ONE BIOLOGIST'S VIEW OF MORPHOMETRICS

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INTRODUCTION

For this biologist, morphometrics is the characterization of biologically relevant forms and patterns in ways that allow their quantitative handling: a considerably wider definition than usual. There are many different methods by which we may carry out this characterization, many different types of structure to be characterized, and many different ways in which the results may be used within systematics and evolutionary biology. The methods range from the use of a measurement and univariate statistics, to holographic techniques. The forms to be characterized may be the external dimensions of some simple biological object, the complex internal patterns revealed by such methods as dissection and radiography, or the complicated and multidimensional "structure" of data relevant to a biological problem. Problems of systematics and evolution may be attacked through straightforward descriptions of organisms on the one hand, or, on the other, through elucidation of the conceptual patterns associated with ontogenetic, genetic, phylogenetic, functional, environmental, populational, geographic, and other issues.

At the beginning of the century when the science of morphometrics was still in its infancy, Karl Pearson prophesied that "Twenty years hence our successors, working by improved methods and with better training, will no doubt reach fitter definitions and more exact values for vital coefficients." He added that by this time, morphometric methods will not "have to justify themselves to a non-mathematical biological world; mathematical knowledge will seem to be as much a part of the biologist's equipment as today of the physicist."

Yet in spite of what may appear to be an enormous spate of papers using morphometric approaches, seventy years later it is still scarcely appropriate to review the contributions of morphometric techniques to biological thought. Many of the

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investigations do little more than introduce us to the problems and difficulties that arise in their use.

Thus, some of the methods are applied to entirely artificial data sets [e.g. Caminálcules (173)] (sometimes computer generated) in order to allow us to discover and demonstrate possibilities. Other investigations are indeed aimed at "real" biological data, but at data rather specially chosen to help reveal the properties of the various methods [e.g. Anderson's measurements on the Iris (22, 31, 69, 119, 150)]. Yet other investigations attack "real" biological problems but ones for which an answer is already known (or presumed known). Here the rationale is to supply confirmation that the morphometric method is producing answers not totally at variance with what can be learned by more classical methods [e.g. compare (3) and (70)]. Some morphometric investigations have been directed toward a few unsolved biological problems, but so far they present little more than examples of what may be achieved; they are scarcely extensive enough yet to make a major contribution to evolutionary biology. Only multivariate statistical and clustering methods have been used extensively to tackle new biological problems, but even here there is far to go. Not a few of the methods so intrigue their users that they are applied willy-nilly to every available biological problem, sometimes without much inquiry into their particular relevance.

None of the above comments is intended to depreciate morphometric investigations, which represent, after all, a profession's general discovery of the utilities and inutilities of a series of tools imported for the most part from outside the profession itself.

We must realize also that many of the methods of morphometrics are scarcely past their infancy even within the disciplines responsible for their theoretical development and underlying justification. This comment does not, of course, apply to all of these tools. Statistical methods in general, and multivariate statistical morphometrics in particular, have been thoroughly examined by generations of statisticians. The studies of Francis Galton in the last century were refined by Karl Pearson during the first quarter of this; there followed the work of Ronald Fisher in England, Harold Hotelling in America, and Mahalanobis in India. Some later texts, still most useful to practitioners are those of Rao (140) and Kendall (96), and these lead through a variety of even more recent descriptions to a most useful current book by Gnanadesikan (75). Many descriptions apply directly to biology (25, 92, 155, 163) or to other scientific disciplines, such as the behavioral sciences (28, 48). Several symposia and bibliographies are available (6, 35, 54, 117). The problems inherent in these approaches have not been worked out fully by any means. Nevertheless, a great deal is known about them, and if they are used carefully (with professional assistance, consultation, or collaboration when necessary) they are unlikely to lead us far astray.

But many of the other methods now becoming available to biologists are by no means in such a polished state of readiness. Various cluster-finding procedures are close to statistics but have not yet received a full enough theoretical treatment to make their foundations safe and sure. Yet considerable work is being carried out in these areas, and several books useful for biologists are available [(47, 82, 92) and
(165), now superceded by (163)]. Again, texts from workers in other areas [e.g. (178), psychology] may be useful. Theoretical treatises and symposia from workers in statistics [e.g. on cluster analysis (23) and especially on multidimensional scaling (158)] indicate that these methods overlap with multivariate statistics and in some cases are inseparably fused with that more mature field.

Some procedures are even less well worked out. One example, optical data analysis, promises major breakthroughs for those interested in the analysis of complex patterns; but even though the underlying mathematics has been known since the time of Fourier (77), the many technical problems in its usage are only now being solved (160, 177). As another example, digital image processing (8, 9) is clearly a method that can be used to look at biological shapes and patterns (127); yet it is at an early enough stage that its analytical procedures are still being invented and tested (149, 177). The biologist who uses such methods must do so in the knowledge that it is easy to be misled.

The number of techniques grows daily. We must be willing to look to fields as disparate as engineering, electronics, communications, optics, applied mathematics (especially applied topology), stereology, image analysis, computer graphics, pattern recognition, and so on. We must be aware of the work of other investigators who may be using these methods as we would—for example in geology, geography, microscopy, metallurgy, meteorology, astronomy, and biomedical science. Seeing how methods have been applied in other disciplines suggests possible applications in our own.

MORPHOMETRIC METHODS

It is usual to view the characterization of form and pattern as being achieved through measurement. Yet forms and patterns can also be handled quantitatively by methods that attempt to describe the envelope of a form in its external entirety, the weave of a pattern in all its internal complexity. This dichotomy between handling structure through discrete measurement and analyzing structure as a whole is artificial: The two are merely the ends of a continuous spectrum. Let us review the entire range.

Biological shapes have been characterized most often by means of a single measure or other descriptor, or by a very small number of measurements or other parameters. It is common, for instance, to study growth through analysis of body length or height only (or of body weight); to describe the shape of a petal, or a shell, or a bone, or a tooth by means of their greatest lengths, breadths, and heights; to encapsulate the form of entire animals by means of the lengths of the head, the trunk, the limbs and the tail. Such measures are hallowed, but are in fact rarely useful in solving real biological problems. They cannot describe most biological forms and patterns nearly as well as the human eye. At their best they are components in 'keys' that can be used for subsequent 'classifications' once the real biological problems have been elucidated [but see (124)].

However, the descriptive powers of measurement can be greatly increased by taking more of them and by analyzing them in ways that look at the interactions
among them. The problems of taking more measurements are slowly being solved by the introduction of new methods and instruments (see below). The problems of making better sense of large data sets now devolve from methods of analysis such as multivariate statistics, and from instruments such as computers and computational programs. For instance, although univariate study of traditional morphological descriptors of various prosimian primates such as bushbabies, mouse lemurs, and indrises suggests that the structure of their hip and thigh is related to their ability to leap (118), study using many new measurements and multivariate statistical methods shows rather clearly that each of these groups has a different structure of the hip and thigh and that several different anatomical arrangements for leaping exist. This in turn suggests the behavioral hypothesis that they may leap in rather different biomechanical ways; and the currently available information about the behavior of these rare animals suggests that this is indeed true ([(121, 168); C. E. Oxnard, R. German & J. McArdle, work in progress].

Furthermore, although an increase in the number of dimensions required to describe shapes may result in a more creative choice of measurements, even rather nondescript measurements, such as overall lengths, widths, and heights, or overall bodily proportions, may yield new insights when analyzed by the new methods. Thus multivariate statistical investigations of simple lengths and breadths of teeth have supplied quite unexpected information about the overall shapes of some of the fossil teeth found in Africa (15); and the new results of studying the detailed structure of the hip and thigh in leaping prosimians described above are confirmed by multivariate statistical analysis of simple measures of the overall proportions of the upper and lower limbs of these creatures (C. E. Oxnard, R. German, F. Jouffroy & J. Lessertisseur, work in progress).

As the numbers of measurements increase, so the difficulty of taking them increases. Rulers and calipers give way to other kinds of physical apparatus to maintain accuracy and to increase speed. One simple device to obtain information about a complexly shaped edge is the artist's Copy Cat\(^2\) described for use in characterizing transects of faces as a “contourometer” (167). A somewhat similar “profile copying machine” was invented in 1953 to characterize the shapes of birds' eggs (137). Other standard equipment, such as goniometers, osteometric boards, depth gauges, diagraphs, and so on, have been used to produce particular forms of measurement. A variety of novel instruments, such as craniometers (13), pelvimeters (43), cranial radiometers (51), and goniometers (37) have been devised to aid in the measurement of complexly shaped parts. Perhaps the ultimate in such instruments are the stereometric craniostat (126) and the head-measuring device (44), both of which resemble gentle forms of an “iron maiden.” Compared with other techniques to be discussed below, most such physical inventions, although once useful, have now become overly cumbersome.

A next step, then, is the combination of physical with electronic measuring devices. These run a gamut from calipers that are electronically linked to recording instruments (34) to “on-line automated osteometric data collectors” (57), in which

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impulses from "digital calipers" are relayed through a number of recording and analytical devices to produce direct computer printouts of statistical analyses [see also (174, 186)]. Such automatic methods go too far whenever they prevent the examination of the original data and of the many internal steps in the procedures. However, a variety of approaches are now capable of measuring biological objects without using calipers, rulers, and other invasive instruments (regardless of how they may be augmented electronically). Some of these involve ultrasonic and optical devices, and all are capable of producing numerous accurate measurements in two- or three-dimensional coordinate form if required. Thus in our own laboratory the Graf/Pena\(^3\) utilizes ultrasonic signals to produce two-dimensional (for photographs, radiographs, etc) or three-dimensional (for actual objects) coordinates of either individually chosen points or of continuous lines. Other techniques use stereopairs of photographs of biological objects, and a variety of methods are available for obtaining measurement information from them [(80) provides an excellent summary description and bibliography of a large literature; see also (2, 73, 111, 152)]. When used with the understanding that particular orientations of objects are not necessary, that data can be readily obtained using stereoplotters like those originally designed for map making, and that automaticity, speed, transformation and analysis can all be carried out by linked systems—for instance, as described and used by Creel [(50) and personal communication]—these methods make very considerable advances possible.

Once it is realized that measurements from one point to another upon an object may be replaced with two- or three-dimensional coordinates for each point on an object, it seems obvious that further information may be obtained simply by increasing the number of such sets of coordinates. This cannot easily be done when the definitions of the points are biological—there may be large areas of many biological objects that are relatively featureless or that do not easily provide well-defined and repeatably locatable points. But in theory, the number of measurements that can be taken upon an object can be increased by increasing the fineness of some grid or network that has been placed over it. Thus a variety of methods have arisen that depend not so much upon the biological details of the shape or pattern as upon the sensitivity of the system available for its geometric characterization. Many of these tools use digital information obtained by showing the shape or pattern to a computer by means of an image-reading device.

Examples of the use of such methods abound outside of biology—e.g. in physics for understanding the nature of patterns in bubble chamber experiments (192), in geophysics for studying the pore spacing and pattern in sedimentary rocks (145), and in meteorology for the study of aerial and cloud photographs (40). Many of these methods have also been applied in biology—e.g. for the characterization of chromosomes (33, 83), fingerprints (40, 157), animal cell movements in vitro (19), and for a variety of microscopic biological studies: autoradiography (136), nerve fibers (133), bone structure (114), and muscle patterns (63). They have even been used to study living, growing specimens (138). But again, although capable of

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descriptions that might be useful in evolutionary and systematic studies, they have scarcely if ever been so used.

Once such methods can produce digital representations of a structure it is necessary to discover how to handle the representations in order to make biological comparisons. Many of the earlier studies use a variety of simple ad hoc parameters for this purpose—e.g. diameters, perimeters, and areas. By using such simple characters it is often possible to calculate such information as numbers, volumes, and distributions of elements in a given field, and to go from information in two-dimensional sections to estimates about three-dimensional objects. It is this that has formed the major part of the field of stereology [e.g. see Underwood (182); for more recent information see the Proceedings of the International Congress for Stereology, from 1969 to the present (183)]. However, now that such methods have become more refined, further advances have stemmed from considering the kinds of elements that may make up a pattern or a form. This is the subject of the fields of pattern recognition and image analysis.

Many of these studies have isolated the features inherent in structures. Thus analyses of edges, corners, nodes, tangents, vectors, inflection points, medial axes, curve-fitted images, skeletal transforms, and so on (1, 61, 138, 147, 166, 191) may provide form and pattern descriptors important in a variety of situations. The use of tangents and inflection points is described by Attneave & Arnoult (18) and illustrated in a biological example by Oxnard (120). Likewise the medial axis transform is described by Blum (26, 27) and Philbrick (130), who use simplified biological structures as some of the examples; actual demonstrations of the method for describing biological shapes are noted by Oxnard (120), and its possibilities are emphasized by Waddington (185). Curve-fitted images have been applied if not to a real biological object at least to a representation of one [a Barbie doll(1)].

Finally we turn to the various methods that attempt to capture forms and patterns holistically. In each case these methods depend upon making transformations of the entire form or pattern.

For example, a field picture of overall shape can be generated from the contours of an object. This method has been applied in biology for the study of the parts of the human body (80, 190). The very difficult and time-consuming reconstructions of the middle ear (106, 107) might have been rendered much simpler had this technique been available when those were undertaken.

There are, however, other ways of tackling this same problem. Some make use of moiré fringe methods. Takasaki (169) demonstrates that contour moiré pictures of a full-size living body with good contrast can readily and accurately be obtained using incoherent (white) light, regular cameras, and grating shadows. These methods have now been improved considerably over the rather crude characterizations obtained for pelves of living and fossil men and apes in an early demonstration by the author (120). It is also possible to produce moiré fringe contours using lasers (coherent light) and a variety of holographic techniques. These methods are now applicable to studies of animal structure, including characterizations of living tissues.

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But the methods have been applied mainly to those anatomical structures whose complicated surfaces have proven very difficult to quantify in both clinical and evolutionary situations using regular mensurational techniques—e.g. the surfaces of teeth (42, 64, 65, 195).

The information in a picture can be analyzed by means of a whole range of methods that depend upon Fourier and related transforms. These may be carried out computationally or optically. The computational methods are far more accurate, and for investigations in various physical sciences (e.g. analysis of earth or moon pictures) they are superior. The optical techniques require less expensive hardware; although their accuracy is necessarily less than that of the computational methods, it is still easily greater than the accuracy of most biological studies. Furthermore, the optical procedures can sometimes be carried out more quickly and easily than the computational.

Computational Fourier analysis has been used for the study of the perimeters and internal structures of organs and organisms (11, 94, 101, 112, 119, 159, 187). But most applications of these optical Fourier transforms are in sciences other than biology. An early description is provided by Cutrona (52), who shows how the methods may be used for the detection of patterns within apparently less-patterned arrangements. Dobrin, Ingalls & Long (60) and Jackson (91) show how such methods may be used to detect patterns in seismographic data. A number of authors (53, 55, 59, 66, 131, 132, 134, 166) demonstrate various improvements of the techniques for analyzing a variety of earth patterns, such as those in rock sections, aerial photographs, and contour maps. Holeman (86) illustrates their use for the automatic reading of printed characters, words, and other patterns. A variety of other transformations (10, 97, 135, 141) are capable of yielding information about the elements of a picture (e.g. the Hadamard/Walsh and the Haar transformations). These studies have been concerned especially with the analysis of aerial photographs of the moon and Mars, and with the improvement of television picture quality. But from the evidence in these publications it is clear how they might be used to help solve biological problems.

Radiography and microscopy have used these approaches to enhance biological images. They may also be used for the optical filtering (dissection) of the information contained in radiological images (20, 21, 76, 90, 129, 156). Rather more recently the methods have been taken up by biological microscopists to enhance images and analyze the pattern hidden within more complex visual representations (84, 98, 170, 172).

These methods have been only little used to study form and pattern in a systematic or evolutionary context. Walsh transforms were used as early as 1967 in a pilot comparison of the outlines of the leaves of Althea and Coleus (116). Fourier transforms analyze the complex internal structure of bone and suggest how the methods may be used in evolutionary studies in the direct comparison by subtraction of one form from another (119, 120, 153, 154, 189).

Finally it is not uncommon for several different morphometric methods to be applied one upon another for both analytical and display purposes. It is standard, for instance, to apply various cluster-finding procedures to the statistics resulting
from multivariate statistical analysis of data (119, 121). In the same way, harmonic amplitudes demonstrate information revealed through multivariate statistical shape descriptors (193); sine-cosine functions display information in orthogonal canonical axes or principal components (7, 68, 89, 121). A particularly early attempt to display and communicate the results of morphometric analyses was that of Anderson (5), who used semi-pictorial glyphs to record variations in kernel shape and texture in maize. This has been followed by a recent surge in activity on the part of data analysts to try to discover useful visual summaries (179, 180). One of the most visually pleasing is the two-dimensional stereodiagram (62, 71). Another is the use of D'Arcy Thompson's Cartesian coordinate transformations to display information within individual canonical axes in multiple discriminant function analyses (119). Yet a third is the use of various mapping procedures for displaying information derived from a variety of multivariate statistics (36, 119, 121). For even “higher dimensional” results, displays by means of “clouds,” “stars,” and “faces” (41, 191) have considerable promise for summarizing and communicating the results of complex data analysis. The fact that many of these techniques can now be used in an interactive mode is of enormous value both for revealing useful results and for letting the investigator know at a very early stage when analyses are wrong or inappropriate, or that some other problem exists.

FEW MEASUREMENTS VERSUS MANY

Our survey of morphometric approaches, necessarily superficial and incomplete, indicates that shape may be characterized by any number of measurements. How many measurements are in fact necessary for the multivariate morphometric approach? Some investigators believe that morphometric problems are not as complicated as presented here and that a single cleverly defined measurement or some very small suite of measurements can supply the important part of the information. Some shapes can indeed be characterized by a very small number of measurements. For example, a single measurement of a circle or sphere (if we know that the shape is a circle or sphere) supplies us with all of the information inherent in them. Two measures completely define a rectangle and three a box (if we know that the shapes and structures are truly rectangles and boxes). Biological objects, however, are more complicated; we may not know even their approximate shape, and more measurements are likely to be necessary. At the other extreme are those investigators who believe that if two measurements are better than one, then two hundred must be better than one hundred. Such thinking can be reduced to the absurdity mentioned by Howells (87), who reminds us of the old study in which the morphometric description of a human skull was said to require 5,000 measurements.

In our laboratory we have undertaken to characterize the shoulder girdle by using three, six, nine, or seventeen measurements. The analysis of these suites using multivariate statistical methods makes it clear that for an object of this degree of macroscopic complexity, nine measurements produce far more information than three or six measurements, but scarcely any less than seventeen (14). An object of roughly comparable macroscopic complexity, the talus (one of the bones of the
ankle), has been analyzed by means of four, eight, and sixteen measures. Eight measures provide a great deal of information not present in four, but sixteen measures do not provide any significant information not already revealed by eight (104).

On the other hand, eight or nine measures do not suffice to characterize the pelvis. The pelvis is a more complicated shape than the talus or scapula, and analysis of four, five, nine, eighteen, and finally thirty measures shows that new orders of information are added until the level of eighteen measurements. A reasonably full characterization of an object as macroscopically complex as the primate pelvis thus requires twice as many measures as does that of the shoulder ([6], C. E. Oxnard, R. German & J. McArdle, work in progress). Howells (88) has shown that an object as complicated as the human skull may not be adequately described, at this level of macroscopic complexity, unless something of the order of fifty or seventy measurements are used [see also (32)].

**TWO DIMENSIONS VERSUS THREE**

Many morphometric methods characterize form and pattern in two dimensions (indeed, sometimes in only one). This is often because of two-dimensional simplicity. Objects as different as leaves (116, 143) and shoulders (16) are relatively flat and easily examined through two-dimensional representations. D'Arcy Thompson's original use of Cartesian coordinates (173) was demonstrated through two-dimensional examples, and this practice has continued each time the method has been used [e.g. (142, 144) on growth of amphibian larvae; (115) on the stages of human growth; (110) on growth in ceratopsians; (100) on Permian amphibians; (161) on the formation of the avian egg; (39) on the form of rhynchosaurs; and most recently perhaps (12) and (72) in expositions of how the method can be improved using computer graphics]. Other morphometric applications that have stemmed at least in part from the method of deformed coordinates are also two-dimensionally confined. Sneath (162) uses third and fourth order curves and surfaces for defining differences between hominoid skulls; he displays the results using two-dimensional, angularly deformed grids. The notion has been taken by Bookstein in another direction using bio-orthogonal grids in which deformations are linear, not angular, but remain two-dimensional (130, 176). Yet an application in mathematics (78) shows us how the three-dimensional coordinate system can work. The various usages of Fourier coefficients (4, 101, 109), the few attempts to use medial axis transformations (26, 27, 119, 185), and some of the applications of optical data analysis (120, 153) have confined themselves, necessarily at this stage, to two-dimensions. In order to make it clear that I am not making pejorative criticisms of these various studies I have included some of my own investigations in the above lists. Almost every worker who has used these methods has been aware of their two-dimensional limitation; almost every worker has noted that extension to the three-dimensional situation is intellectually trivial. Every investigator also knows that such an extension is crucial to elevating these methods beyond the level of mere examples (29, 30, 102, 103, 120, 162).
It is in the realm of multivariate statistical and clustering analyses of measurements and the holistic appreciations of shape through optical data analysis that the greatest strides towards three-dimensionality have been made. For multivariate statistical and clustering analyses it is usual to use (a) measurements taken in three dimensions, (b) measurements made within planes aligned at known angles to one another, or (c) measurements in the form of three-dimensional coordinates of points. Likewise, optical methods, although especially valuable for the analysis of two-dimensional patterns, may be used to characterize three-dimensional surfaces by analyzing deformations of patterns projected upon objects [e.g. of skulls (154) and contour maps (166)].

KEEPING VERSUS LOSING GEOMETRIC RELATIONSHIPS

Geometric relationships seem at first to be the important element for morphometrics. This is why many of the techniques using deformed grids have been employed so frequently. Many morphometric studies of the face, jaws, and teeth lead to dental applications for which the shape of the final object may be of particular importance. Maintenance of geometrical relationships are crucial to studies of change in shape during the movements of an organism [slime molds (146, 147)] or during organismal growth and development (143, 144); it is crucial also to studies of differences in shape between separately evolved organisms (30, 162, 176) or even of differences between shapes stemming from the actions of forces upon those shapes either during their (biological) formation (161) or during their (geological) deformation (12).

But the attractiveness of keeping geometrical relationships to the fore sometimes overshadows the importance of other relationships to which the geometry may speak. And it is probably too little realized that geometrical information can be retained even though the results of analyses are not presented as the relationships of compared pictures. Thus the vectors, axes, and distances of statistical methods, the minimum spanning trees and dendrographs of cluster-finding techniques, and the polar coordinate arrangements of the optical densities of image-analytical methods still contain the original geometrical relationships of the biological shapes [see examples in (119, 121, 122)].

SPECIAL VERSUS GENERAL MORPHOMETRIC POINTS

Many studies, especially earlier ones that depend most upon measurement, rest heavily upon the definition of various kinds of special points. Some are geometrical points that can be repeatedly defined, such as most distal, most proximal, most medial, most lateral, and so on. Others are defined for a priori biological reasons, e.g. so-called homologous points. There is an enormous literature on the meaning and application of homology. Without going into that matter, it is clear that useful biological points are produced by similar developmental processes acting during the ontogenies of the animals being compared. However, the definition of developmentally defined points depends upon the availability of correct developmental information. Points can also be defined using biomechanical assessments. Again, good biomechanical information must be available, and that is sometimes a pipe dream.
Some studies, however, are carried out without defining points. Such is the case with many of the methods already mentioned—for instance, those of image analysis. This circumstance is deliberately sought by many investigators in situations where it might generally be expected that special points would be required. Sometimes the desire to lose specific points may result from the need to characterize areas or regions that are relatively featureless (e.g. the vault of the skull, the form of an egg); at other times it may result from the desire to interpolate many more points between a small number of easily defined points; sometimes it is a genuine desire to produce "reference-free" characterizations. It is worth pointing out that specially defined points can easily be retained alongside general points in many systems such as bio-orthogonal grids (29) and medial axis transforms (119).

TWO SPECIMENS VERSUS MANY

Technically, the word *morphometrics* denotes the characterization and handling of a form or pattern. This is exactly what is required in many of the nonbiological applications that have been noted. Biological problems, however, almost always require comparison and this can be achieved by placing two characterizations of forms or patterns side by side or by superimposing them. The wide variety of optical methods are especially interesting for comparing two forms or patterns. They run from the use of optical diffraction of two pictures placed side by side, through filtering techniques that involve subtracting everything except what is of interest from each of the two patterns, to the actual subtraction of one pattern from another (40, 119, 154, 156).

But the great majority of the problems of morphometrics in evolution and systematics require the comparison of many different specimens. For this purpose the most attractive methods, especially the geometric or visual ones, have not yet been developed far enough. Coordinate transformations, trend-surface analyses, bio-orthogonal grids, and medial axis transforms can all, in theory, provide sample parameters. They have not yet been so utilized. The conceptual development of these methods to include this additional matter is trivial—the statistical background exists. But the practical work necessary is by no means easy. Until it is done these methods and many similar ones not referenced will remain elegant, much quoted, but little used examples. The univariate and multivariate statistical approaches have, of course, been developed especially with this problem in mind.

Everything suggested under the problem of characterizing specimens applies a fortiori to the problem of comparing populations. The only methods so far available that take the latter into account are those that utilize the multivariate statistical approach or one of the modern offshoots of it. Yet many of the other morphometric methods could serve if modified. A start has been made with optical data analysis, by means of which "average" faces among "populations" of faces can be obtained (184).

Such studies assume that there are no difficulties in defining biological groups; they undertake to determine the nature of relationships among known groups. Most biological problems depend, in fact, upon a wide variety of older studies that assume the prior existence of groups. The author’s own studies of primates, where limi-
tions of materials almost always force work at the generic level, are a case in point. Although there is a great deal of debate concerning primate subspecific entities, most primate genera are well defined. But in many investigations the very point at issue may be the existence of particular groupings. At the subspecific level the existence of already known objective groupings cannot be taken for granted (3). Under these circumstances, group-finding procedures are especially important. A wide variety of these exist. Some utilize multivariate statistics in a group-finding mode, some depend directly upon nonstatistical cluster-finding procedures, and some combine the two.

There are problems even more complex than the above, for with biological materials it is possible that genuine fuzziness may exist between groups. Under such circumstances the best realization of the biological relationships may be obtained by means of fuzzy set theory. The underlying mathematical and computational methods for this theory are being worked out by investigators from disciplines such as electronics, engineering, and space technology (38, 74, 151, 194). Biological fuzzy set theory has so far been applied to medical diagnosis and to the investigation of human sleep (99, 188). Bezdek (22) has shown how well the method works on Anderson’s four-dimensional data from Iris.

The problems raised by the placing of an unknown sample or unknown specimen within or among other populations or specimens are especially severe. Although not necessarily simple, placing an unknown sample is obviously the least difficult. Statistical parameters can be derived from the unknown sample; it can therefore make its own genuine contribution to the determination of its position within a set of known groups. Studies of the primate genus Daubentonia are good examples. Data from samples (albeit very small) of specimens of Daubentonia demonstrate their uniqueness among all other primate genera (119). With single specimens, however, extra care is necessary. A spurious result was obtained for Daubentonia when only a single specimen was available (14). This problem is especially marked in dealing with fossils. Thus initial treatment using multivariate statistical methods (58) seemed to confirm an intuitive view of the Olduvai foot (56), that the foot and thus the talus of the fossil were similar to man’s. But further studies taking into account the problems of interpolation show that the Olduvai talus is not like that of man but is similar to those of some living and fossil apes and monkeys (104, 105). A return to the remaining elements of the Olduvai foot shows that they, too, confirm this new picture; the initial realignment of the fossils into an arched foot resembling that of man was incorrect (125).

SOME PROBLEMS SPECIAL TO MULTIVARIATE STATISTICAL MORPHOMETRIC METHODS

So far, the various multivariate statistical approaches for handling measurements are the morphometric techniques most fully developed for use in real biological situations. [Blackith & Reyment (25) provide an excellent series of examples that run throughout biology.] These approaches have been subjected to criticism, some of which is significant, some spurious. “Evidently,” writes Hershkovitz [(81), p. 64],
"the more extensive the mathematical interventions, the more complicated become the statistical analyses, and the more sterile, futile, and unrealistic their results." And it is sometimes suggested (e.g. 108) that, because multivariate statistics are so complicated and so selectively affected by the precise ways in which they are used, each analysis by each separate investigator provides a different result. Lovejoy (108) asks, not unreasonably, which result are we to trust?

However, it can be shown rather easily that for a given problem, markedly similar results are often achieved despite different investigators, different measurements, different specimens, and even, to a degree, different groups of animals. An example is available for the primate forelimb. A single group of investigators obtained the same result in three separate investigations (study of sets of nine, eight, and seventeen dimensions of the shoulder). Their result has been replicated in the same laboratories by three investigations of other forelimb parts (123, 124). Finally, the same results have been obtained by independent investigators working by chance upon the same anatomical areas of the forelimb [(49, 67), both summarized in (124)]. Similar correspondences are demonstrated (124) in separate studies of the pelvis (113, 119, 196) and foot (58, 104, 105).

These replications show that the multivariate statistical method can be remarkably robust. Yet Lovejoy's assertion that different analyses sometimes produce different results is indeed sometimes correct. When discrepancy exists, however, we should not automatically reject the analyses; we should try to discover what has gone wrong.

Albrecht (personal communication) gives a good example here of the way an incorrect use of the method can produce an incorrect result. On the basis of multiple discriminant function analysis of a set of mensural data, Callithrix was thought to comprise three subgroups. C. humeralifer was believed to be intermediate but to tend more closely toward C. jacchus than toward C. argentata (46). The scale of the separations between these groups (30 standard deviation units) provided the warning that Albrecht noticed; it is most unusual indeed to obtain such large-scale differences among objects as closely related as putative subspecies or racial variants. Albrecht's reexamination of the data [communicated briefly in (124)] showed that the groups cannot be distinguished with statistical significance by the combination of the particular dimensions reported.

A spurious increase in degrees of significance is a not uncommon phenomenon in multivariate statistical analyses. It may result from causes other than the above. It may occur when an investigator ignores a fundamental prerequisite of the use of multivariate statistical analysis, that the variance-covariance matrix be approximately even. Thus it seems that when dimensions of individual teeth are included in analyses together with dimensions of jaw and face, there is sometimes a marked disparity between the variance-covariance matrixes of the two sets of dimensions within closely related groups. This matrix imbalance may produce artificially large differences (sometimes of the order of 20–30 standard deviation units). I have now noted this effect in four studies that combine dental and jaw dimensions (for man, macaques, lions, and deer). Separations of the order of hundreds of standard deviation units have been reported for the combination of dimensions of jaws and teeth.
of subgroups of man, a degree of separation likely to be spurious and presumably the result of similar mechanisms (24).

It is also worth recording that although the packaged programs for many multivariate statistical procedures are useful, some or parts of these analyses can easily provide incorrect results. Thus the misclassification tables set up by many of these programs provide far too high a probability figure for the inclusion of individuals within groups; this can be seen by scanning some of the generalized distances also provided by these programs. Because investigators in systematics and evolution sometimes rely upon such tables, drawing attention to this point seems worthwhile (Aitchison, personal communication). Modification of the way these tables are drawn up may yet provide us with a most useful tool.

One further comment about statistical significance in morphometrics may be in order. Although most investigators recognize problems of statistical significance and probability, this understanding is sometimes forgotten when discussing results. The pattern in a dendrogram is only as good as the statistical limits of the distances used to construct it. When the differences between items (whatever they may be) are as great as ten, twelve, fifteen, or more units (standardized in some fashion to the variance of the groups), then there will be little doubt about the picture presented by a given dendrogram. But when the distances between groups are as small as one to three units (measured in the same way) then, whatever the pattern presented by a dendrogram, and however good the overall significance, the lability in the system makes a number of other dendrograms possible. In at least one example drawn from the literature almost every possible dendrogram is as likely as the one that was presented (124).

However, misapplication of the multivariate statistical method is not the primary reason that independent analysts obtain differing results. The discrepancy usually depends on either (a) the inclusion of different data by different investigators, or (b) the exclusion of parts of the multivariate result from the conclusions of different investigators.

Thus the apparent difference between the results of multivariate studies of the pelvis (113, 196) and shoulder (49, 119) are due to the inclusion of more morphological information by the respective second set of investigators. This is clearly evident because the result obtained by the first investigations is replicated in subinvestigations of the second studies (124).

Likewise, apparent differences in conclusions may result from exclusion of part of the multivariate-statistical result. Earlier investigations (58) on ankle bones of primates provide conclusions different from later ones (104, 105, 119) because the former workers (58) based their assessment upon a single canonical axis—only a part of the multivariate result. When the full result as represented in the generalized distance is taken into account, the results of both groups are similar (124); at least approximately similar conclusions should follow.

Yet another problem stems from an overly critical view of some of these multivariate statistical methods. Clearly a blind approach to such techniques should be abhorred. Recently, however, application of these methods has been denigrated because they are not (and given the nature of biological materials they cannot be)
used perfectly. Let me give examples. One precondition of such methods is that data distributions be normal, and the careful worker attempts to test for this where possible. Nevertheless, it has been determined that nonnormality of biological data does not upset the methods to any great degree as long as the nonnormality is not gross and the differences between groups are reasonably large. Another axiom of such methods is that sample sizes should be subequal and greater than the number of variables. The careful worker attempts to meet this criterion if materials allow, but it can be shown in the practical case that the picture presented by the use of such methods may not be significantly distorted if the departures from these requirements are not great and if the differences between groups are already known to be large. The over-reaction is to suggest that the methods should not be used at all if these criteria cannot rigorously be met.

And there is even some lack of understanding of the advantage of using multivariate statistics. We are not infrequently told that if variables considered separately cannot distinguish two groups then variates taken together certainly cannot (81, 148). Such remarks are not only incorrect, but also hide an important fact: There is often much information in the original data that is not known to the investigator exactly because it is contained within patterns of variances and covariances that have not yet been calculated and examined. Two variables taken singly may not separate two groups, but when taken together they may indeed separate the groups. The multivariate statistic certainly cannot "create" anything, but it certainly can reveal totally new information to the investigator.

A final problem besetting many multivariate statistical approaches to morphology results from considerations of size. The fact that animals are of different sizes, and that some aspects of shape seem to be size-dependent and others size-independent (in statistical senses), has led many investigators to exclude size because it seems to be such a nondescript factor. This has been attempted by carrying out various allometric "corrections" that remove both size itself and all aspects of shape that seem to be correlated with it. But the fact that some aspects of shape are correlated with size does not mean they are size.

It is becoming clearer and clearer that size-related shape effects are inextricably mixed up with almost every biological feature of organisms that we may wish to investigate (128). Although differentiation between "size" and "size-related shape" effects may be of interest there is no reason to remove size-related shape in order to reveal differences of "real" biological import. Such attempts often leave behind data that are so denuded that they scarcely contain any significant information.

Many earlier suppositions—e.g. that size is contained in a first principal component of a factor analysis or in a first canonical axis of a multiple discriminant study—are now problematical. In early, uncomplicated studies of small numbers of groups, size and other aspects of shape correlated with size do seem to have appeared in individual axes (93). But in multivariate studies involving many groups, large samples, and secondary variables, size-related shape effects may be far more complicated, may be involved in many multivariate axes, and are in general badly dealt with if attempts are made to separate them (and all the other features correlated with them) from the rest of the data.
One useful way of dealing with size effects (so that it is understood what has been done) may be through the elimination of those simple parts of size that relate to isometry. This is, of course, what is achieved by the use of ratios. Ratios may pose difficult problems for multivariate statistical methods because of the curious distributions that they sometimes possess (17); but given that such problems can be overcome, they may not be a bad way to deal with simple size. The factors discussed above may explain why studies using ratios have been so successful in the past.

CONCLUSION

We can now characterize and compare, by a wide variety of methods, many biological forms and ask what relationships we can see among them. The resulting answers may suggest new systematic arrangements of known forms, provide for better placement of unknown forms, and affect our assessment of possible phylogenetic relationships.

Such relationships may be suggested by investigations that look at aspects of form and pattern without regard to biological principles. Much that is valuable may come from such "hypothesis-free" approaches, even though some parts of the data may confuse the picture presented by others. Such relationships may also be determined by using more restricted data based upon prior phylogenetic hypotheses; but such results will be channeled by the prior hypotheses (which may of course, be wrong).

Morphometric methods may also prove valuable to systematics and evolution by testing other hypotheses about geographic variation and racial affinity. An excellent review of the major methods and problems in this area is presented by Thorpe (175).

Understanding ontogenetic changes in structure is usually revealed by experimental investigations in particular groups of animals. But morphometric observations of structure in many different species may reveal a group's underlying ontogenetic patterns or channels; in this way multivariate morphometrics may provide interpretative materials for systematics and evolution. Its use for modeling biological growth and development is particularly valuable (45, 85, 95, 171).

Studies of functional adaptation of animal form also help interpret relationships among structures. Like direct ontogenetic investigations, direct functional or biomechanical studies are experimental and can usually only be performed upon an infinitesimal "selection" of the animals of interest to systematics and evolution. Such information is of vital importance in providing overall pictures of the nature of biomechanical adaptation to function. On the other hand, morphometric methods may well allow large selections of animal forms and patterns to tell for themselves, as it were, something of their functional adaptation.

Finally, morphometric methods may be applied to structures other than the real, three-dimensional forms of animals. The structure of population interactions, of physiological variables, of ecological and environmental parameters, of temporal paleontological sequences, and of the arrangements of biological taxa are some of the structures whose analyses by morphometric methods contribute to systematics and evolution. (I have made no attempt to review this fascinating, wider field.)
Now is not the time for a summary of the contributions of morphometrics to thought in systematics and evolution. In spite of the very large bulk of morphometric work now being done, the approach is generally too young and the newer methods currently too little used to make the kind of impact upon systematics and evolution that, for instance, several hundred years of light microscopy or several decades of electron microscopy have made upon cellular biology. What this review makes clear however is that we have begun to apply to the investigation of biological structure many fascinating tools that promise to make major inroads into the problems of systematics and evolution.

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