

Form, Function, and Geometric Morphometrics

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ABSTRACT

Geometric morphometrics (GM) has increasingly become an important tool in assessing and studying shape variation in a wide variety of taxa. While the GM toolkit has unparalleled power to quantify shape, its use in studies of functional morphology have been questioned. Here, we assess the state of the field of GM and provide an overview of the techniques available to assess shape, including aspects of visualization, statistical analysis, phylogenetic control, and more. Additionally, we briefly review the history of functional morphology and summarize the main tools available to the functional morphologist. We explore the intersection of geometric morphometrics and functional morphology and we suggest ways that we may be able to move forward in profitably combining these two research areas. Finally, this paper provides a brief introduction to the papers in this special issue and highlights the ways in which the contributing authors have approached the intersection of GM and functional morphology. *Anat Rec*, 298:5–28, 2015. © 2014 Wiley Periodicals, Inc.

Key words: geometric morphometrics; functional morphology; methodological comparison; comparative methods; biological anthropology

INTRODUCTION

The past 20 years have seen the rapid expansion and adoption of quantitative methodologies designed to capture and describe complex two- and three-dimensional shapes (Rohlf and Marcus, 1993; O'Higgins, 2000; Adams et al., 2004, 2013). Chief among these has been the group of methods making up the geometric morphometric toolkit. Although founded on a relatively new theoretical and mathematical framework, the tools employed in geometric morphometrics (GM) rely heavily on common statistical techniques, which help to make these methods intuitive and user-friendly. Furthermore, the ever-increasing processing power of personal computers has made these tools more accessible than ever.

Geometric morphometrics has been employed across a number of fields where quantifying morphological variation is of interest (e.g., paleontology, anthropology, biology, medicine, and engineering). These studies have addressed a wide range of questions including assessing phenetic differences among taxa (e.g., Lockwood et al.,

2002; Cardini and O'Higgins, 2004; Harvati et al., 2004; Baab, 2010), examining the relationship between shape and phylogeny (e.g., Lockwood et al., 2004; Gilbert, 2010) or shape and dispersal across geographic space (e.g., Frost et al., 2003), and creating reconstructions of ancestral morphotypes (e.g., Wiley et al., 2005). However, while GM is successful at capturing complex shapes, these methods fall short when applied to functional questions derived from the biomechanical and functional literature. GM methods are not easily applied to the evaluation of biomechanical hypotheses because they examine correlations between representations of

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three-dimensional shape and function, rather than testing hypotheses about specific mechanical relationships and function usually specified by particular linear measurements.

To try to address these deficits and to develop novel ways in which to approach functional questions using this increasingly valuable GM toolkit, a symposium was held at the 2013 meetings of the American Association of Physical Anthropologists (AAPAs). In preparation for this symposium, and for this special issue of *The Anatomical Record* which stems from it, we asked our participants and contributors a simple question, but one that has many answers: can geometric morphometrics and functional shape analyses be used to address similar functional hypotheses? Here, we briefly summarize the field of geometric morphometrics and its intersection with functional morphology, with the goal of providing an introduction for readers of this special issue. We approach this topic from an applied, not a mathematical, perspective, with the hope that this material will prove accessible to newcomers and experienced morphometricians alike. For more detailed mathematical descriptions of the methods presented here, we refer readers to several volumes that have been published on the subject including: *Morphometric Tools for Landmark Data: Geometry and Biology* (1991) by Fred L. Bookstein, *Geometric Morphometrics for Biologists* (2004) by Miriam Zelditch et al., *Modern Morphometrics in Physical Anthropology* (2005) edited by Dennis E. Slice, *Virtual Anthropology* (2011) by Gerhard W. Weber and Fred L. Bookstein, and *Measuring and Reasoning: Numerical Inference in the Sciences* (2014) by Fred L. Bookstein, as well as a variety of chapters and journal publications.

Although we focus our discussion on the application of GM to functional morphological questions in biological anthropology, we hope that this discipline is by no means the only one for which this review will be applicable. We conclude this contribution by introducing the studies presented in this special issue, which tackle the question assigned above through topics ranging broadly across mammalian taxa and across morphological regions, including analyses of dentition, jaw biomechanics, and locomotor adaptations. Through this diverse collection of papers, we hope to stimulate discussion and highlight new directions for future work in this commonly employed but often debated research area.

GEOMETRIC MORPHOMETRICS

Morphometrics as it is broadly defined seeks to evaluate shape variation and the covariation of shape with other variables (Bookstein, 1991; Dryden and Mardia, 1998). The approach now defined as 'traditional morphometrics' (Marcus, 1990; Reyment, 1991; Rohlf and Marcus, 1993) has typically relied on the univariate or multivariate analysis of variables such as distance measures, angles, and/or ratios. While powerful in many ways, and still a mainstay in many fields (including biological anthropology), these methods lack the ability to characterize the entire shape of an organism and the measurements themselves are often treated as independent of one another, although they are part of a larger structure and may therefore covary. This lack of geometric retention of the object or region under investigation subsequently led to the development of new morphomet-

ric techniques that purposefully sought to retain the geometric form of specimens for analysis: geometric morphometrics. Originally employed primarily to capture the shape of two-dimensional (2D) structures (or 2D images of three-dimensional [3D] structures) using specifically defined homologous landmarks, recent years have seen an explosion of the use of these methods for complex 3D structures and the use of increasingly sophisticated data collection tools (i.e., Microscribe digitizer, surface scans, computed tomography scans, etc.). Furthermore, where the strict biological homology of landmarks was originally emphasized, sliding (semi-)landmarks in both 2D and 3D have become commonplace, and these original rules regarding homology have been relaxed to allow for the identification of landmarks that may not be strictly biologically homologous but which are instead mathematically homologous (Bookstein, 1991; Polly, 2008; Klingenberg, 2008; Weber and Bookstein, 2011; Gunz and Mitteroecker, 2013). This same time period has also seen the rise of what has recently been termed the 'Procrustes paradigm' (Adams et al., 2013), a collection of GM approaches that stem from the statistical theory of shape originally defined by Kendall (Kendall, 1981, 1984, 1985; Slice, 2001), and the relative decrease in the use of other morphometric approaches (e.g., Euclidean Distance Matrix Analysis [EDMA; Lele, 1993]).

The GM Toolkit

In the following sections we provide a brief introduction to the GM toolkit, a continuously evolving group of methods for analyzing GM data, with explanations of uses and applications of various statistical techniques. In addition, we have also provided an example dataset (Appendix), which will supply the interested reader with a practical illustration of how these techniques are applied.

Landmarks, superimposition, and shape space. Once acquired, geometric morphometric data are simply a configuration of x , y (and z in the case of 3D data) landmarks. Landmarks may be categorized in multiple ways, but can broadly be subdivided into landmarks and semilandmarks (see Table 1 for definitions). Landmarks have typically been further subdivided into Bookstein types (Bookstein, 1991) and more recently this typology has been revised to incorporate semilandmarks (Weber and Bookstein, 2011).

The first step in any GM analysis must necessarily be superimposition of the landmark configurations. This process removes the unwanted effects of differences in specimen position and rotation, and scales all specimens to a common unit centroid size (see Appendix Fig. A3). By definition, what remains after this superimposition process is the shape of each specimen, and the original centroid size of the specimens can be extracted for further analysis. By far the most common superimposition method is generalized Procrustes analysis (GPA; previously known as generalized least squares superimposition; Rohlf [1990]), but other methods may be employed depending upon the research question and landmarks in use (i.e., two-point registration, generalized resistant fit superimposition; see Zelditch et al. [2004] for a general overview of these methods). Following superimposition,

TABLE 1. Definitions of Geometric Morphometric Terms

Term	Definition
Bending energy	A quantity that summarizes the amount of non-uniform (non-affine) shape difference between landmarks or specimens. This measure is based on a thin plate spline (TPS) metaphor, where bending energy is the amount of energy required to deform an idealized steel plate and where the displacements of landmarks in the x, y plane are depicted as displacements in the z-axis of the plate.
Canonical variate analysis	An ordination method that functions to identify the axes along which two or more groups are best discriminated by maximizing the between-group variance relative to the within group variance.
Centroid Size	The square root of the sum of squared distances from each landmark in a landmark configuration to the centroid of that configuration (Kendall, 1984; Bookstein, 1989, 1991).
Consensus configuration	The mean (average) configuration of landmark coordinates, typically computed following Procrustes superimposition. Also known as the Procrustes average or mean shape.
Form (GM definition)	Shape and size of an object.
Form space	Also known as size-shape space, this space contains information regarding shape and the natural log of centroid size. A principal component analysis evaluating form space is conducted by including the natural log of centroid size along with the Procrustes residuals in the calculation of the variance/covariance matrix. This analysis functions to compress the size-related shape variation common to all specimens in the sample onto the first principal component axis (Mitteroecker et al., 2004).
Geometric morphometrics	A collection of approaches for the multivariate statistical analysis and visualization of Cartesian coordinate data.
Landmark	Discrete anatomical loci that may be either biologically or mathematically homologous. Bookstein (1991) originally defined three types of landmarks: Type 1= discrete juxtapositions of tissues (i.e., the intersection of two sutures); Type 2= maxima of curvature (i.e., the deepest point in a depression, or the most projecting point on a process); and Type 3= extremal points or points that are defined by virtue of information at other locations on that object (i.e., the endpoint or centroid of a curve or feature). This definition of Type 3 landmarks originally encompassed semilandmarks, but Weber and Bookstein (2011) more recently redefined this system to identify Type 3 landmarks as those landmarks characterized by information from multiple curves and symmetry (i.e., intersection of two curves, or the intersection of a curve and a suture) and identified three subtypes (3a, 3b, 3c).
Landmark configuration	A collection of two- or three-dimensional coordinates describing an object and containing information about size, shape, location, and orientation.
Mahalanobis distance	The squared distance between two group means divided by the pooled variance-covariance matrices.
Principal component analysis	An ordination method for reducing the dimensionality of the dataset. Principal component analyses (PCA) function to reduce dimensionality by performing a singular value decomposition of the variance-covariance matrix and extracting the resulting eigenvectors, which then form the principal components. The associated eigenvalues describe the percentage of variance in the sample that is explained by each axis. Principal component scores represent the position of each specimen along each axis.
Procrustes distance	The square root of the summed squared distance between homologous landmarks in two landmark configurations after Procrustes superimposition. This measure may be a full Procrustes distance or partial Procrustes distance, depending upon the scaling employed during superimposition. This distance also refers to the distance between two landmark configurations in Kendall's shape space, and is therefore the metric that defines Kendall's shape space.
Procrustes residuals	Landmark coordinates that have been subjected to Procrustes superimposition and are ready for shape analysis. These residuals are described as deviations of each specimen from the mean (i.e., consensus) configuration.
Semilandmark	Originally identified as a special form of Type 3 landmark (Bookstein, 1991), a semilandmark refers to any point on a geometric feature defined in terms of its position on that feature (i.e., 10 equally spaced semilandmarks along the length of a curve). Weber and Bookstein (2011) have further identified three types of semilandmarks: Type 4= semilandmarks on curves; Type 5= semilandmarks on surfaces; Type 6= constructed semilandmarks (i.e., the start and finish of a curve).
Shape	All geometric information that remains in an object after differences in location, scale, and rotation have been removed (Kendall, 1977).
Shape space	Generally, this term can refer to any space defined by a particular mathematical definition of shape. In a geometric morphometric framework, shape space is also known as Kendall's shape space, the dimensionality of which is calculated as $2k-4$ (for 2D configurations) or $3k-7$ (for 3D configurations), where k = the number of landmarks. In the simplest version of this shape space (where shape

TABLE 1. (continued).

Term	Definition
Superimposition	<p>variation in planar triangles is examined) this shape space is represented by the surface of a two-dimensional sphere. However, when a least-squares superimposition method is employed (i.e., generalized Procrustes analysis), the shape space is more appropriately modeled as the surface of a hemisphere (Slice, 2001; thus, Slice's space). This difference is due to the different treatment of size in the superimpositions used to create these shape spaces; in Kendall's shape space all specimens are scaled to unit centroid size (i.e., partial Procrustes distance is minimized between configurations), whereas in Slice's space centroid size is allowed to vary, thus minimizing the full Procrustes distance between specimens.</p> <p>The process by which two or more landmark configurations are transformed so that trivial differences (i.e., rotation, position) are removed prior to further analysis. Also referred to as "registration" or "fitting". Types of superimposition methods that vary in their optimality criteria include two-point registration, sliding baseline registration, generalized Procrustes analysis (GPA; also known as generalized least squares [GLS] superimposition), and resistant fit registration superimposition (GRF).</p>
Tangent (Euclidean) space	<p>The linear space tangent to a curved space. In geometric morphometrics, the tangent space (also referred to as Euclidean space) is a projection of Kendall's space into the tangent plane. Distances in this tangent space are linear, in contrast to Kendall's shape space, which is curved. When the configurations under analysis are close to the point of tangency (i.e., at the mean form), linear approximations in the tangent space approximate distances in curved space.</p>
Thin plate spline	<p>An interpolation function that models the difference in shape between two landmark configurations by minimizing the bending energy required to deform a uniform grid (represented by the reference configuration) to a given landmark configuration (i.e., target configuration).</p>
Wireframe diagram	<p>A collection of straight lines connecting landmarks in a given two- or three-dimensional landmark configuration. Connections between landmarks are typically chosen to represent relevant features of the object under examination, although it is not necessary that all landmarks be connected to one another in this diagram. This usage in geometric morphometrics differs from the common usage of the term wireframe in 3D graphical modeling, where lines are used to identify the points at which two smooth surfaces meet, and where lines may be curved or straight.</p>

Unless otherwise indicated, these definitions are drawn from Zelditch et al. (2004), Mitteroecker and Gunz (2009), and Weber and Bookstein (2011).

the Procrustes coordinates (aka, Procrustes residuals) of each specimen are represented by a single point in a common shape space (for GPA, the resulting space is referred to as Kendall's shape space [Kendall, 1984, 1985]). The dimensions of this shape space are defined by the number of landmarks and dimensions (i.e., for 2D configurations the number of dimensions is calculated as $2k-4$ and for 3D the number of dimensions is calculated as $3k-7$, where k =number of landmarks). Notably, this shape space is non-linear; projection of these data into a Euclidean space that is tangent to the mean configuration is therefore necessary for further statistical analyses (Dryden and Mardia, 1993, 1998; Kent and Mardia, 2001).

Ordination methods. Because of the high-dimensionality of all but the most simple landmark configurations (i.e., a triangle), the resulting shape spaces can be difficult to visualize and interpret. Ordination methods are therefore typically employed to summarize variation in shape space. The most commonly employed of these techniques is principal components analysis (PCA), a method that performs a rigid eigendecomposition of the covariance matrix and examines the distribution of specimens along each of the resulting eigenvectors (i.e., principal component [PC] axes). The

resulting PC axes are thus linear combinations of the original data that are statistically independent of one another. However, it is notable that the only resulting PC axis that is likely to actually represent a biological phenomenon is PC 1, which typically represents allometric shape variation in a single species or population, if present (Klingenberg, 1998; Mitteroecker et al., 2005; Mitteroecker and Gunz, 2009) because all subsequent axes are constrained by being orthogonal to the first axis.

Several recent extensions of PCA have been proposed and are beginning to be more frequently employed in the GM literature: form space (i.e., size-shape space; Mitteroecker et al., 2004) and between-group PCA (Mitteroecker and Bookstein, 2011). The former method places size, represented as the natural log of centroid size (LnCS), back into the PCA by including LnCS as an additional variable in the calculation of the variance/covariance (V/CV) matrix. Because of the increased variance in LnCS relative to the Procrustes coordinates, including LnCS in the V/CV matrix forces almost all of the size-related shape variation that is common to the entire sample onto the first axis of the subsequent PCA. Compressing allometric shape variation onto a single axis in this way is especially useful where analyses incorporate multiple species across a wide range of sizes; in contrast, in a multi-species sample subjected to a

standard PCA, the first PC axis is likely to represent a combination of size-correlated shape differences and shape differences among taxa unrelated to size. This technique is rapidly gaining utility in ontogenetic and allometric shape analyses (e.g., Mitteroecker et al., 2004, 2005; Baab and McNulty, 2009; Singleton et al., 2011; Singleton, 2015), and has recently been extended to the evaluation of shape differences relative to a functionally significant size measure such as mandible length or body mass (Terhune, 2013).

The second of these extensions of PCA is a between-group PCA (bgPCA), which projects data for individual specimens onto a PCA originally calculated using group means (Mitteroecker and Bookstein, 2011). The main advantage of this method is that separation among (*a priori* defined) groups can be increased relative to a standard PCA. Perhaps more importantly, by allowing the inclusion of unequal covariance matrices for each group being examined and allowing the data matrix to contain more variables than specimens, bgPCA may provide a more robust alternative to canonical variate analysis (CVA). Although similar to PCA, CVA functions to differentiate *a priori* defined groups by maximizing the between-group variance relative to the within-group variance, therefore distorting the original relationships among specimens (Zelditch et al., 2004; Klingenberg and Monteiro, 2005). Originally more frequently used in GM analyses to differentiate among groups (e.g., Adams and Rohlf, 2000; Harvati, 2003), the appropriateness of CVA for GM analyses has been debated (see Klingenberg and Monteiro, 2005) since this method assumes a homogeneous covariance structure among groups and requires that the data matrix be invertible. This method, and its corresponding distance metric the Mahalanobis distance, has therefore been employed less frequently as of late. Notably, however, one way to avoid these pitfalls is to first reduce the dimensions present in the data by using a tool such as PCA, and then employ only the first few PC axes in the calculation of the CVA, or discriminant function analysis (DFA).

Visualizing shape variation. Shape variation in a sample can be visualized in several ways. Perhaps the simplest way to examine a landmark configuration is through the use of wireframe diagrams. These diagrams are a collection of lines connecting selected landmarks in a given configuration; these connections are often chosen to represent relevant features of the object being examined. Shape variation can be visualized by warping the landmark configurations and corresponding wireframes along PC axes. This is accomplished by adding or subtracting the eigenvectors of that PC axis multiplied by the position on the axis to the mean (reference) configuration.

Some of the earliest attempts to visualize shape differences among different animals were performed by D'Arcy Thompson (1917) in *On Growth and Form*. These studies did not employ statistical analyses, but simple mathematical models were used to show morphological differences. These methods remained largely unexplored until they were extended to form the basis for thin-plate spline analysis (TPSA) (Bookstein, 1991). This technique employs the thin plate spline (TPS) metaphor, where displacements in landmarks take place on an infinitely thin

and uniform metal plate where the energy required to bend this plate (i.e., bending energy) is minimized. These visualizations require a reference configuration, often the average specimen after landmarks have been GPA-aligned, to which the landmarks of the specimen or specimens under study can be compared. At each landmark coordinate, the study specimen's landmarks will be either more positive or negative than the reference configuration, and these differences can be visualized as bending or deforming the grid or metal plate. Although TPS has more commonly been employed for 2D configurations, this method can be used to examine shape variation in a single plane of a 3D structure, and more recently the TPS function has been extended for warping entire 3D surfaces (Mitteroecker and Gunz, 2009).

Statistically assessing shape variation. It's important to note that the above ordination and visualization methods are largely exploratory in nature and other statistical analyses are employed for testing hypotheses. In most scenarios, standard multivariate statistical techniques can be used; these methods include (but certainly aren't limited to) multivariate analysis of variance (MANOVA), analysis of distances between specimens in shape space (i.e., Procrustes or Mahalanobis distances), regression analysis, and/or partial least squares (PLS) analysis.

The first of these methods, MANOVA, is used for examining statistically significant shape differences among groups related to categorical variables which will be considered simultaneously (e.g., sex, locality, species, different experimental treatments, etc.). MANOVA is often performed on the shape variables projected into the tangent space (Zelditch et al., 2004) or the significant principal component scores (e.g., Cobb and O'Higgins, 2007; Pierce et al., 2008).

Distance measures are highly versatile and are used in many parts of the GM toolkit. For example, the Procrustes distance (either full or partial, see Table 1) between homologous landmarks is the measure that is minimized during a generalized Procrustes analysis. The Procrustes distance is the fundamental unit of Kendall's Shape Space; thus, this metric can also be employed to describe the distance between two landmark configurations in this space. When the question at hand is "do two groups differ significantly in shape space?", the Procrustes distance between the means of each group can be examined and the statistical significance of this distance assessed via a permutation test. Furthermore, more recent implementations of ANOVA/MANOVA in GM take a Procrustes-based approach, and employ the Procrustes distances among specimens as the metric of interest (i.e., Procrustes ANOVA) and are combined with permutation approaches for assessing significance. Another metric that measures the distance between two groups in shape space is the Mahalanobis distance, which is employed in CVA. This metric differs from the Procrustes distance because this distance is scaled by the pooled within-group covariance matrix; thus, this metric reflects the degree of separation between groups and does not take into account the nature of the distribution of specimens around the mean forms (i.e., isotropic or nonisotropic variation) (Klingenberg and Monteiro, 2005). Importantly, this scaling assumes that

all of the groups in the analysis have similar covariance structures, which can be a tenuous assumption when sample sizes are small and unequal to one another (Klingenberg and Monteiro, 2005).

If the hypothesis in question is focused on examining the relationship between shape and one or more continuous variable, regression is an appropriate statistical method. One of the most basic implementations of regression analysis in GM is to examine the relationship between individual PC axes and size (i.e., LnCS). These basic linear regressions contrast with multivariate and/or multiple regressions that may be employed to examine how shape variation varies in relation to other external factors. In the case of multiple regression, PC scores may be regressed on multiple explanatory variables to examine which of these variables more strongly influences shape variation along a single PC axis. Alternatively, in the case of multivariate regression, coordinate data describing all shape variation in the sample (i.e., Procrustes residuals) may be regressed on a single variable (i.e., size) or multiple variables. Use of these regression techniques will necessarily depend upon the research question being investigated.

Like regression analysis, partial least squares (PLS) analysis (aka, singular warps analysis) examines the relationship between two (or more) 'blocks' of data (Rohlf and Corti, 2000; Bookstein et al., 2003). However, one benefit of PLS over regression analysis is that PLS does not assume that one dataset is dependent upon the other. Instead, this method examines patterns of covariation between two or more blocks of data; in GM, at least one of these blocks of data contains shape data. This technique proceeds by performing a singular value decomposition of the cross-covariance matrix of the two datasets, and produces linear combinations of the original datasets that maximize covariance between the blocks of data. The relationship between any two sets of axes is described by the PLS correlation, whereas the overall relationship between the two blocks of data can be summarized using the RV coefficient (Escoufier, 1973; Klingenberg, 2009).

Depending upon the sample under investigation and because of the non-independence of samples taken from closely related groups in a phylogeny, a consideration of how phylogenetic covariance influences the statistical tests described above may also be in order. At present, evaluating the role of phylogeny in GM analyses is performed primarily in two ways: by examining the extent to which shape variation in the sample covaries with phylogeny, and/or by statistically "controlling for" phylogenetic covariance.

The former method estimates the phylogenetic signal in the dataset given a specific phylogeny (and typically assuming a Brownian motion model of evolution) by calculating the total amount of squared change summed over all branches of the phylogenetic tree and performing a permutation test (i.e., shuffling the shape data among the tips of the phylogeny) to assess the significance of this test-statistic (Klingenberg and Gidaszewski, 2010). This phylogenetic signal can be visualized by overlaying the phylogenetic tree on a PC plot of any two (or three) PC axes of interest.

The latter method for assessing the role of phylogeny is to essentially "remove" phylogeny from the analysis in question. This is typically done either through phyloge-

netically independent contrasts (PIC; Felsenstein, 1985; Nunn and Barton, 2001) or via phylogenetic generalized least squares (PGLS; e.g., Martins, 1996; Martins and Hansen, 1997; Pagel, 1999; Rohlf, 2001; Freckleton et al., 2002) methods. Given a phylogeny, PIC operates by calculating the difference between species tips and between a species value and an ancestral node. Thus, for each node in a tree there is a contrast value, which is then used in further statistical analyses (i.e., correlation, regression). This method differs from PGLS in that PGLS incorporates phylogenetic covariance into the error term in a regression model, and thus adjusts for the relationship between two variables given this estimated phylogenetic covariance. Phylogenetic covariance can be accounted for in ANOVA models in a similar fashion (i.e., phylogenetic ANOVA; Garland et al., 1993).

Applications of Geometric Morphometrics

The true strengths of GM methods lie in qualitatively describing and statistically evaluating complex, three-dimensional shape differences between and among groups of specimens. This relatively simple research question has perhaps been by far the most commonly addressed question for which GM has been employed (e.g., Lockwood et al., 2002; Harvati et al., 2004; Kawakami and Yamamura, 2008; Gunz et al., 2009; Freidline et al., 2012; Rosenberger et al., 2013; Terhune, 2013). Similarly, assessment of the influence of external variables on shape (i.e., ontogenetic and allometric analyses, geography, diet) also represents a large number of GM analyses (e.g., O'Higgins and Jones, 1998; Frost et al., 2003; McNulty et al., 2006; Freidline et al., 2013; Martin-Serra et al., 2014; Terhune et al., 2014), and the assessment of shape covariation, integration, and modularity is rapidly becoming more and more common (Bookstein et al., 2003; Klingenberg et al., 2003; Mitteroecker and Bookstein, 2008; Klingenberg, 2009). Finally, the incorporation of phylogenetic comparative methods (as reviewed above) into the GM framework has increased (e.g., Sidlauskas, 2008; Figueirido et al., 2010; Klingenberg and Gidaszewski, 2010; Polly et al., 2013; Martin-Serra et al., 2014) although these methods have primarily been used to examine the distribution of specimens in morphospace relative to a known (or assumed) phylogenetic tree (i.e., *phylo*morphospace plots).

But where the above areas have been strengths, there are certainly areas in GM that can be improved upon. For example, although there are methods for estimating missing landmarks on bilaterally symmetric structures (i.e., reflected relabeling; Mardia et al., 2000), and techniques for virtually reconstructing damaged or distorted fossil specimens are becoming more commonplace (e.g., Motani 1997; Zollikofer et al., 2005; Ogiwara et al., 2006; Gunz et al., 2009; Ghosh et al., 2010), there are few statistical methods for accommodating missing landmarks in current geometric morphometric analyses (but see Adams and Otárola-Castillo, 2013).

Of particular interest in this special issue is the intersection of geometric morphometrics and functional morphology. Although numerous studies have linked particular aspects of shape variation to functional or biomechanical differences among taxa, the overarching weakness of the use of GM in functional questions is that these methods examine correlation but not

causation. This shortcoming is of course also true for non-GM analyses, but traditional functional methods employ biomechanical variables that are specific to a given mechanical problem, and thus are often best measured as well-defined vectors or linear quantities that are more straight-forwardly interpreted (e.g., a longer lever arm will provide greater mechanical advantage and one would expect to observe this trait under specific circumstances). Critically, GM analyses are confined to evaluating shape in total and are not typically “pre-designed” to only capture meaningful aspects of biomechanics; consequently, the portions of the shape that are the result of functional differences cannot easily be disentangled from the portions of shape that are due to phylogeny, allometry, or other factors. In other words, there is a low signal to noise ratio in analyses seeking to use GM to evaluate functionally significant shape variation. This may be improved by a more careful consideration of the features under examination (i.e., limiting landmarks to functionally important features) and/or by statistically controlling for extraneous factors.

An additional problem encountered by researchers using GM for biomechanical studies involves controlling for size and scaling. Centroid size is often used as a variable within analyses to remove or incorporate size information (e.g., generalized Procrustes analysis, form space), but this may not always be the most appropriate size adjustment in functionally-oriented studies. More work need to be done in this area to provide researchers with a roadmap to choose among the methods available for adjusting/controlling/accounting for size. Other options include employing variables such as body mass, molar length, or mandible length (e.g., Hylander, 1985; Vinyard, 2008; Terhune, 2013; Terhune et al., 2015), which are tied more directly to the size of the organism and are functionally relevant.

One growing area of utility for GM analyses is in finite element analysis (FEA). Although not commonly employed until the last few years (e.g., Pierce et al., 2008; Cox et al., 2011; O’Higgins and Milne, 2013), the utility of GM in FEA was first mentioned by Rohlf and Marcus (1993). This research area has increasingly been seen as one way to bridge the GM/ functional morphology gap (Richmond et al., 2005; O’Higgins et al., 2011; Adams et al., 2013; O’Higgins and Milne, 2013). FEA can be used to estimate the stress and strain patterns in a biological specimen under specific loading regimes. Importantly, by coupling GM methods and finite element models, biomechanical performance can be quantified and compared across models with different assumptions (i.e., trabecular structure, material properties) and different loading regimes (i.e., incisor loading vs. molar loading) (O’Higgins et al., 2011; O’Higgins and Milne, 2013). These methods have been used for a number of research questions, including analyses of masticatory forces in extant and extinct organisms (e.g., Ross et al., 2005; Pierce et al., 2008; Fitton et al., 2015; Smith et al., 2015). FEA has not escaped criticism, however. Major critiques of this method revolve around model validation (i.e., how well do FEA models match *in vivo* or *in vitro* experimental data?), model assumptions and simplification (i.e., is the morphology under examination representative of a given species and/or are there simplifications of the FEA model that may impact the results?), and model parameters (i.e., muscle force inputs, boundary

conditions, material properties; how sensitive are models to variation in these parameters?) (e.g., Grine et al., 2010; Adams et al., 2013; Walmsley et al., 2013). Furthermore, the mathematical interpretation of GM data based on FEA models remains unclear (Adams et al., 2013).

FUNCTIONAL MORPHOLOGY

The major goal of functional morphological studies is to understand the relationship between an organism’s form and its function. To this end, researchers have employed a great variety of techniques in attempts to quantify movement, understand how muscles cause movement, and evaluate the biomechanical advantages that certain morphological forms may have over other similar forms. Functional morphology as a “discipline” is relatively diffuse in contrast to GM, as functional morphological studies not only sometimes contain GM methodologies, but also encompass a wide variety of other methods. For this reason, our review of the history of this field will not be exhaustive, and we refer interested readers to works such as *Form and Function: A Contribution to the History of Animal Morphology* by Russell (1916; republished in 1982) and “A brief history of vertebrate functional morphology” by Ashley-Ross and Gillis (2002).

Evolutionary Theory and Functional Morphology

The theoretical underpinnings of functional morphology are primarily centered in the ongoing debate regarding how form, function, and adaptation are defined and operationalized, both in living and fossil organisms. We summarize this debate briefly here, and refer interested readers to the vast literature on the relationship between form, function, and adaptation (e.g., Bock and von Wahlert, 1965; Gould and Lewontin, 1979; Clutton-Brock and Harvey, 1979; Bock, 1980; Gould and Vrba, 1982; Mayr, 1982; Harvey and Pagel, 1991; Reeve and Sherman, 1993; Lauder, 1990, 1995; Ferry-Graham et al., 2002; Ross et al., 2002; and more).

Russell (1916) distinguished between at least two approaches to morphological studies, which still resonate in functional morphology to this day. The first, what Russell termed the functional or synthetic view (exemplified by Georges Cuvier), holds that function is the primary determinant of form. In contrast the second view, the formal or transcendental view (championed by Étienne Geoffroy Saint-Hilaire), posits that form determines function. This historical debate between functionalism (i.e., adaptationism) and structuralism can in many ways be resolved in the post-Darwinian era where the theory of natural selection allows for similarities due to common ancestry and allows for differences due to adaptation during descent (Szalay, 2002). Thus, this debate has largely shifted to evaluating the extent to which features may have arisen as a result of selective processes, or whether features may hold no particular adaptive significance but instead were produced by constraints (developmental, mechanical, phylogenetic) within an organism that may have mediated the effects of natural selection (e.g., Gould and Lewontin, 1979).

Of particular importance to this special issue is the argument that form and function cannot be examined in isolation from one another. In their now classic work on "Adaptation and the Form-Function Complex" Bock and von Wahlert (1965) argue that the fallacy of many morphological studies is that they divorce form from function, which doesn't allow for the examination of the "phenomenon of biological adaptation" (Bock and von Wahlert, 1965: 270). Instead, they argue that studies should focus on the form-function complex (aka functional units), which themselves are defined as a feature or group of features of an organism that work together to carry out a common biological role. This biological role, as argued by Bock and von Wahlert (1965), is closely linked to, but not necessarily inferable from, the form-function complex, except through observation of the organism in its natural environment. The study of form-function relationships is intimately tied to understanding adaptation, and in many cases, the identification of a specific form-function complex that is used for a particular biological role allows for the inference that the complex in question is an adaptation.

The topic of how specifically an adaptation is defined is a broad one, and thorough discussion of this debate is beyond the scope of this paper. Most simply, an adaptation can be defined as a feature shaped by natural selection for the function it is currently performing (e.g., Bock and von Wahlert, 1965; Reeve and Sherman, 1993). This nonhistorical definition contrasts with the historical perspective, which defines an adaptation as a feature that arose as a result of selection for a particular function, but need not necessarily be the function it currently performs (Gould and Lewontin, 1979; Harvey and Pagel, 1991; Ross et al., 2002). The identification of adaptations relies heavily on the comparative method, which in essence searches for correlated evolution among characters or between characters and environments (Harvey and Pagel, 1991). An observed correlation can only suggest a particular adaptive scenario, however, not prove its validity (Harvey and Pagel, 1991). The finding of a correlation between a particular form and a particular environment therefore necessitates further study of the form-function relationship and biological role of Bock and von Wahlert (1965). Notably, the direct linkage of a form-function complex to a specific biological role is a difficult task to undertake when the organism of interest is extinct. Two main methods therefore predominate for inferring function from structure in extinct taxa: the phylogenetic method, which examines convergences in forms that perform the same function, and the paradigm method, which examines how well-adapted and efficient a feature is for a given function via a biomechanical modeling approach (Rudwick, 1964; Lauder, 1995).

The Functional Morphologist's Toolkit

Today's functional morphologists have a great variety of techniques at their disposal, many of which are used in combination with each other. Some major research foci have examined gait and leaping patterns, body and head carriage, masticatory forces and their effects on cranial and mandibular morphology, as well as dental functional morphology. These studies have taken place both in the lab and in wild populations of animals.

Below, we review some of the most important methodologies that have proved essential for studying functional morphological questions.

Comparative morphological analysis. Comparative anatomy, which itself finds its roots in some of the earliest scientific literature from the western tradition (in particular, Aristotle discussed animal anatomy in his seminal work, *Historia Animalium*, *De Partibus Animalium*) provides the foundation for many later analyses of functional morphology. Notable contributors to our early understanding of variation in human and animal form, and the relationship of these forms to function, include Galen (129–201 A.D.), who is often considered the father of human anatomy; Leonardo da Vinci (1452–1519), whose exquisite drawings were some of the first accurate anatomical representations of the human form and which allowed him to study the mechanical function of the skeletal and muscular systems; and Giovanni Borrelli (1608–1679), whose work on animal locomotion and his application of simple lever systems and physical principals to muscle function has earned him the title of "father of biomechanics" (Russell, 1916; Ashley-Ross and Gillis, 2002). Perhaps the most notable historical character in the comparative anatomical tradition is Georges Cuvier (1769–1832) who, in addition to his work on catastrophism and debates with Étienne Geoffroy Saint-Hilaire (1772–1844) (Appel, 1987), is famous for his examination of the relationship between function and anatomy, including aspects of locomotor anatomy as well as dental functional morphology. Cuvier is often considered to be the first comparative functional morphologist.

By the end of the 19th century, much of this groundwork was incorporated into an evolutionary framework and in particular Cuvier's contributions to the development of this framework were recognized (e.g., Russell, 1916). Studies of the dentition became particularly important during this period with a focus on the evolutionary morphology of mammals. Cope and Osborn developed their model of the tribosphenic molar, and while largely focused on cusp homology, their model did not ignore how the dentition worked to effectively shear, grind, and crush food items (e.g., Cope, 1883a,b; Osborn, 1888, 1907). This research laid the foundation for many later studies of mammalian molar function (e.g., Kay and Hiiemae, 1974; Kay, 1975; Rosenberger and Kinzey, 1976). Nearly simultaneously, researchers were developing a variety of measures of anatomical form intended to capture functionally significant postcranial variables, many of which are still in use today. Mollison (1911) introduced the intermembral index—a measure of the relative lengths of the primate fore- and hindlimb, which correlates tightly with locomotor profile. Schultz among others published extensively using this measure and solidified its importance in understanding body proportion and locomotion (e.g., Schultz, 1926, 1930, 1933, et seq.).

These types of comparative analyses dominated physical anthropology during the first half of the 20th century, until Sherwood Washburn (1951) implored physical anthropologists to move beyond simple correlations and to employ laboratory-based methods for the study of functional morphology. Importantly, this paradigm shift suggested that the conclusions of comparative morphometric analyses could be seen as forming the foundation

for future experimental studies of form and function such as those outlined below. Virtually all functional morphological studies today take into account some aspects of comparative morphological analysis.

Kinematic analysis. The latter half of the 19th century also saw the advent of new techniques for evaluating movement as it related to form and function. Eadweard Muybridge made a substantial contribution in understanding gait and motion by photographically documenting movement in thousands of images of animals and humans walking, running, and performing various tasks. These images are still used today. Muybridge's contemporary, Etienne-Jules Marey invented graphical methods of documenting animal locomotion, which established the beginnings of methodologies invented to capture data as an animal was moving (Ashley-Ross and Gillis, 2002). Additionally, Ryder (1878, 1879) examined the relationship between jaw movement and mammalian dental anatomy and noted animals with a greater transverse component to mastication also tended toward having more complex dental anatomy in the form of more ridging, cresting, and enamel infolding.

While 19th and early 20th century scholars understood the importance of the study of movement, it wasn't until the middle of the 20th century that methodologies were developed to allow researchers to scientifically examine how organisms move and how that movement relates to anatomy. Chief among these methods is the use of high-speed photography, video analyses, cineradiography, and 3D motion capture systems (Vicon, XROMM), which allow researchers to track skeletal and soft tissue movement either through manual digitization of images or through the use of software (e.g., Unimark by R. Voss, Tübingen) designed to capture and measure skeletal markers placed on bony or soft tissue landmarks (e.g., knee, ankle, dentition, etc.). From these digitized images, functionally relevant angles, distances, and even range of motion can be calculated (e.g., Demes et al., 1996; Schmidt, 2005a,b; Stevens et al., 2011). Often measurements obtained from these images are combined with data collected simultaneously from force plates, strain gauges, electromyography, or with static morphological measurements taken on the same animals (e.g., Hylander et al., 1987; Schmidt, 2005b; Ross et al., 2010; Stevens et al., 2011; Terhune et al., 2011).

Kinematic analysis has been particularly important in analyzing locomotor and masticatory behaviors. Of particular importance for understanding primate locomotion is the work of Brigitte Demes, Susan Larson, and colleagues who have utilized multiple kinematic methods in all major lineages of primates as well as some other mammals (e.g., Demes et al., 1995, 1996; Schmitt and Larson, 1995; Larson et al., 2000; Demes, 2011). While much of this work has taken place in a controlled laboratory setting, some researchers have tried to bridge this gap by examining locomotion in the wild as well. While data on the proportions of different locomotor behaviors in wild populations is readily available, and some functional morphological studies have used these data in analyses of anatomical forms (e.g., Ward and Sussman, 1979; Fleagle and Meldrum, 1988), it is rarer in the literature to link kinematic laboratory analyses with wild observation (e.g., Stevens et al., 2011). In addition to

kinematic studies of locomotion, analyses of primate mastication have also used kinematic techniques. A number of researchers have examined masticatory movement in laboratory settings including Kay and Hiemae (1974) who correlated jaw movement with molar form and Hylander et al. (e.g., 1987) who have used a combination of techniques to correlate masticatory movement, strain, and force.

Electromyography. Electromyography (EMG) is often used in combination with kinematic analyses (e.g., Hylander et al., 1987; Vinyard et al., 2006a). The initial discovery of electrical impulse in muscle was made at the end of the 18th century (Ashley-Ross and Gillis, 2002), but technological developments in the 19th and 20th centuries, such as the fine wire electrode (Basmajian and Stecko, 1962), allowed the detection of impulses in single muscles. By the 1960s, extensive research on human muscular function had been conducted for nearly all muscles of the body (e.g., Basmajian and Bazant, 1959; Travill, 1962; Hirano and Ohala, 1969; Basmajian and de Luca, 1985) including those muscles on which no one would be happy to have an electrode placed (e.g., Floyd and Wall, 1953). Researchers subsequently turned their interest to various other organisms including domestic dogs and cats (e.g., Dedo and Ogura, 1965; Cohen et al., 1964; Wienbeck et al., 1972; Griffiths and Duncan, 1978) with the specific purpose of understanding disease processes and the clinical applications of electromyography.

Non-clinical inquiry also began to flourish in the 1960s and researchers perused a broad array of questions. Henson (1965) examined bat middle ear musculature; many studies were conducted on fish feeding and swimming (e.g., Hughes and Ballintjin, 1968; Osse, 1969; Davison et al., 1976). Primates have and continue to receive considerable attention. Among the primate studies, work by William Hylander, his students and colleagues (i.e., Kirk Johnson, Matthew Ravosa, Callum Ross, Chris Vinyard, Christine Wall, Susan Williams) on masticatory musculature has been particularly important in understanding the mechanics of chewing and for determining which muscles and muscle groups fire during different points in the chewing cycle (e.g., Hylander and Johnson, 1985, 1994; Hylander et al., 2005; Vinyard et al., 2006b). EMG studies of locomotion and primate grasping, which have often been combined with kinematic analysis have also elucidated how primates grasp (e.g., Boyer et al., 2007; Kingston et al., 2010), jump and leap (e.g. Jungers et al., 1980; Anapol and Jungers, 1987), knuckle walk (e.g., Tuttle et al., 1972; Tuttle and Basmajian, 1974a,b), and brachiate (e.g., Jungers and Stern, 1980, 1981). Finally, many studies have also examined muscle use in *Homo sapiens* with the goal of understanding some of the unique aspects of our own biology such as tool use (e.g., Hamrick et al., 1998) and bipedality (e.g., Stern and Susman, 1981; Shapiro and Jungers, 1988; Jungers et al., 1993).

Measuring forces. As an organism moves, forces are produced both within the body and between the body and the object with which it is in contact. Understanding how these forces affect morphology, both ontogenetically and through selection for particular morphological traits,

has proved to be a rich area of inquiry. Multiple methods exist for assessing forces, many of which were developed during the mid-20th century. In studying the strain on bones themselves, some early researchers covered bones with a thin coat of colophonium or a brittle lacquer (stress coat) and then placed the bones under strain. Cracks would appear in the location of highest strain, and these cracks were photographed and analyzed (e.g., Gurdjian and Lissner, 1944; Gurdjian et al., 1947; for a review of these methods see Evans, 1953).

The same researchers who pioneered the use of a stress coat also introduced the strain gage to measure bone deformation *in vivo* (Gurdjian and Lissner, 1944). To attach a strain gage, the bone is exposed, stripped of periosteum, the gage is attached using an adhesive, and the surgical wound is closed (Hylander, 1977, 1984). Once recovered, the animal is then allowed to move and strains are recorded during normal behaviors. Measurement of bone strain continues to be used heavily in studies of primate masticatory forces most commonly in *Macaca fascicularis* (e.g., Behrens et al., 1978; Hylander 1984; Hylander et al., 1987; Hylander and Johnson, 1997), but research on other taxa has also been conducted (e.g., Hylander, 1977; Ross and Hylander, 1996; Ross and Metzger, 2004). Strain gages measure the deformations of the surfaces of bones that are a result of external forces applied to those surfaces. The bite force is a reaction force that is applied to food objects and that results from the recruitment of the jaw muscles. An isometric bite force can be measured *in vivo* using a bite force transducer (Hylander, 1978; Dechow and Carlson, 1983; Chazeau et al., 2013). Bite forces can be estimated in a variety of ways, most frequently by estimating muscle contractile force in combination with two- or three-dimensional measurement of lever arms and load arms (e.g., Demes et al., 1986; Demes and Creel, 1988).

Finally, force plates have been instrumental in determining the forces that occur between the limbs and the ground during locomotion. Force plates themselves were developed as an outgrowth of strain gages (Cavagna, 1975), and have been applied to a wide variety of questions. Of particular interest to primatologists are the forces produced by the unusual diagonal sequence primate gate which has been suggested to be an adaptation to walking on thin flexible branches (e.g., Schmitt and Lemelin, 2002). Primates are also unusual in being hind limb driven in contrast to most other mammals (Kimura, 1992; Demes et al., 1994). Understanding the forces produced between the limbs and the substrate elucidates what mechanically is occurring in the body. Additionally, researchers have used force plates to examine how other variables such as body size (Demes and Günther, 1989) or substrate type (e.g., Schmitt and Hanna, 2004) might affect locomotion.

Combining Geometric Morphometrics and Functional Morphology

How can we move forward with combining the strengths of geometric morphometrics with those of functional morphology? In fact, these two disciplines are already intertwined. As discussed in the historical review above, functional morphology initially grew out of a comparative anatomical tradition and still extensively utilizes these tools to examine functionally meaningful

shape variation. However, the functional morphology toolkit has expanded beyond comparative anatomy to such a degree that functional analyses solely utilizing comparative anatomy can be viewed as too simplistic and lacking a rigorous interpretive framework. In many ways, GM analyses that seek to address functional questions also fall into this trap, where correlations between shape and function may be observed but clear mechanical links cannot be demonstrated, hampering inferences concerning adaptation. Furthermore, GM analyses of functionally interesting shape variation can be plagued by confounding factors that are not easily evaluated (i.e., inclusion of non-functional shape variation, phylogeny, allometry). This low signal to noise ratio (Baab et al., 2012) is a major hurdle over which GM analyses of functional shape variation are just beginning to jump.

The integration of geometric morphometrics into other portions of the functional morphology repertoire is already underway. Procrustes motion analysis (Adams and Cerney, 2007) represents one existing method for the analysis of kinematic data in a geometric morphometric framework. However, this method has not been widely adopted by functional morphologists and its utility in functional analyses remains to be demonstrated. In contrast, GM methods are steadily becoming more frequently incorporated into finite element analyses (i.e., O'Higgins et al., 2011; O'Higgins and Milne, 2013; Fitton et al., 2015; Smith et al., 2015), which themselves are designed to model strains in such a way that mirror *in vivo* strain gage analyses.

THIS SPECIAL ISSUE

This issue contains sixteen papers that have each attempted to address the original question posed to our symposium and special issue participants: can geometric morphometrics and functional shape analyses be used to address similar functional hypotheses? Our goal was ambitious, and we hope that the reader finds these contributions helpful in beginning to address the intersection of geometric morphometrics and functional morphology. The contributions range from the theoretical to the practical and run the gamut in terms of specific methodologies employed.

Using coordinate landmark data, several authors examined the functional morphology of the masticatory apparatus. Terhune and colleagues examined covariation between dental morphology and craniofacial shape, with a particular focus on the temporomandibular joint, in a broad sample of platyrrhine primates. While the relationship between cranial and mandibular shape and diet and between dental morphology and diet has been extensively studied, little work has been conducted to examine how components of this morphological system covary. Noback and Harvati (2015) also examined covariation between different parts of the masticatory apparatus and focused their analyses on variation between different modern human populations, and found that including relative position, orientation, and size of the components of the masticatory complex reveals stronger patterns of shape covariation than evaluating shape alone. Taking a different approach to masticatory studies, Singleton used GM to examine masticatory development in papionins with the particular goal of testing the hypothesis that the timing of eruption and relative

position of molars is biomechanically constrained. She found that the distalmost molar maintains a consistent position relative to the temporomandibular joint throughout ontogeny, suggesting similar functional capacities among specimens of different ages. Although not strictly part of the masticatory apparatus, Pagano and Laitman (2015) round out the craniofacial contributions to this special issue by examining the nasopharyngeal boundaries using both coordinate and linear data. Their data support previous results that human nasopharyngeal shape is distinct from other extant apes, and suggest that nasopharyngeal boundaries are related to variation in the facial skeleton and external basicranium of great apes and humans.

The combination of GM methods and FEA also features prominently in this special issue with the contributions from Smith et al. (2015) and Fitton et al. (2015). The first Smith et al. (2015) study employed GM as a method for identifying individuals at the extremes of cranial shape variation in *Pan troglodytes*; finite element models were then made of these individuals and intraspecific strain patterns were examined. The second Smith et al. (2015) study builds on this understanding of intraspecific strain variation to evaluate strain distributions in *Paranthropus boisei* (as represented by OH 5), suggesting that *P. boisei* would have been capable of efficiently producing high bite forces. Where Smith et al. (2015) use GM on the front end of their work to identify specimens which should be examined using FEA, Fitton et al. (2015) take the opposite approach and use GM methods to examine the output of their FEA analyses. Specifically, Fitton et al. (2015) examine a single FEA model of a *Macaca fascicularis* cranium and use Procrustes size and shape analyses to compare differences in deformations between models with different assumptions regarding material properties and segmentation. Their results reveal that, although model simplifications do have an impact on FEA outcomes, these impacts are small relative to strain patterns produced by differences in bite point location or among species.

Several papers used GM to address specific functional questions relating to postcranial morphology and locomotion. Almécija and colleagues explored the relationship between hamate shape in a sample of apes and locomotor categories while also taking phylogeny into account. Their findings indicate a significant relationship between different types of arboreal locomotion and shape. Tallman also explored shape in the wrist, but examined the morphology of the distal ulna across a sample of humans, great apes, and two hominin species, *Australopithecus afarensis* and *A. africanus*. Her primary goal was to assess functional morphology of this region in the australopiths; she found broad similarity with ape morphology, perhaps indicating the possibility of continued use of trees for foraging or shelter. Green et al. (2015) used the morphology of the scapula as a test case for examining the efficacy of different GM approaches to quantifying shape. They were particularly interested in addressing how complex scapular shape could be captured with homologous landmarks or sliding semilandmarks and how those shapes relate to scapular function. Macias and Churchill (2015) also explored scapular morphology, but with the goal of understanding whether differences between Neanderthal and modern *Homo sapiens* scapular morphologies are best attributed

to functional differences or if other explanations such as size or development are more strongly supported. Lewton (2015), concentrating on pelvic morphology of strepsirrhines, employed both GM methodologies and linear measures derived from 3D coordinate data to test functional hypotheses. She found that a combination of linear and 3D measures allowed her to capture pelvic shape fully; while the linear measures were used to test specific functional hypotheses, the 3D data augmented these data and in some cases further supported her hypotheses.

The contributions of Curran (2015) and Knigge et al. (2015) use GM to explore the relationship between functional morphology and ecology. Curran employed GM to quantify the shape of hind limb bones in cervids and to examine the relationships between these morphologies and the environment (i.e., dry vs. wet habitats) and to infer the habitat occupied by an extinct cervid, *Eucladoceros*. Knigge et al. (2015) examined morphological differences in the talus of western, mountain, and grauer gorillas. Since these different populations have somewhat different locomotor repertoires, the authors explored how talar shape differed among the taxa and what relationship these differences might have to functional demands of the different substrates.

Finally, two papers concentrated on the development of new or the modification of existing techniques to expand the range of GM capabilities. In their article, Boyer et al. (2015) introduce a new technique for the automatic placement of landmarks on 3D surface models. Using a sample of primate calcanei, the authors compared data gathered automatically to data collected by an observer. Additionally, they introduce an *R* package for the automatic placement of landmarks. Bookstein (2015) presents a new method for evaluating shape variation in a sample given an *a priori* measure of function such as a distance or index. This technique calculates a vector in shape space against which landmark configurations can be aligned.

The concluding contribution in this issue provides a critical review of the status of geometric morphometrics and functional morphology, and points the way forward. McNulty and Vinyard (2015) particularly highlight how extracting functional information from three-dimensional shape coordinates is a complex process as much of the shape is dominated by phylogenetic factors. Additionally, they suggest that an expansion of statistical methods currently in use is essential for maximizing the potential of GM for functional questions and, like Bookstein (2015) suggest the field must move beyond the most commonly used statistical techniques (e.g., principal component analysis). Finally, the authors suggest that forming collaborations with behavioral ecologists, geneticists, and physiologists (among others) are critical for incorporating multiple lines of data into GM datasets, including genetic information and/or behavioral and ecological data.

As a group, these papers push the current boundaries of how GM has been traditionally used in analyses of functional morphology. These contributions employ newly developed methods (i.e., Bookstein, 2015; Boyer et al., 2015), examine the comparability and complementarity of traditional and geometric morphometrics (i.e., Lewton, 2015; Pagano and Laitman, 2015), highlight the increasing adoption of existing methods such as

semilandmarks, PLS, and phylogenetic techniques for functional analyses (Almecija et al., 2015; Green et al., 2015; Knigge et al., Noback and Harvati, 2015; Tallman, 2015; Terhune et al., 2015), expand the application of commonly used GM methods to new contexts and questions (Singleton, 2015; Macias and Churchill, 2015; Curran, 2015), and meld quantitative techniques such as GM and FEA to produce novel insights into shape variation in a biomechanical context (Smith et al., 2015; Smith et al., 2015; Fitton et al., 2015).

CONCLUSIONS

Although we are unapologetic advocates of the GM approach, it's critical for us to emphasize that GM is simply a toolkit. Fundamentally it is a set of techniques in search of a question. We emphasize that there are certainly other ways of tackling complex questions regarding form, function, and adaptation, and perhaps GM isn't always the best method for addressing these questions. Whether GM is appropriate should be weighed carefully and chosen only if appropriate to the research at hand. These caveats aside, as we think is exemplified by the contributions in this special issue, the future for geometric morphometrics and functional morphological analyses is bright. It is notable that the analyses presented here largely fall into the "comparative anatomical analysis" portion of the functional morphology toolkit. This is indeed the region of the strongest overlap between GM and functional morphology, and will likely continue to be a commonly investigated research area. The major challenges for the future should be to expand geometric morphometric analyses to other portions of the functional morphology toolkit, and to couple GM methods with experimental analyses of the form-function complex. It is clear that although GM has the analysis of complex forms largely sorted out, the incorporation of a strong theoretical consideration of how these forms are best linked to function is less resolved.

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APPENDIX

EXAMPLE GEOMETRIC MORPHOMETRIC ANALYSIS

Our goal in this review paper was to provide a practical guide to those researchers planning to undertake geometric morphometric analyses and particularly those with functional questions in mind. To this end, here we provide examples of some of the analyses that can be conducted using the techniques outlined in the main body of the text. These examples are illustrated using a dataset of 20 3D landmarks describing the facial morphology (and the relationship of the face to the cranial base) of a wide cross-section (40 species) of anthropoid primates (Tables A1 and A2, Figs. A1 and A2). These data were collected by one of us (CET) using a Microscribe G2X digitizer; please refer to Terhune (2010) for more specific details of the data collection protocol and a description of intraobserver error for this dataset. All specimens chosen for analysis are non-pathological adults, with minimal dental wear (where possible). Males and females are pooled in all analyses. We employ this dataset to illustrate the wide variety of GM

TABLE A1. Landmark Descriptions for the Example Dataset

Landmark #	Landmark Description
1	Gnathion
2	Infradentale
3	Most inferior point on the mental foramen
4	Point on lateral alveolar margin at the midpoint of mandibular P4
5	Point on lateral alveolar margin at the midpoint of mandibular M2
6	Prosthion
7	Nasospinale
8	Nasion
9	Glabella
10	Bregma
11	Basion
12	Midpoint of sphenoccipital synchondrosis
13	Point on alveolar margin at the midpoint of maxillary P4
14	Point on alveolar margin at the midpoint of maxillary M2
15	Orbitale
16	Maxillofrontale
17	Frontomolare orbitale
18	Jugale
19	Point on the superior border of the zygomatico-temporal suture
20	Most anterior point on the cranial masseteric scar

TABLE A2. Specimens Examined as Part of the Example Dataset

Species	Abbreviation	Clade	Female	Male	Mandible Length (mm)
<i>Ateles geoffroyi</i>	<i>Age</i>	Atelidae	12	11	61.54
<i>Alouatta seniculus</i>	<i>Ase</i>	Atelidae	11	10	69.78
<i>Lagothrix lagotricha</i>	<i>Lla</i>	Atelidae	11	11	60.14
<i>Aotus trivirgatus</i>	<i>Atr</i>	Cebidae	11	10	35.54
<i>Cebus apella</i>	<i>Cap</i>	Cebidae	10	12	50.87
<i>Cebus capucinus</i>	<i>Cca</i>	Cebidae	13	11	53.83
<i>Saimiri sciureus</i>	<i>Ssc</i>	Cebidae	10	5	29.87
<i>Chiropotes satanas</i>	<i>Csa</i>	Pitheciidae	11	11	46.83
<i>Pithecia pithecia</i>	<i>Ppi</i>	Pitheciidae	11	10	44.80
<i>Cercopithecus mitis</i>	<i>Cmi</i>	Cercopithecini	11	11	65.50
<i>Cercopithecus nictitans</i>	<i>Cni</i>	Cercopithecini	9	12	63.19
<i>Erythrocebus patas</i>	<i>Epa</i>	Cercopithecini	8	11	80.08
<i>Miopithecus talapoin</i>	<i>Mta</i>	Cercopithecini	5	7	38.08
<i>Macaca fascicularis</i>	<i>Mfa</i>	Papionini	11	10	66.79
<i>Macaca fuscata</i>	<i>Mfu</i>	Papionini	12	9	81.00
<i>Macaca nemestrina</i>	<i>Mne</i>	Papionini	11	11	87.89
<i>Macaca sylvanus</i>	<i>Msy</i>	Papionini	8	4	78.08
<i>Cercocebus torquatus</i>	<i>Cto</i>	Papionini	4	5	81.22
<i>Lophocebus albigena</i>	<i>Lal</i>	Papionini	11	10	73.79
<i>Mandrillus sphinx</i>	<i>Msp</i>	Papionini	5	6	131.91
<i>Papio anubis</i>	<i>Pan</i>	Papionini	9	11	126.58
<i>Papio cynocephalus</i>	<i>Pcy</i>	Papionini	9	9	110.42
<i>Theropithecus gelada</i>	<i>Tge</i>	Papionini	3	9	109.63
<i>Colobus polykomos</i>	<i>Cpo</i>	Colobini	12	11	68.42
<i>Ptilocolobus badius</i>	<i>Pba</i>	Colobini	12	12	63.43
<i>Procolobus verus</i>	<i>Pve</i>	Colobini	10	12	49.26
<i>Nasalis larvatus</i>	<i>Nla</i>	Colobini	11	12	71.37
<i>Trachypithecus obscurus</i>	<i>Tob</i>	Colobini	10	9	57.26
<i>Semnopithecus entellus</i>	<i>Sen</i>	Colobini	12	11	71.77
<i>Hylobates agilis</i>	<i>Hag</i>	Hylobatidae	8	12	58.82
<i>Hylobates klossii</i>	<i>Hkl</i>	Hylobatidae	8	8	54.97
<i>Hylobates lar</i>	<i>Hla</i>	Hylobatidae	9	12	59.88
<i>Symphalangus syndactylus</i>	<i>Ssy</i>	Hylobatidae	10	11	75.69
<i>Pongo abelii</i>	<i>Pab</i>	Hominidae	7	10	124.08
<i>Pongo pygmaeus</i>	<i>Ppy</i>	Hominidae	11	9	125.33
<i>Pan paniscus</i>	<i>Ppa</i>	Hominidae	12	8	88.85
<i>Pan troglodytes</i>	<i>Ptr</i>	Hominidae	12	11	107.44
<i>Gorilla beringei</i>	<i>Gbe</i>	Hominidae	6	8	147.27
<i>Gorilla gorilla</i>	<i>Ggo</i>	Hominidae	12	12	132.33
<i>Homo sapiens</i>	<i>Hsa</i>	Hominidae	24	27	83.93

Specimens accessed from the following collections: National Museum of Natural History, Washington DC, USA; American Museum of Natural History, New York NY, USA; Field Museum, Chicago IL, USA; Royal Museum for Central Africa, Tervuren, Belgium; Department of Primatology at the State Collection of Anthropology and Palaeoanatomy, Munich, Germany.

TABLE A3. Results of Regressions of Principal Component (PC) Scores for the Top Five PC Axes Regressed on the Natural Log of Centroid Size (LnCS) for Their Respective Samples, Including the Percentage of Variance in the Sample Explained by the Regression (%variance), the r-Squared Value (r-sq), and the Corresponding Significance (P-value)

	Species Means- Shape space			All Specimens- Shape space			All specimens- Form space		
	%variance	r-sq	P-value	%variance	r-sq	P-value	%variance	r-sq	P-value
PC1	53.0	0.68	<0.0001	42.2	0.60	<0.0001	89.4	0.999	<0.0001
PC2	13.8	0.06	0.13	16.4	0.06	<0.0001	3.4	0.001	0.47
PC3	11.2	0.11	0.04	11.7	0.17	<0.0001	2.3	0.00	0.82
PC4	5.1	0.03	0.28	5.3	0.03	<0.0001	1.0	0.00	0.80
PC5	3.7	0.00	0.96	4.4	0.00	0.08	0.7	0.00	0.99

approaches for assessing shape variation and for examining the relationship between shape variation and other factors. Although this analysis is largely exploratory and for illustrative purposes, we can further ask a relatively simple research question: what is the nature of facial shape variation across anthropoid primates, and how is

this variation distributed relative to size and phylogeny? So that interested readers can work through these same analyses, the two datasets employed in this analysis (the data for each individual specimen in the analysis, and the landmark coordinates of the species mean forms) are provided in the supplementary materials and are

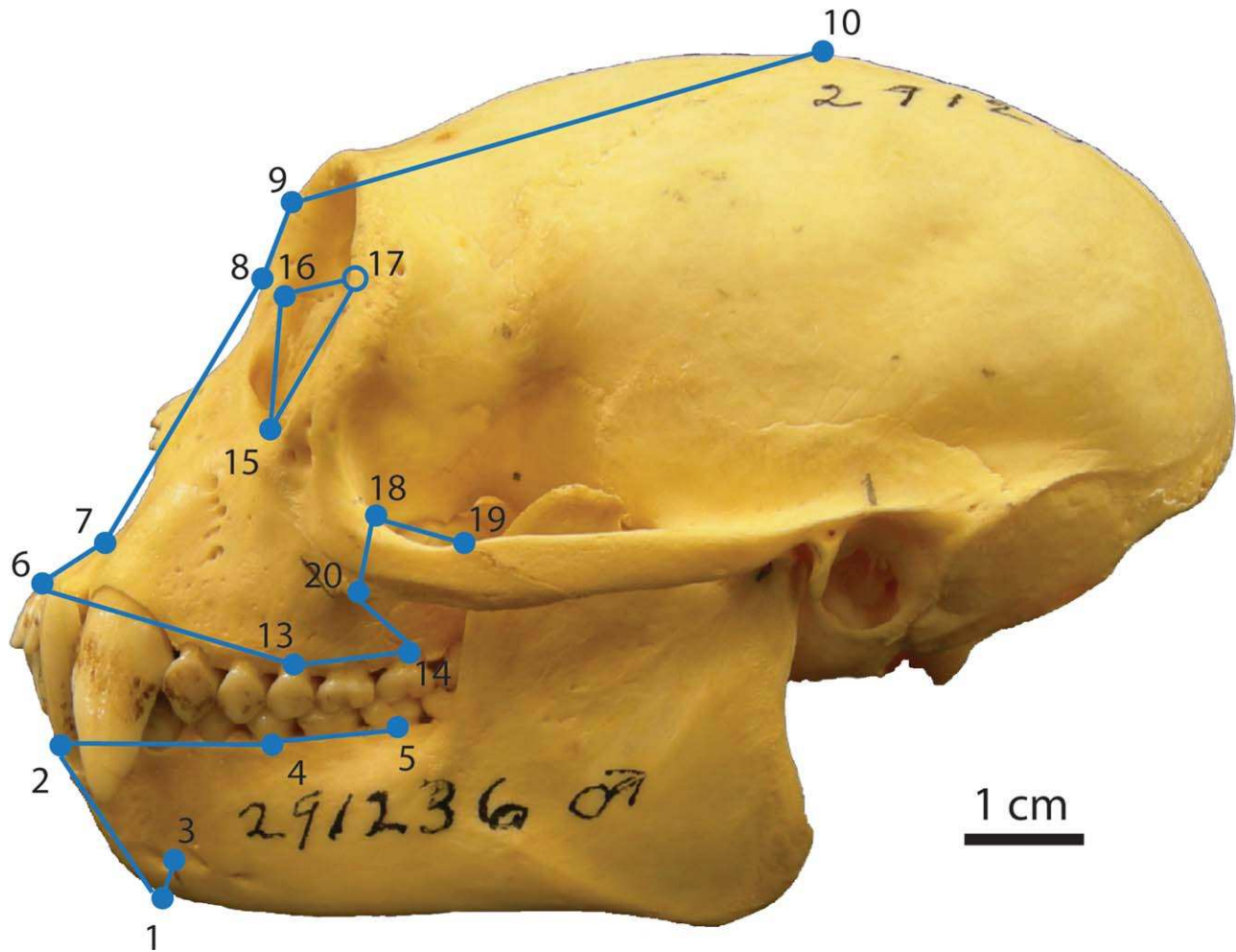


Fig. A1. Lateral view of a *Cebus capucinus* cranium showing the cranial and mandibular landmarks and wireframes employed in this analysis. Landmark numbers correspond to those listed in Appendix.

available at terhunelab.uark.edu. Should these data be used in further analyses we ask that this publication be cited accordingly. The analyses presented here were performed using the programs Morphogika (O'Higgins and Jones, 1998), MorphoJ (Klingenberg, 2011) and the 'geomorph' package for R (R Development Core Team, 2008; Adams and Otárola-Castillo, 2013).

Ordination Methods

Following superimposition via Generalized Procrustes Analysis (GPA) (Fig. A3), variation in shape space for the dataset describing the primate face was assessed via a principal components analysis (PCA), results of which are shown in Figure A4. Figure A4A shows variation in a shape space consisting of species mean forms. Principal component (PC) 1 explains approximately 53% of the shape variation in the sample and is significantly correlated with centroid size variation ($r\text{-sq}=0.68$, $P<0.0001$; Table A3). PC 2 (not significantly related to centroid size) explains less shape variation in the sample (13.8%), and largely separates humans and papionins on the negative end of this axis from hominoids and *Alouatta seniculus*,

which load positively on PC 2. A similar distribution of taxa in shape space is demonstrated when all specimens for each of these species are included in the PCA (Fig. A4B). However, the distribution of specimens along PC 2 differs considerably in this shape space, with the distinctive facial morphologies of *Alouatta seniculus* and *Homo sapiens* falling at either end of this axis with no overlap with other taxa along PC 2. It is worth noting that the top four PC axes in this shape space are all significantly related to centroid size, although only PC 1 has an r -squared value that exceeds 0.2. Not surprisingly, the form space PCA (Fig. A4C) shows a different distribution of specimens along the first two PC axes, with PC 1 (89.4% of shape variation) significantly and highly correlated with centroid size ($r\text{-sq}=0.999$, $P<0.0001$). At the far negative end of PC 1 is *Aotus trivirgatus*, while papionins and great apes load positively on this axis. It's also worth noting that PC 2 (3.4% of shape variation) largely distinguishes papionins (which load positively) from *Homo sapiens* (which loads negatively) on this axis.

A comparison of standard PCA, bgPCA, and CVA plots for a subsample of the primate face dataset (i.e., great apes and humans) is shown in Figure A5. Although the

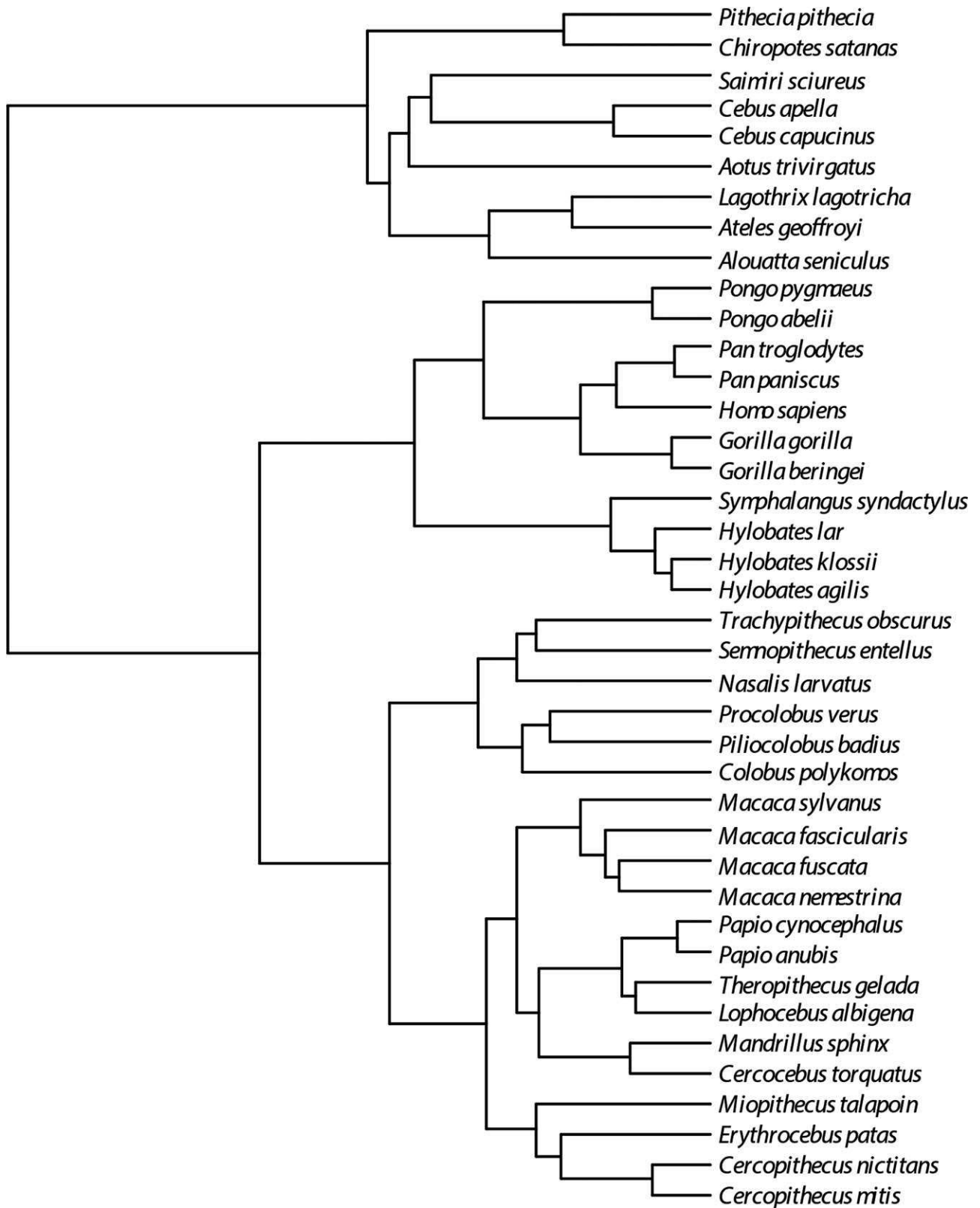
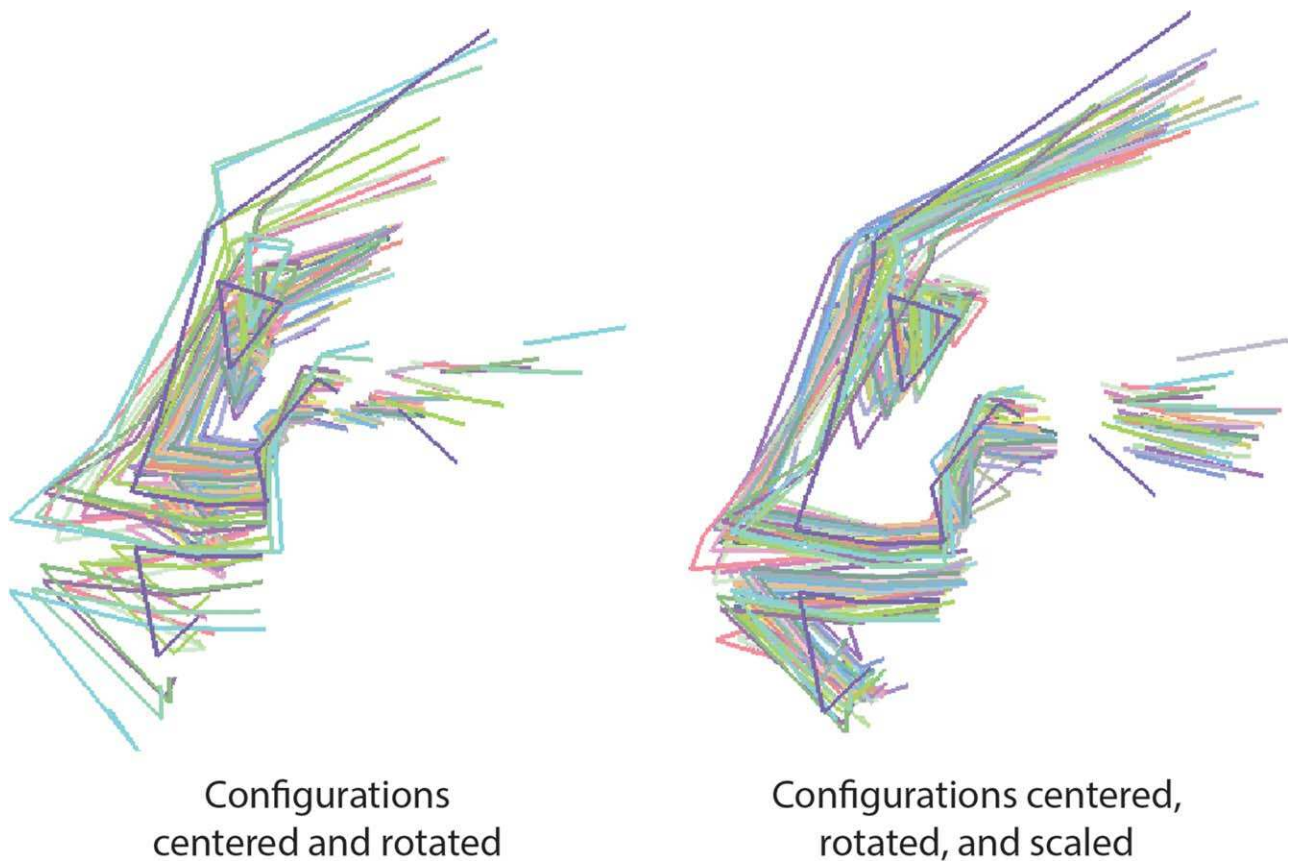


Fig. A2. Consensus tree with branch lengths (downloaded from 10Ktrees.fas.harvard.edu; version 3; Arnold et al., 2010).



Configurations centered and rotated

Configurations centered, rotated, and scaled

Fig. A3. Species mean configurations after centering and rotating (left) and after full generalized Procrustes analysis (centering, rotating, and scaling; right).

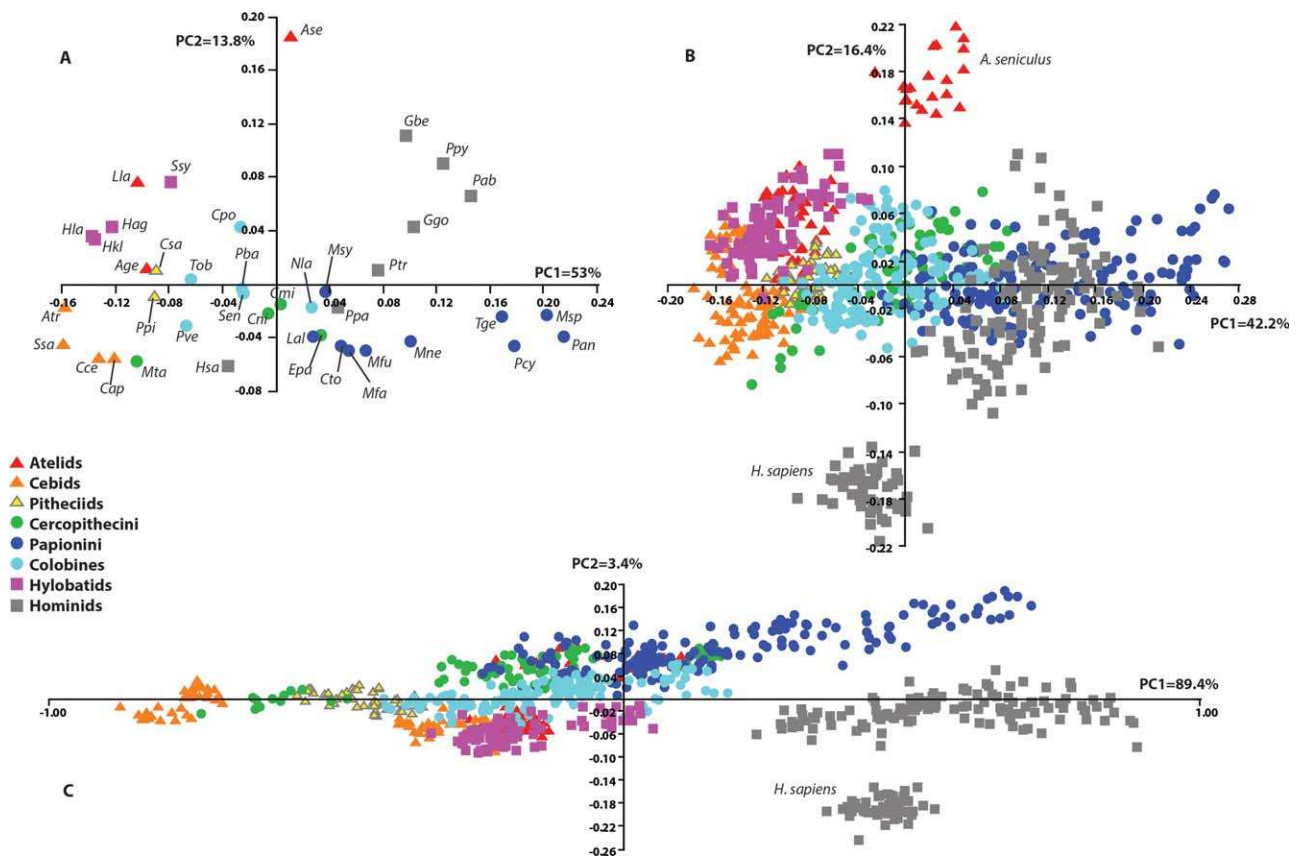


Fig. A4. Principal component plots of the first two PC axes for the species means dataset (A), the dataset where all individuals for all species are included (B), and the form space PCA of all individuals (C). Abbreviations for A are provided in Table A2.

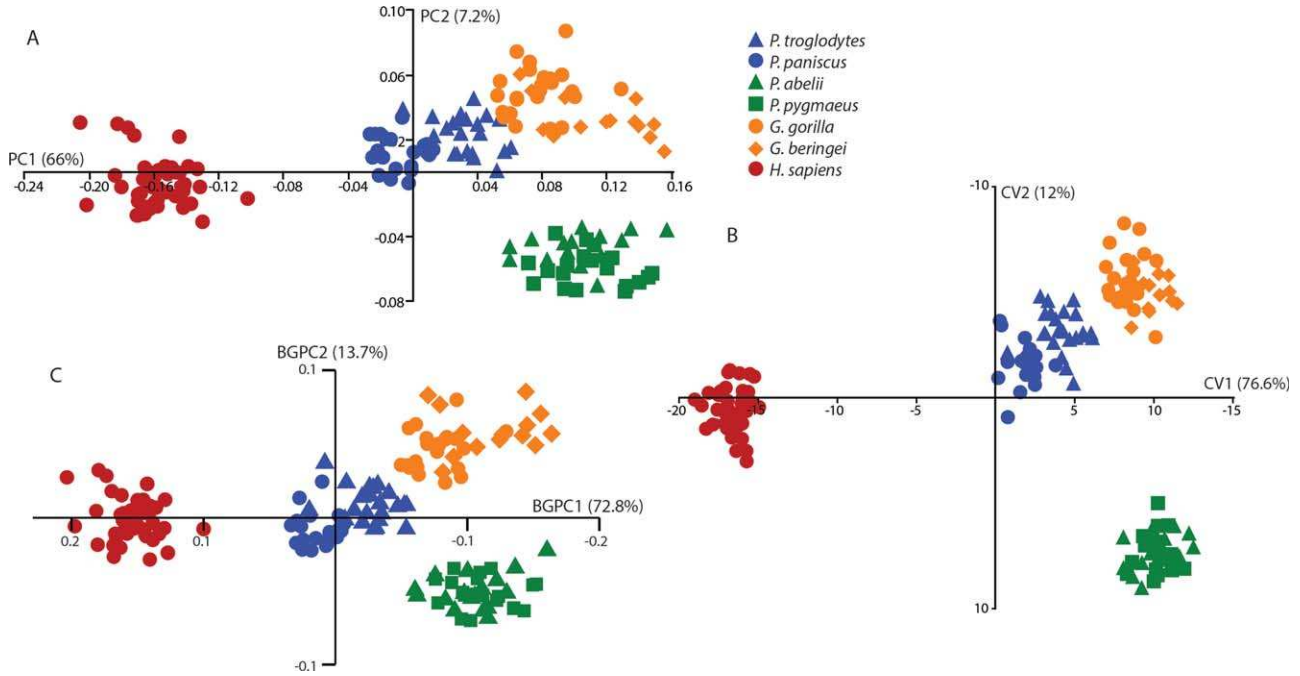


Fig. A5. Bivariate plots illustrating shape variation in the great ape and human dataset for a standard principal component analysis (A), a canonical variate analysis (B), and a between group PCA (C).

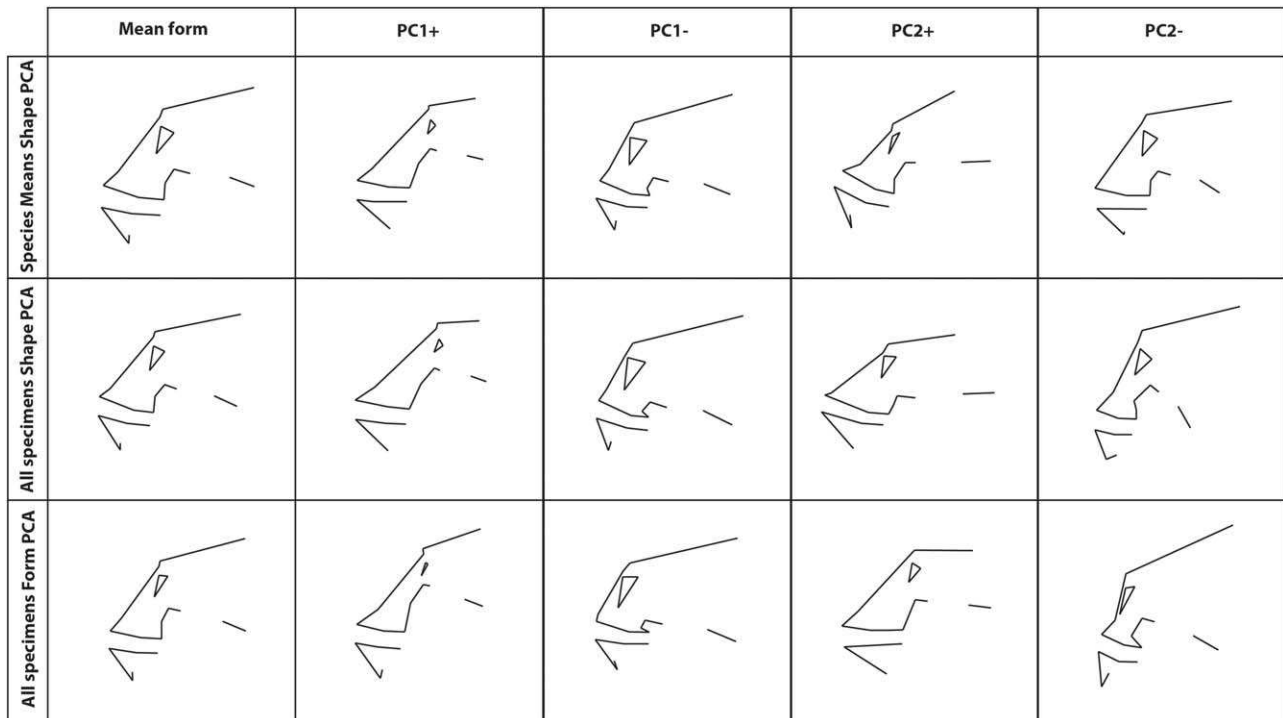


Fig. A6. Wireframe diagrams illustrating shape variation in each of the shape spaces depicted in Figure A4. Wireframes illustrate the average configuration for each sample (mean form) as well as the positive (+) and negative (-) extremes of the first two PC axes (PC1+, PC1-, PC2+, PC2-).

TABLE A4. Procrustes (upper triangle) and Mahalanobis (lower triangle) Distance Matrices for the Great Ape Subsample

	<i>G. beringei</i>	<i>G. gorilla</i>	<i>H. sapiens</i>	<i>P. abelli</i>	<i>P. pygmaeus</i>	<i>P. paniscus</i>	<i>P. troglodytes</i>
<i>G. beringei</i>		0.09	0.28	0.12	0.11	0.17	0.13
<i>G. gorilla</i>	8.96		0.24	0.11	0.12	0.12	0.08
<i>H. sapiens</i>	28.18	26.18		0.26	0.27	0.16	0.19
<i>P. abelli</i>	15.01	13.64	27.80		0.05	0.14	0.11
<i>P. pygmaeus</i>	14.30	14.01	27.80	5.62		0.15	0.12
<i>P. paniscus</i>	16.23	12.69	20.33	14.71	14.70		0.06
<i>P. troglodytes</i>	13.24	9.70	22.12	13.70	13.52	5.71	

All distances are statistically significant at $P < 0.0001$.

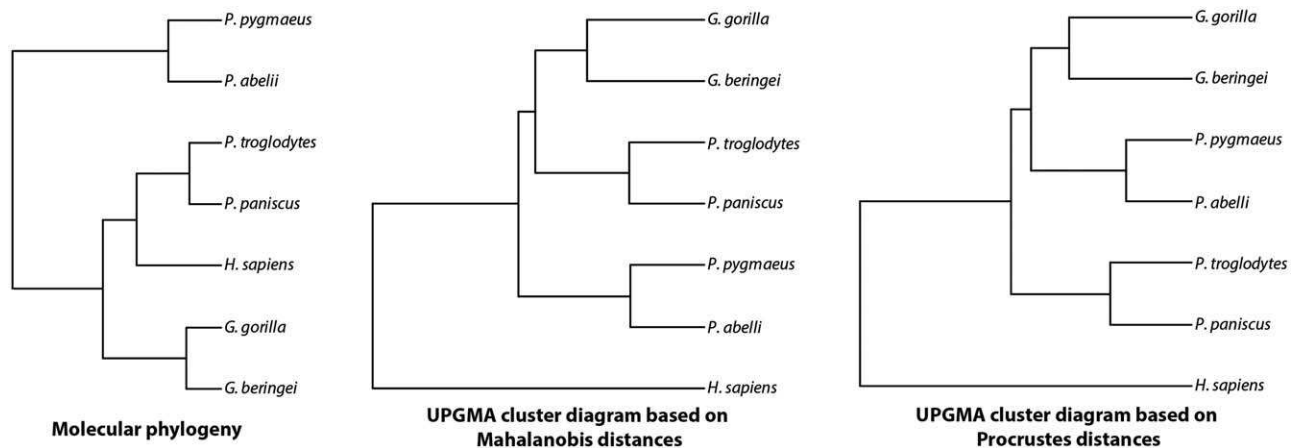


Fig. A7. Consensus molecularly phylogeny with branch lengths (downloaded from 10Ktrees.fas.harvard.edu; version 3; Arnold et al., 2010) for the great ape and human subsample (A); unweighted pair group method with arithmetic mean (UPGMA) cluster diagrams calculated using the Mahalanobis distance (middle) and Procrustes distance (right) matrices.

standard PCA (Fig. A5A) shows relatively good separation among great ape genera, the bgPCA and CVA illustrate more marked separation among taxa and tighter clustering of specimens within genera. Notably, the bgPCA also preserves much of the original distribution of taxa in shape space, whereas the CVA, as a type of discriminant analysis, more markedly separates taxa as a result of its scaling of the distances among taxa by within-group variance, thus finding the linear combination of variables that maximizes separation—the discriminant function.

Visualizing Shape

Wireframe diagrams describing shape variation in the example dataset employed here are shown in Figure A6. These wireframes correspond to variation in the shape spaces depicted in Figure A3A. For each of these shape spaces (PCA of species means, PCA of all specimens, form space PC of all specimens), the mean (or reference) configuration is shown, and this mean configuration is warped to the negative and positive ends of the first two PC axes. In all three of these shape spaces, shape variation along PC 1 illustrates variation in the relative size of the face and orbits, with specimens loading more negatively (*Saimiri*, *Aotus*) having relatively small, short faces, and specimens loading positively (*Mandrillus*, *Papio*) having large and long faces. PC 2 in all of these shape spaces is

primarily related to cranial base flexion and facial flattening, with positively loading specimens (*A. seniculus*) having very unflexed cranial bases and airorhynch crania, and specimens loading negatively (*H. sapiens*) having very flexed cranial bases and klinorhynch crania.

Statistically Assessing Shape Variation

One major way that the differences between and among groups in shape space can be examined is by quantifying the distance between group means and assessing whether this distance is statistically significant. Differences in the two major distance measures employed, Procrustes and Mahalanobis distances, can be illustrated by performing a PCA and CVA (Fig. A5) of the great ape sub-sample from the example dataset here, and by calculating the corresponding Procrustes and Mahalanobis distances for each of these shape spaces (Table A4). Although similar, the Procrustes and Mahalanobis distance matrices do differ; these differences are particularly obvious when these distances are employed in a UPGMA cluster analysis (Fig. A7). Notably, however, neither distance metric fully recovers the molecular phylogeny of this group.

The relationship between size and shape in the example dataset here are illustrated in Table A3, where, for each of the three PC analyses performed, the top five PC axes were each regressed on the natural log of centroid

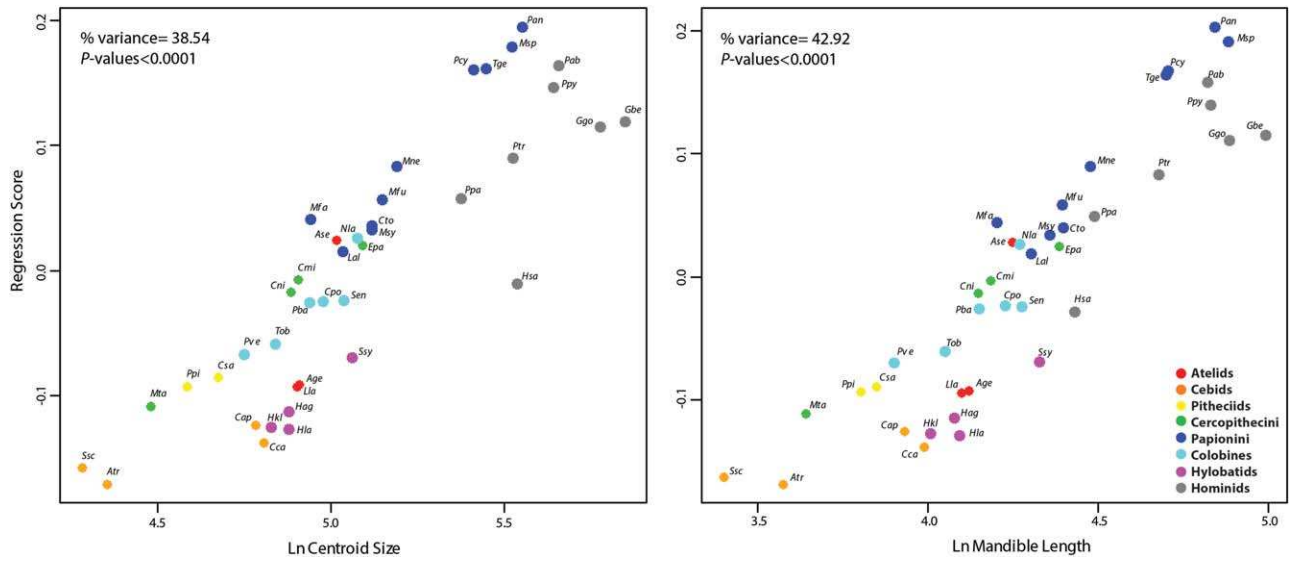


Fig. A8. Multivariate regressions of the entire species means sample on the natural log (Ln) of centroid size (left) and mandible length (right). Species abbreviations are provided in Table A2.

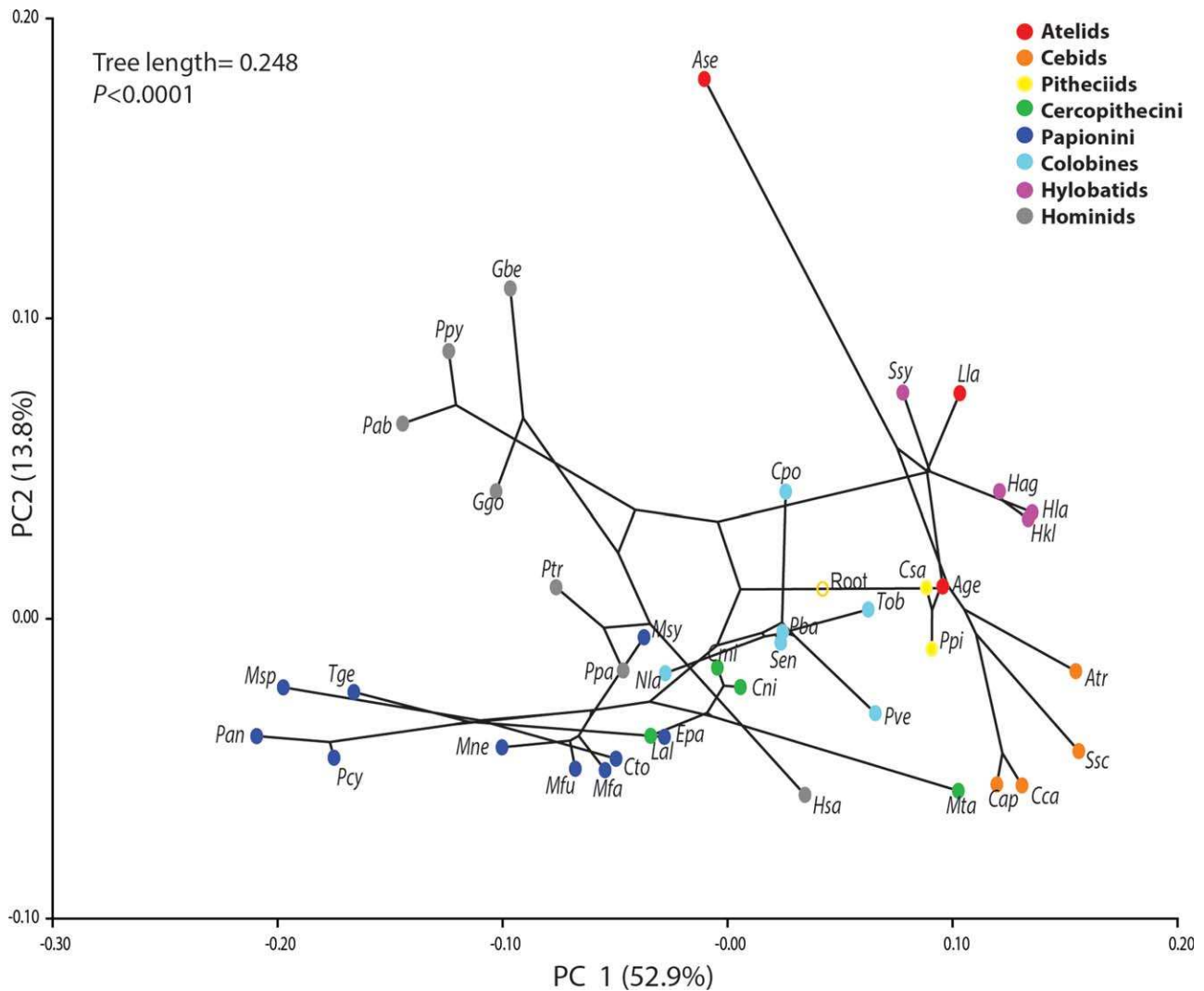


Fig. A9. Phylomorphospace plot of the species means dataset. Tree length equals the sum of squared changes in shape along the branches of the consensus phylogeny; the corresponding P-value for this relationship is also provided. Species abbreviations are provided in Table A2.

TABLE A5. Results of the Multivariate Regressions of the Procrustes Residuals on the Natural Log of Centroid Size (LnCS) and the Natural Log of Mandible Length (LnMandLg) Before (Non-PGLS) and After (PGLS) Adjustment for Phylogenetic Covariation, Including the Percentage of Variance in the Sample Explained by the Regression (%variance) and the Corresponding Significance (P -value)

Shape vs.	Non-PGLS		PGLS	
	%variance	P -value	%variance	P -value
LnCS	38.54	<0.0001	42.78	0.0018
LnMandLg	42.92	<0.0001	43.21	0.0008

size (LnCS). The results highlight the condensing of size-related differences onto the first PC in form space. This is particularly striking when examining the regression of all specimens in shape space where the first four PCs are correlated with size.

We also illustrate the use of multivariate regression by regressing the Procrustes residuals of the species means dataset onto LnCS as a measure of configuration/cranial size, and onto a biomechanically relevant size measure, the natural log of mandible length (LnMandLg; Fig. A8, Table A5). Both regressions are statistically significant at $P < 0.0001$, with the regression of shape on LnCS explaining 38.54% of the variance in the sample, and the regression between shape and LnMandLg explaining 42.92% of the sample variance.

In our example dataset, calculating the phylogenetic signal in the dataset reveals that there is a statistically significant relationship between primate face shape and phylogeny ($P < 0.0001$) (Fig. A9). Thus, not surprisingly, closely related taxa tend to share more similar face shapes than more distantly related taxa.

We can further examine the relationship between shape and size (LnCS and LnMandLg) by performing

PGLS regressions using the same data as for the non-phylogenetic regressions (Table A5). Both the regressions of shape on LnCS and shape on LnMandLg remain statistically significant after phylogeny is taken into account, and while the percentage variance explained by LnMandLg stays roughly the same, the percentage variance explained by LnCS increases. Thus, although there is a phylogenetic signal in the dataset, there remains a significant relationship between size and shape even when this signal is statistically accounted for.

Conclusions

These analyses are meant as a guide and example of the utility of GM methods. In this example dataset, we were able to show the range of cranial shape variation seen across anthropoids and how that variation correlates with size, phylogeny, and other factors. Specifically, we examined the nature of facial shape variation. The example analyses here indicate that, not surprisingly, there is considerable shape variation in the cranium of extant anthropoid primates, and that much of this shape variation is linked to size and phylogeny. Furthermore, these data indicate that basicranial flexion and relative facial size play a major role in the observed shape variation in this sample.

Moving forward, we encourage beginning users of GM methods to explore the utility of the GM tools illustrated here for a wide range of questions including not only those which purely assess shape, but also questions exploring the functional reasons for those shapes. While this example dataset is by no means exhaustive in terms of the range of analyses available to GM user, we hope that the reader is able to use these example analyses as a starting place for gaining a practical understanding of these rich analytical techniques.