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*Annual Review of Ecology and Systematics*, Vol. 13. (1982), pp. 451-470.

Stable URL:
http://links.jstor.org/sici?sici=0066-4162%281982%2913%3C451%3AFOM%3E2.0.CO%3B2-0

*Annual Review of Ecology and Systematics* is currently published by Annual Reviews.

*Ann. Rev. Ecol. Syst. 1982. 13:451–70*


# FOUNDATIONS OF MORPHOMETRICS

*Fred L. Bookstein*

The University of Michigan, Ann Arbor, Michigan 48109

## *Introduction*

Whether broadly (58, 60) or narrowly (10, 11, 14, 33, 34, 63) construed, morphometrics clearly has something to do with the assignment of quantities to biologic shapes. In most fields, the advent of quantification is followed a few years later by a systematization of the exploratory quantitative styles. At that time one encounters studies of the nature of information captured and discarded by the various conventions, general families of mathematical or statistical models mimicking relevant behaviors of the natural phenomena under study, and so forth: in short, the contemplation of *foundations.* In morphometrics this passage to introspection has not occurred. There is one classic in the field, D'Arcy Thompson's *On Growth and Form* (80), which argues that form should be modelled as the expression of physical laws. This stance, now badly dated, has not been replaced by any other consistent point of view. The only more recent paper I have encountered that speaks of a discipline for information captured in the course of morphometric investigation is Green's critique of methods for studying axial growth in plants (36). Otherwise, the morphometric literature is entirely application-oriented rather than methodological.

In this essay I attempt a preliminary remedy: a framework into which specific morphometric methods can be fitted (with more or less difficulty, as will become clear from my section headings). The rationale for that framework lies in a duality underlying comparisons among biologic forms.

## *Morphometrics as Biology and Geometry*

Morphometrics, in my view, is the empirical fusion of geometry with biology. Its methods must explicitly take cognizance of two wholly distinct sources of information—geometric *location* and biologic *homology.*



0066-4162/82/1120-0451$02.00

"Homology" is here construed as a smooth correspondence that transforms any two related forms one onto another in accord with appropriate ontogenetic or phylogenetic criteria. Morphometric quantifications arise from the interaction of these two sorts of information. Practitioners of morphometrics should be extracting information from the geometry of biologic shape for particular comparative purposes, such as the study of growth, abnormality, or taxonomic differences.

In this preliminary exploration I restrict the notion of "shape" to boundary information only, rather than extending it to measure textures and other spatial fields and densities. The boundaries of which I speak are to be simple closed curves (in the plane) or closed surfaces (in space) with analytically proper, piecewise-smooth insides and outsides. For instance, the notion of homology as a differentiable mapping cannot be easily extended to biologic fractals (50).

In the presence of a homology function, a set of biologic shapes can be measured in a great many ways. We might measure the finite distance between the homologs, in the general form, of any two points in any particular form. Should we wish the segments to begin and end on the boundary, there is a two-fold infinity of transects we might choose from. We may further consider arbitrary ratios of these quantities, integrals, and so forth. From this range of possibilities the morphometrician's task is to construct measures optimal for particular explanatory purposes—trends, contrasts, comparisons. In this role its purpose is distinct from that of multivariate statistics, which from a vector space of variables tries to construct the most useful linear combination. The space over which morphometric methods search is geometric, not algebraic; their purpose should be to generate a scheme of best simple measurements, not a single best composite. The exercise of morphometrics, then, lies squarely in-between "digitization" (acquisition of purely geometric information) and familiar statistical manipulations upon measured variables; it represents a specialized task, the optimizing of variables that will be measured. For instance, the biorthogonal method (14, 19) extracts a one-parameter family of finite distances that best capture the contrast of a pair of forms. From these, single proportions that discriminate well can be selected by inspection. In an analysis of multiple populations, various geometric regions into which the form can be fragmented may give rise to their own excellent discriminators; once the geometric investigation has been completed, the multivariate statistics may then distill these into a single optimal score.

In this context of the interplay between geometric location and biologic homology, consider Thompson's method of Cartesian transformation (14, 80), the fundamental construct of morphometrics. In this strategy one mathematical object, a deformation, is used to represent explicitly the rela-

tion of a pair of forms. Although we may view these objects in pairs of sketches each displaying one form, in essence the method relates two coordinate systems upon the same figure (in the classic example, upon the deep-bodied fish, *Mola*). One of the coordinate systems is the ordinary Cartesian one on that form—it is not ordinarily drawn, of course; the other, which *is* drawn, is the coordinate system for homologous points in the comparison form. By this device the essentially biologic information, about homology, is communicated most efficiently.

In another version of this same interplay, a sample of the homology function upon a form may be taken in a special way, by a collection of named landmarks, as in cephalometrics. Not all "landmarks" are in fact homologous according to biologic criteria, however; for a discussion, see Moyers & Bookstein (55) or chapter iii of Bookstein (14). Only the biologic homology of two configurations makes meaningful their scientific description by collections of geometric points, distance measures, or coordinates. There are far more homologous measures on configurations than are used in typical multivariate morphometric data sets; success in selecting particular raw variables in the absence of protocols is a matter of luck.

## *Data*

A morphometric data set ought to consist of a set of forms, archived by an adequate number of strongly patterned distances, and a set of homology maps relating the forms in pairs. The forms may be archived by either Cartesian coordinates or distances among landmarks. The ordered format of the data as collected is a convenient device allowing the reconstitution of these maps, the transformations between forms, from the separate coordinates or distances.

DISCRETE SAMPLES If a form is to be modelled as a polygon of straight sides, it is most conveniently sampled at its vertices. These must of course be landmarks; their homology, *sensu* Jardine (42a), will then be implicit in the sequence of data entry. A polygon may be archived either by its Cartesian coordinates in an arbitrary or standardized system of axes or by a pattern of interpoint distances that comprises at least a determinate triangulation. A scheme of measured distances is inadequate if it does not permit the reconstruction of the polygon it purports to measure, since information is thereby lost permanently. Data sets of discrete landmarks in three dimensions are digitized either by their explicit Cartesian coordinates in a three-dimensional digitizing apparatus, or by photogrammetric synthesis of a pair of two-dimensional projections (8, 32, 67). For most morphometric investigations, no other quantities (e.g. angles or proportions) are of any use in the archive. As we do not yet know what quantifications will ultimately emerge

as variables for statistical analysis, there is no point in presuming their identities so early in a study.

CONTINUOUS SAMPLES In the discrete sample each point bears its full dimensional complement of degrees of freedom: for plane data, two; for spatial data, three. When boundaries are sampled continuously, each point carries only one degree of freedom, its distance normal to the line or surface through its neighbors, even though two or three coordinates must be used to record its position. In two dimensions the digitizing of continuous traces is fairly standardized: An underpaid clerical traces around an outline on an electronic digitizing tablet, sampling points at a spacing approximately inverse to curvature of the boundary. [See, for instance, the introduction to Riolo et al (65).] For three-dimensional data there is a much greater diversity of techniques conveniently assembled in two SPIE proceedings (4, 27). [I also encourage the reader to view Robert B. Livingston's magnificent movie *The Human Brain* (47).] For the typical points of a surface, recording schemes include serial sections, moiré projections, grid projections, stereopair photography, and others. A more recent technique is the automatic extraction of boundaries from solid computed tomography (5).

All these schemes archive points, with their one or two coordinates of redundancy. One may instead sample *lines* on forms in two dimensions (e.g. 15), or circles touching twice (12, 86). These geometric objects often quantify meaningful features of form much more directly. Other two-dimensional schemes are reviewed in Bookstein (14). For spatial data a similar variety is geometrically possible: one may represent forms, for instance, with spheres (6, 57). In general, the varieties of surface representation—planes, spheres, quadrics—depend on the number of derivatives coded for small regions (16). All these schemes would be more efficient than the record of Cartesian coordinates; as of this writing, none has been seriously tried.

COMPUTING HOMOLOGY In the discrete schemes, homology is embedded in the order of data entry. Otherwise it must be computed by one or another interpolation rule using the landmarks as points of calibration for some nonlinear function. For instance, homology can be extended along boundary arcs between landmarks linearly in arc-length; this one-dimensional homology, in turn, may be extended throughout the interior of a pair of related forms by relaxation according to the elastic equation (14a). Tobler (82) interpolates according to the same partial differential equation but starts with data in the form of a correspondence between two discrete meshes. Others have tried the simplest explicit nonlinearities of finite-element analysis of displacement (46), which correspond to no particular

constitutive equation. Yet another solution denies the problem by digitizing quasilandmarks, proportional divisions along otherwise landmark-free arcs, and ignoring all other points of the plane (85). In this same spirit of ignoring interiors some workers define a body axis, then make homology of boundary points either side of the axis to be linear with respect to the axial coordinate.

All these homology functions depend on extensive listings of data. Sneath (77) attempted instead to compute homologies by a single polynomial; but this scheme, in spite of the interest it has evoked, seems incapable of being brought into a biologic framework, since some homologies are fitted much more exactly than others. A recent statistically robust version (71) separates the form into two regions, in one of which homology is geometrically simpler.

A COMMENT ON COORDINATES Coordinate pairs or triples, the elements of the geometric record, are not the quantities we want to send on to statistical analysis: They are no good as variables. Under continuous sampling, of course, they are not aligned from form to form; but even in the discrete case they are not of themselves homologous quantities. A coordinate is a function on the form. The sets where it is constant are coordinate curves (in the plane) or surfaces (in space) linking points that are quite literally *co-ordinated* (20). Cartesian coordinates, for instance, are simply distances from point to line, or point to plane; but the lines and planes of reference, in their straightness, misrepresent homology of position inside the form. Usually one axis is chosen to link two landmarks and the other is taken perpendicular to the first through some third landmark. The former axis can be biologically meaningful only between the two landmarks delimiting it; the latter axis is generally not homologous at all from specimen to specimen (21). Other coordinate curves as interesting as the Cartesian flats—circles or spheres, confocal conics, bicircular quartics (20)—likewise have no a priori claim to be measuring anything biologically meaningful. One would do better to invoke coordinates fitted from features of the form itself. For instance, Hansell et al (37) fitted a standardized coordinate system to describe the position of mite setae in a consistent scheme. [For another example, see (69).] As a sample of distances, Cartesian coordinates have the severe additional flaw of representing displacements in only two (or three) directions, whereas the general morphometric measurement scheme requires an even sampling of directions.

This is not to say that coordinates are not worth archiving. Where points can be followed homologously the various models of continuous deformation all proceed by taking derivatives coordinate by coordinate; in the Cartesian scheme the formulas for this manipulation are by far the simplest. For the testing of some hypotheses the statistical assessment of reduced sets

of coordinates is sufficient. For instance, Holloway (40) computes mean spherical coordinates of the points of a brain endocase placed in standardized relation to the coordinate system. Using these he shows that the lunate sulcus of the Taung specimen is not particularly intermediate in one ostensible phylogenetic sequence. Surfaces can be represented on a plane by use of certain standard cartographic tricks as well (7). Corruccini (29) executes multivariate discriminations via Cartesian coordinates in three dimensions (and by their log-transforms and shifted log-transforms), then discovers these to discriminate about as well as other systems of arbitrary distance analyses. Brower and his colleagues (23–25) model series of forms by predicting the exact values of coordinates from their own factor loadings. Yet in the typical "advanced" application the arbitrariness of the Cartesian framework is compounded. For instance, Luder (48) computes group mean differences in growth by vector subtraction in three Cartesian systems overlapping on the craniofacial form. The origin of each is interpreted to have been translated in the system of another.

GEOMETRY WITHOUT HOMOLOGY One can measure forms that bear only two landmarks, or one, or none. The methods of orthogonal decomposition, such as Fourier analysis, treat form as a function of some uniform abstract parameter, such as azimuth out of a point, or, for basically linear forms, aliquots along an axis. Relations between forms must then be modelled as differences in the value of functions evaluated at the same parameter, so that "change" must be along lines of unchanging parameter; the biologic geometry of transformation is thereby wholly lost (22). One version (83) of the craniofacial "growth profile," for instance, is essentially the first term of a difference of Fourier series, subject to this limitation and others as well (18).

Moss and his colleagues (53) have proposed a protocol for optimal polar coordinates. They would locate an "allometric center" with respect to which divergence of growth homology from radial displacement, properly weighted, was a minimum. In that it would inspect the information that all other versions of this tactic have discarded, the method is enlightened. In fact the model fails (54): No such center seems to exist. The linear equivalent of this is superposition along a curving medial axis (19, 86).

Many workers have considered the direct reduction to parameters of outline forms or arcs by functions from simple families. Sampson (68), for instance, used two landmarks (the centers of the first molars) to delimit the maxillary dental arch, then modelled the sequence of observed tooth centers between by a single arc, a best-fitting conic section bearing three degrees of freedom. There is an elegant geometry to the statistics of these arcs. For

instance, the confidence region for an arc of highest probability (equivalent to a "mean") can be drawn directly around that mean. Sampson does not ascertain the extent to which subsequent statistical analysis might depend on the pair of teeth picked to anchor the arc, nor does he estimate the information from the coordinate base that is discarded by the three parameters of the arc—for instance, the relative spacing of teeth along the arch. Most other procedures fitting parametric forms to scatters must be questioned in the same way. For instance, Schudy (70) models the outline of a beating heart by a linear combination of low-order spherical harmonics; but it is not known whether the information discarded in the fitting, phase by phase, is important in the analysis of the cardiac cycle. See also Geiser et al (35) and Kovatz (45) for the intuitive treatment of complex forms using only a few coordinates.

These imprecise representations of geometry are most often used for estimates of volume or area. See Cook & Cook (28) and Pierce et al (62) and many of the papers in Heintzen & Bursch (38). The American school of biostereometrics under Herron (e.g. 39) likewise concentrates upon these integral measures, for which the notion of homology enters only weakly: The volume of the legs must be measured homologously, of the trunk, upper limbs, etc.

HOMOLOGY WITHOUT GEOMETRY In another style of incomplete morphometrics the form is mostly lost but its contrasts are nevertheless closely followed. Alberch et al (2), for instance, represent size and shape variables by the Greek letters $\sigma$ and $\Sigma$ but otherwise do not define them. The resulting analysis is basically a model of ontogenetic and phylogenetic time; it tends to be applied to real data only in a univariate or bivariate context (1).

In other cases, the "form" is an assemblage of independent organisms that can be followed by computerized image analysis. See, for instance Potel & MacKay (64) on slime mold aggregation, or Katz et al (44) on measures of fish schooling behavior.

Many shapes change reversibly by rigid motion between articulated parts, as at joints. Measurement of this change involves only the usual screw analysis of classical mechanics; one need not measure forms at all. A goodly portion of the biomechanical literature is presented in terms of these purely kinematic parameters; for a critical review, see Soudan & Audekercke (78). Lupkiewicz et al (49) measure dysfunction of the temporomandibular joint by variance in the screw parameters over time. For most problems in evolutionary and developmental biology, however, the assumption of rigid motion cannot be sustained. Rune et al (66) conclude that descriptions of

craniofacial growth based on observations of metallic implants in the maxillae are simply inconsistent with descriptions from the positions of landmarks. Attempts (e.g. 42) to refer to "kinematics of growth" as rotation are flawed in that the model does not allow for linear extension between landmarks over time.

## *The Tensor Method*

Recall my characterization of morphometrics as the extraction of information from the interplay between geometric coordinates and biologic homology. In my view, successful morphometric analyses are all variants of a single approach, the modeling of form-change as *deformation.* I have discussed the historical development of this approach elsewhere (13–14).

There are two systems of notation for arriving at the proper formalization, differing only in the stage at which one chooses to differentiate coordinates. In one approach, points are considered to be simultaneously undergoing displacements in a single coordinate system: They have "velocities"; the model is borrowed from compressible fluid flow. I do not review this formulation here, but instead refer the reader to several good sources (30, 31, 72–74). In the remainder of this section I present another explanation of the method, in terms of material derivatives. These, in effect, analyze change at any point in a coordinate system registered precisely *there,* so that nothing has any velocity but nevertheless all pairs of points move apart.

The method grows out of my earlier technique of *biorthogonal analysis,* a quantification of D'Arcy Thompson's old method of Cartesian transformation. It was Thompson who realized that shape change was not to be measured by numerical differences among measures of shapes separately. Rather, shape change is a geometric object in its own right, the deformation taking one form into the other in accord with biologic homology. Thompson suggested this object be depicted by its effect on a grid laid over one form; he always began with a Cartesian (square) grid. The figures produced in this style are endlessly intriguing but do not directly lead to any effective quantification or feature extraction.

The fundamental problem of Thompson's original method is the selection of that starting grid, which leads to an asymmetry: A grid strictly square over one form is transformed into a curvilinear grid having in general no mathematical regularities. I suggested drawing instead a grid that has the same geometric properties in both forms: the grid along the pairs of directions that begin and end at 90° to each other. One of these directions manifests the least *dilatation* (specific rate of change of length between forms) and the other the greatest, of all directions, locus by homologous locus (14).

In its original form this technique applies to forms only in pairs. It executes its geometric computations in full spatial detail, but it is unable to aggregate over sets of starting forms, even though the distinctions among them are irrelevant to the description of their transformations. It was the specific aim of the present method to lift this limitation, at the lowest cost in lost information, so that a representative average transformation could be computed over diverse populations undergoing similar shape changes. The average will approximately preserve the optimal properties of the original biorthogonal formalism—one direction of maximum rate of change, one of minimum, symmetrically placed (at 90°) and varying over the forms.

The order of computations will vary depending on the style of comparison under investigation. For a study comparing shape changes longitudinally observed in multiple groups, the method has five steps, as follows.

1. Each outline is simplified into a configuration of anatomical landmarks. We consider the landmarks in triples as vertices of many overlapping triangles. These are not biologic entities (except for their vertices) but planar abstractions. Their edges may pass through various tissues and through air.

2. Case by case and triangle by triangle, we deform the whole area of one triangle onto the other, Figure 1. For triangles, these maps may be taken as homogeneous or uniform, and take circles to ellipses the radii of which, Figure 2, are proportional to dilatations in each direction. The ellipses have a longest and a shortest radius—the principal directions, Figure 3, directions of greatest or least percent change in the course of the deformation. These lie at 90° both before and after deformation.

The analysis separates the observed change into one component for size change and a second for shape change. The product of the dilatations is the ratio by which the area of the triangle has increased; their quotient is a measure of the *anisotropy,* or directionality, of this size change. One may think of any distortion as the composition of a pure size change, altering nothing but scale, and a pure shape change, leaving area alone. Note that

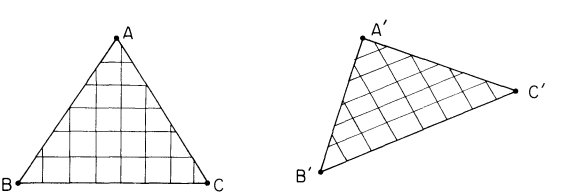


*Figure 1* In the tensor approach, we model the relation between two homologous triangles as a uniform deformation linking their interiors.

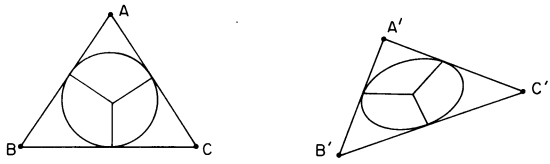


*Figure 2* Uniform deformations take circles to ellipses expressing *dilatations,* dimensionless rates of change of length direction by direction.

even though form cannot be decomposed as "shape plus size," form change can be so decomposed, triangle by homologous triangle.

One arm of the cross is along the direction of largest dilatation, the other along the direction of smallest dilatation. These ratios are taken between images for distances along homologous segments. We can instead compute *proportions,* ratios within a single form. Change in proportion may be measured as the quotient of the dilatations in the two directions that the proportion is comparing. Then of all proportions within the triangle, that of distance along the major axis to distance along the minor axis increases fastest over the change. We thus arrive at a simple optimal shape discriminator. Proportions between pairs of directions placed symmetrically with respect to the principal axes are invariant across the deformation. When a principal axis makes an angle of 45° with the bisector of a vertex angle of the triangle, the angle measured at that vertex is approximately constant.

Lines drawn in the principal directions through any vertex intersect the edge opposite in points directly toward or away from which that vertex is being displaced. In any deformation of one triangle into another, after adjusting for general change of scale, one vertex may be viewed as moving toward a point between the other two, and one away.

The appropriate polarity for description of shape change is not horizontal/vertical, the language of coordinates, but rather stretch/shrink, the language of tensors. Changes in the relation of point to line segment are expressed not by a vector of displacement but by a tensor of deformation:

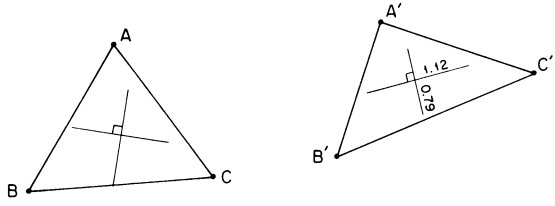


*Figure 3* The *biorthogonal analysis* of a transformation is the pair of crosses of directions, one in each form, which are at 90° both before and after transformation. These are the axes of the ellipse in Figure 2 and their preimages in the circle. They bear the extremes of dilatation.

two rates of change in two orthogonal directions. This descriptor resembles not at all a simple contrast of coordinates or interlandmark distances taken from the archives of forms separately.

3. Triangle by triangle, we average dilatations in directions connecting any vertex to a point dividing the opposite edge in a fixed fraction. For instance, an average dilatation is computed separately for each of the three edges of each triangle of landmarks; for each of the three median lines, which divide the sides opposite in the ratio 50:50; and so on. This accords with the homology function induced by the uniform transformation of Figure 1 for deformations between triangles of a series.

4. Triangle by triangle, we determine and depict for each group the greatest and least mean dilatations over all directions within the triangle. These may be taken as the appropriate mean biorthogonal analysis. Like any other means, they have standard errors of sampling, and also some selection bias.

If all the crosses for all the shape changes of a population are aligned in the same directions (as determined by our homology convention), the maximum of the mean dilatations would be the mean of the separate maxima, and likewise the minimum. The anisotropy of the mean change would then be just the mean of the anisotropies of the separate changes being averaged. If the directions of extreme dilatation for the individual deformations wander far from mutual alignment, then the averages will mix extremal dilatations along principal directions of certain shape changes with middling dilatations along others, attenuating the extrema of those averages. The ratio of anisotropy of the means to mean anisotropy is a useful statistic, a sort of fraction of variance explained by shape change.

5. Group by group in pairs, for any triangle we determine and depict as well the algebraically greatest and least *differences* in dilatation. These lie in the directions along which distance change in one group most exceeds, or most falls short of, growth in the other group. These last derived data, dilatations along the (homologously defined) directions of algebraically greatest and least difference in dilatation between the groups, constitute the quantification of group differences in deformation.

The analysis proposed here for a single pair of triangles is fully equivalent to the simplest case of the *finite-element* description familiar in other branches of biomechanics (74). That literature, however, seems nowhere to have considered the problem of averaging over whole populations that are continuously changing their shapes. Alternative procedures can be imagined that average shapes rather than shape changes or that map all deformations upon a "standard." In such approaches the computed mean, although arbitrary in certain crucial particulars, will be an exactly linear map with principal strains at exactly 90°. But this does not extend to comparisons between groups.

AN EXAMPLE Figure 4 displays two adjacent triangles describing the history of two groups of human children undergoing orthodontic treatment [see (21), Sec. V]. Each child was radiographed at two ages separated by about two years and the changes averaged according to the procedure just reviewed. The landmarks are the points Sella, Anterior Nasal Spine, Menton, and Nasion of the lateral cephalogram; the data were in the form of coordinates digitized carefully as described by Baumrind & Miller (9). The two groups are a Control group and one subjected to cervical traction (i.e. orthodontic headgear) in an effort to lessen overbite.

Consider first the lower triangle, S-M-A. The panel at the upper left, above the one naming the vertices, presents the mean annualized Control history. The empirical maximal dilatation, printed as "2.08," represents a mean increase in length of 2.08%/yr in the direction from Menton to a point .3 of the way from Sella to ANS; the observed minimum represents a mean increase of .71%/yr in the direction from ANS to a point .45 of the way from Menton to Sella.

Passing to the right along the top row, still looking at the triangle S-M-A, we discover principal axes for the treatment group that are nearly perfectly aligned (to the .05 fractional spacing the computation relies on) with those we just noted for the Controls. The dilatations in these directions are, however, altered.

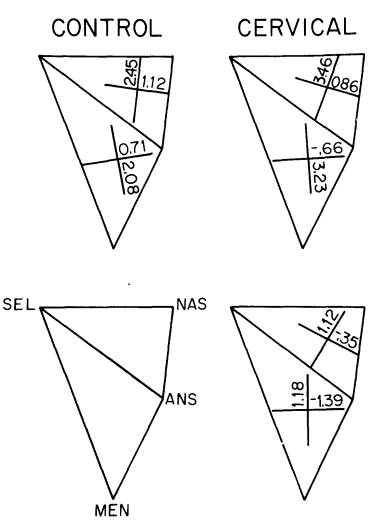


*Figure 4* Mean annualized observed deformation over about 24 months in two triangles of cephalometric landmarks for two populations of children, one undergoing orthodontic treatment. Analysis from (21); data courtesy of S. Baumrind (9). In the top row are principal axes of mean change; at lower right is the relative tensor, the "treatment effect" optimally contrasting the mean deformations between the groups. Dilatations are reported in units of percent increase per year.

The "relative dilatations," the algebraic differences of treatment and Control dilatations, are presented in the bottom row of the Figure. The contrasts consists in distortion by an additional 1.18%/yr of vertical extension and a shortfall of 1.39%/yr horizontally. ("Vertical" and "horizontal" are defined here with respect to the coordinate system of the diagram, oriented on Sella-Nasion.)

For the upper triangle, Sella-ANS-Nasion, the histories and also the treatment effect are somewhat different. For Controls, the deformation of this triangle, due to growth, is again approximately along vertical and horizontal principal axes, with an anisotropy of 1.3%. But for the treatment group, note (in the lower right panel) the additional expansion of the distance from Nasion to the Sella-ANS line by 1% per year. This is described, in cephalometric jargon, as "rotation of the lower face downward and backward."

The method this example demonstrates has important implications for all comparative studies of geometric form. Note that the shapes have not been measured, merely archived; no preconceptions of specific variables have interfered with the technique's construction of optimal discriminations and optimal descriptions of change. The orthodontist can thereby detect regularities in the action of the cervical appliance that he was unable to ascertain in any other elementary way. For systematics this approach implies the construction of measures *after* analysis of shape change, a complete reorientation of multivariate morphometrics.

## *Multivariate Morphometrics*

I have left to the last the discussion of multivariate morphometrics, the commonest version of morphometrics in our journals and the one taking least note of biologic homology. [For instance, none of the texts in the field (cf 11, 63) seem to have any figures of organisms; they are filled instead with explanatory statistical diagrams and scatters.] The multivariate tradition assumes that homology has been somehow automatically arranged, outside the statistician's ken, in the course of variable definitions. Any operational, reproducible definition of a quantity—"the distance from the anteriormost point of structure A to structure B," or "the diameter of region six at its narrowest"—is assumed to yield a measure homologous from form to form. In practice some are homologous, some not; I have sketched the general rules elsewhere [(14), Ch. iii]. The situation can be made quite a bit worse by passing too soon to "shape variables," which are arbitrary ratios or regression residuals [cf (41, 51) and references therein]. These, although technically dimensionless, are still generally correlated with size; because they are measured indirectly they complicate geometric modeling still further. The linear scores produced by the usual multivariate techniques serve as input to clustering or ordination procedures, which are then interpreted

biologically. I refer the reader to several good examples of this style of analysis (2, 59, 61, 81). The most recent general review of the field is by Neff & Marcus (56).

In my opinion the success of this general approach is surprising, since no care is taken to determine whether crucial information has been discarded. Multivariate morphometrics proffers no model for generating the measurements it studies out of the fundamental geometrics of plane or spatial shape (70a). Good morphometrics, I believe, is incompatible with the notion of a predetermined character set. Rather, the characters should be defined post hoc as a reflection of the comparisons they are intended to capture. "Shape variables," for instance, *report* an analysis but ought not to drive it; they are *latent,* to be inferred, not observed.

The lack of sophistication in the generation of variables leads to logical problems and paradoxes. For instance, seriation of forms cannot be accomplished unambiguously by separate measurements (17). For any two forms there are arbitrarily many homologous measures on which they agree, so that a third form, whatever it may be, cannot lie unambiguously in-between. One ought not to let the algebraic machinery of statistics select from a motley collection of distances a linear combination optimal by some scalar criterion. One must ask what information is omitted and what distorted to fit the statistical conventions, and also what geometric information is wasted that could have been invested in more sensitive measures.

To make biologic sense of multivariate morphometrics, in particular of the general level of satisfaction expressed by its users, one needs a conceptual model of the step its practitioners are skipping: the link between linear combinations of variables and form-change. This link is best expressed in the factor model introduced by Sewall Wright in the 1930s (88) and rediscovered by Jolicoeur (42b). Any variable selected from a space of possible measures will have *loadings* on hypothetical factors emerging from statistical analysis. These loadings specify the ordinary simple regression of the variable upon the factor. A change in the factor score thereby alters all variables simultaneously to manage the geometry of change, difference, or growth of forms.

The joint log-linearity of all these relations over large ranges of variation is the general subject of multivariable *allometry* (26, 51, 75, 76, 79). Many writers (e.g. 43) miss the point of this exercise. Allometry is a discussion of the role of latent variables, like "general size," not of detailed bivariate associations among observables. The general philosophy underlying the role of unmeasured variables in empirical science has been reviewed (87).

In the previous section I showed how the generalized morphometric analysis of comparisons demands a sampling of loadings in all directions at

typical points of the form. The two dimensions of possible distance measures between boundary homologs, for instance, can be counted as one dimension's worth of directions per interior point. The directional dependence of these rates at a point is a straightforward two-factor model, with trigonometric loadings. One best quantifies this directional variation by noting the two loadings in the two principal directions. Therefore that sample of directions and distances is best that minimizes the expected failure of one of the finite measures to align with these directions. This is true regardless of the nature of the transformation represented by the loadings, whether it be an actual observation of growth averaged over a population, a comparison between forms, a comparison between growth patterns, or a comparison between forms corrected for growth pattern. For species difference at constant size, for instance, Humphries et al (41) construct, as a linear combination of the first two interspecific principal components, a factor orthogonal to size. In fish growth morphometrics, principal axes seem to be at 45° to the axis of the fish (B. Ç hernoff, personal communication). The traditional measurement scheme of axial lengths and body depths thereby loses as much information as it possibly could lose; but a collection of measures including those at 45° to the axis shows much greater diversity of factor loadings and much better discrimination (78a).

The optimal summary of any of these comparisons is a single tensor variable, combining size-change and shape-change information, computed at every locus of the form; and its approximation in multivariate morphometrics is the entire pattern of loadings *interpreted as a transformation.* It is essential that the system of linear measures permit a full reconstruction of the original object geometry, so that the predicted values at any factor score form an archive of a *predicted form.* Furthermore, it is best if the distances measured be generally short instead of long, that they not be overlapping as vectors, and that their directions be well-distributed around the compass. This is neatly managed by taking edges and diagonals of quadrilaterals of landmarks (78a).

When this discipline of measurement design is accepted the results of multivariate morphometrics will serve a dual role. (*a*) As factors they give rise to expected values for all distances, excpected values that change as "size" or "species" changes, so that change in the factor may be interpreted explicitly as a transformation, a change of form in accord with homology. That is, the factors capture an approximation of the information necessary to continue with the morphometrics of the configuration under study. (*b*) As patterns of loadings they will suggest optimal contrasts between poles of the comparisons they embody—large versus small, or species A versus species B, or male versus female—even if the possibility of further measurement is absent.

## *Concluding Remarks*

I have explained the relation between the two main styles of contemporary morphometric analysis, the measurement of transformation via geometrically ordered tensors and the measurement of form via geometrically unordered vectors. These may be expected to arrive at similar but not equivalent analyses of particular comparisons, trends, or contrasts; but the findings of the transformation point of view have priority, as they may determine variables for a subsequent multivariate study.

There is no clear next step, but instead a multitude of intellectual problems remain to be addressed. The transformation model, for instance, need not accord with the diverse mechanisms by which organisms actually bring about changes or distinctions of form. The expression of displacements among landmarks by use of the tensors is meaningful only to the extent that the transformation is a smooth deformation. There should be no tearing of the picture plane, with points previously close becoming widely separated—no slip of one structure relative to another, no passage of points from interior to exterior of closed curves, and no discontinuous opening of an angle. There should be little motion of one part over another by projection from other planes, nor drift of one structure through another; and there should be no creation of new "coordinate mesh," no tissue not smoothly accounted for in earlier triangulations. To all these problematic variants will correspond geometric adjustments of the model. For instance, the tensor treatment of accretionary growth, wherein coordinate mesh is continually created, is sketched by Moss and colleagues (52, 84).

The statistics of these tensors are likewise in a preliminary state, as I have reported in another essay (21). The machinery of that essay yields average deformations for populations. For the technique to be of more utility, quantitative correlation of growth with form should be allowed to adjust the mean deformation. For instance, contrasts between species are different at different sizes; this covariance is itself a tensor field worth extracting (78a). We also have some technical needs regarding the sampling variation of these mean principal dilatations, as they are chosen to be extreme values. And averages should be computed that themselves average over all the triangles as they pertain to each interior point, just as the extended biorthogonal grid does (14).

Further work is needed to extend these foundations conceptually. It is necessary that this notion of the two sorts of information, geometric and biologic, be put on an axiomatic basis. For discrete configurations of landmarks, when we measure distances of all points to all others, what is the nature of the redundancy? Can we come up with optimal triangulations by reference to some model of measurement error at the landmarks in various

directions? For continuous traces, the very space of functions we use to represent the computed homology needs to be formalized and refined. Complete information lies in a combination of position, tangent direction, and curvature; how might it best be homologously sampled? For an early suggestion, see Bookstein [(14), Ch. iv].

A resurrection of morphometrics from such foundations will make possible the design of sound measurement schemes in all manner of applied contexts. The user of these techniques will then be justifiably confident that his measures extract, without bias, the biologic shape information that has been there all along.

ACKNOWLEDGMENT

I acknowledge the support of N.I.D.R. grants DE-03610 and DE-05410 in the course of preparing this essay. I have benefited greatly by discussions with the Morphometrics Study Group at the University of Michigan: Barry Chernoff, Ruth Elder, Julian Humphries, Gerry Smith, and Richard Strauss.

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