, & Rylands, 2012b). We quantified the face and palate using 18 landmarks and quantified the basicranium using 8 landmarks (Fig. 1; Table II). We quantified calvarium shape by placing a 9*13 landmark patch (117 landmarks) using a patch placement method previously described by Balolia et al. (2020). We placed the calvarium patch using 17 guiding landmarks, of which 9 landmarks (A, B, C, D, E, g, j, o, q) are homologous. The remaining eight landmarks (f, h, i, k, l, m, n, p) were autopositioned (i.e., landmarks were automatically positioned along the surface of the 3D model, guided by the positions of the relevant guiding landmarks), or autopositioned and then aligned to the correct position on the neurocranium (Fig. 2; Table III). Of the 117 landmarks used to quantify calvarium shape, we used a subset of 20 landmarks to quantify frontal bone shape to examine this
| Species                  | Males | Females | Original specimen locations                        | Repository                                                                 |
|-------------------------|-------|---------|---------------------------------------------------|-----------------------------------------------------------------------------|
| *Cebus albifrons*       | 8     | 8       | Cesar and Magdalena, Colombia                     | Smithsonian National Museum of Natural History, Washington, DC             |
| *Cebus capucinus*       | 5     | 4       | Panama                                            | Smithsonian National Museum of Natural History, Washington, DC             |
| *Cebus olivaceus*       | 8     | 7       | Kartabo and Tumatumtai, Guyana                   | American Museum of Natural History, New York                                |
| *Cebus (Sapajus) macrocephalus* | 8     | 8       | Meta, Colombia                                    | American Museum of Natural History, New York; Smithsonian National Museum of Natural History, Washington, DC |
| *Cebus (Sapajus) libidinosus* | 8     | 8       | Minas Gerais and Goyaz, Brazil                   | American Museum of Natural History, New York                                |
morphological region in isolation. (Fig. 2; Table III). We have not used the term “semi-landmarks” to describe autopositioned landmarks to avoid confusion with the use of this term to describe computationally derived landmarks (Gunz et al., 2005).

**Measurement Error**

We assessed measurement error for the calvarium patch (including frontal region landmarks) by collecting landmarks on a single cebine specimen (*Cebus albifrons*) 3 days and 7 days after collecting the initial patch. We calculated the Euclidean distances between Procrustes residuals for repeated measurements and compared these values to the Euclidean distances between Procrustes residuals for ten specimens of the same species (5 males and 5 females), similar to the procedure described in Balolia et al. (2020). Results show that measurement error was low, i.e., intraspecimen Euclidean distances were lower than between specimen values.

**Statistical Analysis**

For all shape analyses, we removed the effects of isometric size by performing generalised Procrustes analysis (GPA) on 3D landmarks for each of the four craniofacial measures separately (the face and palate, the basicranium, the calvarium, and the
### Table II

3D Landmarks Used to Quantify Craniofacial Shape in *Cebus albifrons, C. capucinus, C. olivaceus, C. (Sapajus) macrocephalus,* and *C. (S.) libidinosus.* Landmarks are Depicted in Fig. 1.

| LM # | Landmark and definition                                                                 | Face and palate | Basicranium |
|------|----------------------------------------------------------------------------------------|-----------------|-------------|
| 1    | Glabella: the most anteriorly projecting point of the frontal bone, adjacent to the supraorbital ridges | X               |             |
| 2    | Nasospinale: the point on the lower rim of the nasal cavity                             | X               |             |
| 3    | Prosthion: the most anterior point on the premaxilla between the two central incisors  | X               |             |
| 4    | Staphylion: the point on the median palatine suture that crosses a line drawn from the deepest part of the arches of the horizontal plate of the palatine bones, or the most posterior point of the median palatine suture when no arches are present | X               |             |
| 5    | Basion: the anterior-most point of the foramen magnum                                   | X               |             |
| 6    | Opisthion: the posterior-most point of the foramen magnum                               | X               |             |
| 7    | Opisthocranion: the most posterior point of the cranium at the Frankfurt Horizontal      | X               |             |
| 8    | The point at which the frontozygomatic suture intersects with the outer orbital rim      |                 |             |
| 9    | Frontomalar orbitale: the point at which the frontozygomatic suture intersects with the inner orbital rim | X               |             |
| 10   | Point of maximal curvature on the inner orbital rim (medial) (left)                     | X               |             |
| 11   | The most superior point on the upper orbital rim (left)                                 | X               |             |
| 12   | The most inferior point on the lower orbital rim, perpendicular to the most superior point on the upper orbital rim (left) | X               |             |
| 13   | The point corresponding to the largest width of the piriform aperture (left)            | X               |             |
| 14   | The most anterior point on the buccal side of the canine alveolus, projected onto the alveolar margin (left) | X               |             |
| 15   | The most distal point on the buccal side of the canine alveolus, projected onto the alveolar margin (left) | X               |             |
| 16   | The most mesial point on the alveolar margin of the buccal side of the fourth premolar (left) | X               |             |
| 17   | Midpoint of the alveolar margin of the buccal side of upper M1 (left)                  | X               |             |
| 18   | Midpoint of the alveolar margin of the buccal side of upper M2 (left)                  | X               |             |
| 19   | Maximum curvature of the anterior upper margin of the zygomatic arch (left)            | X               |             |
| 20   | Anterior termination point of the zygomatic process (left)                             | X               |             |
| 21   | Superior margin of the zygomatic arch at the widest point (left)                       | X               |             |
| 22   | Porion: the most superior and lateral point of the external auditory meatus (left)      |                 |             |
| 23   | Most posterior and lateral point of the external auditory meatus (left)                 | X               |             |
| 24   | Most anterior and lateral point of the external auditory meatus (left)                 | X               |             |
| 25   | Most inferior and lateral point of the external auditory meatus (left)                 | X               |             |
| 26   | Maximum curvature of the lateral edge of the foramen magnum (left)                     | X               |             |
**Fig. 2** Visual representation of the 117 3D landmarks used to quantify calvarium shape, applied to a *Cebus albifrons* 3D surface model. The subset of 20 landmarks used to quantify frontal region shape is shown in purple. Manually positioned (guiding) landmarks are shown using orange or green arrows, and autopositioned landmarks are shown using blue landmarks. Guiding landmarks are defined in Table III.

**Table III** 3D Landmarks Used to Quantify Calvarium Shape in *Cebus albifrons*, *C. capucinus*, *C. olivaceus*, *C. (Sapajus) macrocephalus*, *C. (S.) libidinosus*. Landmarks are Depicted in Fig. 2

| Landmark | Description |
|----------|-------------|
| A        | Midpoint between bregma and posterior termination point of the zygomatic process |
| B        | Opisthocranion: the most posterior point of the cranium at the Frankfurt Horizontal |
| C        | Glabella: the anterior point between the orbits |
| D        | Most inferior point of the temporal fossa |
| E        | Most lateral meeting point of the mastoid part of the temporal bone and supraoccipital |
| f        | Autopositioned, then aligned to the sagittal plane (specimens without a sagittal crest), or the superior margin of the sagittal crest (crested specimens) |
| g        | Bregma: the junction of the coronal and sagittal sutures |
| h        | Autopositioned, then aligned to the sagittal plane (specimens without a sagittal crest), or the superior margin of the sagittal crest (crested specimens) |
| i        | Autopositioned, then aligned to the contour along the most inferior edge of the cranial vault |
| j        | Posterior termination point of the zygomatic process |
| k        | Autopositioned, then aligned to the contour along the most inferior edge of the cranial vault |
| l        | Autopositioned, then aligned to the contour along the most inferior edge of the cranial vault or the nuchal crest |
| m        | Autopositioned, then aligned to the contour along the most inferior edge of the cranial vault or the nuchal crest |
| n        | Autopositioned, then aligned to the contour along the most inferior edge of the cranial vault or the nuchal crest |
| o        | The most anterior point of the right upper orbit at midpoint |
| p        | Autopositioned, then aligned to the contour of the temporal fossa |
| q        | The point of the upper lateral margin of the postorbital plate at postorbital constriction (as viewed in superior view) |
frontal region of the calvarium). We scaled landmarks to a standard centroid size, translated them so that the centroid of each specimen was positioned at the same location, and rotated them to minimise the squared distance between each landmark set (Rohlf & Slice, 1990). To quantify the morphological distances between taxonomic groups (i.e., between gracile and robust capuchin monkey groups or between species pairs), we measured the Procrustes distance (PD) between the mean shapes using the Procrustes shape coordinates obtained from the GPA. To test for statistical significance of PDs, we used permutation tests (10,000 permutations per analysis). To assess how much of the shape variation was influenced by taxon size (i.e., the allometric component), we performed pooled regression within subgroups analyses. We conducted analyses using Procrustes shape coordinates obtained based on either combined-taxon or group-specific GPA, depending on the analysis in question, in MorphoJ 1.07a (Klingenberg, 2011).

To assess which craniofacial regions are good taxonomic indicators between gracile and robust capuchin monkey groups, we first performed Principal Components Analysis (PCA) on Procrustes shape coordinates obtained from performing a GPA on the entire dataset. We then performed cross-validated stepwise Discriminant Function Analysis (DFA), retaining PCs that accounted for at least 1% of the sample variation for all analyses. Across the four craniofacial regions, this resulted in the inclusion of 1-18 PCs, which accounted for 89-99% of the sample variation. To assess which craniofacial regions are good taxonomic indicators at the species-level, for analyses considering only two taxa, we performed cross-validated stepwise Discriminant Function Analysis (DFA), i.e., similar to genus-level analyses. For analyses with more than two taxa, we ran stepwise canonical discriminant analysis (CDA), again retaining PCs that accounted for at least 1% of the sample variation. For species-level analyses, we first performed group-specific GPA, i.e., sampling only the subset of gracile or robust capuchin monkey groups species required for the analysis in question. For gracile capuchin monkeys, this resulted in the inclusion of 1-18 PCs, which accounted for 93-98% of the sample variation. For robust capuchins, this resulted in the inclusion of 1-16 PCs, which accounted for between 93-98% of the sample variation. To assess the pattern of cross-group misclassification rates at the species level, we repeated these analyses using Procrustes shape coordinates obtained from performing GPA on the entire cebine dataset. We then performed PCA using the resulting Procrustes shape coordinates and ran stepwise CDA. To assess whether the effects of sexual dimorphism impacted correct classification rates, we conducted GPA and PCA on males and females separately for use in sex-specific DFA and CDA. For these analyses, we included 1-17 PCs, which accounted for 93-100% of the sample variation. We acknowledge that there are limitations of CVA and DFA (Mitteroecker and Bookstein, 2011) and note that our results are less likely to be affected by some of the problems described by these authors based on a relatively low number of PCs being used to sample craniofacial shape in our paper. We used SPSS v. 27 to conduct DFA and CDA. We used the EVAN Toolbox v. 1.71 to perform PCA, and MorphoJ 1.07a (Klingenberg, 2011) to conduct shape visualisations. We conducted shape visualisations within the limits of the sample variation.
Ethical Note

No ethical clearance was required for this study. The authors declare that they have no conflict of interest.

Data Availability  The dataset used in this study is available via Figshare: https://doi.org/10.6084/m9.figshare.20009996.

Results

Gracile and Robust Capuchin Group-level Analyses

Presence of Intergroup Shape Differences Between Gracile and Robust Capuchins

There are statistically significant shape differences between gracile and robust capuchin groups across all four craniofacial measures (Table IV). The frontal region of the calvarium shows the most pronounced shape differences between gracile and robust capuchin groups, followed by the face and palate, basicranium shape, and calvarium shape (Table IV). Size accounts for between 4–16% of the shape variation (allometric component) across the four craniofacial regions, and the frontal region of the calvarium shows the greatest amount of size-related shape variation (Table IV).

Which Craniofacial Regions are the Best Taxonomic Indicators Among Gracile and Robust Capuchin Groups?

All four craniofacial shape measures show high classification rates and can discriminate between gracile and robust capuchin groups, with 82-97% of specimens being correctly classified across all measures (Table V). The frontal region of the calvarium and face and palate shape measures show the highest correct classification rates, with more than 95% of specimens classified correctly when using the sex-combined sample for both measures. Calvarium shape and basicranial shape also yield high correct classification rates (90% and 82%, respectively) when considering the entire sample. Sex-specific analyses do not yield substantially different results to those obtained using the entire sample, with sex-specific correct classification rates of 84-100% achieved across analyses (Table V).

Table IV  Procrustes Distance Comparisons and the Amount of Shape Variation Explained by Taxonomic Size (Allometric Component) Between Gracile and Robust Capuchin Groups

| Craniofacial region | Procrustes distance | Pooled within-group allometry |
|---------------------|---------------------|-----------------------------|
| Face and palate     | 0.0434, $P < 0.0001$| 8% of shape variation predicted by genus size, $P < 0.0001$ |
| Basicranium         | 0.0381, $P < 0.0001$| 4% of shape variation predicted by genus size, $P = 0.001$ |
| Calvarium           | 0.0349, $P = 0.008$ | 4% of shape variation predicted by genus size, $P = 0.0281$ |
| Frontal region of the calvarium | 0.0745, $P < 0.0001$ | 16% of shape variation predicted by genus size, $P < 0.0001$ |
Table V  Cross-Validated Stepwise Discriminant Function Analysis (DFA) Classification Results for Four Craniofacial Regions Between Gracile and Robust Capuchin Groups. Values Highlighted in Bold Indicate the Percentage of Specimens that are Correctly Classified.

| Craniofacial region | Group   | Predicted group membership % | Overall Correct Classification rates % |
|---------------------|---------|------------------------------|----------------------------------------|
|                     |         | Entire Sample | Males | Females | Entire Sample | Males | Females |
| Face and palate     | Gracile | 97             | 3     | 90       | 100           | 0     | 100     |
|                     | Robust  | 3              | 97    | 13       | 87            | 0     | 100     |
| Basicranium         | Gracile | 80             | 20    | 86       | 14            | 84    | 16      |
|                     | Robust  | 16             | 84    | 19       | 81            | 0     | 100     |
| Calvarium           | Gracile | 90             | 10    | 95       | 5             | 83    | 17      |
|                     | Robust  | 10             | 90    | 0        | 100           | 13    | 87      |
| Frontal region of the calvarium | Gracile | 94             | 6     | 100      | 0             | 92    | 8       |
|                     | Robust  | 3              | 97    | 0        | 100           | 6     | 94      |
These results show that all four craniofacial measures show statistically significant shape differences between gracile and robust capuchins and can distinguish between these two groups with high classification accuracy (>80%). Of these four measures, frontal region of the calvarium shape, and face and palate shape show the highest magnitude of shape differences between groups and are the best taxonomic predictors. Shape visualisations show that frontal region differences between gracile and robust capuchin groups are associated with a more steeply sloped frontal bone at the midline in robust capuchins, in contrast to a lower, flatter frontal bone in gracile capuchins (Fig. 3). For the face and palate, shape visualisations show that gracile and robust capuchin groups differ in their glabellar morphology, shape of the piriform aperture and aspects of zygomatic arch shape (Fig. 4).

Fig. 3 Wireframe graph showing the mean frontal region of the calvarium shape for gracile capuchin species (Cebus albifrons, C. capucinus, C. olivaceus; shown in grey) and robust capuchin species (C. (Sapajus) macrocephalus, C. (S.) libidinosus; shown in purple). Frontal region landmarks are depicted in Fig. 2 and definitions for guiding landmarks (C, h, and o) are provided in Table III.

Fig. 4 Wireframe graph showing the mean face and palate shape for gracile capuchin species (Cebus albifrons, C. capucinus, C. olivaceus; shown in grey) and robust capuchin species (C. (Sapajus) macrocephalus, C. (S.) libidinosus; shown in purple). Face and palate landmarks are depicted in Fig. 1 and landmark definitions are provided in Table II.
Species-level Analyses

Presence of Interspecific Shape Differences Among Gracile and Robust Capuchins

There are statistically significant interspecific shape differences between cebine species across all taxonomic comparisons for face and palate shape and for basicranium shape (Table VI). Of a total of ten interspecific comparisons per craniofacial region, seven are significant for calvarium shape and eight are significant for frontal region of the calvarium shape. Nonsignificant comparisons comprise those within and between gracile and robust species pairs (Table VI). The magnitude of interspecific shape differences for the face and palate exceeds that of the basicranium for comparisons between *C. albifrons* vs. *C. capucinus* and *C. albifrons* vs. *C. olivaceus*. Similarly, the magnitude of interspecific shape differences for the frontal region exceeds that of the entire calvarium for these same interspecific comparisons (Table VI). A similar pattern is not found for interspecific comparisons between *C. capucinus* vs. *C. olivaceus* and *C. (S.) macrocephalus* vs. *C. (S.) libidinosus*. For all four craniofacial regions, interspecific comparisons between gracile and robust capuchin species do not uniformly exceed those within gracile and robust capuchin groups, indicating that shape distances between species from different purported genera (*Cebus* and *Sapajus*) can be more similar than shape distances of species within the same genus (Table VI).

Which Craniofacial Regions are the Best Taxonomic Indicators at the Species Level?

Among gracile capuchin species, three of the four craniofacial shape regions (face and palate shape, calvarium shape, and frontal region of the calvarium shape) show high classification rates (classification accuracy >80%), with 81-84% of specimens correctly classified (Table VII). Face and palate, and calvarium shape measures show the highest correct classification rates among gracile capuchin species, with 84% of specimens classified correctly when using the sex-combined sample for both measures. Frontal region of the calvarium shape also yields a high correct classification rate of 81% when considering the entire sample. For most craniofacial regions, sex-specific analyses yield less accurate classification results than do analyses that include the entire gracile capuchin sample, except for face and palate shape for females (100% of specimens were correctly classified) and calvarium shape for males and females (96% and 100% of specimens were correctly classified, respectively) (Table VII).

Among robust capuchin species, similar to the gracile species, three of the four craniofacial shape regions (face and palate shape, calvarium shape, and frontal region of the calvarium shape) show high classification rates, with 81-97% of specimens correctly classified (Table VIII). Face and palate, and calvarium shape measures show the highest correct classification rates among robust capuchin species, with 97% and 84% of specimens, respectively, classified correctly when using the sex-combined sample for both measures. Frontal region of the calvarium shape also yields a high correct classification rate of 81% when considering the entire sample. For the majority of craniofacial regions, sex-specific analyses do not yield
substantially different results to those obtained using the entire sample, with the exception of basicranium shape for males and females (100% and 87% of specimens were correctly classified, respectively) (Table VIII).

When gracile and robust capuchin species are considered together, only face and palate shape shows high classification rates, with 86% of specimens correctly classified (Table IX). The other three craniofacial regions (basicranium, calvarium, and frontal region of the calvarium) show low correct classification rates of 66-72% (Table IX). Of the four craniofacial regions, face and palate shape show low misclassification rates at the genus level, with 2-3% of specimens being classified to the wrong genus compared with misclassification rates of 4-20% for the basicranium, calvarium, and the frontal region of the calvarium (Table IX).

To summarise, these results show that of the four craniofacial measures, face and palate shape, calvarium shape, and frontal region of the calvarium shape diagnose gracile and robust capuchin species with high classification accuracy (>80%) when the two groups are considered in isolation. However, when gracile and robust capuchin species are considered together, only face and palate shape shows high classification rates and is consistently shown as the best taxonomic predictor at the species-level among cebines. Shape visualisations show that face and palate differences between cebine species are associated with glabellar morphology, shape of the piri-form aperture, and aspects of zygomatic arch shape differences, similar to what was observed between gracile and robust groups, although to varying degrees (Figs. 4 and 5). In addition, some species pairs show orbital shape differences (Fig. 5). Visualisations of shape differences between species pairs (Fig. 5) is consistent with results showing that interspecific face and palate comparisons between gracile and robust capuchin species do not uniformly exceed those within gracile and robust capuchin groups (Table VI).

**Table VI** Species-Level Procrustes Distance Comparisons (and P values in parentheses) Among Cebine Species. Significant Results Based on Permutation Tests are Presented in Bold. Cells Representing Cross-Genus Interspecies Comparisons are Shaded in Grey to Aid the Interpretation of the Table

| Craniofacial region | Species              | C. albifrons | C. capucinus | C. olivaceus | C. (S.) macrocephalus |
|---------------------|----------------------|--------------|--------------|--------------|-----------------------|
| Face and palate     | C. capucinus         | 0.0655 (< 0.0001) | X            | X            | X                     |
|                     | C. olivaceus         | 0.0556 (< 0.0001) | X            | 0.0476 (< 0.0001) | X                     |
|                     | C. (S.) macrocephalus| 0.0521 (< 0.0001) | 0.0526 (< 0.0001) | 0.0466 (< 0.0001) | X                     |
|                     | C. (S.) libidinosus  | 0.0656 (< 0.0001) | 0.0654 (< 0.0001) | 0.0677 (< 0.0001) | 0.0460 (< 0.0001) |
| Basicranium         | C. capucinus         | 0.0301 (0.0284)  | X            | X            | X                     |
|                     | C. olivaceus         | 0.0436 (0.0001)  | 0.0543 (0.0002) | X            | X                     |
|                     | C. (S.) macrocephalus| 0.0416 (< 0.0001) | 0.0496 (0.0001) | 0.0380 (0.0034) | X                     |
|                     | C. (S.) libidinosus  | 0.0623 (< 0.0001) | 0.0654 (< 0.0001) | 0.0491 (0.0001) | 0.0460 (0.0001) |
| Calvarium           | C. capucinus         | 0.0623 (0.0337)  | X            | X            | X                     |
|                     | C. olivaceus         | 0.0778 (0.0003)  | 0.0543 (0.0160) | X            | X                     |
|                     | C. (S.) macrocephalus| 0.0536 (0.0536, ns) | 0.0426 (0.1418, ns) | 0.0566 (0.0049) | X                     |
|                     | C. (S.) libidinosus  | 0.0498 (0.0187)  | 0.0538 (0.0056) | 0.0568 (< 0.0001) | 0.0263 (0.3533, ns) |
| Frontal region of the calvarium | C. capucinus | 0.0901 (0.0006)  | X            | X            | X                     |
|                     | C. olivaceus         | 0.0869 (0.0007)  | 0.037 (0.4398, ns) | X            | X                     |
|                     | C. (S.) macrocephalus| 0.1002 (0.0001)  | 0.0725 (< 0.0001) | 0.0692 (< 0.0001) | X                     |
|                     | C. (S.) libidinosus  | 0.1078 (< 0.0001) | 0.0863 (< 0.0001) | 0.0806 (< 0.0001) | 0.0306 (0.280, ns) |
Table VII  Species-Level Cross-Validated Stepwise Canonical Discriminant Analysis Classification Results for Four Craniofacial Regions Among Cebus Species. Values Highlighted in Bold Indicate the Percentage of Specimens that are Correctly Classified

| Craniofacial region | Species       | Predicted group membership % | Overall Correct Classification rates % |
|---------------------|---------------|-------------------------------|----------------------------------------|
|                     |               | Entire Sample | Males | Females | Entire Sample | Males | Females |
| Face and palate     | *C. albifrons* | 94             | 60    | 25      | 0             | 100   | 0       | 0       | 84 | 58 | 100 |
|                     | *C. capucinus* | 0              | 88    | 12      | 25            | 50    | 25      | 0       | 0  | 100 | 0   |
|                     | *C. olivaceus* | 7              | 22    | 71      | 12            | 38    | 50      | 0       | 0  | 0   | 100 |
| Basicranium         | *C. albifrons* | 63             | 25    | 12      | 50            | 25    | 25      | 63      | 37 | 0   | 72  |
|                     | *C. capucinus* | 22             | 67    | 11      | 40            | 60    | 0       | 50      | 50 | 0   | 66  |
|                     | *C. olivaceus* | 13             | 0     | 87      | 12            | 0     | 88      | 0       | 43 | 57  |
| Calvarium           | *C. albifrons* | 82             | 9     | 9       | 100           | 0     | 0       | 100     | 0  | 0   | 84  |
|                     | *C. capucinus* | 0              | 88    | 12      | 0             | 100   | 0       | 0       | 100| 0   |
|                     | *C. olivaceus* | 8              | 8     | 82      | 0             | 13    | 87      | 0       | 0  | 100 |
| Frontal region of the calvarium | *C. albifrons* | 73             | 0     | 27      | 83            | 17    | 0       | 40      | 20 | 40  |
|                     | *C. capucinus* | 0              | 87    | 13      | 0             | 60    | 40      | 33      | 67 | 0   |
|                     | *C. olivaceus* | 17             | 0     | 83      | 12            | 38    | 50      | 50      | 0  | 50  |

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Table VIII  Species-Level Cross-Validated Stepwise Discriminant Function Analysis Classification Results for Four Craniofacial Regions Among Robust Capuchin Species. Values Highlighted in Bold Indicate the Percentage of Specimens that are Correctly Classified

| Craniofacial region       | Species          | Predicted group membership % | Overall correct classification rates % |
|---------------------------|------------------|-------------------------------|----------------------------------------|
|                           |                  | Entire sample | Males | Females | Entire sample | Males | Females |
| Face and palate           | C. (S.) macrocephalus | 94   | 6     | 87    | 13     | 100  | 0     | 97   | 87 | 94 |
|                           | C. (S.) libidinosus | 0    | 100   | 13    | 87     | 13   | 87    |      |    |    |
| Basicranium               | C. (S.) macrocephalus | 75   | 25    | 100   | 0      | 87   | 13    | 72   | 100 | 87 |
|                           | C. (S.) libidinosus | 31   | 69    | 0     | 100    | 13   | 87    |      |    |    |
| Calvarium                 | C. (S.) macrocephalus | 87   | 13    | 71    | 29     | 100  | 0     | 84   | 79 | 94 |
|                           | C. (S.) libidinosus | 19   | 81    | 13    | 87     | 13   | 87    |      |    |    |
| Frontal region of the     | C. (S.) macrocephalus | 87   | 13    | 86    | 14     | 75   | 25    | 81   | 87 | 75 |
| calvarium                 | C. (S.) libidinosus | 25   | 75    | 13    | 87     | 25   | 75    |      |    |    |
Discussion

Our study findings show that among cebines, the craniofacial shape differences between intergroup species pairs are not sufficient to justify gracile and robust capuchin species being separated into different genera. While our findings are consistent with research that documents craniofacial differences between gracile and robust capuchin groups (Lynch-Alfaro, Silva Jr, & Rylands, 2012b; Silva, 2001; Wright et al., 2015), our findings also show that the magnitude of interspecific craniofacial shape differences among gracile and robust capuchin species are more reflective of what is expected under a single-genus (Cebus). These findings align with research based on a comprehensive genetic analysis, which similarly shows that genetic distances between gracile and robust capuchin species pairs are consistent with species of both groups being placed within a single genus (Ruiz-García et al., 2016). Although the magnitude of craniofacial shape differences between gracile and robust capuchins are insufficient to separate these groups at the genus level, craniofacial shape differences do exist, where gracile and robust specimens can be distinguished with high accuracy (>82% correct classification rates). Our frontal region of the calvarium shape, and face and palate shape measures show particularly high (>95%) correct classification rates. Of the four craniofacial shape measures we employed, our face and palate shape measure yields the highest correct classification rates for interspecific comparisons, with >84% of specimens being correctly classified using this measure. The calvarium shape and basicranium shape measures used in this study also show high classification rates across analyses (72-84%). Face and palate shape is the most reliable morphological region by which to diagnose cebine species, although other craniofacial regions can also provide reliable species-level taxonomic information.

Our findings that cebines reliably show interspecific face and palate shape differences can be considered in the context of research documenting interspecific phenotypic variation among cebines (Aristide et al., 2014; Avila, 2004; Byron, 2009; Cáceres et al., 2014; Masterson, 1997; Wright, 2005; Wright et al., 2009; Wright et al., 2015). Interspecific craniofacial differences are hypothesised to be associated with multiple evolutionary forces, including variables such as diet, ecological factors, and genetic drift (Aristide et al., 2014; Avila, 2004). Research that specifically examines the relationship between cranial morphology and diet among cebines shows that cranial morphology and musculature associated with mastication varies in response to dietary factors. For example, cebids show interspecific differences in temporalis and masseter muscle position and morphology, the degree of postorbital constriction, as well as zygomatic arch robusticity and zygomatic flaring associated with dietary differences and hard-object feeding (Masterson, 1997; Wright, 2005). Further findings show that masticatory adaptations are especially exaggerated in C. apella who incorporate exceptionally hard and tough plant foods in their diet during times of food scarcity (Wright, 2005). Similarly, C. apella have more complex sagittal suture morphology compared with C. albifrons, C. capucinus, and C. olivaceus, inferred by the authors to be a modelling response to greater reliance of tough and obdurate foods (Byron, 2009).
Further studies investigating the relationship between ecology, ecogeographical variation and evolutionary history and craniofacial morphology indicate that derived craniofacial features among cebines are associated with ecological differences related to terrestrial environments, forest aridity, evolutionary history, and sympatry with other capuchin species (Wright et al., 2015). Research that specifically investigates ecogeographical variation in cebine skull shape further indicates that skull shape is associated with climatic variables including those associated with temperature annual range, minimum temperature, seasonality, precipitation, and latitude (Cáceres et al., 2014). Species living in southern regions of South America for which there is less rainfall and larger temperature and environmental variability show narrower skulls and a relatively long snout compared with northern species (Cáceres et al., 2014).

Combined, evidence showing that interspecific differences in the craniofacial skeleton are associated with dietary, ecological, geographical, and climatic differences among cebine species (Byron, 2009; Cáceres et al., 2014; Masterson, 1997; Wright, 2005; Wright et al., 2009; Wright et al., 2015) is consistent with our findings of interspecific craniofacial shape differences among the capuchin species employed in this study, including those of the piriform aperture, glabella, orbits, and zygomatic arch. If selective pressures associated with dietary and ecological differences are the main underlying reasons for the interspecific face and palate shape differences observed among capuchin taxa, it is possible that convergent evolution among taxa with similar diets and/or living in similar environments may confound attempts to use the face and palate as a taxonomic indicator. However, the high

Table IX Species-Level Cross-Validated Stepwise Canonical Discriminant Analysis Classification Results for Four Craniofacial Regions Among Cebine Species. Values Highlighted in Bold Indicate the Percentage of Specimens that are Correctly Classified. Cells Representing Cross-Genus Interspecies Comparisons are Shaded in Grey to Aid the Interpretation of the Table

| Craniofacial region | Species    | C. albifrons | C. capucinus | C. olivaceus | C. (S.) macrocephalus | C. (S.) libidinosus | Overall correct species classification rates (%) | Misclassification rates (%) | Predicted group membership (%) | Gracile | Robust |
|---------------------|------------|--------------|--------------|--------------|-----------------------|---------------------|-----------------------------------------------|-----------------------------|-----------------------------|--------|--------|
| Face and palate     | C. albifrons | 81           | 0            | 19           | 0                     | 0                   | 86                                            | 2              | 86              | 3      |        |
|                     | C. capucinus | 11           | 89           | 0            | 0                     | 0                   |                                               | 2              | 14             | 0.6    |        |
|                     | C. olivaceus | 7            | 0            | 86           | 7                     | 0                   |                                               | 7              | 14             | 0.6    |        |
|                     | C. (S.) macrocephalus | 0  | 0  | 0  | 94                    | 6                    | 61                                            | 4              | 61             | 55     |        |
|                     | C. (S.) libidinosus | 0  | 6  | 0  | 13                    | 81                   |                                               | 13             | 13             | 0.6    |        |
| Basicranum          | C. albifrons | 56           | 32           | 6            | 0                     | 0                   | 72                                            | 4              | 72             | 13     |        |
|                     | C. capucinus | 0            | 89           | 11           | 0                     | 0                   |                                               | 0              | 0              | 0      |        |
|                     | C. olivaceus | 7            | 0            | 86           | 7                     | 0                   |                                               | 7              | 14             | 0.6    |        |
|                     | C. (S.) macrocephalus | 13 | 0  | 66           | 56                    | 25                   | 56                                            | 13             | 13             | 0.6    |        |
|                     | C. (S.) libidinosus | 6  | 0  | 0  | 19                    | 75                   |                                               | 8              | 8              | 0.6    |        |
| Calvarium           | C. albifrons | 73           | 0            | 9            | 9                     | 9                   | 72                                            | 20             | 20            | 17     |        |
|                     | C. capucinus | 0            | 75           | 0            | 12                    | 13                   |                                               | 13             | 13             | 0.6    |        |
|                     | C. olivaceus | 0            | 0            | 83           | 17                    | 0                   |                                               | 17             | 17             | 0.6    |        |
|                     | C. (S.) macrocephalus | 13 | 7  | 77           | 60                    | 13                   | 60                                            | 13             | 13             | 0.6    |        |
|                     | C. (S.) libidinosus | 6  | 0  | 0  | 25                    | 69                   |                                               | 16             | 16             | 0.6    |        |
| Frontal region of the calvarium | C. albifrons | 73           | 0            | 9            | 9                     | 9                   | 66                                            | 16             | 16            | 0.6    |        |
|                     | C. capucinus | 0            | 50           | 37           | 13                    | 0                   |                                               | 4              | 4              | 0.6    |        |
|                     | C. olivaceus | 17           | 17           | 66           | 0                     | 0                   |                                               | 0              | 0              | 0      |        |
|                     | C. (S.) macrocephalus | 7  | 0  | 0  | 73                    | 20                   |                                               | 20             | 20             | 0.6    |        |
|                     | C. (S.) libidinosus | 0  | 0  | 0  | 31                    | 69                   |                                               | 69             | 69             | 0.6    |        |
Fig. 5 Wireframes showing the mean face and palate shape for gracile and robust capuchin species: *Cebus albifrons* (red), *C. capucinus* (blue), *C. olivaceus* (green), *C. (Sapajus) macrocephalus* (black), *C. (S.) libidinosus* (pink). Face and palate landmarks are depicted in Fig. 1 and landmark definitions are provided in Table II.
correct classification rates using face and palate shape observed in the current study, and the fact that multiple ecologically driven pressures have been shown to play a role in interspecific variation in craniofacial morphology (Byron, 2009; Cáceres et al., 2014; Masterson, 1997; Wright, 2005; Wright et al., 2009; Wright et al., 2015), indicate that convergent evolution in craniofacial regions in response to isolated selective pressures is unlikely to negatively affect the utility of craniofacial shape as a taxonomic indicator.

Our conclusion that cebine species should be placed within one genus, Cebus, is inconsistent with the viewpoints of other authors who have proposed that the robust capuchin monkeys be placed in a separate genus, Sapajus, based on distinct morphological differences between the two groups (Lynch-Alfaro, Silva Jr, & Rylands, 2012b; Silva, 2001; Wright et al., 2015). Our findings that the magnitude of craniofacial shape differences among gracile and robust capuchin species pairs do not exceed inter-gracile or inter-robust species comparisons provides a clear basis to include all cebine species within the same genus, Cebus. In considering assertions made by other authors surrounding what constitutes a genus within the field of primatology, such disagreements may reflect differences in perspectives surrounding what a genus represents, i.e., whether unique, derived features observed within a group are important in making genus-level distinctions, or whether shared features should be emphasised (Garbino, 2015). Our view is that even under a scenario in which unique, derived features should be emphasised in making genus-level classifications, the relatively small degree of shape differences between gracile and robust species pairs does not support such a genus-level distinction. Similarly, the craniofacial evidence presented in this paper does not support classifying gracile and robust capuchin groups into different genera using the alternative framework surrounding delineations of adaptive zones based on hard tissue morphology (Wood & Collard, 1997, 1999; Wood & Lonergan, 2008). Despite the genus taxonomic rank, including how to classify taxa on this basis, being discussed by numerous authors (Mayr, 1943; Simpson, 1943; Cain, 1956, 1958; Clayton, 1983; Lemen & Freeman, 1984; Stevens, 1985; Atran, 1987; Garbino, 2015; Sigward et al., 2018; Garbino et al., 2019), primatologists continue to hold different opinions about what the genus level of classification represents. Future thought and consideration among researchers may be required to move towards more widespread agreement about how to best classify species into genera, which may subsequently pave the way towards consensus surrounding the number of genera represented within the cebinae.

Conclusions

In this study, we show that craniofacial evidence is a reliable taxonomic predictor among cebines. We further show that the magnitude of craniofacial shape differences between gracile and robust capuchin species pairs is consistent with what would be expected under a single-genus hypothesis, i.e., that gracile and robust
capuchin species do not show sufficient interspecific craniofacial differences to be considered as separate genera. We suggest that all cebine species should be considered under one genus, *Cebus*. The methodology we employed serves to quantitatively assess the magnitude of differences between species pairs of members of different purported genera using craniofacial shape evidence. This method of delineating genera, i.e., assessing whether craniofacial shape differences between species pairs representing different hypothesised genera uniformly exceed those of within-genus pairs, may be particularly useful for making genus-level assessments in the fossil record among groups of specimens for which other criteria for making taxonomic assessments, e.g., soft tissue, pelage, or behavioural variables, are not available. Such applications may include testing whether interspecific craniofacial shape differences between gracile and robust australopith species pairs, which often have been categorised into separate genera: *Australopithecus* and *Paranthropus*, are consistent with a one- or two-genus scenario as has been proposed by some authors (Wood & Constantino, 2007). Further comparative research examining whether craniofacial shape is a good taxonomic predictor among other nonhuman primate groups, including the great apes, has not yet been conducted. The results we present here suggest that quantification of craniofacial shape using geometric morphometric techniques may be a reliable method to make robust taxonomic assessments as part of future research endeavours.

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**References**

Arístide, L., Soto, I. M., Mudry, M. D., & Nieves, M. (2014). Intra and interspecific variation in cranial morphology on the southernmost distributed Cebus (Platyrrhini, Primates) species. *Journal of Mammalian Evolution, 21*, 349–355.
Atran, S. (1987). Origin of the species and genus concepts: an anthropological perspective. *Journal of the History of Biology, 20*, 195–279.

Avila, I. (2004). Morphological variation between two subspecies of *Cebus libidinosus* (Primates: Cebidae). *Boletin del Museo Nacional de Historia Natural del Paraguay, 15*, 1–8.

Balolia, K. L., & Massey, J. S. (2021). How does scanner choice and 3D model resolution affect data accuracy? *Journal of Anatomy, 238*, 679–692.

Balolia, K. L., Jakeman, E. C., Massey, J. S., Groves, C., & Wood, B. (2020). Mandibular corpus shape is a taxonomic indicator in extant hominids. *American Journal of Physical Anthropology, 172*, 25–40.

Byron, C. D. (2009). Cranial suture morphology and its relationship to diet in *Cebus*. *Journal of Human Evolution, 57*, 649–655.

Cáceres, N., Meloro, C., Carotenuto, F., Passaro, F., Sponchiado, J., Melo, G. L., & Raia, P. (2014). Ecogeographical variation in skull shape of capuchin monkeys. *Journal of Biogeography, 41*, 501–512.

Cain, A. J. (1956). The genus in evolutionary taxonomy. *Systematic Biology, 5*, 97–109.

Cain, A. J. (1958). Logic and memory in Linnaeus’s system of taxonomy. *Proceedings of the Linnean Society of London, 169*, 144–163.

Clayton, W. D. (1983). The genus concept in practice. *Kew Bulletin, 38*, 149–153.

Feijó, A., & Langguth, A. (2013). Mamíferos de médio e grande porte do Nordeste do Brasil: distribuição e taxonomia, com descrição de novas espécies. *Revista Nordestina de Biologia, 22*, 3–225.

Fruciano, C., Celik, M. A., Butler, K., Dooley, T., Weisbecker, V., & Phillips, M. J. (2017). Sharing is caring? Measurement error and the issues arising from combining 3D morphometric datasets. *Ecology and Evolution, 7*, 7034–7046.

Garbino, G. S. (2015). How many marmoset (Primates: Cebidae: Callitrichinae) genera are there? A phylogenetic analysis based on multiple morphological systems. *Cladistics, 31*, 652–678.

Garbino, G. S., Serrano-Villavicencio, J. E., & Gutiérrez, E. E. (2019). What is in a genus name? Conceptual and empirical issues preclude the proposed recognition of Callibella (Callitrichinae) as a genus. *Primates, 60*, 155–162.

Groves, C. P. (2001). *Primate Taxonomy*. Smithsonian Institution Press.

Groves, C. P. (2004). The what, why and how of primate taxonomy. *International Journal of Primatology, 25*, 1105–1126.

Groves, C. P. (2014). Primate taxonomy: inflation or real? *Annual Review of Anthropology, 43*, 27–36.

Gunz, P., Mitteroecker, P., & Bookstein, F. L. (2005). Semilandmarks in three dimensions. In D. E. Slice (Ed.), *Modern Morphometrics in Physical Anthropology* (pp. 73–98). Springer.

Kerr R. (1792). The animal kingdom, a zoological system of the celebrated Sir Charles Linnaeus. Edinburgh.

Klingenberg, C. P. (2011). *MorphoJ*: an integrated software package for geometric morphometrics. *Molecular Ecology Resources, 11*, 353–357.

Lemen, C. A., & Freeman, P. W. (1984). The genus: a macroevolutionary problem. *Evolution, 38*, 1219–1237.

Lynch-Alfaro, J. W., Boublí, J. P., Olson, L. E., Di Fiore, A., Wilson, B., Gutiérrez-Espeleta, G. A., Chiou, K. L., Schulte, M., Neitzel, S., Ross, V., Schwchoow, D., Nguyen, M. T. T., Farias, I., Janson, C. H., & Alfaro, M. E. (2012a). Explosive Pleistocene range expansion leads to widespread Amazonian sympatry between robust and gracile capuchin monkeys. *Journal of Biogeography, 39*, 272–288.

Lynch-Alfaro, J. W., Silva Jr., J. D. S. E., & Rylands, A. B. (2012b). How different are robust and gracile capuchin monkeys? An argument for the use of *Sapajus* and *Cebus*. *American Journal of Primatology, 74*, 273–286.

Marcy, A. E., Fruciano, C., Phillips, M. J., Mardon, K., & Weisbecker, V. (2018). Low resolution scans can provide a sufficiently accurate, cost-and time-effective alternative to high resolution scans for 3D shape analyses. *PeerJ, 6*, e5032.

Martins-Junior, A. M. G., Amorim, N., Carneiro, J. C., de Mello Affonso, P. R. A., Sampaio, I., & Schneider, H. (2015). Alu elements and the phylogeny of capuchin (*Cebus* and *Sapajus*) monkeys. *American Journal of Primatology, 77*, 368–375.

Martins-Junior, A. M. G., Carneiro, J., Sampaio, I., Ferrari, S. F., & Schneider, H. (2018). Phylogenetic relationships among Capuchin (Cebidae, Platyrrhini) lineages: An old event of sympathy explains the current distribution of *Cebus* and *Sapajus*. *Genetics and Molecular Biology, 41*, 699–712.

Masterson, T. J. (1997). Sexual dimorphism and interspecific cranial form in two capuchin species: *Cebus albifrons* and *C. apella*. *American Journal of Physical Anthropology, 104*, 487–511.
Mayr, E. (1943). Criteria of subspecies, species and genera in ornithology. *Annals of the New York Academy of Sciences, 44*, 133–139.

Mitteroecker, P., & Bookstein, F. (2011). Linear discrimination, ordination, and the visualization of selection gradients in modern morphometrics. *Evolutionary Biology, 38*, 100–114.

Nascimento, F. F., Lazar, A., Seuánez, H. N., & Bonvicino, C. R. (2015). Reanalysis of the biogeographical hypothesis of range expansion between robust and gracile capuchin monkeys. *Journal of Biogeography, 42*, 1349–1357.

Rohlf, F. J., & Slice, D. (1990). Extensions of the Procrustes method for the optimal superimposition of landmarks. *Systematic Biology, 39*, 40–59.

Rosenberger, A. L. (2012). New World monkey nightmares: science, art, use, and abuse (?) in platyrrhine taxonomic nomenclature. *American Journal of Primatology, 74*, 692–695.

Ruiz-García, M., Castillo, M. I., Lichilín-Ortiz, N., & Pinedo-Castro, M. (2012). Molecular relationships and classification of several tufted capuchin lineages (*Cebus apella, Cebus xanthosternos* and *Cebus nigritus*, Cebidae), by means of mitochondrial cytochrome oxidase II gene sequences. *Folia Primatologica, 83*, 100–125.

Ruiz-García, M., Castillo, M. I., Luengas-Villamil, K., Shostell, J. (2016). It is misleading to use *Sapajus* (robust capuchins) as a genus? A review of the evolution of the capuchins and suggestions on their systematics. In M. Ruiz-García and J. M. Shostell (Eds.) Phylogeny, Molecular Population Genetics, Evolutionary Biology and Conservation of the Neotropical Primates. Nova Science Publisher Inc., New York, pp. 209–268.

Sigward, J. D., Sutton, M. D., & Bennett, K. D. (2018). How big is a genus? Towards a nomothetic systematics. *Zoological Journal of the Linnean Society, 183*, 237–252.

Silva, J. S. (2001). Especiação nos macacos-prego e caiararas, genero *Cebus* Erxleben, 1777 (Primates, Cebidae). PhD Thesis, Universidade Federal do Rio de Janeiro, Rio de Janeiro.

Simpson, G. G. (1943). Criteria for genera, species, and subspecies in zoology and paleozoology. *Annals of the New York Academy of Sciences, 44*, 145–178.

Stevens, P. F. (1985). The genus concept in practice: but for what practice? *Kew Bulletin, 40*, 457–465.

Wood, B., & Collard, M. (1997). Grades and the evolutionary history of early African hominids. *Pan, 2*, 2–9.

Wood, B., & Collard, M. (1999). The human genus. *Science, 284*, 65–71.

Wood, B., & Constantino, P. (2007). *Paranthropus boisei*: fifty years of evidence and analysis. *American Journal of Physical Anthropology, 134*, 106–132.

Wood, B., & Lonergan, N. (2008). The hominin fossil record: taxa, grades and clades. *Journal of Anatomy, 212*, 354–376.

Wright, B. W. (2005). Craniodental biomechanics and dietary toughness in the genus *Cebus*. *Journal of Human Evolution, 48*, 473–492.

Wright, B. W., Wright, K. A., Chalk, J., Verderane, M. P., Fragasy, D., Visalberghi, E., Izar, P., Ottoni, E. B., Constantino, P., & Vinyard, C. (2009). Fallback foraging as a way of life: using dietary toughness to compare the fallback signal among capuchins and implications for interpreting morphological variation. *American Journal of Physical Anthropology, 140*, 687–699.

Wright, K. A., Wright, B. W., Ford, S. M., Fragasy, D., Izar, P., Norconk, M., Masterson, T., Hobbs, D. G., Alfaro, M. E., & Alfaro, J. W. L. (2015). The effects of ecology and evolutionary history on robust capuchin morphological diversity. *Molecular Phylogenetics and Evolution, 82*, 455–466.