Geometric Morphometrics

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Abstract

Morphometrics, the field of biological shape analysis, has undergone
major change in recent years. Most of this change has been due to
the development and adoption of methods to analyze the Cartesian
coordinates of anatomical landmarks. These geometric morphome-
tric (GM) methods focus on the retention of geometric information
throughout a study and provide efficient, statistically powerful anal-
yses that can readily relate abstract, multivariate results to the phys-
ical structure of the original specimens. Physical anthropology has
played a central role in both the development and the early adoption
of these methods, just as it has done in the realm of general statistics,
where it has served as a major motivating and contributing force be-
hind much innovation. This review surveys the current state of GM,
the role of anthropologists in its development, recent applications
of GM in physical anthropology, and GM-based methods newly in-
troduced to, or by, anthropology, which are likely to impact future
research.

shape: geometric properties of an object invariant to position, orientation, and isometric (global magnification/ reduction) size differences

morphometrics: examines central tendencies of shape, shape variation, group differences in shape, and associations of shape with extrinsic factors

Geometric morphometrics (GM): morphometric methods, often based on Cartesian coordinates of landmarks, that retain all geometric information in the data throughout an analysis

INTRODUCTION

Many questions in biological research are concerned with shape: What is the average shape of a bone/organ/structure in a population? What is the pattern of variation in a population around that average shape? How do groups differ in shape? What is the functional importance of those differences? Morphometrics is the field of multivariate statistical analysis concerned with the methods necessary to rigorously address such questions. Historically, these methods have involved the analysis of collections of distances or angles, but recent theoretical, computational, and other advances have shifted the focus of morphometric procedures to the Cartesian coordinates of anatomical points that might be used to define the more traditional measurements. The direct study of landmark coordinates requires special techniques but yields powerful, concise, and comprehensive analyses. This latest approach to shape analysis is called geometric morphometrics (GM), in recognition of its emphasis on the complete retention of geometric information throughout the research process. As in many areas of statistics, the field of anthropology has played a surprisingly important role in the development and adoption of these new methodologies.

In this review, I summarize the major developments in morphometrics that have occurred in the past few years and their relationships to physical anthropology. I begin with an overview of GM methods and illustrate the historical alliance between anthropology and statistics, including morphometrics. I provide an overview of how geometric methods are being used in contemporary anthropological research, and I outline some of the latest methods that, though already having been applied and possessing a justifiable theoretical basis, have yet to be widely deployed. These latter methods, though relatively unfamiliar at the moment, are likely to become increasingly important in physical anthropological studies and

serve as models for similar research in other fields.

The reader is encouraged to peruse older reviews such as Rohlf (1990), Rohlf & Marcus (1993), Bookstein (1996), and O'Higgins (2000) to appreciate the extent to which the field has developed. Adams et al. (2004) is a recent, general review examining the influence of morphometrics beyond the field of anthropology. Bookstein et al. (2004) also address the role of anthropology in contemporary morphometrics, and Slice (2005a) provides more emphasis on introductory material.

METHODOLOGY

What is often called the traditional approach to morphometric analysis usually involves the application of multivariate statistical procedures to collections of distances, angles, or distance ratios. Problems with these methods are well-documented (Bookstein et al. 1985, Slice 2005a). Of primary importance is that the analysis of a limited set of linear distances, ratios, or angles frequently fails to capture the complete spatial arrangement of the anatomical points (landmarks) on which the measurements are based. As more landmarks are included in an analysis, the minimum number of distances (or angles) needed to fix the relative landmark positions increases to the point of being impractical. Coordinates of these same landmarks, however, concisely encode all the information in any subset of distances (or angles) between them. This complete retention of geometric information from data collection through analysis and visualization is the reason coordinate-based approaches are generally referred to as geometric morphometrics, a term first used by Corti (1993).

The analysis of landmark coordinates is not without its own problems. The coordinates must be recorded with respect to some defined coordinate axes, and their numerical

values reflect the unique location and orientation of each specimen with respect to those axes. Furthermore, specimen size is also encoded in the coordinates. A number of methods have been proposed to address these issues including the conversion of the coordinates to exhaustive or sufficiently complete sets of interlandmark distances or angles (Bookstein et al. 1985; Lele & Richtsmeier 2001; Rao & Suryawanshi 1996, 1998) and the registration of specimens with respect to a common interlandmark line segment, or "baseline," to standardize the sets of coordinates for location, orientation, and size (Bookstein 1986, 1991). The most widely embraced methods today, however, and those with the most thorough theoretical development, are the so-called Procrustes methods, which are based on the least-squares estimation of translation, rotation, and, sometimes, scaling parameters that optimally, in the least-squares sense, align sets of landmark coordinates for pairs of specimens (Dryden & Mardia 1998, Gower 1975, Gower & Dijksterhuis 2004, Rohlf & Slice 1990).

I will not take up the limited space of this review with a complete description of the mathematical and algorithmic details of Procrustes analysis and its underlying theory. Such coverage can be readily found in the original literature (see references above) and/or other recent and general reviews (e.g., Adams et al. 2004, Slice 2005a). Nor would it be fruitful to review proposed alternatives and attendant controversies (see Lele & Richtsmeier 2001; Rao & Suryawanshi 1996, 1998; Rohlf 2000a,b, 2003). Instead, I provide only a summary (**Figure 1**) of the familiar Procrustes approach to the analysis of landmark coordinates as applied to the question of, "Do the scapulae of male and female west-African lowland gorillas differ in average shape as captured by five landmarks in two dimensions?"

As seen in **Figure 1**, the coordinates of landmarks used to characterize specimen shape vary owing to the location and orientation of each specimen with respect to the digitizing axes, and their numerical values encode specimen size (**Figure 1a,b**). Generalized Procrustes analysis (GPA) addresses these issues by translating and rotating each specimen to minimize the squared, summed distances (squared Procrustes distance) between corresponding landmarks on each configuration and an iteratively computed mean (or consensus) configuration. Specimens are individually scaled to the same, unit Centroid Size—the square root of the sum of squared distances of the landmarks in a configuration to their average location (for a justification of this size measure see Bookstein 1991). This process brings the landmark configurations of all specimens into a common coordinate system in which differences in landmark coordinate values reflect differences in configuration shapes (**Figure 1c**). The coordinates of landmarks on each (superimposed) specimen are usable as shape variables (geometric descriptors invariant to position, orientation, and scale) and can be subjected to the usual kinds of multivariate testing procedures to quantify and identify covariance structure, group differences, and functional (in the statistical sense) relationships. The transformed configurations are all a common size, but the scale factor used to standardize them can be retained as a size measure.

It is important to recognize that the constraints introduced by GPA (i.e., mean centering, size standardization, distance minimization by rotation) insure that coordinate covariance matrices will be singular and many parametric procedures (MANOVA using the Wilks' lambda statistic, for instance) are guaranteed to be computationally undefined—they will involve the matrix equivalent of division by zero. Steps may be taken to address this problem by either projecting the data onto an appropriately dimensioned space tangent to the curved spaces of superimposed shapes (Rohlf 1999, Slice 2001) or availing oneself of nonparametric methods that are not
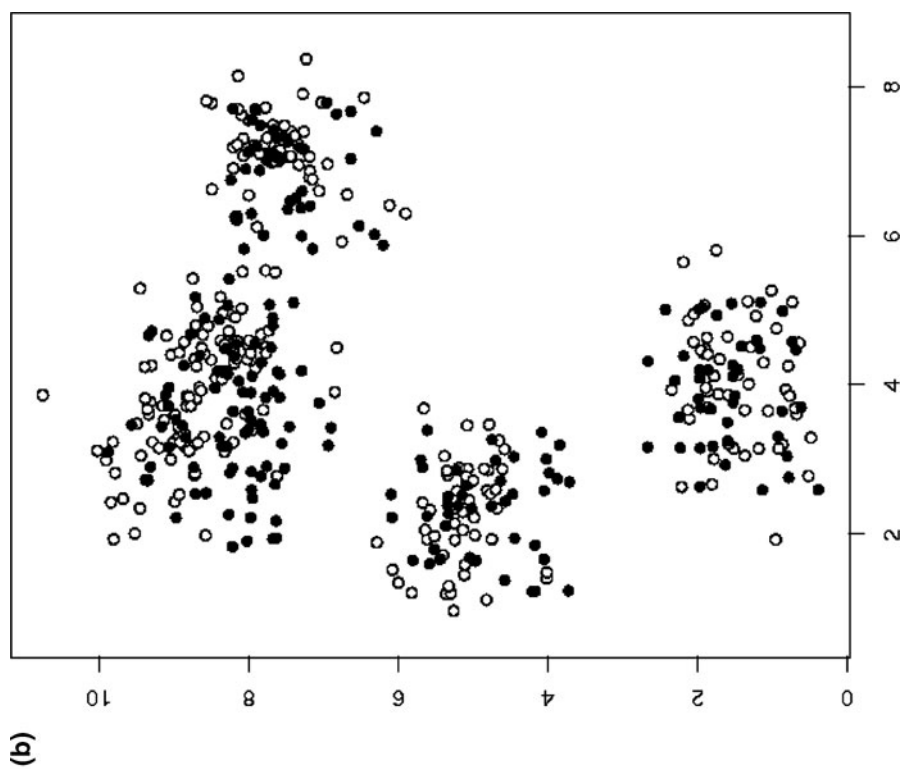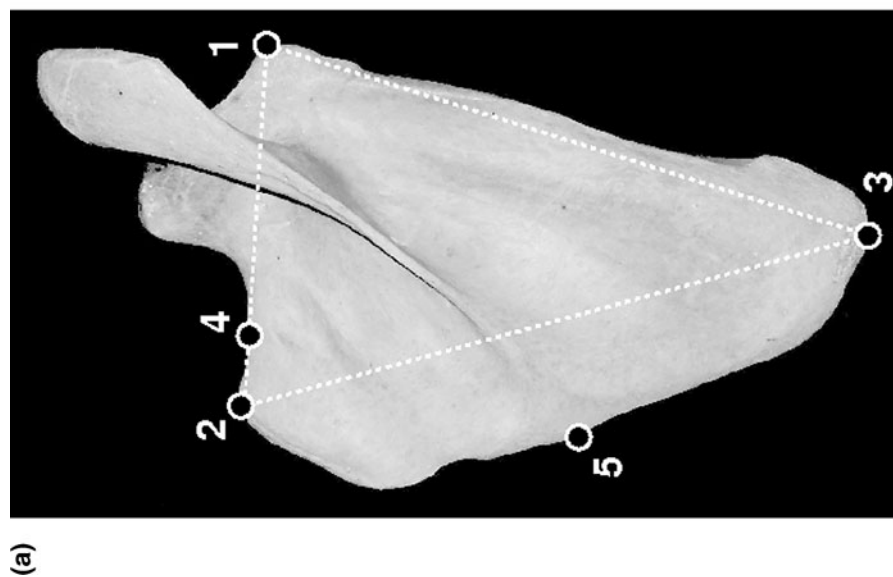
Procrustes analysis: the analysis of shape coordinates generated by the least-squares superimposition of configurations of landmarks

GPA: generalized Procrustes analysis

shape variable: geometric variables invariant to position, orientation, and isometric size. Superimposed landmark coordinates are shape variables. Raw coordinates are not
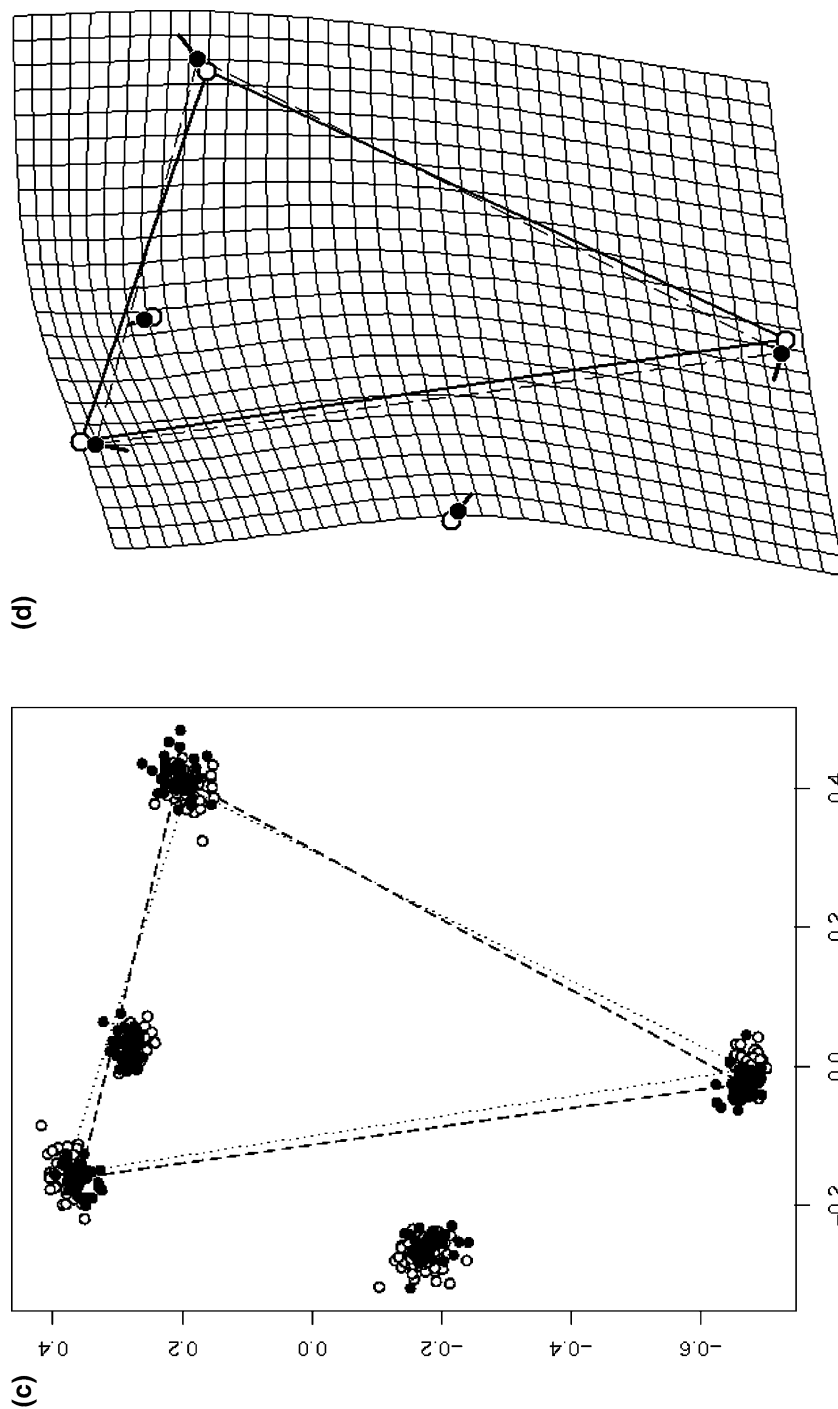
(a)

(b)

(d)

(c)

Generalized Procrustes analysis (GPA), the foundation of geometric morphometrics, is illustrated here through the examination of differences in the average shape of the scapula of male ($n = 52$, *open symbols*) and female ($n = 42$, *closed symbols*) western African lowland Gorillas (*Gorilla gorilla gorilla*). Data from images provided by A. Taylor. (*a*) First, the coordinates of homologous points are recorded for each specimen. Data here are two-dimensional, but this is not a constraint imposed by the method. (*b*) The coordinates vary owing to the shape of the specimens, but also encode the location and orientation of each specimen with respect to the digitizing axes used to record the coordinates and vary owing to size differences between specimens that are often best analyzed as a separate variable. (*c*) GPA superimposes sets of configurations into a common coordinate system so that the coordinate values of their landmarks represent shape variables that can be subjected to further statistical analysis. In the present example, a randomization test for group differences shows the males and females to differ significantly in average scapular shape with a p-value of 0.001. (*d*) The geometric nature of the data can then be used to generate intuitive visualizations of statistical results such as the male-female difference shown here as both difference vectors and as a thin–plate spline deformation grid—both exaggerated by a factor of two.

Thin-plate spline:
a visualization tool
based on the
interpolation of
landmark differences
mapping one set of
landmark locations
exactly onto another

so dependent on distributional assumptions and full-rank covariances (e.g., Manly 1997). Once these statistical issues have been addressed, analysis can proceed following the lines of inquiry outlined in multivariate texts. In the present case, a nonparametric, randomization test for sex differences identifies a highly significant difference in the average scapula shape of the male and female gorillas ($p = 0.001$).

With GM, one can also take advantage of the fact that statistical analyses address the full geometric variation in the sample and, as such, statistical results can be readily related back to the physical space of the original specimens. Suitable graphical displays to achieve this (**Figure 1***d*) include difference-vector diagrams, in which differences in the mean location of landmarks between groups are shown as vectors from one set of mean landmark locations to their corresponding positions for the other group. These vectors can be magnified to aid interpretation as in the current example. One can also use the compelling graphical device that is the thin-plate spline (Bookstein 1989, 1991). The thin-plate spline provides an exact mapping of the landmarks of one configuration (e.g., a group mean) onto another (e.g., another group mean) and supplies a maximally smooth (minimally bent) interpolation of the interlandmark space. When viewing such displays, either difference vectors or thin-plate splines, one must remember that specific results at a particular landmark must be interpreted in the context of the entire set of landmarks in the analysis (Adams et al. 2004, Slice 2005a).

Figure 1*d* shows both modes of visualization of the differences in mean scapular shape between the male and female gorillas. The vectors and spline map the locations of landmarks from their average position in males to their average position in females—note a straightening of the medial (leftmost) border in the females as evidenced by the relative positions of landmarks 2, 3,

and 5 and a relative reduction in the notch at the top of the scapula characterized by landmarks 2, 4, and 1. Such observations can then be interpreted in terms of the functional anatomy of muscle attachments, mechanical advantages, etc. For a more detailed analysis of similar data for subspecies of gorillas and common chimpanzees, see Taylor & Slice (2005).

The computational steps for all the above can be expressed in terms of matrix algebra and can easily accommodate two-, three-, or even higher-dimensional data.

THE ANTHROPOLOGIST AND THE STATISTICIAN

Anthropology has long played a central role in the development and application of new methods in quantitative biology, in general, and morphometrics, in particular. In the nineteenth and early twentieth centuries, the founders of modern statistics were frequently motivated by questions concerning patterns of variation, association, causation, and inheritance in human populations. Polymaths such as Francis Galton,[1] the president of the Anthropological Institute of Great Britain, whose discoveries concerning "regression" in seeds and human stature provide a significant proportion of today's introductory statistics courses, genuinely blur the distinction between statistician and anthropologist. He was the first to use, for instance, the baseline-registration approach to shape comparisons mentioned above and so thoroughly developed by Bookstein (1986, 1991). Galton's eminent protégé Karl Pearson was similarly drawn to applications of newly developed statistical techniques to the analysis of human variation and heredity. Their

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[1]A comprehensive bibliography including many facsimiles of Galton's papers can be found at **http://www.galton.org**.

shared concern with the statistics and morphometrics of human identification would have surely secured both scholars significant funding from today's governmental security agencies.

At the same time, professional anthropologists were eager consumers of the new methodologies and immediately applied them to research questions within their own domains. G.M. Morant (e.g., 1939) made substantive contributions to both the anthropological and the statistical literature, as did Franz Boas (1912, 1922; see also Gravlee et al. 2003a,b; Sparks & Jantz 2002). The latter even outlined the method of least-squares landmark registration that lies at the heart of much contemporary (Procrustes-based) morphometric analyses (Boas 1905, Cole 1996).

The role of the anthropologist as adopter and promoter of sophisticated methods of shape analysis continued throughout the twentieth century. This is represented perhaps nowhere better than in the pioneering work on worldwide craniometric variation by W.W. Howells (1973, 1989), and it is impossible to consider the contributions of anthropologists to morphometric analysis without recognizing the work of Charles Oxnard, who continually found and employed sophisticated and innovative methods in physics and engineering that could be usefully applied to questions of functional anatomy. The breadth and comprehensiveness of Oxnard's contributions to applied morphometrics are noted by Bookstein & Rohlf (2004) in a volume dedicated to him, where the authors state "Oxnard's 1973 book is subtitled 'Some mathematical, physical, and engineering approaches,' and Bookstein quickly learned that if Oxnard had not noted an approach here, it was not worth noting or it had been invented after 1973." (p. 378)

This historical relationship between statistician and anthropologist has persisted through the recent shifts in the methodology and data of morphometric analysis from the study of the traditional subsets of distances, ratios, and angles to the current focus on the analysis of landmark coordinates, a development anticipated by both Galton (1907) and Boas (1905). Early contemporary work in the development of these new methods was often motivated by questions in anthropology (Sneath 1967) and archaeology (Kendall & Kendall 1980). Still today, many of the latest innovations, extensions, and new applications in this field are to be found (or widely appreciated) first in the anthropological and anatomical literature, e.g., Hartman's (1989) early three-dimensional GM study of hominoid molars, O'Higgins & Jones's (1998) GM modeling of three-dimensional facial growth in mangabeys, Bookstein et al.'s (1999) use of sliding landmarks to study frontal bone morphology, Schäfer et al.'s (2006) use of GM to examine genetic and environmental components of asymmetry (discussed later), and various chapters in Slice (2005b).

Why should this be so? There are several reasons. First, statisticians, like the public in general, are strongly attracted to questions about our own species, its origins, and variation. If one is going to develop methods for assessing associations between sets of variables, why not let those variables be measurements of past or present human populations? This, in turn, feeds into medical research, further justifying the association between anthropology and statistics. Second, anthropologists, especially paleoanthropologists, are almost uniquely faced with the problem of a paucity of data. How many fields are in the habit of referring to individual data points by name, names such as "Lucy," "Mrs. Ples," or "KNM-ER 1470," and who else is so often faced with crucial samples of size less than one—a bit of mandible or a fragment of calvarium—that are so critically important to research in the field? It is no wonder that anthropologists are ever vigilant for new methods to help them wring every last bit of

insight from their rare material. Finally, and its impact should not be underestimated, is the fact that anthropologists often deal with material of a, well, human scale that often admits access to new data collection protocols. An early, affordable, robust, and portable 3D digitizer, the Microscribe 3D by the Immersion Corporation, has had a major impact on morphometric data acquisition. However, it is really too large and clumsy to use with, say, mice crania or small fish or insects, and it is too small for elephants and hippos. But for human skulls or scapulae or pelves, the Microscribe is just right. Together, the generally attractive nature of the research, the desirability of maximally efficient analytical methods, and the utility of the newest data collection modalities provide the motivation and opportunity for what continues to be a highly productive interaction between the anthropologist and the statistician.

MORPHOMETRICS IN ANTHROPOLOGY

One can group applications of morphometric analysis in anthropological research in many ways. Here, I examine them under three main headings: statistics, anatomy, and process. Of course, considerable overlap occurs in these categories, but I will try to keep the redundancy in check. Citations are meant to be illustrative, not comprehensive.

Statistics

A fundamental goal of statistical analysis is the computation of a reduced set of values or variables that meaningfully summarizes a larger set of data. In morphometrics, this usually involves the estimation of mean shapes and the covariance structure of the sample around that mean. Such estimates are not usually an end in themselves but instead are an initial step in the examination of more complex questions. One associated statistical procedure, however, is

worth special mention: principal components analysis (PCA). With a single homogeneous sample, one can view PCA as an estimator of some parametric structure characteristic of the population. Otherwise, PCA is purely a dimension-reduction technique that identifies orthogonal linear combinations of the original variables that most efficiently reproduce sample variability. The latter use is particularly important in morphometric research because (*a*) the number of shape variables to be analyzed can be very large and often exceeds reasonable sample sizes and (*b*) the constraints of the GPA superimposition insure that the resulting residual coordinates will not have a covariance structure of full rank. PCA is one way to address both of these problems by using only scores on a reduced number of principal components in subsequent analysis [the use of relative warp scores including a uniform component (see Rohlf & Bookstein 2003) is another way to address the second issue], but it must be kept in mind that such variables are constructed by a variance-maximizing criterion and may not be aligned with the variation relevant to the biological question(s) being addressed.

PCA, especially when combined with visualization tools in a GM analysis, may provide insight into the covariation among the shape variables, but far more diverse associations can be explored by considering correlations of shape with other factors. One rather unique example is the work of Bulygina et al. (2006), who found adult cranial shape in humans to have low correlations with their newborn morphology, but high correlations with their skull shape at three years of age. Note, high correlation does not necessarily mean morphological similarity; the actual head shapes at different stages could be quite different. Partial least-squares analysis (PLS) is a method for extracting linear combinations of two sets of variables that best account for the pattern of covariation across the sets (Bookstein 1991), and it can be used in morphological research to examine

the relationship between morphology and be-
havioral or other nonmorphological variation
(Bookstein et al. 2002, Rohlf & Corti 2000).
PLS can also be used to examine covaria-
tion in the shapes of different structures and
has been used most often in anthropology
to examine morphological integration (Bastir
et al. 2005, Bastir & Rosas 2006, Bookstein
et al. 2003). Correlation studies can even tran-
scend a single mode of analysis. McKeown
& Jantz (2005) use nonparametric Mantel
tests to consider the relationships between ge-
netic, temporal, and geographic distances and
coordinate- and distance-based morphologi-
cal comparisons of Native American (Arikara)
populations.

Given an estimate of mean shape and shape
(co)variation, one can ask questions about the
significance of group differences. Sexual di-
morphism has been a direct target of such in-
quiry (Kimmerle et al. 2007, Oettle et al. 2005,
Pretorius et al. 2006, Steyn et al. 2004; see also
more complex designs cited below), as have
been morphological differences at the pop-
ulation, subspecies, species, and higher-taxa
level (e.g., Bruner & Manzi 2004, Guy et al.
2003, McNulty 2004, Lockwood et al. 2004,
Ross 2004). Here, too, the constrained covari-
ance structure of Procrustes shape variation
must be addressed either through tangent-
space projections prior to classical statistical
testing (Rohlf 1999, Slice 2001) or by taking
advantage of distribution-free nonparametric
procedures.

Regression analysis can be used to re-
late shape to variables such as size for allo-
metric studies (e.g., Frost et al. 2003, Penin
et al. 2002) or extrinsic variables such as
time (Jonke et al. 2003, Kimmerle & Jantz
2005, Wescott & Jantz 2005) or developmen-
tal environment (Fink et al. 2005, Schäfer
et al. 2005). This type of analysis can be
combined with hypotheses of group differ-
ences through multivariate analysis of covari-
ance (MANCOVA) as was done by Rosas &
Bastir (2002), who identified independent ef-
fects of sex and size on cranial shape in mod-

ern humans. Similarly sophisticated analy-
ses include the study of ontogeny and sexual
dimorphism in data from the Bolton-Brush
growth study by Dean et al. (2000), the study
of facial growth and sexual dimorphism in
the papionin face by O'Higgins & Collard
(2002), the interspecific allometric compar-
isons of African apes by Berge & Penin (2004),
and the study of sexual dimorphism and al-
lometry in extant hominids by Schäfer et al.
(2004).

GPA-derived shape variables are just as
amenable to other familiar multivariate tech-
niques such as cluster analysis (Couette et al.
2005; Frost et al. 2003; Lockwood et al.
2002, 2004) and discriminant function anal-
ysis (Berge & Penin 2004, Delson et al.
2001, Penin et al. 2002, Vidarsdóttir & Cobb
2004) in anthropological studies. The latter
possesses considerable practical utility in the
forensic setting (e.g., Kimmerle et al. 2007,
Pretorius et al. 2006, Ross et al. 2004, Vi-
darsdóttir et al. 2002).

Anatomy

As in traditional morphometric analyses,
the anatomical distribution of investigations
with GM methods has not been uniform.
The skull has received most of the attention
with respect to both the entire cranium
(e.g., Bastir et al. 2006; Bruner et al. 2004;
Mitteroecker et al. 2004a, 2005; Neves et al.
2005; Singleton 2002; Zollikofer & De Leon
2002) and its constituent parts (e.g., Bastir
& Rosas 2005, Bookstein et al. 1999, Bruner
et al. 2003, Bulygina et al. 2006, Collard &
O'Higgins 2001, Delson et al. 2001, Guy et al.
2003, Harvati 2003, Lockwood et al. 2002,
Singleton 2005) including teeth (Boughner &
Dean 2004, Hartman 1989, Martinon-Torres
et al. 2006). The postcranial skeleton, how-
ever, has not been completely overlooked.
Researchers have used Procrustes-based
morphometrics to examine variation and
differences in vertebrae (Albert et al. 2003;

Manfreda et al. 2006), scapulae (Taylor & Slice 2005; Young 2006), and the pelvis (Bouhallier et al. 2004, Bouhallier & Berge 2006, Steyn et al. 2004), and the femur (Shepstone et al. 1999, Weaver 2003) and humerus (Bacon 2000) have received attention as well. Important early work in the challenging area of joint surface analysis is that of Niewoehner (2001, 2005), who used the projection of grid points to address the lack of discrete, homologous points on the metacarpal articular surface.

Process

One can, of course, use the tools of modern morphometric analysis to examine processes underlying observed morphological variation, and allometry, ontogeny, and heterochrony, especially, have been major themes (e.g., Cobb & O'Higgins 2004, Leigh 2006, Rozzi et al. 2005, Vidarsdóttir & Cobb 2004, Zollikofer & De Leon 2004). The comparative study by Mitteroecker et al. (2004b) of cranial ontogenetic trajectories in great apes and humans provides a useful review, and their helpful appendix gives details of the mathematical and statistical frameworks for such studies using Procrustes methods. Their appendix also outlines the proof of log Centroid Size being the appropriate size variable to attach to Procrustes shape variables to combine size and shape into a single principal component or other analysis. The space so constructed can logically be called "Procrustes size-and-shape space." Another particularly creative ontogenetic study is that of McNulty et al. (2006). The authors used ontogenetic trajectories of extant hominine species estimated by GM methods to "grow" the Taung fossil and assess its probable adult affinity. They undertake exhaustive validation of their methodology and ultimately reject the possibility that Taung is a juvenile robust australopithecine. An equally interesting finding of this study is that the results are not substantively affected by the specific growth trajectory used, be it one of a

subspecies or a population of *Pan*, *Gorilla*, or *Homo*.

THE FUTURE

The core methodology for coordinate-based shape analysis is fairly well-established. One selects a set of anatomical points that are believed to capture relevant aspects of shape variation. The coordinates of these landmarks are digitized for each specimen by some convenient data collection modality. The coordinate values are subjected to a preprocessing step to either minimize (location and orientation) or standardize (scale) differences due to nonshape variation. Then subject to constraints of the data set (e.g., sample size versus variable number) and any imposed by the preprocessing step (e.g., singular covariance structure due to superimposition), one subjects these shape data to standard sorts of multivariate analyses and tests to address the research question(s) at hand. Finally, the geometric origin of the data and the geometric conservatism of the methodology are revisited as the multivariate results are visualized in the space of the original specimens.

The stability and, by now, familiarity of the above process in anthropological research should not be taken as an indication that the methodology is fixed or that its full potential has been realized. Active research is underway to extend the basic paradigm to accommodate unique aspects of specific data sets and research questions, and some of these sophisticated methodologies, though theoretically developed, have yet to be widely applied in anthropological research. The following sections examine some of these.

Sliding (Semi-) Landmarks

Not all landmarks are created equal (Bookstein 1991). Some are insufficiently

determined by surrounding anatomy to render their spatial position well-defined in all directions. For example, the shapes of curves can provide important biological information but may lack obvious points at which they should be sampled. One solution is to sample a curve at points along its length on each specimen according to some spacing rule. Variation in the position of the sample points along (locally parallel to) the curve, then, generally lacks discernible biological importance, whereas variation orthogonal (at right angle) to the curve can provide meaningful shape information.

Such landmarks are called "deficient" or "semi" landmarks in recognition of the fact that the dimensionality of their coordinate locations exceeds that of their biologically relevant content (Bookstein 1991). Bookstein suggested this situation could be addressed by allowing the points to slide in the preprocessing step along directions of arbitrary variability (usually the tangent to the curve) to minimize some reasonable criterion: bending energy (BE) (Bookstein 1997) or Procrustes distance (Bookstein et al. 2002). Despite the reasonableness of this approach, it has seen very little application in biomedical and/or anthropological research beyond that of Bookstein and his associates (e.g., Bookstein 1997; Bookstein et al. 1999, 2002). The main problem, of course, has been the lack of software that can carry out the necessary computations. This problem has been addressed for two-dimensional data by adding sliding-landmark support in the TPS series of programs, e.g., tpsRelw (Rohlf 2006). For three-dimensional data, only Bookstein and Green's *Edgewarp* software (**http://brainmap.stat.washington.edu/edgewarp/**) offers any sliding landmark capabilities at this time, and these are best considered "under development." This is likely to be a short-term problem. The necessary equations for three-dimensional sliding to minimize BE have been published by Gunz et al. (2005), and

minimization of Procrustes distance along a tangent requires only relatively simple vector algebra.

Even with the availability of good software, questions about the mode and general applicability of sliding landmark methods still need to be addressed. For instance, in two dimensions semilandmarks are always associated with curves, whereas in three dimensions one can be faced with deficient landmarks residing either on curves in space or on surfaces. A distinct difference between curves and surfaces can affect the implementation and applicability of a sliding algorithm. Specifically, curves have a natural ordering of points along them that can, and should, be preserved throughout any manipulations—a particular, nonendpoint landmark always and unambiguously lies between its neighbors on the curve. This ordering is not found or defined in points scattered on a surface, and the use of "neighbors" in, for instance, the approximation of tangent directions must be extended to a "neighborhood." Gunz et al. (2005) provide a reasonable methodology to address such issues, but the final word must await further study.

Similarly, one can slide landmarks to remove extraneous variation according to at least two criteria: minimum Procrustes distance or minimum BE. Both are reasonable. GPA is oriented largely toward minimizing Procrustes distance, but Gunz et al. (2005) provide compelling reasons for opting for a minimum BE approach. Unfortunately, the choice of criterion can affect the interpretation of the results (Perez et al. 2006). BE minimization is the obvious choice if one is going to construct thin-plate spline visualizations (using Procrustes distance could retain or introduce "features" due to semilandmark variation in a direction deemed uninformative), but Procrustes distance minimization is consistent with the criterion used for other aspects of configuration comparisons. This is an area of great potential

importance and requires further thoughtful investigation.

Asymmetry Analysis

Asymmetry analysis has been a compelling and contentious area of biological research (Auffray et al. 1999; Palmer & Strobeck 1986, 2003). The basic idea is that under ideal conditions development should generally produce nearly symmetric final forms. In contrast, disruptions of normal development due to inhospitable genetic and/or environmental backgrounds can be recognized as changes in observed patterns or levels

of asymmetry. From a traditional approach, asymmetry is usually characterized as some function of right- and left-hand measurements of an organism (Palmer & Strobeck 2003). It is reasonable that modern methods of morphometric analysis could be useful in such research, but the focus on landmark-based methodologies requires a new mathematical formulation. A geometric approach was outlined by Bookstein (1991) and has been applied outside of anthropology by Smith et al. (1997), Klingenberg & McIntyre (1998) and Auffray et al. (1999). Mardia et al. (2000) provide a rigorous mathematical treatment (see also Bock & Bowman 2006) that was finally brought to anthropological research in the elegant study of dental asymmetry in Croatian populations by Schäfer et al. (2006; other anthropological studies of asymmetry include Kimmerle & Jantz 2005, Willmore et al. 2005).

Schäfer et al. (2006) examined dental arch asymmetry in a number of Croatian populations selected to address potential influences of both environmental and genetic background using the Mardia et al. (2000) methodology (**Figure 2**). An outbred population on the island of Hvar (presumed to represent a relatively stressful environment) was found to have a significantly higher level of fluctuating asymmetry (FA, random differences between right and left sides or structures) than did a similarly outbred population from the capital city of Zagreb. Within the common environment of Hvar, FA increased with presumed inbreeding (genetic stress). Patterns of directional asymmetry (DA, systematic differences between right and left sides or structures) also varied with environment and genetic background, and patterns of DA and FA differed in the mandible and maxilla. This study presented a powerful, but relatively unknown, methodology to the anthropological and general biological research community, and it did so in the context of a sophisticated design that addressed substantive issues in its field of
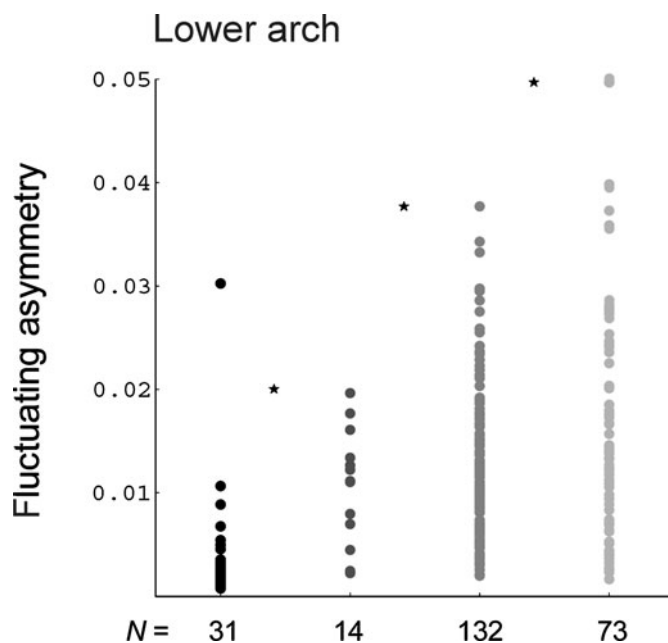

Figure 2

Fluctuating asymmetry (FA) values for the lower (mandibular) dental arch of individuals from Schäfer et al. (2006). The leftmost set is for individuals from the outbred, mainland population of Zagreb, Croatia, and it has significantly lower FA than does a similarly outbred sample from the island of Hvar (*second set of values*) indicating an environmental effect. Within Hvar (*the three rightmost sets of values*), FA increases with increased inbreeding, suggesting a genetic component. After figure 4 of Schäfer et al. 2006.

application. As such, this report is likely to serve as a template for future investigations into the utility of asymmetry analysis in the determination of genetic and environmental influences on development. Such progress is again hampered by a lack of tools for the application of the methodology, especially for three-dimensional data sets, but this is likely to be addressed in the near future.

Evolutionary History and the Fossil Record

As a number of papers cited earlier attest, coordinate-based morphometric analysis provides a sophisticated suite of tools with which to address evolutionary questions. However, even this potential is only just being tapped. Recent collaborative work by computer scientists, anthropologists, and morphometricians at the University of California at Davis, the American Museum of Natural History, and Stony Brook University has produced some remarkable preliminary results illustrating the extent to which modern morphometric methods can be used to probe the evolutionary history of organisms (Wiley et al. 2005).

This research group used landmark-based morphometric methods to combine molecular phylogenetic trees with laser range surface data for extant Old World monkeys to generate detailed and mathematically justifiable estimates of ancestral morphology (**Figure 3**). Given an evolutionary tree, the process involves using GPA to generate shape coordinates from landmarks associated with surface scans of representative terminal taxa. These coordinates are then used to estimate shape-coordinate values for hypothetical taxonomic units (HTUs = presumed ancestral forms) at tree nodes using a generalized least-squares (GLS) regression procedure described by Rohlf (2001). The GLS regression results are the equivalents of squared-change

parsimony estimates (Maddison 1991) that are reasonable assuming a constant Brownian-motion model of evolutionary change. The surface scans are then warped onto the estimated HTU configurations and averaged using new methods developed by the computer visualization group. The result is a detailed estimate of ancestral morphology implied by the phylogenetic tree and the assumed model of evolutionary change. Such models can, for instance, be studied or compared with fossil material to assess the adequacy of the tree and assumed model of change to account for morphological evolution or used to assess the putative position of fossil material in relation to the extant species. Although this work has been initiated by anthropologists, such capabilities offer considerable potential for the advancement of research throughout evolutionary biology, paleontology, systematics, and other fields.

SUMMARY

Anthropology has played an important role in the development of statistical methodologies both through its provision of compelling questions with which to intrigue statisticians and through its adoption and dissemination of novel techniques to wring every last bit of insight from often rare data sets. In no place has this been more true than in the field of statistical shape analysis: morphometrics. This relationship continues today as anthropologists contribute to the development of modern morphometric methods and embrace these methods in their own research. As a result, geometric morphometrics stands as a mature and widely used analytical paradigm. Still, this is not a static field. New, innovative, and lesser-known extensions of the basic analyses are likely to figure in future anthropological research, and anthropologists are likely to contribute to their development.

DISCLOSURE STATEMENT

The author is not aware of any biases that might be perceived as affecting the objectivity of this review.

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RELATED RESOURCES

Numerous sources of information, advice, and tools are available to researchers seeking to incorporate modern morphometric methods into their projects. Two of these sources can provide access to others. First, MORPHMET is the online mailing list started by Leslie F. Marcus and currently moderated and maintained by the author. Subscribed to by more than 600 researchers, students, and other interested parties around the world, this list allows members to post questions and comments about morphometric methods, analytical procedures, applications, and hardware to a knowledgeable and helpful community. Also, the original morphometrics Web site, **http://life.bio.sunysb.edu/morph**, developed and maintained by F. James Rohf at Stony Brook University, contains links to software, data sets,

workshop and book reviews, morphometricians, Web sites, and other resources of value to morphometricians. Information about MORPHMET, including subscription information, and links to the Stony Brook page can be found at **http://www.morphometrics.org**, which also maintains a list of job announcements of relevance to those proficient in morphometrics.

Chlorocebus aethiops

Papio hamadryas ursinus

Macaca nemestrina

Pygathrix nemaeus

Colobus guereza

16   12   8   4   0

millions of years ago
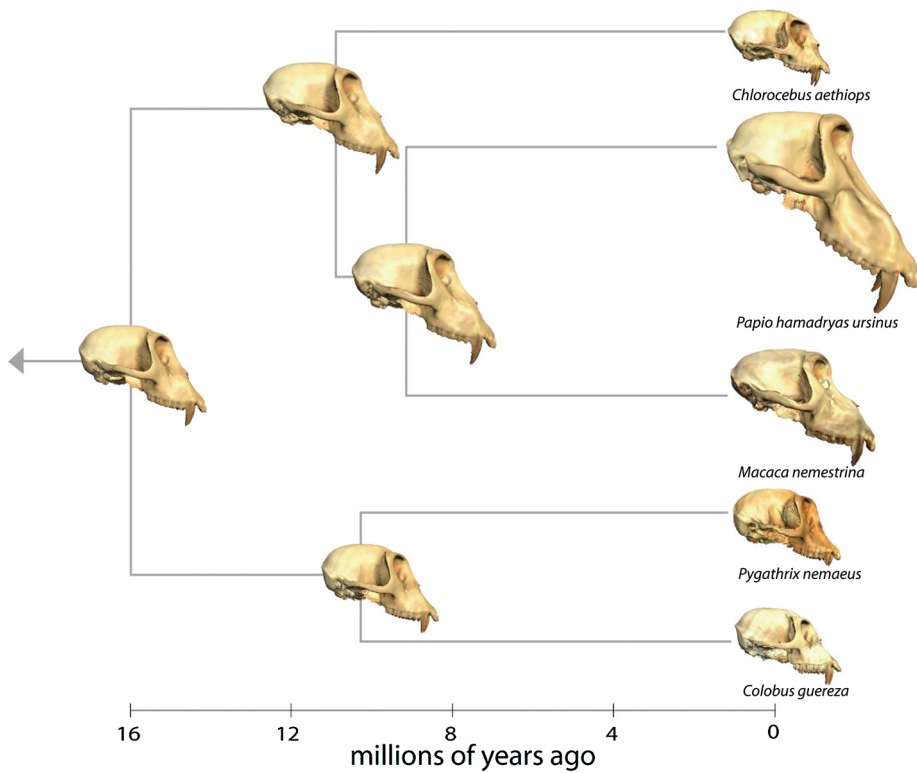
Figure 3

Estimating ancestral morphology. The tree is based on molecular data. The images of terminal taxa are
from laser scans of representative specimens. Landmark data recorded from terminal taxa were interpo-
lated into the tree and the terminal scans mapped onto the estimated configurations and averaged.
Image from **http://graphics.idav.ucdavis.edu/research/EvoMorph** with permission.

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