



Morphometrics

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MORPHOMETRICS

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INTRODUCTION

Morphometrics—the quantitative description, analysis, and interpretation of shape and shape variation in biology—is a fundamental area of research. Techniques of description and comparison of shapes of structures are needed in any systematic study (whether phenetic or cladistic) that is based on the morphology of organisms. Measurements of morphological diversity are of interest in ecological and genetic studies. Ways of dealing with shape change are also important for developmental studies and for practical applications in the medical sciences.

It is impossible to cover adequately such a broad and active field. Thus, the scope of this review is limited to developments in methodology—rather than to the numerous applications of quantitative morphometric methods. Morphometrics is, I believe, in the midst of fundamental change. During such a period, disagreements are expected about issues such as the relative importance of different approaches and the interpretation of the results of different methods. While I have tried to be objective, the relative emphasis given to different approaches undoubtedly reflects my perceptions of where the field is heading.

Traditionally, of course, the variables used in morphometric analyses are distances between landmarks, and these are measured directly on the specimen. With the availability of image acquisition hardware and image analysis systems, it is useful to distinguish the problems of data acquisition (e.g. capturing information about an image in machine readable form) from those

of feature extraction (selecting variables and making measurements) and morphometric analysis. This review follows this structure. There are important advantages to the use of image acquisition and feature extraction techniques. For example, one does not have to decide in advance which variables should be measured. This means that one can evaluate the usefulness of alternative suites of variables without handling the original specimens again. Image enhancement techniques may also make it easier to see certain features. If measurements are made by hand, then variables other than linear distances between landmarks are difficult. As Strauss & Bookstein (108) point out, such measurements usually give very incomplete and redundant information about the shape of a structure. With more comprehensive data more powerful morphometric analyses are possible—ones that take the geometrical relationships among the variables into account. But there are alternative techniques that can be (and have been) used, and they can yield very different results. The selection among them should be based on ontogenetic, phylogenetic, or other models. There has been some progress in this area, but much remains to be done. It is, however, beyond the scope of the present review.

DATA ACQUISITION

It is desirable to capture enough detailed information in a machine readable form that the shapes of the structures are “archived.” It is then possible to consider alternative sets of measurements (perhaps automatically). To be able to do this, information about the shapes of the structures must be captured with sufficient detail that the alternative measurements one might wish to use are defined. One test of adequacy is whether or not it is possible to reconstruct the shapes of the structures of interest from the recorded information. For example, one cannot later decide to use area as a variable if the recorded information is not sufficient to allow one to reproduce the general outline. A simple method, when suitable landmarks are present, is to take distance measurements in the form of a truss (108)—a network of relatively short and nonoverlapping distance measurements that allows one to infer the geometrical arrangement of the measurements (i.e. to reconstruct the coordinates of the landmarks). This is especially useful for large specimens that cannot be placed on a digitizing tablet.

One goal in the selection of variables for archiving is efficiency—to reduce the volume of data as much as possible while retaining the ability to adequately represent the shape of a structure. Elegant examples are given by Barnsley et al (6) and Barnsley & Sloan (7). They show that the entire form of a Black Spleenwort fern frond, for example, can be expressed by very few parameters (many of which are zero), using an algorithm based on fractals. Another goal

is to obtain variables, e.g. coordinates, that can easily be decoded and transformed into other kinds of variables for alternative morphometric analyses. One can also use a video framegrabber and just save entire images. With microcomputer-based image analysis systems and large hard disks, this is quite feasible (see MacLeod, 72, for a general discussion and Fink, 42, for practical issues and lists of vendors). But this is not always the best solution since image files are large and often require interpretation. One would thus have to deal with each image twice—once while digitizing and then again when locating landmarks or other features. Alternatively, the coordinates of selected landmarks and the outlines of structures of interest can be directly recorded. Outlines can also be stored compactly as chain codes and easily converted back to a list of coordinates when needed. Simple coordinate digitizers are very effective for recording landmarks and simple outlines. Sophisticated software is not needed since the human operator makes all of the important decisions about what to measure. Video-based systems have the advantage that image enhancement algorithms can be applied to the raw image to make the features of interest easier to see. There is also the possibility of use of automatic and semi-automatic techniques to assist in the isolation of structures of interest. A disadvantage of standard video-based systems for morphometric work is their relatively low resolution (usually about 500×500 in comparison to about $2,000 \times 2,000$ for even inexpensive digitizers). Desktop scanners are also high resolution devices, but they are relatively slow and do not seem to have been used yet for image acquisition in morphometrics.

The general literature on image processing and analysis techniques is very large and cannot be reviewed adequately here. There are, however, a number of general texts (e.g. 5, 54, 84, 98) and overviews oriented toward systematics (42, 72, 92, 96).

FEATURE EXTRACTION

This step is concerned with the selection of morphometric variables for analysis. The variables that are most convenient for archiving an image are not necessarily those that are the most appropriate for morphometric analysis. Different kinds of analyses also require different kinds of variables. The problem of selection of sets of variables is nontrivial, because different, but seemingly equally reasonable, sets of variables can yield very different results. The variables that one selects define a feature space—a multivariate space with the variables as axes and the specimens as points in this space. If one's purpose is to distinguish automatically between two populations, then what matters most is that the clouds of points representing the two populations overlap as little as possible. It matters very little whether or not the variables

make sense. But in most other applications one wants distance between points in the feature space to be a reasonable measure, however defined, of morphological difference between specimens. The selection of different ways to represent a configuration of landmarks or an outline corresponds to different transformations within this space. While some alternative selections correspond to orthogonal linear transformations, which leave distances between points invariant, most alternatives correspond to oblique affine or to nonlinear transformations which can give radically different distances between the points. This is especially true in taxonomic applications. It is clear that the particular selection of variables used in a study needs to be justified.

One strategy is to select variables that describe the expected pattern of shape variation in a simple "natural" manner (for example, related in some simple way to the function or to the development of the structure). If one is interested in variation in the degree of elongation of a particular part of a structure, then it would be convenient to have a variable that directly measures such elongations. On the other hand, if one expects a structure to vary in the degree to which it is bent, then other variables would be more appropriate. In some studies one knows enough about how a structure develops (either ontogenetically or phylogenetically) that particular variables seem appropriate. A classic example is Raup's (86, 87) study of shell growth in molluscs. He developed an intuitively simple spiral model in which the shell aperture revolves around the coiling axis and expands at a rate W and translates along the axis at a rate T . On the other hand, Ackerly (1) finds these shell parameters to have no obvious biological significance. He then develops an alternative—a growth function that specifies the magnitude of the growth vector at any given point on the margin and the rate of divergence of adjacent growth vectors. Points of growth maxima and minima are located along the margin and used as "programmable" landmarks. Though mathematical constructs, he argues they are biologically relevant because they reflect cellular processes of mantle secretion. Thus such considerations need not lead to a unique set of variables since alternative models can usually be developed. The simplest strategy may be just to use a suite of descriptive variables that efficiently spans the universe of possible shape variation. Some examples are given below for landmark and outline data. Other types of data, such as surface texture and pattern, are more difficult to quantify and have not been used as much as morphometric studies.

Landmark Data

Analyses of landmark data are usually based either on distances between selected pairs of landmarks or on the coordinates of the landmarks. Strauss & Bookstein (108) discuss the advantages of using distances in the pattern of a graph called a *truss*. They showed that discrimination between populations was improved by the use of measurements representing distances along a truss

rather than in the pattern of conventional measurements used in previous studies. A number of papers have discussed the issue of whether or not the linear measurements should be used as is, log-transformed, or converted to ratios in order to correct for the effects of having specimens of different sizes (see below).

When coordinates are used as variables, the coordinates in the archive often have to be transformed because their initial origin and orientation may be with respect to the measuring device (e.g. the axes of digitizing tablet). Brower & Veinus (29) aligned their axes with respect to landmarks and then used the logarithms of the absolute values of the coordinates of the landmarks as variables. It is also possible to use constructed points such as the geometric centroid for alignment of the axes (but this is more common in studies of outline data). Other coordinate systems can also be used.

Bookstein (18–20) uses features that are simple linear transformations of the original coordinates. Assuming configurations do not differ by a reflection, he first selects a pair of landmarks (*A* and *B*, perhaps the most distant) to serve as a baseline and then scales, translates, and rotates all specimens so that the coordinates of *A* are (0, 0) and those of *B* are (1, 0). Then the *x,y*-coordinates of the other landmarks are called “shape coordinates relative to the *A-B* baseline” and can be used as descriptors rather than the raw coordinates. They are an improvement over linear measurements since small changes in shape can be expressed as linear combinations of shape coordinates and standard multivariate linear statistical methods can be used to detect and test hypotheses about these differences between populations. The choice of baseline is arbitrary, but the effect of different choices is mainly to translate, rotate, and rescale. When differences are small, the results of most statistical tests should be unaffected by choice of baseline.

Bookstein (23–25) suggests a very different approach—the use of “principal warps” as features with which to describe configurations of landmarks relative to a reference configuration. He showed how configurations of points can be expressed as deformations of a reference configuration (a single specimen or an average). These deformations can be decomposed into a linear part (an affine transformation) and a nonlinear part (thin-plate splines of weighted sums of the principal warps). The principal warps are geometrically independent nonlinear functions of the reference configuration of landmarks. They are eigenvectors of what Bookstein (23) calls a “bending energy matrix.” The matrix is, however, based only on the reference configuration of landmarks and not on how the configuration must be “bent” to match a particular target configuration. Free of the effects of affine transformations, the warps correspond to the geometrically independent ways in which the reference configuration could be bent. The eigenvalues corresponding to each warp are inversely related to the scales of deformation. Large eigenvalues correspond to principal warps with small-scale bending, and small eigen-

values correspond to principal warps large-scale bending. Affine transformations correspond to global features and do not involve any bending. The weights necessary to produce a thin-plate spline fitting a target configuration can be used as variables to describe the target configuration separate from any affine (uniform) size or shape change. This scheme captures information on landmarks in a very elegant manner. Since the variables are based on a continuous transformation of the landmarks, it is possible to reconstruct configurations corresponding to hypothetical points—such as sample means, points two standard deviations from the mean along PCA axis 1, etc. as routinely done with outline data (e.g. 34, 93). Further study of the properties of this feature space is needed. One obvious inconvenience is its dependence upon a reference configuration.

Outline Data

Many studies are based on outlines when there are few clear landmarks in the structures of interest. Outlines are usually recorded as either a sequence of x, y -coordinates along an outline or, more compactly, as a sequence of chain codes. Chain codes are usually decoded back into coordinates, but White & Prentice (112) investigated the use of features based directly on chain codes to describe leaf outlines. Their descriptors performed poorly in discriminating between species in their study—possibly because the differences between the species did not correspond to fine details of the outline for which their chain code descriptors would be better suited.

A sequence of transformations is usually applied to the initial set of coordinates to align them or to express them in terms of special coordinate systems. The origin is placed at a landmark or, more commonly, at the centroid of the object (2). The axes are rotated to pass through a landmark or the greatest width (for example, using the principal axes of the image—41). Lohmann (70) rotated each object until it had a maximum covariance with a standard reference object. The sequence of points around the outline is also adjusted so that the first and last points correspond to homologous landmarks (the same point in the case of closed outlines). In most early studies outlines were transformed to polar coordinates relative either to a central morphological landmark or to the centroid of the object. Workers now usually use Zahn & Roskies' (116) method of expressing an outline as the slope of a tangent to the outline as a function of distance, t , around the outline (t scaled to range from 0 to 2π). The normalized form, $\phi^*(t)$, is used as a descriptor of the outline shape (e.g. 41, 93). In elliptic Fourier analysis (69), $\Delta x, \Delta y$ is expressed as a function of distance, t , around the outline (t scaled from 0 to 2α). Kincaid & Schneider (66) described a related approach.

In eigenshape analysis (see below), the tangent slopes describing the outline are used directly as variables, but a more common approach is to fit a

function to the outline and then use the parameters as variables. For example, in Fourier analysis a trigonometric function is fitted to an outline, and the Fourier coefficients are used as variables for subsequent multivariate analyses. Kaesler & Waters (63) is one of the earliest examples. Since that time, many studies have been performed using this approach. The harmonics represent an elegant, although arbitrary, decomposition of a shape into a series of orthogonal components—analogue to the decomposition of a non-linear curve into linear, quadratic, cubic, etc components. It is doubtful that the individual harmonics themselves will have useful biological interpretations (27; but see also 38). However, since they capture the form, the coefficients may be highly correlated with variation in whatever parameters influence the shape of an organism. When there are no landmarks and the outlines cannot be aligned, information on phase angle is lost (115). When the outline is more complex, alternative methods have to be used. One choice is to use Fourier analyses of Zahn & Roskies' (116) ϕ^* function. An alternative is elliptic Fourier analysis (69) of the x, y -coordinates themselves. Other types of functions can be used in a similar way. For example, Evans et al (40) described the use of cubic splines and Engel (39), the use of Bezier curves. Rohlf (91) reviews these approaches.

Another approach is to model an outline as a probability density surface by defining the height of the surface to be a positive constant within the outline of the object and zero everywhere else. Bivariate moments can then be used as descriptors of this surface. Hu (55) and others have formulated functions called moment invariants that have the desirable property of being invariant with respect to rotation, translation, and reflection of the image. Rohlf (92) reviews the various formulations that have been proposed. But F. J. Rohlf & S. Ferson (unpublished) found their computation to be very sensitive to rounding error (denominators of some coefficients can go to zero). They also found that there were strong nonlinear relationships among some of the descriptors (different invariants were in part functions of the same moments) and that this greatly influenced the apparent relationships among the objects. White & Prentice (112) did not find this a problem in using moment invariants to discriminate between species.

Median axis transformations reduce the interiors of a structure to stick-figures or "skeletons." One definition of a skeleton is the locus of centers of circles that touch the object's edge at more than one place (12). Another is the result of thinning an object until the structure is only 1 pixel wide (84). For thin objects, skeletons often have a structure that seems biologically appropriate. For example, branch points tend to behave as landmarks (16). Applications to shape description are given by (12, 13, 16, 26, 107). An important problem is the sensitivity of the medial axis transformation to small changes in the outline. For instance, a small bump or indentation can cause drastic changes in the form of the skeleton. Different definitions of a skeleton

give somewhat different results, but it is not clear which definition is most reasonable biologically.

There are many additional ways to describe outlines. How does one know which one to use, and does it make a difference? Rohlf (90) points out that the Fourier coefficients represent an orthogonal linear transformation of the data on which they are based. Thus the multivariate analyses of distances will be identical whether based on Fourier coefficients or the original variable—which may make the use of Fourier descriptors seem somewhat pointless. But usually just the lower-order harmonics are used. This has the effect both of reducing the number of descriptors one has to deal with and of smoothing the outline (which may reduce the effects of digitization error). An important advantage of fitting a function to an outline is that one can interpolate in the feature space and invert the function so that one can visualize the shapes of hypothetical objects. A problem with the fitting of functions is that the coefficients from different functions may imply different relationships among the objects, and hence subsequent multivariate analyses may give different results. For example, Rohlf (91) shows that while Fourier, cubic spline, and Bezier curve coefficients are linearly related, the transformations among them are not orthogonal. Thus, the pattern of proximity of points in the different features spaces is not the same, and multivariate analyses based on distances between points (e.g. cluster analyses and ordination analyses) need not give the same results. This is unfortunate since it means that an arbitrary choice among methods that are mathematically equivalent—in the sense that one can transform from one representation to another without error—can have a serious effect upon one's results. On the other hand, multivariate analyses relative to a within-group variance-covariance matrix (e.g. generalized distances) are invariant under linear transformations and thus will yield statistically identical results among alternative set of variables that differ only by affine transformations.

MORPHOMETRIC ANALYSES

How should morphometric data be analyzed? There are several strategies. One is to use conventional multivariate statistical methods to analyze sets of morphometric variables. If the various assumptions can be met, this approach provides a means to perform statistical tests. Another approach is to use special methods that explicitly take into account the fact that one has landmarks in a two- or three-dimensional physical space. These are described in the subsections that follow. Present methods do not integrate information on both landmarks and outlines very well. When landmark methods are used, outlines serve only as visual references. Another problem is that morphometric methods are unable to deal with missing data or else deal with missing information in a rather arbitrary manner.

Multivariate Statistical Methods

The measurement of many variables naturally leads to the use of multivariate analysis (although there has been some controversy—35, 113, 114). If one has adequate sample sizes, multivariate analyses allow one to make overall tests as well as proper a posteriori tests of sets of variables that look interesting. The reader is referred to reviews (52, 58, 80) and to useful texts such as (53, 59, 68, 85, 88) since there is not space here to review the general application of multivariate statistics in morphometrics.

Coefficients of functions fitted to outlines (e.g. Fourier, cubic spline, and Bezier coefficients) have often been used as variables in multivariate analyses. Lohmann (70) suggested the use of “empirical shape functions” rather than the use of coefficients of a priori defined functions. His eigenshape analysis is a singular-value decomposition (37, 45) of matrix, \mathbf{A} , of ϕ^* -values with p rows corresponding to p equal-length steps around the outline and with n columns corresponding to specimens. The matrix is expressed as the product $\mathbf{U} \mathbf{\Lambda} \mathbf{V}^t$, where the columns of \mathbf{U} are the shape functions, $\mathbf{\Lambda}$ is a diagonal matrix of eigenvalues, and the columns of \mathbf{V} give the relative contributions of the shape functions to the outline of each specimen. Linear combinations of columns of \mathbf{U} (perhaps defined by the results of a multivariate analysis) can be interpreted as ϕ^* -values for a hypothetical outline. Plots of these outlines are very useful as they allow one to visualize means of clusters, extremes of principal component axes, etc. Examples are given by Lohmann (70) and Lohmann & Malmgren (71), but see Full & Ehrlich (43) for critical comments. The idea of eigenshape analysis can be readily generalized to the singular-value decomposition of any data matrix rather than of a matrix of coefficients of a function fitted to the data. If the coefficients correspond to an orthogonal linear transformation of the coordinates, then the results will be statistically equivalent and the choice will depend upon computational convenience (90). If not, then a decision must be made as to which metric gives the “correct” results.

This approach can now be applied to landmark data by using principal warps. A configuration of landmarks can be described as a deformation from a reference configuration by the use of a thin-plate spline based on a weighted linear combination of the principal warps of the reference configuration. The weights can be used as variables in a multivariate analysis. The configuration corresponding to the average of these weights in a sample can then be visualized as a thin-plate spline. In a similar manner one can visualize the configurations corresponding to the results of other statistical computations made on the weights.

The results of canonical variates analysis, one of the most used methods in morphometrics, are often misinterpreted. Plots of canonical variate scores, $\mathbf{Y} = \mathbf{C}^t \mathbf{X}$, and canonical variate coefficients, \mathbf{C} , are usually superimposed so that one can see the variables on which groups differ. This is done in analogy

to a biplot (44). But \mathbf{Y} and \mathbf{C} do not represent a decomposition of the data matrix, \mathbf{X} , as required for a biplot. The matrices \mathbf{C} and \mathbf{X} are a decomposition of matrix \mathbf{Y} . One solution is to plot the columns of $\mathbf{C}(\mathbf{C}^T\mathbf{C})^{-1}$, the least-squares inverse of \mathbf{C} , rather than \mathbf{C} .

Conventional multivariate analysis cannot take into account the geometrical relationships among the variables (15, 83). While a multivariate analysis does take the correlations among the variables into account, it has no knowledge of the spatial pattern of the variables on the organism—whether the variables are linear measurements, raw coordinates, or coefficients of functions. Methods that can take this additional geometrical information into account should be more powerful and allow one to see more subtle relationships in the data.

Geometrical Methods

How should morphometric data be analyzed so as to take into account geometrical relationships among the variables? Several methods have been developed, and all emphasize graphical displays in terms of the original objects, synthesized hypothetical specimens, or deformations of objects—instead of simple tables of numerical results. If no true landmarks are present, then all one can do is analyze size and what might be called “pure shape.” That is, one can determine only whether the outline is circular, oval, triangular, etc without any knowledge of its orientation. If a single landmark exists (e.g. a starting point on an outline), then outlines of different objects can be synchronized. This permits, for example, multivariate analyses based on the ϕ^* function. With two landmarks it is possible to align two outlines in a nonarbitrary manner or to study open curves. More landmarks are needed to understand in a more detailed way just how the components of an outline change.

One method is to superimpose one specimen's configuration of landmarks onto another's, rotating and scaling to fit, and then studying the differences in the positions of the landmarks. One can then see (by the lack of fit) how the relative positions of landmarks differ. The numerical technique of Hurley & Cattell (57) was first applied in morphometrics by Sneath (104). In this method one configuration of landmarks is used as a reference, and a second is scaled, translated, and rotated until the sum of the squared differences in the positions of homologous landmarks (called a Procrustes distance coefficient) is as small as possible. This is a least-squares fitting procedure. Gower (50) provided an explicit solution to this problem. This general approach has been extended in several ways. Gower (51) developed a generalized Procrustes algorithm to fit any number of configurations to a consensus configuration. Siegel & Benson (101) made the important observation that a least-squares fit usually results in a general lack of fit at most landmarks—even if the configurations are identical except for the position of a few of the landmarks. This makes the differences between two configurations seem more complex

than is necessary. They proposed a nonparametric approach that they call *resistant-fit theta rho analysis*, based on robust regression techniques (99, 100). It works very well when the two organisms differ in the positions of only a few of the landmarks. Tobler (111), Goodall (46), and Bookstein & Sampson (28) present other least-squares methods with slightly different assumptions. These methods have been used in a number of studies (8–11, 32, 82, 102). Olshan et al (82) used least-squares and resistant-fit methods to compare coordinates of points distributed along a pair of outlines. Rohlf & Slice (97) extend the resistant-fit method so that any number of configurations can be superimposed. Goodall & Green (48), in their study of cell growth, suggested using affine transformations to allow for differences in uniform shape change (a stretching in orthogonal directions—28) rather than global size differences. Rohlf & Slice (97) refer to this as an oblique rather than an orthogonal rotational fit. They also extend the resistant-fit and the generalized least-squares methods to include affine transformations.

Another method for studying the relationships among more than two specimens is to use the Procrustes distance between pairs of configurations as a measure of their difference. A matrix of such distances can then be clustered or an ordination performed using principal coordinates (49) or nonmetric multidimensional scaling (67) analyses. This approach seems reasonable if the differences are like digitization error in that there are independent homogeneous small differences at all landmarks (47). However, this approach has several limitations. (a) The Procrustes distance coefficient defines a very complex metric (64, 65). (b) By analyzing only distance coefficients one considers only the magnitude of the differences and not the details of the ways in which organisms differ, which are often of most interest in a morphometric study. (c) The distance coefficient based on orthogonal rotations combines differences in shape due both to uniform shape changes and deformations. Bookstein (23, 25) shows that the metrics for uniform and nonuniform shape differences are incommensurate and that there is no good way to combine these into a single nonarbitrary metric.

Rather than modeling uniform shape change by simple affine transformations, and then examining the residuals to discover evidence for local and nonuniform changes, one can fit a more complex model that includes nonuniform shape change. There are two main approaches: (a) Fitting a continuous function that expresses one specimen as a deformation of another, and (b) breaking structure into a number of small regions and computing the size and shape-change parameters for each. A classic example of the former is the transformation grid of Thompson (110), and finite element analysis is an example of the latter. These approaches seem particularly appropriate when one has samples along a developmental or phylogenetic sequence.

In a finite element analysis the organism is divided into many small regions (usually triangles in two dimensions or tetrahedrons in three dimensions)

based on lines or planes connecting homologous landmarks. For a given set of landmarks there will be many alternative ways in which regions can be defined. The regions should be small and compact, and the tissue they represent should be as homogeneous as possible. The differences between two organisms are analyzed by comparing each cell on a reference organism with the corresponding cell on another. For each cell one can compute descriptors such as the ratio of areas (or volumes), the principal axes of the deformation of one cell into another (the arms of a strain cross), the principal dilatations (lengths of the axes), and measures of anisotropy (ratio of the principal dilatations). Goodall & Green (48) give a good description of strain cross parameters and their estimation. These results are conveniently shown on a drawing of one of the organisms with strain crosses centered in each cell. An early example is given by Niklas (81). Discussion of this approach is given by (e.g. 17, 18, 20, 21, 33, 47, 77–79, 89, 103).

Sneath (104) explored the use of trend-surface analysis to give plots analogous to transformation grids. He computed contours of polynomial surfaces fitted to the x and y residuals from a Procrustes analysis. Bookstein's (14, 15) biorthogonal grid is a direct quantitative implementation of Thompson's idea. He modeled a continuous deformation of a homogeneous elastic membrane stretched across the configuration and constrained at the landmarks. But this elegant approach has been little used. The complexity of the numerical methods inhibited the development of portable software. The use of thin-plate splines as an alternative model has been proposed recently (23, 25). In this model, nonuniform shape change is a deformation like that a thin metal plate would have if the landmarks were forced into new positions corresponding to a second configuration. Since the spline is continuous, a transformation grid can be obtained by transforming a rectangular grid and plotting it. In analogy with the physical deformation of a thin metal sheet, the bending energy can be computed for a given deformation (but any energy needed to shear the sheet appropriately is not included). Bending energy is not directly useful as a measure of distance between configurations because small changes in landmarks close together can require more bending energy than do what look like much larger changes in landmarks far apart. There is also the complication that the energy needed to bend configuration 1 into 2 is usually different from that to bend 2 into 1.

SIZE

Size and size corrections continue to be topics of discussion. An understanding of the results of Mosimann (73), Mosimann & James (76), and Darroch & Mosimann (36) is essential for an understanding of the effects of size. Mosimann (73) considers a variable G to be a size variable if the effect of multiplying linear distances in the specimen by a constant α is to change the

value of G to αG . There are many ways such a size variable can be defined. The particular choice is important since the relationships between size and shape depend upon the size variable selected (76). No single size variable is necessarily the "correct" one to use for all organisms or for all types of analyses (22). It is often helpful to use more than one size variable in a single study to display different relationships of interest (e.g. 61, 62). But morphometric methods based on particular morphometric and statistical models should suggest which size variable or at least which class of size variables is most appropriate. Bookstein (22) gives five different definitions for size and a context within which each seems natural.

Darroch & Mosimann (36) investigate models with lognormally distributed variables. For such models, dividing by a generalized geometric mean (which is equivalent to a weighted mean of log-transformed data) yields shape variables. They show that the results of canonical variates and principal component analyses of these log-transformed shape variables do not depend on the particular generalized geometric mean used—thus the usual geometric mean can be used. Mosimann (75) and Campbell & Mosimann (31) investigated Dirichlet models in which the variables are proportions and the sum of the measurements for each specimen is the measure of size. Somers (105, 106) calls such a measure "isometric size." Mosimann & James (76) point out that since shape can be independent of at most one size variable, discussion of "isometry" must be relative to a specified size variable.

In many studies the interest in using shape variables is in the practical problem of removing the effects of size from a dataset so that one may compare samples from different populations that may have different age (and hence size) distributions. Mosimann (73, 74) shows that shape can be independent of at most one size variable. Thus, the method of constructing shape variables and the definition of size must go together in order for there to be a proper correction. Most studies, however, seem to treat these independently. The traditional use of ratios is often criticized (e.g. 3, 4). Another method is to use residuals from regressions of each variable onto a particular variable (such as total length or weight). Humphries et al (56) and Bookstein et al (26) suggest a method of "shearing" to adjust for the effects of size based on a model with size estimated as a factor. Rohlf & Bookstein (94) review this approach and suggest the use of Burnaby's (30) method if the purpose is size correction alone, instead of the estimation of a factor model. This method corresponds to the projection of the data onto a space orthogonal to a size vector. This directly ensures that the resulting variables are orthogonal to whatever variable is used to define size. The first principal component axis is often used as a size vector (60). Its use assumes that the major source of variation in the sample is size and not outliers, polymorphisms, or inadvertent mixing of different species. Somers (105, 106) suggests the use of the isometric size vector $(1, \dots, 1)$ based on the assumption that all variables

(regardless of type) contribute equally to overall size (22). Unfortunately, there were problems with the Somers algorithm (94, 105, 109).

CONCLUSIONS

Many new tools have been developed during the past decade that greatly facilitate the capture of morphometric information and its transformation into appropriate features. New analytic techniques now also allow one to analyze shape variation and shape change, with the relationships between the features and the geometry of the organism taken into account. However, there are still many technical problems. For example, missing data are not handled very well, and comparing large numbers of diverse organisms is often awkward. Landmark and outline-based techniques are not integrated very well at present. There has also not been much work on understanding the implications of using alternative, but equally reasonable, sets of landmarks and descriptive features. While the use of alternative kinds of features and methods of analysis usually provides additional insights in morphometric studies, taxonomists would like to know which methods give the most reliable information about overall similarity and cladistic relationships. Relatively little progress has been made toward an answer to this question. Solutions to these questions cannot come from methodological studies alone. Theoretical work on the foundations of morphometrics, called for near the beginning of this last decade (17), must continue, because without theoretical work and models one has little basis for choosing among methods—no matter how ingenious they may be.

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