Reviews

Syst. Zool., 29(1), 1980, pp. 102–104

The Measurement of Biological Shape and Shape Change.—Fred L. Bookstein. 1978. Lecture Notes in Biomathematics, No. 24, Springer-Verlag, New York. 191 pp. $8.90.

The perception, comparison, and interpretation of shape constitute the core of systematics: first, we must be able to describe the shape of structures in a manner sufficient and relevant to the question at hand; second, comparative judgments must be made about the similarity or dissimilarity of those shapes; the third, we must ask the meaning of those judgments, that is, we must consider how they are to be used to answer specific biological questions.

Traditionally, systematists have described shape in a qualitative, narrative way. In recent years, following the quantitative uprisings during the 1960's and 1970's, systematists and morphologists adopted approaches designed to express shape in terms of "objective," quantitative measures. The spirit of this quantification was born in the works of D'Arcy Thompson, but by modern standards his writings contain little mathematical application. Likewise, Julian Huxley is the one most responsible for introducing the allometric power function into the analysis of size and shape, but again its efficacy in description has been limited. Along the way there have been more sophisticated techniques suggested, such as multivariate allometrics, polar coordinates, and Fourier transformations, but none of these has been widely applied.

This monograph by Bookstein is the most ambitious, and probably the most successful, attempt yet to forge a quantitative approach to shape description and shape change. In the introduction (chapter 1) he recognizes three great methodological inventions indigenous to biometrics: the analysis of variance, population genetics, and quantitative phyletics. The latter is also indigenous to systematics and, he notes, "has risen to guide construction of the most crucial formalism in modern evolutionary theory, the cladogram or chart of evolutionary relationships, out of the chaos of contemporary and surviving data" (p. 1). Placed within this setting, Bookstein's monograph represents an attempt to fill a fourth great need within biometrics, the quantitative measurement of shape. His goal is two-fold: first, to redefine morphometrics as a branch of applied modern geometry and to formalize shape geometrically so that it can be quantified, and second, to develop a method to investigate the quantitative description of shape change.

In chapter 2 he presents a short discussion of formal definitions of shape ("an outline-with-landmarks from which all information about position, scale, and orientation has been drained," p. 8), shape change ["a map of one shape onto another which sends arcs (or surface patches) smoothly onto arcs and corners (or edges) onto corners; then it sends landmarks onto landmarks," pp. 8–9], and shape measurement ("a *function* on some domain into the real line which is the same for all elements of an equivalence class," p. 9). The formalizations get "worse" (i.e., to the geometrically naive student) as the book continues, but as Bookstein explains so clearly, such formalizations are required if concepts such as tangent angle and curvature are to be a part of shape measurement (see below). Only with their use—in contrast to deciphering shape from distance measures—can important aspects of form such as bulges, bumps, and curves be quantified.

Chapter 3 presents a critique of conventional cephalometrics, emphasizing that traditional linear distance measures cannot describe curving form. Landmarks do not define form, they merely lie upon it (arcs, curves), and "to understand the changes of growth and remodeling, we need to know how each landmark is moving away from the others" (p. 14). He proposes to solve this problem by the introduction of two measures taken in the immediate neighborhood of identifiable landmarks (p. 17): the *tangent angle* ("the azimuth of a straight line lying along the outline at the landmark") and the *curvature* ("the inverse of the radius of the circle closest-fitting to the outline"). As he notes, these two measures can be directly ascertained from digitized cephalogram tracings, but they have not been used in prior work on shape.

Chapter 4 presents Bookstein's statistical analysis of shape data, based on the input of tangent angle and curvature. A major criticism of prior techniques (like Fourier analysis) is that the results are not diagrammable: we ought to be able to retrieve from measurement data, and display in a diagram, a close fit to the original shape. Bookstein's method does this very nicely, judging from his examples. Detailed understanding of his technique will be accessible only to the statistically and geometrically sophisticated reader, but generally speaking it involves conic splining by "polynomial spline regression." What this amounts to is fitting two or more conics (curves) together at landmark points and minimizing their error fit at those points. Hence, with his computer algorithm shape is faithfully recreated with minimum error.

In 1917 D'Arcy Thompson introduced the method of transformation grids in order to study the change in shape from one organism to another (either ontogenetically or phylogenetically). This method, familiar to most systematists and morphologists, entails mapping points of one shape (derived from a superimposed, lined grid) onto corresponding points of the second shape and then smoothly deforming the first grid to fit the points of the second shape. Transformation grids have been used extensively in the literature. In chapter 5 Bookstein reviews and critiques this method. As he notes, a revolution in morphometrics has not emerged from this method: virtually all its applications are entirely within the confines of Thompson's original formulation.

As one might expect from the contents of the preceding chapters, Bookstein is critical of the effectiveness of transformation grids to describe shape change: Thompson's method did not really express shape change quantitatively or with precision; construction of the transformations is replete with arbitrary decisions affecting the accuracy of the renderings of shape.

In order to provide a solution to the problem of quantifying shape change Bookstein introduces in chapter 6 the method of biorthogonal grids (see also *Science* 197:901; 1977). The method is not easy to explain in words, and the results are calculable only with the aid of a computer. Very simplistically, outlines of two shapes are covered by a grid of points, "corresponding point for point between the images, which summarize the homologies of the interiors" (p. 99). For each point, in both images, there exist two local principal axes perpendicular to each other, the only difference being the ratios of the lengths of the axes that signify the dilations (stretch) necessary to derive one shape from the other. Curves can be generated that are tangent to the two principal axes, so that a family of curves intersect at right angles over the interior of each figure. In Bookstein's own words (pp. 97–98):

> "Through almost every point of a differentiable transformation pass just two differentials which are at 90° both before and after transformation. The integral curves of these differentials form a grid whose intersections are at 90° in both images. These are called the *biorthogonal grids* for the transformation, for there are two of them, one in each image, corresponding curve for curve, intersection for intersection .... We quantify shape change by extracting the two dilations at every point of either shape, measured along the local canonical axes. Thompson's fundamental error was the construction of diagram pairs which were unsymmetrically specified: rectangular grid on one side, unrestricted grid on the other .... Since all angles within the [biorthogonal] grid are unchanging by construction, such change of form as has occurred is a matter of changes of relative curve-spacing only, of differential *dilation* (stretch) from point to point in the two local principal directions."

Bookstein thus has created the algorithms necessary to compute dilation (shape) changes and he presents examples in chapter 7. He reinterprets Thompson's famous transformation of *Diadon* and *Mola,* but readers of *Systematic Zoology* probably will find his discussion of primate craniology the most interesting. He compares, for example, a primitive *Cebus* skull with the relatively derived howler monkey, *Alouatta.* Bookstein also looks at the immatures and finds that the infant howler is identical to the adult of *Cebus.* He continues these comparisons among additional species of cercopithecids, and then turns his attention to ontogenetic series of the great apes and man. The power of his technique to generate important systematic data is nowhere better illustrated than with these studies. His results are significant (pp. 148–149):

> "The *ontogenies* of chimp and man are likewise similar . . . *not to the ontogenies of the other great apes* but to the relations among their infant forms .... The chimp and man manifest similar gradients in ontogeny, so that the relation of their infant forms is concordant with the relation of their adult forms, indicating an intensification of the retardation of the chimp with respect to the main anthropoid line. *Both their ontogenies are unlike the ontogenies of the other apes .... The discrete shift, the neotenization, appears in common between* Homo *and* Pan, *and is merely intensified in the former ontogeny in comparison with the latter*" (italics added).

Bookstein's results, then, suggest a sister-group relationship between *Homo* and *Pan* (the synapomorphy being the derived ontogenetic pattern), not between *Homo* on the one hand and *Pan* + *Gorilla* on the other, as many previous workers have suggested. If this is correct then there is justification for maintaining *Gorilla* and *Pan* in separate genera (and placing, obviously, *Homo* and *Pan* together in some supraspecific taxon).

Much has been written in recent years about an "emerging science of form." Over the last decade or so influential morphologists have extolled the virtues of a new approach to the so-called dreary descriptive anatomy of the past, and have argued, by word and deed, that a functional approach offers something new. Indeed, because of many elegant studies we now have a much better idea as to how morphological complexes work, but in what sense has this led to a "science of form"? Conceptually, at least, old-time anatomy and the new functional morphology are very similar: they are both descriptive. Before a "science of form" emerges, morphologists will have to seek out generalizations and the majority do not seem to be doing that.

To my mind there have been two fundamental contributions to the study of size and shape in recent years. One is interpretive; the other is descriptive. The first derives from the work of Thomas McMahon of Harvard University, who by relating size-dependent shape changes to the maintenance of elastic similarity has made a bold attempt to unify a vast amount of empirical data (morphological and physiological) on allometric scaling (see particularly 1973, Science 179:1201–1204; and 1975, J. Applied Phys., 39:619–627). Regardless whether this work proves successful, it suggests the kinds of generalizations that are possible within morphology.

The second—and descriptive—contribution that has the potential to substantially change the investigation of size and shape is, I think, this study by Bookstein. As he points out in the last chapter (8), the future applications and modifications of this work are enormous. A major problem to be solved is the translation of the complex mathematical underpinnings into a language easily understandable by the common biologist, and to make the computer programs readily available to undertake computations. All this will come in due time, I am sure. It is very possible that biology will view Bookstein's contribution to be one of the most important conceptual and methodological advances in the study of size and shape. For this reason, morphologists and systematists will want to study this monograph.—*Joel Cracraft, Department of Anatomy, University of Illinois at the Medical Center, P.O. Box 6998, Chicago, Illinois 60680.*

Syst. Zool., 29(1), 1980, pp. 104–105

Order in Living Organisms: A Systems Analysis of Evolution.—Rupert Riedl. 1978. Translated by R. P. S. Jefferies (original German edition published in 1975). John Wiley and Sons, New York. xx + 313 pp. $37.50.

Riedl first attempts to synthesize and document the general patterns of morphologic order exhibited by living organisms. He recognizes four and only four basic and universal patterns of morphologic order: (a) standard-part (Section IIB3a, & Ch. 4), (b) hierarchical (Section IIB3b, & Ch. 5), (c) interdependent (Section IIB3c, & Ch. 6), and (d) traditive order (Section IIB3d, & Ch. 7). He then attempts to develop an evolutionary genetic model to explain how each of the patterns arises and is maintained in nature [Ch. 3 on the molecular causes (genetic mechanisms) underlying the patterns of order, Ch. 4–7 in part, and the final Ch. 8], and why, parenthetically, there may be only four such patterns. His explanatory model accepts virtually all of the neo-Darwinian new systematics [perhaps better referred to as the "new in '42 systematics" (after Huxley, 1940, 1942)]: random mutations accompanied by natural selection in the environment and survival of fittest, etc. However, his theory includes much more. In the tradition of German science, he builds a complex theoretical superstructure, and one which cannot be entirely dismissed as a "stack of cards." His superstructure is founded on information theory and general systems theory, which should please most English-speaking taxonomists and evolutionary biologists. By contrast, his superstructure takes as given alleged processes and phenomena which might make some of the latter group of scientists rather uneasy. These include axiomatic acceptance of: 1) a strict version of Haeckel's law—ontogeny recapitulates phylogeny (Section IIB3d, Sect. VIIIB4a), 2) orthogenesis (e.g. Sect. VIIIB5b), 3) the notion of homologs as countable single individualities constant in number for a given group (p. 43), 4) the concept of the morphotype (Sect. IIC3, VIClc, VIIIB2b) or groundplan which embodies the "essential features" of a group of organisms, and 5) the related notion of a corresponding limited number of underlying epigenotypes. The morphotype concept especially is a major element in Riedl's theory. He quotes Goethe (1790) in defining the morphotype as "a consequence or law according to which nature will be expected to act." Riedl admits the morphotype "since Goethe's first formulation . . . has remained an abstraction, which could scarcely be measured, was difficult to show in a figure, and was not easy even to think about" (p. 246).

Consider first Riedl's four basic patterns of order. Standard-part order in the morphology (cytology and histology as well as anatomy) of organisms is the occurrence of structures "agreeing so well with each other in constitution and mode of occurrence that no doubt remains of the presence of identical determinative laws" (p. 95). Examples include a) identical sequences of amino acid residues in Cytochrome-C in groups as diverse as yeast and man (p. 37), b) mitochondria, cilia, and cells in all groups of plants and animals, c) bone cells, Haversian columns, and vertebrae in the Vertebrata; and d) individuals belonging to a species.

The second type of order (hierarchical) arises when the standard building blocks "are fitted inside each other in a system of frameworks which mutually require and determine each other" (p. 53). In particular, homologs are arranged in a hierarchical system, i.e. "most consist, in turn, of subordinate homologues, and several combine to form homologues of a higher rank" (p. 40). Riedl illustrates this with the following nested sequence of mammalian homologs (see his fig. 11; recall homologs to him are discrete, countable, and fixed in number for a given species or higher taxon): 1) vertebral columns with cervical, thoracic, lumbar, etc., regions, 2) neck regions, consisting as a rule of seven cervical vertebrate; 3) axes (=second cervical vertebrae); 4) centra of axes; 5) odontoid processes of axes; 6) ventral articular facets of odontoid processes. Tied into the notion of pervading hierarchical patterns is the difficult but important concept of the *burden* of a morphological feature. The burden "carried by" a feature is the number of features which are functionally dependent on it; the concept forms a key part of Riedl's theory, which ties increase in the fixation of a feature during evolution to an increase in its burden.

Interdependent order (p. 179) arises when two or more features are interrelated but in a non-hierarchical fashion. Functional examples of mutual dependence which fall in this category are (p. 181): gill bases and aortic arches of fishes, myomeres and spinal nerves of vertebrates. An example where the functional connection is not obvious (p. 188) is the