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ABSTRACT

This review, invited by Paleobiology, presents an overview of some of the general techniques available for the analysis of morphology, concentrating on some recent advances in statistical estimation of the deformation of shape. These featured methods graphically utilize homological congruence in form as a means for morphological comparison. Robust statistical methods, such as repeated median techniques, can be employed in order to effectively identify localized regions of shape change.

INTRODUCTION

Morphological or phenotypic variation may in fact only account for a fraction of the genetic variation that controls heritable differences among species (Stebbins and Ayala, 1981; Schopf, 1981) or even bring about the act of speciation. However, paleontology, accustomed to dealing with problems of incompleteness and overcoming inferential hurdles, is founded on comparative morphology. It not only needs to account for the differences that may distinguish basic units of evolutionary change, but also must attempt to link sequential parts of these changes by statements of similarity; i.e., measured similarity.

The current popularity of the cladistic approach has attracted many to the problem of measured comparison. In fact similarity coefficients derived in our present method may be used to express phyletic relationships, although this is not the immediate purpose of this method. In our opinion, many of the present methods based on discrete characters for comparing morphologies suffer from the severe limitations imposed by the categorical imperative, the assumption that character definition is independent of the evolutionary relationship it seeks to describe, and that the characters themselves are as functionally discrete as their definitions suggest.

In this review, we wish to call attention to some of our analytical concerns, such as mentioned above, however, its primary purpose is to describe some recent advances in the statistical estimation of the deformation of shape that graphically utilizes homological congruence in form as a means for morphological comparison. We believe that such visual and quantitative estimates of morphological change will help to describe evolutionary change.

We will conclude that simultaneous measurement and estimates of difference must be founded on conservative changes in homologous proportions and concepts of functioning design in order to be most successful. Always there is the problem of interpreting the fundamental design elements of organic architecture so that one makes the numbers that represent measurement behave like the curved or irregular pathways of structural equilibria. We realize that practical solutions to construction problems using proportions derived from straight line segments and Euclidian logic existed and were used for defining shape for 2000 years before irrational numbers or the computer came into existence. We, like others, struggle within these constraints. However, we wish to point out the limitations of using conventional cartesian space and suggest theoretical avenues that may help to overcome the age old problem of measuring and comparing curved and crooked objects with straight lines.

LIMITATIONS IN PAST STUDIES

The failure or indecisiveness of many past evolutionary studies in paleontology was in part due to the lack of adequate measurement of changing structure. Structure in this sense includes the consideration of the effect of material on shape as distinguished from that of changing form as a shape abstration. The use of calipers to measure relative size may be sufficient for some purposes, but these straight-line distances say very little about the reaction pathways of functional stress that cause most skeletal structure to resist failure and to survive using materials that have real and different tension and compression coefficients. Certainly such measurements indicate a level of variability, including that which is necessary for selection to take place, but they and their statistics may simulate actual adaptive reactions about as well as a tailor's dimensions discriminate among potential olympic contenders.

Most of the morphometric techniques that have become established in evolutionary and systematic research reflect the atomistic philosophy of particulate genetics and the positivism implicit in the Modern Synthesis of Huxley (1963). Changes in morphology were considered as the results of single gene effects and their mutations which ultimately led to inductive covariant estimates from similarity matrices. Simple linear measurements were considered to subsume and differentiate gradual overall trends (Huxley, 1932; Imbrie, 1956; Gould, 1966). These allometric approaches were expanded into multivariate analogues with the assumption that imperfect sampling would be covered by nonspecificity in either the direct single linkage or pleiotrophic effects of genes (Sneath & Sokal, 1973; Blackith & Reyment, 1971). A more Eudoxian or Platonic approach was taken by Raup (1961, 1966) who approximated molluscan shell accretionary growth, in order to *define* the limits of "morphologic space", by comparing real proportions in shape to variations in ideal geometric figures (following the method, if not the example, of Cook, 1914).

Despite a very high degree of popularity, D'Arcy Thompson grids have advanced little since their original proposal in 1915 (expanded on in 1917, 1942). In many respects this is a prime example of a methodological "dead-end", though a wonderfully elegant one. The problems associated with the grids can be summarized as follows.

First, a major limitation of the Thompsonian approach is that it treads on philosophically vague and uncertain territory. Because a rectangular grid is initially fit to one morphology and then deformed to fit another, the result is to imply a deformation of mathematical space with a constant morphology. This is illustrated in Figure 1. The circle shown in Fig. la remains constant throughout all figures. The mathematical space has simply been altered from top to bottom. This allows or forces the observer to perceive different parts of the circle from different relative positions resulting only in the apparent deformation of the object.

Furthermore, the Thompsonian approach is based on the inference of a uniform and gradual morphological development with stable and hypothetical intermediate steps, often used to illustrate the transformation; see Thompson's (1915, pp. 885-888) discussion of Archaeopterix and Apatornis. It can be suggested, however, that many intermediate steps are functionally unsatisfactory because of secondary reactions and problems analogous to evolving a fourth leg on a three-legged stool. This instability is apparently the rule for the architectural design of ostracodes (see Benson, In Press A) and is probably so in other organisms. Consequently transitions will often be quite abrupt reacting to both genetic input and environmental stresses which produce field deformation. If this begs the question of "hopeful monsters" as stated by Frazzetta(1970), so be it.

Finally, probably the greatest difficulty with the

Thompsonian grids is the need for a generally complete, uniform, and perhaps symmetrical transformation. To quote Thompson (1915, p. 861). "... it is essential that our structure vary in its entirety, or at least that 'independent variants' should be relatively few." Although it may be true that whole structures often vary together as a result of a high degree of morphological integration (c.f. Olson and Miller, 1958), many, if not the majority, of transitions between closely related forms will involve localized deformation. This is especially true for growth series, sexual dimorphism and specialized adaptation. Yet D'Arcy Thompson grids apparently also fail whenever change is substantial; Lull and Gray (1949) found that transitions within the ceratopsian dinosaurs necessitated overly complex or impossible grid deformations.

THETA-RHO ANALYSIS

An alternative technique, Theta-Rho Analysis (the name is derived from vector components), has been developed to address, identify and deal with the problem of localized deformation. As first proposed (Benson, 1967), TRA was a coordinate-graphical tool for the study of ostracode shell morphology. Using a standard reference point for the comparison, a conservative muscle-scar or the center of form (the center of gravity of some authors), all points of interest (shell outline, muscle scars, nodes, etc) were located on a polar coordinate system by their angle from the reference point (using a standard orientation), known as Theta, and the distance along that vector, Rho. The technique was successfully used for comparison of shape changes in fresh-water ostracodes with some taxonomic and ontogenetic trends noted but not quantitatively estimated.

Following this study, a major advance was made by Sneath (1967) who recognized the need for a more rigorous quantitative approach to shape analysis. His technique utilized a number of homologous points (h-points) and those of two morphologies were optimally fit using a least-squares algorithm. Sneath's approach was combined with the original Theta-Rho technique by Benson (1976a, 1977) who used constellations of conservative pore-conuli (extensions of the nervous system) in ostracodes as h-points. The results of the study of the genus Costa (Benson, 1976a,b,c; 1979) helped document the biodynamical (ostracodal) changes associated with the Messinian salinity crisis.

Theta-Rho analysis has been refined further to its present state through the introduction of even a "robust" statistical method, principally through the repeated use of medians as the principal statistic combined with the ability of fitting of the h-point matching to also indicate the transformation of the outlines and other structural features. This method, called Resistant-Fit Theta-Rho Analysis (RFTRA), has been applied to primate skulls Siegel & Benson (In Press), ostracodes (Benson, In Press A) and even the caricatures of Leonardo da Vinci (Benson, In Press B; also see Siegel, 1982, Siegel, Olsham & Swindler 1982).

To illustrate the basic process of RFTRA the famous drawing of Leonardo da Vinci (Figure 2; Benson, In Press B) has been taken apart and then reassembled by the computor allowing for the lack of change in conservative structures (body) while the movement of the limbs is indicated by vectors. The application of RFTRA and a subsequent cluster analysis to a series of caricatures (Fig. 3), probably best attributed to Leonardo, allows a "phylogeny" to be constructed for the individuals; fortuitously, the nun and the pope are shown to demonstrate the highest similarity (see the detailed discussion in Benson, In Press B).

RFTRA has been applied, in an exploratory fashion, to various problems in craniometry. For Example, the figures analyzed by Sneath (1967) for the chimpanzee Pan troglodytes and three hominid species were reanalyzed using RFTRA. The results (Figure 4A-C) show the facial features to be far more conservative while the major changes are concentrated in the region of the maxilla and in the cranium, reflecting the latter's great expansion. Also, RFTRA results were compared with those of Bjork analysis (see Enlow, 1975), an important technique used for the positioning of dental elements in orthodontic treatments (see Figures 4A, C and D). The results demonstrate a considerable refinement to those of Bjork analysis, which utilizes only a single base line (from the sella turcica to the distal end of the nasal bone) for its fitting.

RFTRA is performed using the following steps. A more detailed account, including equations and proofs is given in Siegel and Benson (In Press).

1. Using scanning electron micrographs or morphological drawings, the h-points are selected (25 to 30) and an arbitrary

track made from the first to the last. The h-points are then digitized in this order for each specimen and the coordinates recorded. Then evenly spaced series of points, continuously recorded, indicating the outline or other structural features of interest, are digitized and stored as separate strings of data. For ostracodes, the outline is usually digitized using from 300 to 700 points. This process is repeated for each figure or specimen (we are presently using a Tektronix 4052 graphics computer with accessory peripherals). Our analyses usually are made with from seven to twenty specimens.

2. A quick least-squares analysis of overall h-point fit for all possible pairs of specimens is first run to find the approximate relative fits within the group. The average difference in vectorial distance in h-points between each of the pairs of test shapes is given in order to determine the order for the RFTRA. For phylogenetic studies, the comparison between all forms made in this way can provide a distance matrix for further statistical manipulation using standard phenetic or cladistic techniques.

3. To fit one figure onto another with homologous points, the best match among those parts with the greatest degree of correspondence in proportions can be obtained by altering (transforming) the size, orientation and position (but not the shape) of one of the figures to match the other by the following steps:

To adjust the figures to the same size, a scale factor is calculated by first deriving all of the proportionate distances of corresponding h-points of one figure to the other using all possible combinations of these different proportions; i.e., for proportions between the first pair of h-points and each from all the rest, then the second and each of all the rest, etc. This describes a matrix of values representing a network of proportionate distances between all corresponding h-points of the two figures. However, for each time these proportions are taken of one of the h-point pairs to all the others, the resulting values are ranked from lowest to highest and the half-way value (median) is selected. Consequently, one ends up with as many medians as h-points. Then these median values are ranked and a second or summary median is selected that represents them all. This derivation of the repeated median has the effect of arranging the relative distances of corresponding h-points in order with those of least difference being preferred, so that if most of each of the two figures have nearly the same proportions (tends to be isomorphic), the value selected will represent this correspondence in proportion.

The angle needed for rotation of one figure to fit the other is estimated the same way. In this step the repeated median of difference in angles (using the difference in bearing angles made by a ray from one h-point pair to another) is calculated among all possible homologous pairs of such angles. After rotation and adjustment in size using the compensating angle and scale factors, a shifting or translation of the resulting figure is performed in order to superimpose or register it on the other. This is done by moving the figure an amount derived from estimating the ranked median differences of the $\underline{x}$ and $\underline{y}$ coordinate values of the respective h-points of each figure. If the pairs of h-points are then connected by lines in the form of arrows, the result is a set of vectors indicating the relative change in proportions or deformation of the figure.

4. The final step is to use available graphics capabilities and the translated coordinates of the outlines of the morphological figures to produce a representation of the two morphologies superimposed. If desired, smoothed (locally averaged) or unsmoothed vectors can indicate the displacement of the h-points and consequently visually quantify the deformation. Inspection suggests which h-points vary significantly, and therefore, where the major deformation is concentrated. Consequently, the analysisist can examine the area of best fit, the area of deformation, or the effect of the whole. The superimposed outlines give further data on the differences of the morphologies. Theoretically, further quantification is possible on these data either by calculating distances between additional homologous points or at standard angle measurements on the outline and/or other features. This has yet to be applied, however. Localities of either the area of best fit or of deformation can be reexamined quantitatively and separately after the first stage of analysis has been completed.

A least-squares approach will follow the same methodology through step 2. The magnification factor and rotation coefficient, as well as the translated coordinates are all estimated using an algorithm that minimizes the squared differences between the two sets of h-points (Sneath, 1967; Siegel and Benson, In Press).

Figure 5 illustrates the different results that can be obtained using RFTRA and least-squares approaches on two simple two dimensional polygon shapes (Figs 5a and 5b; deformed hexagon and arrowhead). A three dimensional system is now available (Siegel & Pinkerton, 1982) but not yet tried for complex morphology. The least-squares method (Fig. 5c) distributes the fit throughout the whole shape resulting in an overall or averaged fit without registration of parts. The RFTRA, on the other hand, concentrates on the registration of parts where there are the least or no differences (approaching isometry) and suggests the lack of fit where the change actually occurred. Obtaining the closest matches in a gradational sequence would therefore indicate progressive deformation. Fig. 6 gives an ostracode example using sexual dimorphs (Fig. 6a, male; 6b, female). The RFTRA result (Fig. 6d) shows the major region of dimorphy; the elongation of the posterior region to accomodate the larger male reproductive apparatus. In the least-squares results (Fig. 6b), this is far less apparent. RFTRA is especially effective if combined with a vectorial representation of the translation, the vectors showing the major regions of change (Fig. 6e; see Siegel and Benson, In Press; Benson, In Press A, B). An average vectorial distance and direction can be used as a generalized coefficient of deformation or morphological difference (or similarity if a series is linked together).

The differences between the RFTRA and least-squares approaches can be minimal unless the changes are fairly localized. In the absence of localized deformation the results of the two approaches become quite similar; the distribution of the ordered distance values between h-points shifts from a skewed to a normal distribution and the median and mean tend to converge. Consequently, RFTRA is most effective when applied to comparisons of closely related forms where at least 50% of the h-points come close to registration. In practice it has not yet been a problem to find this probable registration as complex morphological systems tend to deform in a non-uniform manner.

OTHER METHODS

Other methods have become available recently for shape analyses. For the most part they follow two major classes; those that are a general modification of the Thompsonian approach, and those that rely on harmonic signal or optical methodologies.

In the former, we have already discussed the important advances made by Sneath (1967) in the application of least-squares methods to grid-like systems (see also Huffman, et al., 1978; Tobler, 1978). Similar, though variable, approaches are available in the literature on craniometry (see Walker and Kowalski, 1971; Bookstein, 1978). Among the most successful of these types of approaches are by Bookstein (1977a,b; 1978; 1980) and Tobler (1977, 1978; references therein). Both describe change between two forms in terms of unique sets of orthogonal axes (Tissot's indicatrix in Tobler) which suggest the major components of the strain that produced the change. The results can be quite instructive in demonstrating growth gradients (sensu Huxley, 1932) and at graphically illustrating them, especially when combined with vectorial representation. Both suffer from the same problems; a very complex mathematical base that limits the intuitive understanding of the researcher trying to interpret the patterns. Further, neither supplies the distance estimates as coefficients and the superimposed morphologies available through RFTRA. Also, Bookstein's methodology has apparently been applied in past studies, although perhaps not intrinsically limited to using h-points on the exterior outline of the shape with internal interpolation, paradoxically where the gradients are best developed. Both techniques show considerable promise, however, and only further application will demonstrate their full potential.

Most prominent of the latter class of techniques is Fourier analysis. Generally, Fourier analysis can be visualized as an additional step to Theta-Rho analysis as proposed originally by Benson (1967; Kaesler and Waters, 1972). Here, Rho distances for evenly spaced intervals of Theta are subjected to a harmonic analysis; cosine waves of varying amplitude and period are fit to the outline of a shape (Davis, 1973). The resulting harmonic amplitudes and phase angles can be used as direct shape descriptors (c.f. Ehrlich and Weinberg, 1970; Kaesler and Waters, 1972; Younker and Ehrlich, 1977) or they can be used as characters for additional statistical manipulation (c.f.

Lestrel, 1974; Kaesler and Maddocks, 1979; Anstey and Pachut, 1980, Healy-Williams and Williams, 1981). Limitations of Fourier analysis include; the difficulties involved with interpreting and incorporating phase angle data, its general restriction to outlines, and further difficulties that are encountered in interpreting the descriptive results in terms of a non-trivial functional or mechanical reality. Certain types of Fourier analysis have been used quite successfully for functional interpretation by Oxnard (1980), however. A satisfactory alternative may be to apply further statistical analyses to Theta-Rho coordinates (sensu Benson, 1967) in a way similar to the approach of Brower and Veinus (1978).

Other optical and scanning methods are quite common also and will probably become more so as additional technology becomes available, especially from the medical sciences (automatic cell counters and identifiers, etc). Useful reviews and bibliographies are given in Oxnard (1973, 1980) and Bookstein (1978). In general, most of these show a limited but useful potential for paleontological analyses, mostly for removing distortion (see Appleby & Jones, 1976) or providing outlines for studies similar to those discussed above. A possible exception is the technique described by Schooley, et al (1981) for obtaining 3-dimensional or cross-sectional information using stereo micrographs. Although still quite early in development, the potential information available to this technique is extensive and important, especially if combined with some of the other methods described herein.

Finally, despite the fact that Moire' photography can provide useful contour diagrams for shape, the technique has seen very limited application to morphological problems. A notable exception is the study by Takeshita, et al (1978, see also Oxnard, 1980) on branchial convexity in crabs. The developing use of optical scanning equipment suggests that important advances may be possible along this line.

SUMMARY AND CONCLUSIONS

A multitude of morphometric techniques are available or are being developed for the analysis of overall organic shape. All have their limitations and strengths, the most common of the latter being difficulties in visual imagery of quantitatively expressed comparisons of the deformation of shape and in taking the major step from description to functional interpretation. We believe the method presented here, Resitant-Fit Theta-Rho Analysis, combines the best characters of many of these different methodologies. The use of many homologous points based on conservative structural features provides a stability to the results. The use of medians is a major refinement to the approach of Sneath (1967) in allowing more robustness and the easier delimitation of the evolving structures. When used with a strong biological or functional insight, RFTRA provides the means for both visualizing and quantifying transitions. The use of additional vectorial approaches to the former, and other statistical manipulation to the latter enable the researcher to more easily make the step to functional interpretation. We do not see its restriction to closely related forms as a serious limitation because this is where the interesting transitions occur. The shortest transitional distance between two distantly related, complexly organized forms will seldom coincide with the path taken in Nature.

One final note concerns the stress on choice of characters in the application of any morphometric technique. It is the opinion of the authors that the whole organism is more than just the sum of its parts (see Benson, 1981, In Press B). Instead, the organismal equivalent of architecture is present (often referred to as "organic" design in architectural engineering). To properly understand morphology and how it changes, the characters chosen should reflect organically related parts of this architecture and the results interpreted in the light of function. The principle of similitude should be applied as closely as possible so that the numbers of the analysis that represent proportions behave in a way similar to the structure they represent. For example, the characters analyzed by Brinkmann (1929) for Kosmoceras are the standard or conventional characters that have been used by ammonite workers for well over a century. They were not chosen to reflect a specific functional reality for the animals themselves. Although any standard measurement will tend to represent some aspects of the organism 's architecture, those chosen without functional insight will more than likely be associated only marginally with a number of different structural units. That evolutionary trends seen in these characters are often indistinguishable from random walks (Raup and Crick, 1981) is hardly surprising.

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Figure Captions

Figure 1. A demonstration of the consequences of changing perceptual position by deforming mathemetical space using a method similar to the grid system proposed by D'Arcy Thompson.

Figure 2. RFTRA of the classic drawing by Leonardo da Vinci. The different postures shown on the left are superimposed on the right using the dotted h-points. The middle illustration shows complete registration for the medial points and vectorial movement for those on the limbs (from Benson, In Press B).

Figure 3. Cluster analysis (Single linkage) of RFTRA produced similarity matrix for the cricatures of Leonardo da Vinci. The pope and num on the right demonstrate the highest similarities All of the faces are fit along the $\underline{y}$ axis with the $\underline{x}$ axis extended (From Benson, In Press B).

Figure 4. Craniometric analysis of the chimpanzee *Pan troglodytes* and *Homo sapiens* using least-squares analysis (a), RFTRA (b), and Bjork analysis (d). The vectorial changes represented in (b) are shown in (c).

Figure 5. Comparison of polygons by the least-squares (A, C) and the TRFA (B, D) methods. See text for discussion (from Siegel & Benson, In Press).

Figure 6. The application of least-square analysis (c) and RFTRA (d) to a comparison of a male (a) and a female (b) of the ostracode *Costa edwardsii*. The RFTRA demonstrates more clearly the posterior inflation that accompanies the larger genitalia in the male (see the shaded regions; from Siegel & Benson, In Press).

Fig. 1

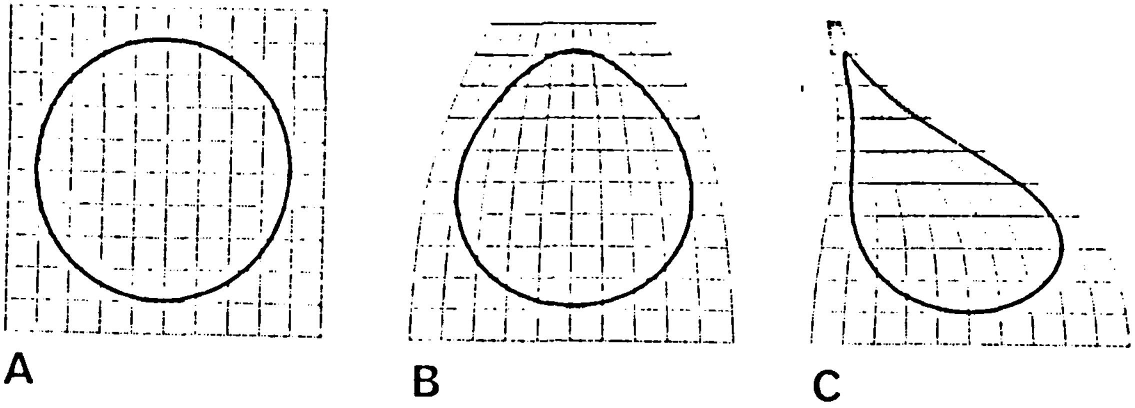


Fig 2

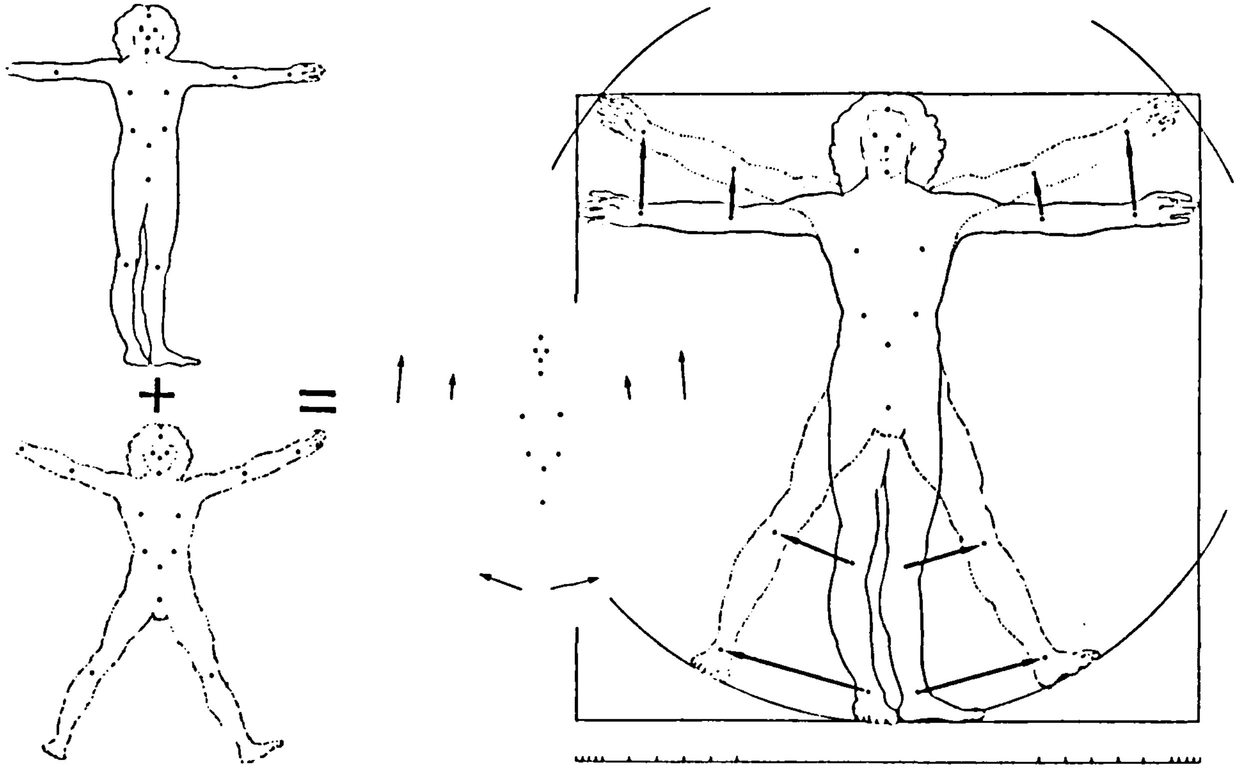


Fig. 3

Fig 4

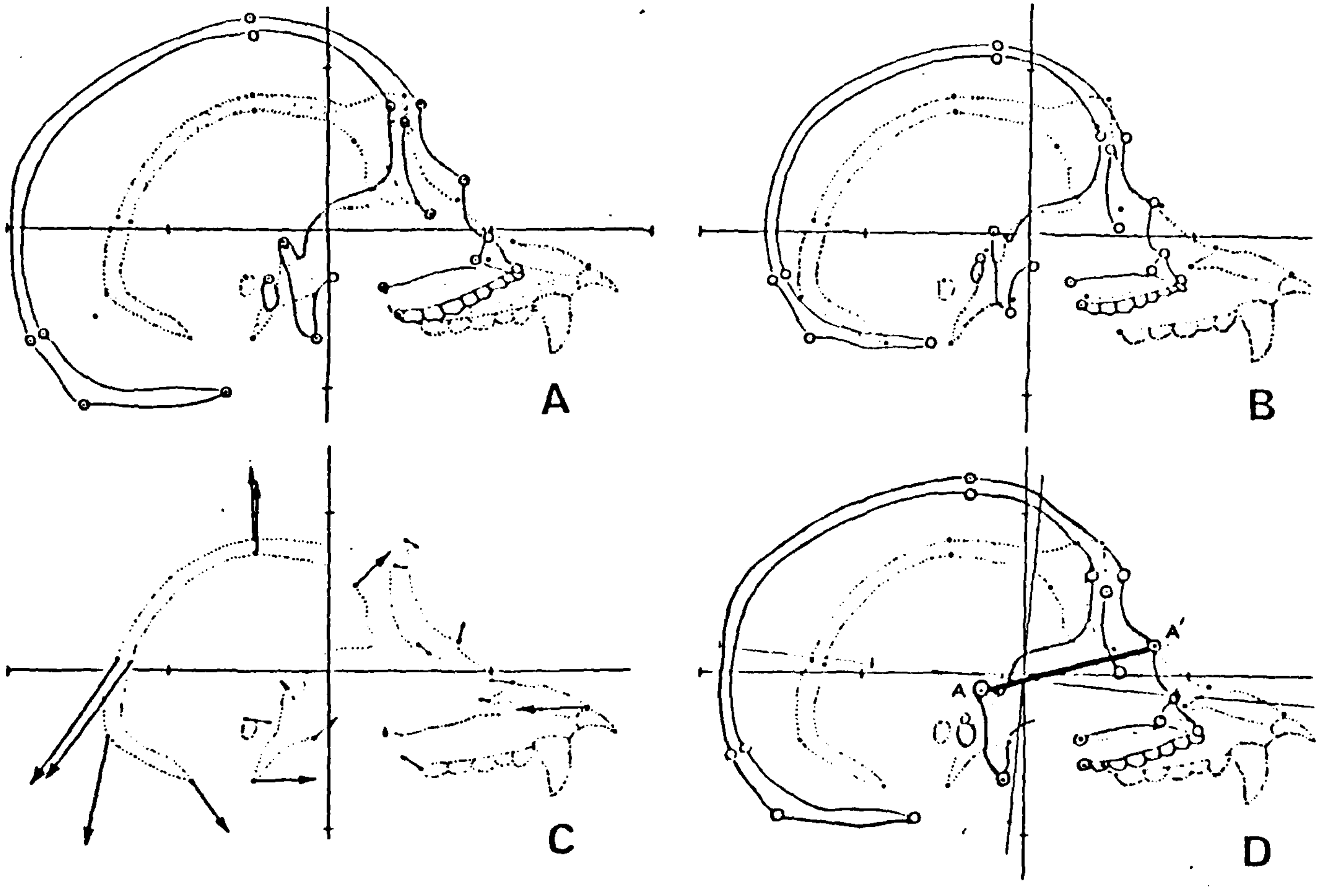
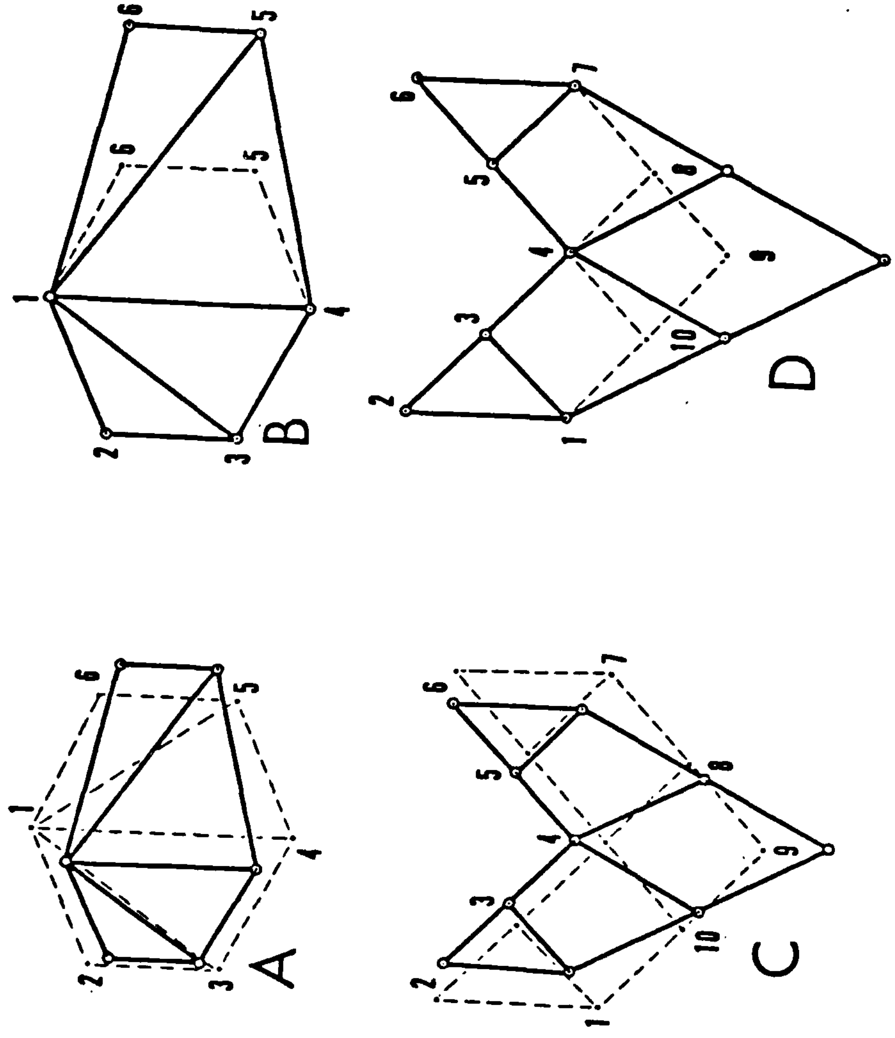


Fig. 5



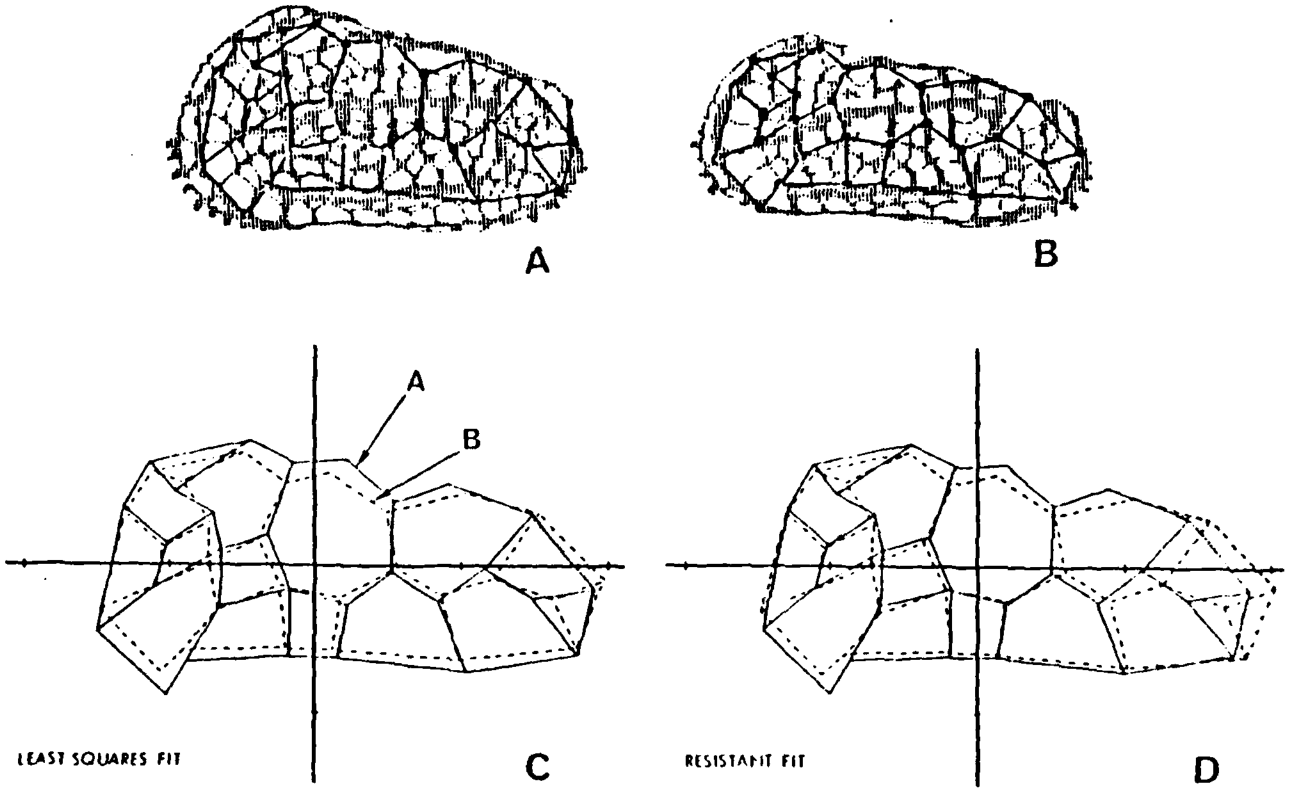


Fig. 6

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8