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Research Article

A field comes of age: geometric morphometrics in the 21st century

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Abstract

Twenty years ago, Rohlf and Marcus proclaimed that a "revolution in morphometrics" was underway, where classic analyses based on sets of linear distances were being supplanted by geometric approaches making use of the coordinates of anatomical landmarks. Since that time the field of geometric morphometrics has matured into a rich and cohesive discipline for the study of shape variation and covariation. The development of the field is identified with the *Procrustes paradigm*, a methodological approach to shape analysis arising from the intersection of the statistical shape theory and analytical procedures for obtaining shape variables from landmark data. In this review we describe the Procrustes paradigm and the current methodological toolkit of geometric morphometrics. We highlight some of the theoretical advances that have occurred over the past ten years since our prior review (Adams et al., 2004), what types of anatomical structures are amenable to these approaches, and how they extend the reach of geometric morphometrics to more specialized applications for addressing particular biological hypotheses. We end with a discussion of some possible areas that are fertile ground for future development in the field.

Introduction

> The study of form may be descriptive merely, or it may become analytical. We begin by describing the shape of an object in the simple words of common speech: we end by defining it in the precise language of mathematics; and the one method tends to follow the other in strict scientific order and historical continuity.
>
> D'Arcy Wentworth Thompson (1915)

For centuries, naturalists have marvelled at the diversity and complexity of life on earth. From the simple observation that organisms differ in both their anatomical attributes and in their use of these traits, scholars have sought to describe morphological and anatomical differences among taxa and explain how these differences have evolved (Darwin, 1859). Indeed, this long-standing fascination with biological form has shaped our current perspectives on many biological topics, including our notions of taxonomic discontinuities, our methods of classification, and our hypotheses of the structure-function relationship. As was accurately prophesized by Thompson in 1915, the study of form has developed into a rigorous quantitative discipline; the field of morphometrics. For much of the 20th century morphometric analyses were accomplished by applying univariate and multivariate statistics to sets of measured traits that included linear distances, ratios, and angles (i.e., traditional morphometrics *sensu*: Blackith and Reyment 1971; Marcus 1990; Reyment 1991; for a unique history of the field see: Reyment 1996). However, over time it became apparent that certain shortcomings limited the biological interpretations that were possible with these methods. For example, graphical depictions of shape and shape changes cannot always be generated from the results of these approaches, as the geometric relationships among variables were usually not preserved in the measurements taken (Strauss and Bookstein 1982; for discussion see: Rohlf and Marcus 1993; Adams et al. 2004). Thus, another approach to the study of shape was required.

In the 1980's, alternative approaches were proposed and developed that represented a radical shift in the way the shapes of anatomical structures were quantified and analysed (but see Boas 1905; Galton 1907; Sneath 1967 for earlier work). These alternatives captured the geometry of the morphological structures of interest and retained this information throughout the analyses. This new approach was called *geometric morphometrics* (Corti, 1993). Not surprisingly, the conversion from traditional to geometric morphometrics could be viewed as a "revolution" (Rohlf and Marcus, 1993). This revolution embodied both a shift in methodology, and in the conceptual and statistical underpinnings of the field. Geometric morphometric approaches generally utilize fundamentally different types of data to quantify shape; landmark coordinates, outline curves, and surfaces. In its early years the field developed at a rapid pace, as methodological advances for shape quantification intertwined with a rich statistical theory for shape analysis (the morphometric "synthesis", *sensu* Bookstein 1996). As a result of this paradigm shift, landmark-based geometric morphometrics (GM) provides a powerful technique in the quantitative biologists' repertoire for the study of shape variation and the identification of its causes. Not surprisingly, these methods are increasingly used to quantify anatomical shapes in a wide range of scientific disciplines.

Nearly a decade ago, we reviewed the field of geometric morphometrics and described the important advantages that these approaches have relative to alternative methods of shape analysis (Adams et al. 2004; for other reviews see: O'Higgins 2000; Slice 2005, 2007; Mitteroecker and Gunz 2009). We also summarized some of the methodological advances that took place in the ten years following the "revolution", and provided an account of the state-of-the field at that time. Much has happened in geometric morphometrics in the years since that review, mandating a new appraisal of this now mature discipline. In this review, we describe some of the theoretical developments that have ensued during the past decade. Our review focuses on advances in landmark-based morphometric approaches, though we recognize that developments in related areas have also occurred (e.g., MacLeod 2008; McPeek et al.

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2008; Shen et al. 2009). Our aim is to provide readers with a succinct summary of the current "toolkit" of geometric morphometrics, and an appreciation for the types of applications and extensions that can be used to address specific biological hypotheses. We also provide our perspective of what the future may hold in store in the coming years.

Geometric morphometrics and the "Procrustes paradigm"

Geometric morphometrics is the statistical analysis of shape variation and its covariation with other variables (Bookstein, 1991). These methods quantify variation in the shape of anatomical objects using the Cartesian coordinates of anatomical landmarks, after the effects of non-shape variation have been mathematically held constant. Geometric morphometric studies are accomplished through what can be called the *Procrustes paradigm*; an approach to shape analysis that emerged from the unification of a rigorous statistical theory for shape (Kendall, 1981, 1984, 1985) with analytical procedures for superimposing landmark configurations to obtain shape variables (Gower, 1975; Bookstein, 1986; Rohlf and Slice, 1990; Rohlf, 1999b). In a typical morphometric analysis, the Procrustes paradigm is implemented as a series of operations (Fig. 1).

First, from each specimen, a set of two- or three-dimensional landmark coordinates is obtained, which record the relative positions anatomically-definable locations. These landmarks can be considered "fixed points", as they define the locations of particular anatomical traits representing discrete biological attributes (see below for a discussion of semilandmarks). Next, a generalized Procrustes analysis (GPA: Gower 1975; Rohlf and Slice 1990) is used to superimpose the configurations of landmarks in all specimens to a common coordinate system, and to generate a set of shape variables. This least-squares procedure translates all specimens to the origin, scales them to unit centroid size, and rotates them to minimize the total sums-of-squares deviations of the landmark coordinates from all specimens to the average configuration. After superimposition, the aligned *Procrustes shape coordinates* describe the location of each specimen in a curved space related to Kendall's shape space (Rohlf, 1999b; Slice, 2001). These are typically projected orthogonally into a linear tangent space yielding *Kendall's tangent space coordinates* (Dryden and Mardia, 1993, 1998; Rohlf, 1999b; Kent and Mardia, 2001), on which multivariate analyses of shape variation are then conducted[1]

The third step of a morphometric study is to test biological hypotheses using multivariate statistical methods. For instance, Hotelling's T^2 or multivariate analysis of variance (MANOVA) can be used to test for shape differences among groups, while multivariate regression or partial least squares (PLS: Rohlf and Corti 2000) can be used to help identify patterns of covariation between shape and other continuous variables. In addition, methods that partition shape variation in particular ways can be utilized to address more specialized biological hypotheses. For instance, shape variation due to directional and fluctuating asymmetry can be quantified and analysed to test hypotheses of symmetry in a sample (Klingenberg and McIntyre, 1998; Mardia et al., 2000; Kent and Mardia, 2001; Klingenberg et al., 2002; Schaefer et al., 2006). Finally, graphical methods are used to visualize patterns of shape variation and facilitate descriptions of shape changes. Here, ordination methods such as principal components analysis (PCA) generate scatterplots representing the dispersion of shapes in tangent space, while thin-plate spline transformation grids can provide a visual description of the shape differences between objects. The latter display shape changes and differences in a manner similar to D'Arcy Thompson's transformation grids (Thompson, 1917) where one object is transformed (or "warped") into another using the thin-plate spline (Bookstein, 1989, 1991). Importantly, transformation grids may be generated for actual specimens in the data set or for estimated specimens, such as group means or predicted specimens along a regression line. Thus, by comparing transformation grids, differences in shape between objects and trends in shape change in specific directions in Kendall's tangent space can be depicted and anatomically described. This combination of rigorous statistical analysis with visualizing shape changes represents one of the more powerful aspects of the Procrustes paradigm.

[1]Note that alternative mathematical approximations of tangent space are possible (see e.g., Weber and Bookstein 2011). These should give very similar results when shape variation is small.

Advances over the past decade

The dawn of the 21st century brought with it the maturation phase of geometric morphometrics and the emergence of the Procrustes paradigm as the standard methodological approach for analysing shape characterized by landmark data. This was due in large part to the realization that Procrustes-based approaches outperformed alternative methods from a statistical perspective (e.g., Rohlf 1999a, 2000, 2003). However, despite the pre-eminence of this approach to shape analysis, much theoretical progress continues in the discipline. Particularly active has been the development of more specialized applications to address particular biological problems and hypotheses. In this section we highlight several of these theoretical advances, and some ways in which they enhance the morphometrician's toolkit.

Use of three-dimensional data

One major change in geometric morphometrics from a decade ago has been the rapid increase in the use of three-dimensional data. Interestingly, there are generally no mathematical limitations for handling data in three dimensions. Indeed the algorithms commonly used for superimposition, projection, and statistical analysis are all generalized to accommodate data of any dimensionality. Instead, the restriction to two-dimensional data has been decidedly more practical. Until recently, acquiring three-dimensional data required specialized equipment and was prohibitively expensive, and the use of many three-dimensional devices was limited to specimens in a restricted size range. However, over the past decade a number of lower-cost options have become available, including surface scanners and other data-collection devices. Because these devices are now more accessible to the research community, many more geometric morphometric studies are conducted using three-dimensional landmark data. This shift is perhaps most pervasive in the field of anthropology, where the specimen sizes are particularly well-matched to the optimal size ranges of three-dimensional data acquisition tools (Slice, 2007).

Semilandmarks and missing landmarks

Geometric morphometric analyses are typically performed on landmark coordinates describing specific anatomical locations (i.e., "fixed"

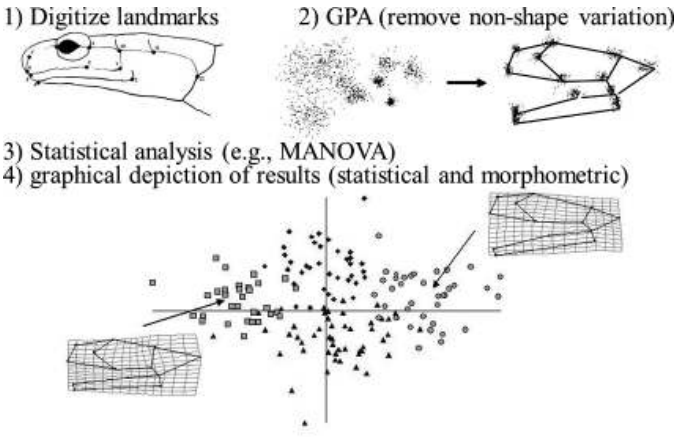


Figure 1 – Graphical depiction outlining the steps of the Procrustes paradigm for landmark-based geometric morphometrics. 1) Digitize raw data (landmarks recorded on head of a *Plethodon* salamander), 2) Generalized Procrustes analysis to remove non-shape variation (landmarks of 156 specimens before and after GPA), 3) statistical analysis (e.g., MANOVA), and 4) graphical depiction of results (ordination plot of specimens with thin-plate spline transformations for the mean specimens of two groups). Data from Adams and Rohlf (2000).

anatomical points), yet the shape of other anatomical features may also be of interest. For example, *semilandmarks* can be used to capture the shape of boundary curves, which can then be included with a set of fixed landmarks in a Procrustes-based shape analysis (Bookstein, 1997; Bookstein et al., 1999). With this approach, a series of locations along the curve are digitized, and an additional step may be incorporated in the Procrustes algorithm which slides these points along vectors tangent to the curve until their positions align as closely as possible with the semilandmarks on the corresponding curve of a reference specimen (for related approaches see: Hammond et al. 2004; McCane and Kean 2011). This algebra for semilandmarks has now been extended to three dimensions, so that the shapes of both curves and surfaces can be quantified (Gunz et al., 2005). Here, semilandmarks on curves are usually slid along their tangent vectors, and semilandmarks on surfaces are slid within their tangent planes, until their positions minimize the shape difference between specimens. This reduces the effect of the arbitrary initial placement of the semilandmarks, and can be accomplished either by minimizing bending energy or Procrustes distance between the reference and the target specimen (Bookstein et al., 1999; Gunz et al., 2005; Rohlf, 2010). It should be emphasized that care must be taken when placing semilandmarks relative to other structures (Oxnard and O'Higgins, 2011). Additionally, these methods tend to work best when used on relatively smooth curves and surfaces, or when many points are included. Nevertheless, by using both landmarks and semilandmarks, information from points, curves, and surfaces may be combined for a more comprehensive quantification and analysis of biological shape variation (Fig. 2).

Methods have also been developed to account for missing landmarks. Because morphometric analyses require that all specimens have the same set of landmarks, incomplete specimens must either be eliminated from the analysis, or missing landmarks must be eliminated from the dataset. Clearly, neither solution is ideal: a far preferable alternative is to estimate the locations of missing landmarks in some way, so that partial specimens can be included. For structures exhibiting bilateral symmetry, one approach is to estimate missing landmark locations by reflecting their corresponding landmarks across the mid-line of the structure (Claude, 2008). Unfortunately, this method can only be implemented for symmetrical objects. Inferring the locations of missing landmarks can also be accomplished through statistical estimation approaches based on regression or expectation maximization (e.g., Neeser et al. 2009; Couette and White 2010). A third alternative extends the logic of semilandmarks to the estimation of missing landmarks (Bookstein et al., 1999; Gunz et al., 2009). Here the locations of missing landmarks are determined using the thin-plate spline, such that they minimize the shape difference between the incomplete specimen and the reference, thereby exerting minimal influence on the resulting patterns of shape variation (the method is presently based on bending energy, but an approach that minimizes Procrustes distances could also be envisioned). Together, these methods greatly expand the utility of the Procrustes paradigm for fields where missing landmarks are common, such as palaeontology and anthropology (see e.g., Weber and Bookstein 2011).

Analysis of symmetry

Biologists have long been interested in identifying deviations in symmetry in populations of organisms, including: fluctuating asymmetry (the random departures from perfect symmetry across individuals) and directional asymmetry (biased departures from perfect symmetry across individuals). Over a decade ago, the methods commonly employed on traditional measurements to analyse patterns of asymmetry were generalized for landmark-based shape data (Klingenberg and McIntyre, 1998; Klingenberg et al., 2002). Subsequently, a mathematical decomposition of shape variation into its symmetry components (for bilaterally symmetric shapes) was derived (Mardia et al., 2000; Kent and Mardia, 2001), and recent extensions of the approach have been proposed for other types of symmetry (Savriama and Klingenberg, 2011). As a consequence of these methodological advances, the analysis of symmetry, and the identification of a lack of symmetry, is now frequently examined in geometric morphometric studies.

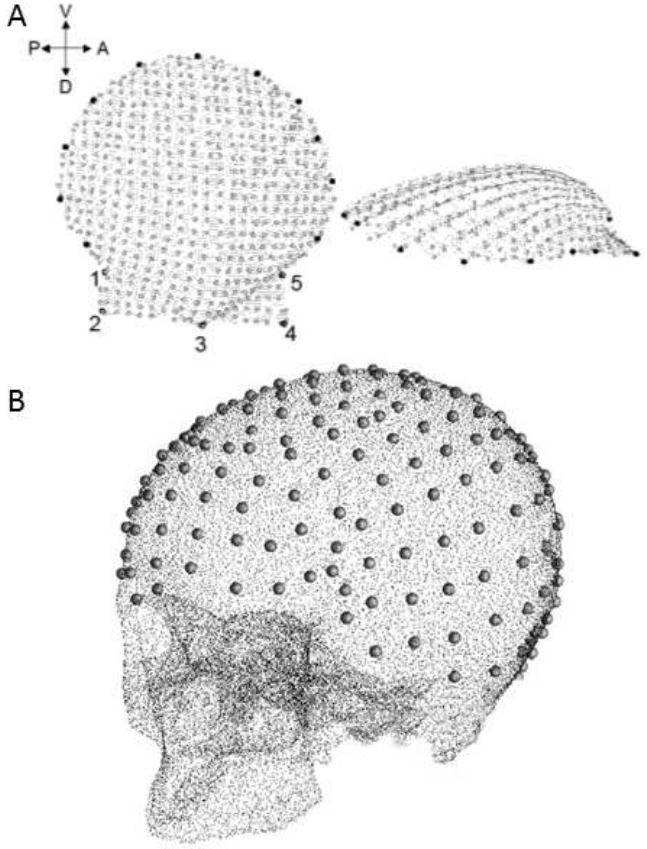


Figure 2 – A) A set of landmarks defining fixed anatomical points, the boundary curve, and the surface of a scallop shell (from Serb et al. 2011). B) Sliding semilandmarks quantifying the surface of a skull (reproduced from Adams et al. 2004; after Mitteroecker 2001; MS thesis, Univ. Vienna).

Visualizing allometry

A nearly ubiquitous property of organisms is that individuals of different sizes also have different shapes. The association of size and shape is investigated through the analysis of allometry. Allometric studies have a long history in morphometrics (Huxley, 1932; Jolicoeur, 1963; Cock, 1966; Klingenberg, 1996; Sidlauskas et al., 2011), yet a recurring challenge has been to generate graphical summaries that adequately illustrate these patterns. This problem is particularly acute for geometric morphometric data, where allometric trajectories describe the multivariate relationship between shape and size. Several recent methods address this issue and help to facilitate biological interpretation of allometric and ontogenetic trends (Fig. 3). For instance, a principal components analysis of the matrix of tangent space coordinates augmented with the vector of log centroid size reveals the major direction of variation in this size-shape space (*sensu* Mitteroecker et al. 2004), which often is due to allometry. When multiple groups are present the common allometric component (CAC: Mitteroecker et al. 2004) can be calculated, which is an estimate of the common within-group trend. Shape residuals from the CAC can then be plotted against size to identify differences among allometric (or ontogenetic) trajectories. A related approach is to estimate shape scores from the regression of shape on size, and plot these against size (Drake and Klingenberg, 2008). It should be noted that for a single group, this approach is mathematically identical to the CAC, as the average within-group trend (i.e. the CAC) is simply the trend for a single group. In a third approach, an allometric trajectory is represented by estimating predicted values from a regression of shape on size, and a stylized graphic is obtained by plotting the first principal component of the predicted values versus size (Adams and Nistri, 2010). Finally, transformation grids representing the shapes of small and large specimens can be included with the

scatterplots to provide a graphical depiction of how shape changes as a function of size. Together, these methods provide complementary visualizations of the allometric and ontogenetic patterns frequently present in morphometric data.

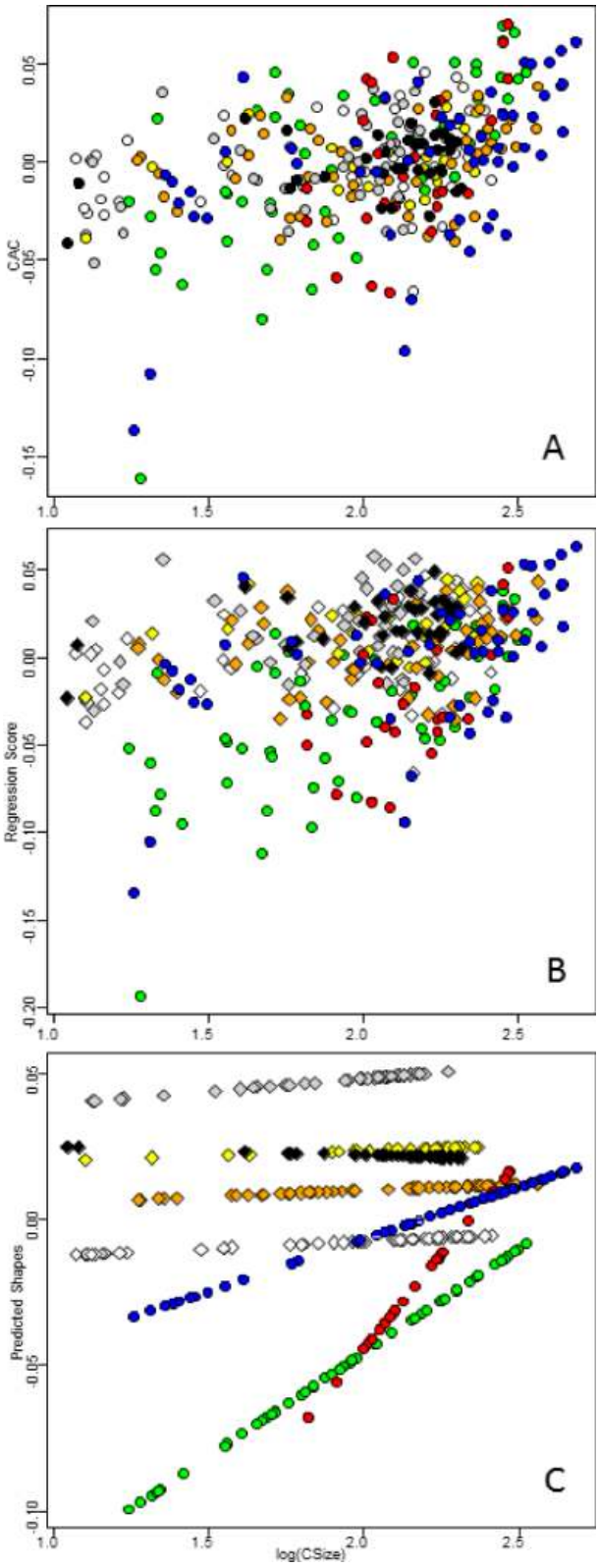


Figure 3 – Examples of various visualizations of shape allometry for eight species of Italian plethodontid salamanders (data from Adams and Nistri 2010). A) The common allometric component (CAC) versus log centroid size; B) Regression scores versus log centroid size; C) PCI of predicted values (from a regression of shape on size) versus log centroid size.

Quantifying phenotypic trajectories and motion paths

The sequence of changes in shape due to allometry corresponds to a path (or trajectory) of shape changes in tangent space. This trajectory reveals how shape changes as a function of size. However, patterns of shape change can also be generated from processes other than allometry; thus a general approach for analysing phenotypic change trajectories is required. Recently, one approach was proposed that examines various attributes of phenotypic change trajectories and uses these for statistical comparison (Adams and Collyer, 2007; Collyer and Adams, 2007; Adams and Collyer, 2009; Collyer and Adams, this issue). Termed *phenotypic trajectory analysis*, this approach quantifies the size, orientation, and shape of phenotypic paths (trajectories) and examines these attributes to determine whether sets of trajectories are similar or different (beyond any differences they may have in their location in tangent space). Importantly, the method can quantify any trajectory of shape change; such as those representing allometric or ontogenetic growth trajectories, temporal sequences, evolutionary shape changes, shape changes resulting from ecological shifts, or shape changes observed in studies of phenotypic plasticity (see Adams and Collyer 2009). Recent applications have identified parallel evolution of shape changes resulting from competitive interactions (Adams, 2010), and patterns of ontogenetic convergence among closely related taxa (Adams and Nistri, 2010; Piras et al., 2010).

A related approach has been proposed for the study of motion paths (Adams and Cerney 2007; for related ideas see: Slice 1999; O'Higgins et al. 2002). Here a motion is represented by a sequence of shapes in tangent space that corresponds to differences in the relative position of their anatomical parts. This sequence forms a trajectory in shape space whose attributes can be quantified and used to identify similarities or differences among motion trajectories (Adams and Cerney, 2007). This method is a special case of the phenotypic trajectory analysis described above. Finally, a complementary procedure quantifies motion paths as the change in relative position of a single landmark during a movement, and sets of these motion paths are then quantitatively compared using Procrustes analysis (Decker et al., 2007).

Applications to quantitative genetics

Another area where considerable development occurred over the past decade is the utilization of shape data in quantitative genetics. For instance, a number of studies have used quantitative trait loci to assess the genetic underpinnings of shape variation (see e.g., Klingenberg and Leamy 2001; Klingenberg et al. 2004; Burgio et al. 2009; Boell et al. 2011). In addition, several methods for linking the algebra of quantitative genetics with that of geometric morphometrics have been proposed. One method is based on Procrustes distance, allowing the estimation of heritability and other quantitative genetics attributes in a univariate framework (Monteiro et al., 2002). An alternative uses the multivariate generalization of the breeder's equation (Klingenberg and Leamy, 2001), retaining the full multivariate nature of the geometric morphometric shape data throughout the analysis and allowing implementations based on the "animal model" (*sensu* Lynch and Walsh 1998). Considerable discussion highlighted the advantages and disadvantages of these two alternatives (e.g., Klingenberg 2003; Monteiro et al. 2003; Klingenberg and Monteiro 2005; see also Myers et al. 2006). Ultimately, for accurate estimates of magnitudes and directions of shape heritability the multivariate approach is preferred (Klingenberg and Monteiro, 2005). Recent applications of this approach can be found in (e.g., Gómez et al. 2009; Klingenberg et al. 2010; Adams 2011; Martínez-Abadías et al. 2012).

Integration and modularity

It has long been observed that some phenotypic traits are highly correlated while other sets of traits display less correlation. Such observations lead Olson and Miller to propose the concepts of morphological integration and modularity (Olson and Miller, 1951, 1958). Morphological integration describes the nature of correlated characters and the cohesion among traits that result from developmental, evolutionary, and functional processes (Klingenberg, 2008; Mitteroecker, 2009).

Several methods have been proposed for empirically identifying modular or integrated components in morphometric data, and these approaches address related, but subtly distinct biological hypotheses. For instance, an exploratory way to identify integration among traits is based on conditional independence (Magwene, 2001, 2009). Here no *a priori* hypothesis of modularity is required; rather, the partial correlations among traits are used to hypothesize combinations of traits that may describe modular structure. However, a number of shortcomings limit the utility of this approach, particularly as the number of traits per module increases (Mitteroecker and Bookstein, 2007, 2009).

When prior evidence exists to posit a hypothesis of modularity, the amount of integration between modules can be assessed through partial least squares (Bookstein et al., 2003). This approach identifies the degree of covariation between sets of traits, and when used with geometric morphometric data, is called *singular warps analysis* (Bookstein et al., 2003; Mitteroecker and Bookstein, 2008). An alternative approach tests the hypothesis that there is modularity according to a given partition of landmarks against the null hypothesis that there is no modularity. This method expresses the degree of covariation between modules relative to variation within modules using Escoufier's RV coefficient (Klingenberg, 2009). This approach can be used to determine whether an *a priori* partitioning of landmarks exhibits covariation expected under the hypothesis of modularity, or to identify putative modules that have minimal covariation between them. Finally, one can test alternative modularity hypotheses by comparing the observed pattern of covariation among traits to patterns of covariation expected under a particular modular hypothesis (Marquez, 2008; Parsons et al., 2012). Here a goodness of fit statistic between the two covariance matrices is obtained and assessed via Monte Carlo methods. Together, these techniques provide new and exciting avenues for examining patterns of integration and modularity in morphometric data.

The next ten years: a possible future

The past twenty five years have seen a surge of methodological developments in geometric morphometrics. What began as an alternative approach to shape quantification has developed into a rigorous discipline that combines a rich statistical theory with shape data from points, curves and surfaces, to test an ever-increasing breadth of biological hypotheses. It is therefore not surprising that geometric morphometric methods are being utilized more than ever before to describe and investigate patterns of shape variation and covariation in many areas of biological research. If history is any guide, the next ten years will be equally exciting, and theoretical developments in geometric morphometrics will continue at a rapid pace. As we did in our review a decade ago (Adams et al., 2004), here we highlight a few areas that we predict are ripe for future development.

Morphometrics and phylogenetics

It is with a sense of irony that we include this topical area under future developments, as a decade ago we commented that the intersection of morphometrics and phylogenetics needs to be further explored (Adams et al., 2004). In some sense this area may remain a perennial candidate for future development, because despite considerable effort, combining these two disciplines in a cohesive manner has remained stubbornly elusive. The power of geometric morphometrics to quantify patterns of shape variation is undeniable; thus it is natural to consider how morphometric variables may be used to estimate phylogenetic trees. However, most attempts to do so have relied on methods based on cladistic parsimony, and unfortunately, there is a fundamental disconnect between these approaches (which require independent, discrete variables) and geometric morphometric shape variables (which are continuous, multivariate, and inter-dependent). Discussions of earlier attempts at bridging this divide can be found in (Fink and Zelditch 1995; Adams and Rosenberg 1998; Rohlf 1998; MacLeod 2002; Swiderski et al. 2002 see also Adams et al. 2011). In fact, even a recent approach for estimating phylogenies from shape data (Gonzalez-Jose et al., 2008) suffers these same shortcomings, as this approach is ultimately based on a rank-based representation of shape differences among species along individual shape axes (for discussion see: Adams et al. 2011; also Klingenberg and Gidaszewski 2010). Other recent work has focused on obtaining a phylogenetically-informed superimposition (see e.g., Goloboff and Catalano 2011; Catalano and Goloboff 2012). Importantly, while these methods use morphometric shape data as input, they fall outside the realm of the Procrustes paradigm, as the landmark-by-landmark parsimony approaches they employ do not conform with shape distances as defined by Kendall's shape space and tangent space (Klingenberg and Gidaszewski, 2010; Adams et al., 2011). Finally, several recent approaches use maximum likelihood methods to obtain estimates of phylogenetic relationship from shape data (Caumul and Polly, 2005; Cardini and Elton, 2008). However, current implementations of this approach assume that the characters evolve independently and with equal variances following a Brownian motion model of evolution; assumptions that are not met with geometric morphometric shape data (see Adams et al. 2011). Nevertheless, because likelihood methods can incorporate continuous multivariate data, we feel that they hold the most promise for this application, and recommend that future work in this area be focused in that direction.

Morphometrics and phylogenetics can also be combined by utilizing an existing phylogeny to address hypotheses of shape change through evolutionary time. For instance, one can visualize predicted patterns of shape evolution by estimating ancestral shapes and projecting both the hypothesized ancestors and the phylogeny into tangent space (e.g., Rohlf 2002; Klingenberg and Gidaszewski 2010). Methods have also been developed for estimating phylogenetic signal from morphometric data (Klingenberg and Gidaszewski, 2010), though more work is required in this area. A few studies have looked at the tempo and mode of macroevolutionary changes in shape (e.g., Monteiro and Nogueira 2011). However, more work is needed to integrate morphometric data, which is both multivariate and multi-dimensional (*sensu* Klingenberg and Gidaszewski 2010), with recent evolutionary methods for comparing models of phenotypic evolution on phylogenies (e.g., Butler et al. 2000; Blomberg et al. 2003; Butler and King 2004), and for estimating rates of phenotypic evolution on phylogenies (e.g., O'Meara et al. 2006; Revell and Harmon 2008; see also Bookstein 2012b for recent Brownian motion models for shape evolution).

Estimating landmark covariances

Another area that represents a hold-over from our previous review is estimating landmark covariance structure. For many reasons, morphologists are interested in evaluating the relative variability within and among landmarks. However, the superimposition procedure itself alters the resulting patterns of landmark covariance, which makes direct interpretation of the resulting covariance matrix challenging (Rohlf and Slice, 1990; Walker, 2000; Rohlf, 2003). While it is important to recognize that this shortcoming does not affect statistical tests of shape differences performed in Kendall's tangent space, the issue still needs to be resolved. One approach to the problem is to perform simulations that can identify the extent to which observed patterns of landmark covariance reflect what is expected under a particular model of shape change. Alternatively, it may be possible to extend recent approaches that evaluate the relative influence of individual landmarks on allometric trends ("jackknife-GPA" *sensu*: van der Linde and Houle 2009), or methods for assessing the relative contribution of each landmark to overall patterns of shape variation (Albert et al., 2003), for the estimation of landmark covariance structure. More work is needed on this issue.

Morphometrics and biomechanics

One area we believe will be fruitful in generating future methodological developments is the intersection of geometric morphometrics and biomechanics. In biomechanics, finite element analysis (FEA) is often used to estimate the stresses and strains that anatomical structures endure when subjected to forces or loadings (e.g., Dumont et al. 2005). Like geometric morphometrics, FEA begins by capturing the geometry of an anatomical structure based on the coordinates of (many) point locations. Therefore it is logical to suppose that the two approaches can

be combined in some meaningful way (for discussion see: O'Higgins et al. 2011; Weber et al. 2011; Parr et al. 2012). Indeed, a number of approaches for combining FEA and GM in the same analysis have recently been proposed. One method uses the thin-plate spline to deform an existing FE model from one specimen into another (e.g., Pierce et al. 2008; Stayton 2009; Rivera and Stayton 2011). Here, geometric morphometric methods estimate the smooth deformation mapping between specimens (based on the locations of their landmarks), and the deformation function is subsequently used to generate a predicted FE model to evaluate stresses and strains for the target specimen. An alternative method combines GM and FEA in a different manner. Here, the thin-plate spline is used to visualize the structural deformations implied by the FE model itself (e.g., Cox et al. 2011; Groning et al. 2011; O'Higgins et al. 2011).

While these approaches represent exciting new developments and hold great promise for future studies in functional and geometric morphometry, a number of serious challenges remain. First, little has been done to validate whether the FE models predicted from morphometric mappings represent what would be obtained from an FEA performed directly on the target specimen. Second, when a single FE model is used to predict models for multiple specimens (e.g., Rivera and Stayton 2011; Parr et al. 2012), distinct FE models are obtained for each target specimen. However, all the information about stresses and strains is based on the geometric and densiometric properties of the original specimen: no new stress information is obtained. As such, this "filtering" of the FE model through the thin-plate spline does not result in novel biomechanical predictions for each specimen, but simply re-expresses the same biomechanical information in some non-linear, but predictable, manner. Further, at present it is not clear how representations of shape differences as displayed by the thin-plate spline relate to the stresses and strains described by FEA. Additionally, even when the densiometric properties of both the reference and target specimens are assumed to be identical (which is unlikely to be the case), predicted FE models generated from thin-plate spline mappings do not provide the correct deformations in terms of the physics of the actual deformations (Bookstein, 2013). Finally, no mathematical theory exists for quantitatively relating difference in shape to differences in stresses and strains that would occur on those specimens (see Weber et al. 2011; Bookstein 2013). Thus, we currently do not know whether the relationship between FE models and shape differences (Procrustes distance) is a one-to-one or many-to-one mapping. As alluded to above, one problem is that the thin-plate spline does not take into account the material properties of the structure, and thus some biomechanical properties estimated by the FE model cannot be directly related to shape deformations. Clearly, additional theoretical work is required to resolve these issues, and to provide a methodological framework for future studies in this area.

Resolution of modularity approaches

The past several years has seen tremendous growth in studies of integration and modularity as applied to morphometric data. In fact, three distinct analytical approaches are currently in use: one based on partial least squares (Bookstein et al., 2003; Mitteroecker and Bookstein, 2008), one based on Escoufier's RV coefficient (Klingenberg, 2009), and one based on comparing observed and expected covariance matrices (Marquez, 2008; Parsons et al., 2012). Further, two of these methods (PLS and the RV coefficient) are mathematically related: they both examine the cross-covariance matrix between sets of traits; only they use this information in different ways. Despite these advances however, a number of issues remain to be resolved in this area. One issue is that the present methods test against an unreasonable null hypotheses of modular structure. That is, present methods test all combinations of contiguous landmarks to see whether their internal level of covariation is higher than that to landmarks not in a putative module. However, these combinations generally ignore the distances between landmarks, yet landmarks cannot usually be sampled uniformly across a structure. A simple alternative to the existence of modules is a model where the level of covariance between landmarks is inversely proportional to their distance. In some datasets, the same modules are obtained by maximizing within-module covariance or by simply clustering landmarks based on interlandmark distances (F.J. Rohlf, unpublished). Thus, in these instances, there is no need to invoke a hypothesis of modular structure, as the observed covariance patterns are simply the result of the relative distances between landmarks. Further, at present it is not clear which approach is most effective at identifying non-spatially determined patterns of integration and modularity, and under what circumstances. Therefore, what is needed is a thorough comparison of the statistical properties of these approaches under known conditions, to determine when each performs relatively well and when each performs more poorly. This would give some much-needed clarity to the field, and provide end-users with clear recommendations on which integration and modularity methods should be utilized, when, and why. We note that this suggestion echoes the approach taken to resolve an earlier issue; namely, which landmark-based morphometric method should be used. Here, statistical simulations determined that Procrustes approaches outperformed alternative methods (e.g., Rohlf 1999a, 2000, 2003).

Software development

As with all quantitative fields, new methods will only be used if researchers have access to software for their implementation. Fortunately, the morphometric community is replete with theorists who also generate software, and thus numerous packages are available. Nearly all morphometrics packages include the standard components of the Procrustes paradigm: including Procrustes superimposition, basic statistical analyses of shape data (PCA, MANOVA, regression), and visualization through thin-plate spline transformation grids. A partial list of these packages includes the `TPS`-series (e.g., `TPSRelw`: Rohlf 2010), `IMP` (Sheets, 2003), the `EVAN` Toolbox (EVAN Society 2012), `MorphoJ` (Klingenberg, 2011), `Morpheus et al.` (Slice, 1998), and several libraries for R (e.g., routines in Claude 2008, and the libraries "`shapes`": Dryden 2013, and "`geomorph`": Adams amd Otárola-Castillo 2013). More specialized analyses, such as mapping shapes on phylogenies, asymmetry analyses, and modularity approaches, are found in fewer software packages, as are methods for incorporating three-dimensional surface semilandmarks in GPA and for estimating missing landmarks using deformation procedures. In the future, we predict that new methodological developments will be incorporated into the software packages mentioned here, and that new software options will become available to the end-user.

Conclusions

It is not an overstatement to say that the past twenty five years in morphometrics has been exciting. We have witnessed a fundamental shift in how morphology is quantified as the field migrated towards the use of landmark coordinates on anatomical points, curves, and surfaces. From the union of statistical shape theory and methods for obtaining shape variables a standard approach to shape analysis has emerged (the Procrustes paradigm), and new extensions based on Procrustes methods continue to be developed to address specific biological hypotheses. Patterns of shape changes are now quantified and compared, and graphical representations of shapes are generated to facilitate biological interpretation of these statistical trends. From all of these developments it is clear that D'Arcy Thompson's dream of investigating biological form in a fully quantitative manner has now been realized. We look forward to the exciting new developments that will emerge in the years to come.

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