Orthogenesis of the Hominids: An Exploration Using Biorthogonal Grids

Abstract. In 1917, D'Arcy Thompson suggested that one should study the change from one biological form to another by examining the unique mathematical object that maps between them in accord with biological homologies. Biorthogonal grids provide a particular coordinate system for visualizing such a map and lead to a quantitative syntax in which a change in shape is reduced to differential changes in size. Application of the method to hominid skull phylogeny has demonstrated three principal axes of evolutionary change anatomically homologous over a fossil sequence.

D'Arcy W. Thompson (1) suggested that a comparison of any two homologous shapes be construed as a single mathematical construct, the transformation between them. This transformation is defined to be the continuous map of one shape into the other that sends each point of one image onto its anatomical homolog. Thompson's "transformation grid" visualizes the transformation by its effect on a Cartesian coordinate system superimposed over one of the images (for example, Fig. 1). Empirical grids drawn according to Thompson's principle (2) are elegant, fascinating-and ambiguous. The hope of locating features in these constructions and extracting usable quantities has not yet been realized in the field of theoretical biology. The difficulty, I believe, derives from the formal asymmetry of the method as Thompson demonstrated it. The two outlines are treated divergently. One grid is very highly constrained, being square; the other is a general coordinate mesh whose spatial variation is difficult to report systematically. It is possible instead to treat equivalently the two shapes being compared by computing a special transformation grid, the biorthogonal grid, whose elements intersect at 90° in both figures, so that the two meshes have the same mathematical constraint placed upon them and the formal asymmetry is removed (3, 4).

Let us mathematically model any change of shape as a correspondence between the points in one shape, or "image," and the points of another, which matches all landmark points with their homologs and which is smooth between the landmark points and inside the outline. Assume that both this correspondence and its inverse have derivatives of first and second order with respect to the Cartesian coordinates. It follows that at every point of either image there exist two directions that are perpendicular and whose corresponding directions in the other image are likewise perpendicular. These directions are tangent to a double system of smooth curves, one in each family through each point in either im-26 AUGUST 1977

age, which themselves correspond under the mapping and which intersect everywhere at 90° (5). Orthogonal coordinate systems of this sort are used in other sciences—cartography, differential geometry, continuum mechanics—wherever Cartesian tensors are applied. Except for my biorthogonal grids, I know of no application in which such a system is derived from an assigned empirical distortion.

A computer algorithm such as that which drew the figures shown here approximately locates the lattice of intersections of suitable samples from the two families of integral curves, but it connects the lattice points with straight segments. The two broken lines crossing at any point represent by chord two smooth curves which intersect at exactly 90° both there and in the other image at the corresponding point. The chords themselves intersect more or less orthogonally as the true curves are changing in curvature more or less sharply there.



Fig. 1. The Cartesian transformation grid from *Homo sapiens* to *Proconsul*, drawn after the fashion of Thompson (1).

By reference to the biorthogonal grid, the summarizing of a transformation becomes simple. Since all angles within the grid are unchanging by construction, such change of form as has occurred is a matter of changes of relative curve spacing only, of differential dilatation (stretch) from segment to homologous segment in the two local biorthogonal directions. The ratios of corresponding segments in two images are referred to as the "relative growth" from one to the other. Along any integral curve, these ratios increase or decrease in growth gradients as defined by Huxley (6). For instance, Fig. 2 shows the biorthogonal grid pair for a transform from square to quadrilateral. The two grids correspond point for point between the images. There is a major axis of increase in size, slightly bowed northeast near the line BD. Along it, relative growth varies at a rate graded from 2.2 at one end to 2.9 at the other. These local dilatations are written on the segments of the upper grid, enlarged at right, to which they refer. Perpendicular to this major axis is a minor axis close to AC, with dilatations graded from 1.3 near C to 1.7 near A. Growth rates are greater near point D than near point B, and greater near point A than near point C. The remaining axes and dilatations intergrade. The biorthogonal display allows the summary of this transformation in but two main gradientbearing curves. There is no need to report changes of angle: there is only change of scale, continuously varying in magnitude and alignment. The method of biorthogonal grids has reduced change in shape to differential changes in size.

In computing these curve systems from data, one must know the one-toone correspondence between the images in advance. Matters are simplest if one assumes a correspondence between boundaries and extends it to the interiors in the absence of data there. I have therefore adopted the following strategy. The homology between two images is to be described by discrete pairs of homologous landmarks, such as the corners of the quadrilaterals in Fig. 2. These landmarks may be connected with straight segments to form polygonal boundaries for the images. Along corresponding sides the homology is presumed to be linear. This boundary correspondence is imagined mathematically to distort the inside of either image into pointwise homologous correspondence with the inside of the other. A convenient model for this correspondence is a complex harmonic function, one without "sources" or "sinks" of distortion. Selecting one image as the domain of the coordinate



Fig. 2. (left) Biorthogonal grids for an artificial quadrangular example. The arrows about the lower outline in this and the following grid pairs point to special axes discussed in the text. (right) Enlargement of the upper grid left, with selected dilatations.

transformation, we may define the x- and y-coordinates of the mapping function as separate solutions of the harmonic equations $\nabla^2 x = 0$, $\nabla^2 y = 0$ on that image the Dirichlet problem with boundary values set equal to the real and imaginary parts, respectively, of the homologous boundary points on the other image. The resulting transform, used for all the figures of this report, is smooth and intuitively pleasing. An algorithm approximately solving the Dirichlet problem can be extended to approximate by segments the integral curves of the field of little perpendiculars. Details of the computation have been described (3).

In each grid pair, the spacing of lines in one image or the other is wholly arbitrary. The curves drawn are but a sample from the continuum of integral curves of the little perpendiculars; it is the orientation of these, and the dilatations along them from one image to the other, that embody the analysis. Relative magnification of the images is irrelevant to the geometry, as it alters only the dilatations (by multiplication by a constant). In some of the engridments, there are small regions where the axes are changing direction in an irregular fashion of sharp bends. These regions enclose singularities of the coordinate system, where the correspondence is locally a pure similarity-rotation and change of scale-and where the principal directions are technically undefined. Around such points all pairs of perpendicular directions are equally suited to be axes. One should thread the coordinate curves through by alignment with better-defined arcs at some remove.

Before applying this method to the description of hominid skull evolution, it is necessary to select a common plane projection and reliable landmarks upon it whose relative displacements fairly summarize the continuous homology. I selected the midsagittal plane (the head's plane of symmetry) and seven landmarks that I could locate in drawings: the frontmost incisor, the rearmost molar, the auditory meatus, the inion or occipital protuberance, lambda, bregma, and the nasion or bridge of the nose (Fig. 4). I noted the coordinates of these points in sections of four craniums from the homi-erectus, Australopithecus, and Proconsul (7)-and also, for comparative discussion, a chimpanzee (Pan) (8). These five outlines, together with a "pseudo-Australopithecus," constitute the data to be analyzed (Fig. 3). The biorthogonal displays between Homo sapiens and ancestral forms are shown in Figs. 4 to 6. They embody the transformation to human shape from approximately 15, 1, and 2 million years ago.

The correspondence between *Proconsul* and modern man is shown in Fig. 4. The arrows about the lower diagram in-



Fig. 3. Six hominoid skulls represented by seven-sided polygons whose vertices are landmarks listed in the text. (A) *Pan*. (B) *Proconsul*. (C) *Australopithecus*. (D) *Homo erectus*. (E) *Homo sapiens* sapiens. (F) Pseudoaustralopithecine, modified from (C) as described in the text. Illustrations A through E are drawn from various sources (7, 8).

dicate three selected curves that fairly summarize the diagram pair. The axis 3-6 participates along its length in two growth processes usually reported separately. The dilatations near the bite are less than unity, representing the shrinkage in length of the midface over hominid phylogeny. Toward its occipital end, near arrow 3, the dilatations along this axis are considerably greater than unity. There is therefore a steep growth gradient along this axis, steeper than along any of its orthogonals. The curve 3-6 is not necessarily a strict optimum among all the axes drawn and undrawn for any of the aspects reported. It merely typifies a systematic variation of these curves and the dilatations thereupon throughout its corridor of the diagram.

Perpendicular to this major axis are two other notable axes. Axis 1-5 bears a monotone gradient from .88 at the lower end to 1.1 at the upper. It represents the change in facial angle by the pushing-out of the orbit from the cranial base. Axis 2-4 is an analog of 1-5 near the back of the head. The dilatations along it are nearly constant, between 1.5 and 1.6; it represents a "vertical" expansion of the braincase at a rate independent of the longitudinal expansion along the major axis. In this manner, the observed shape change from Proconsul to human is described by a smoothly varying pattern of local dilatations along directions fixed unbendingly at 90°. Wherever angles change over finite distances, it is because of differential growth elsewhere in the image.

Now let us skip forward a considerable time to a more recent period of hominid phylogeny, from H. erectus to H. sapiens sapiens (Fig. 5). The irregularity of the curves near arrow 4 is a coordinate singularity of the sort described previously. Near arrow 4 we can draw in any axis; all describe the transform equally well. The expansion of the back of the head is again summarized by the straight line 2-4, just as it was in Fig. 4. The dilatations along this line range from 1.25 to 1.35, smaller than those for Fig. 4, since there is much less change of shape over the shorter term. Likewise axis 1-5 is again manifest, directly pushing out the orbit with a growth gradient between 1.0 and 1.1. Only axis 3-6 has moved slightly. At the bite, as the prognathism of Proconsul has diminished disproportionately, the relative shrinkage which was pulling in point I is no longer operative. The axes for the shortening of the maxilla then terminate farther back, on the tooth row. At the rear of the head, the intersection of this main body axis with the vault is now above bregma rather than below. But axis 3-6 still shows the features that make it useful as summary: greatest variation of growth gradient (.8 to 1.2) and approximate straightness in the earlier form. The exact homolog of this axis can be seen in Fig. 4, beginning just above point 6 but passing above the singularity (inside the five-sided cell) to terminate on the vault.

It would be satisfying if the grids for the change from Australopithecus (Fig. 3C) displayed the same structure. They do not quite. Axis 1-5 runs into the orbit from the mandibular notch as usual; but the homolog of axis 3-6 is bowed, and axis 2-4 is severely bent. Explorations lead me to a "gracilization" of the australopithecine, to wit, moving the auditory meatus forward by .13 of the distance AM in a direction 18° above that segment. This altered outline (Figs. 3F and 6) may be considered a pseudoaustralopithecine from which the robustness of the jaw has been artificially removed by numerical reduction of the ramus.

This gracile australopithecine fits neatly in the sequence of grids between Figs. 4 and 5. Axis 1-5 is straight, pushing out the orbit as usual; axis 3-6 is now the straight line usual in the grid of the ancestral forms, sustaining a steep growth gradient (.87 to 1.33); axis 2-4 (with which the computer program had difficulty, owing to a singularity upon it)



Fig. 4. Biorthogonal grids for the transformation from *Proconsul* (below) to *Homo sapiens*, with selected dilatations. Abbreviations: I, incisor (frontmost); M, molar (rearmost); A, auditory meatus; O, occiput (or inion); L, lambda; B, bregma; N, nasion (or bridge of the nose).

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Fig. 5. Biorthogonal grids for the transformation from *Homo erectus* (below) to *Homo sapiens*.

again summarizes the growth of the back of the head by a dilatation about 1.4. It may be concluded that the australopithecine Sterkfontein 5, which Clark used for his sketch (7), is too robust to fairly represent its grade. Its deviation from the geometric trend, expressed in the idiosyncratically rearward position of the auditory meatus, may be a sizerelated effect, or it may reflect a divergence among the australopithecines, with the ancestor of *Homo* probably closer to the gracile pseudoform.

Although traditional features of human evolution-enlargement of the vault, straightening of facial angle, and so forth-can all be found in these grids, characterization of the evolutionary trend by their three axes corresponds to no conventional craniometric indices. Axis 1-5 approximates the segment from mandibular notch to orbital ridge. Axis 2-4 does not correspond to any conventional end points at all. Axis 3-6 is particularly unprecedented. Not only is neither end point a landmark, but also, the overall length of this segment is not the measure that best indicates a specimen's position in the sequence, but rather the division into two segments according to the intersection with axis 1-5. The lower of these two segments shows negative allometry during hominization, whereas the upper shows positive allometry. Their combination into a single length

would be meaningless. Yet this complex axis—straight in the earlier form and bowed in the later—is always found. The biorthogonal method, geometrically summarizing trends of shape change in all regions of the form, makes it possible to demonstrate their coordination over evolutionary time.

In the biorthogonal grids between H. sapiens and Pan [Fig. 3A and figure 17 in (4)], the same three axes appear. Axis 3-6 is nearly identical to the analogous axis for the transform to H. sapiens from Proconsul and bears a gradient of the same range. The two axes orthogonal to this, 1-5 and 2-4, likewise maintain their positions but have gradients half again as steep as for the comparison in Fig. 4. In fact, the chimpanzee form is derivable from that of modern man by a grid of the same alignments as that associated with Proconsul, by a transform which is nonuniformly intensified, equivalently distorted along the "long axis" 3-6 of the head but steeper and more extreme along the perpendiculars. In traditional terms, the chimp shares the bite-to-lambda distortions of Proconsul relative to Homo but is more prognathic and has a smaller hindbrain height.

The invariance of all these axes over Figs. 4 to 6 suggests that the selection pressures of the last 15 million years have been biomechanically constant with respect to their effects on the shape of the skull in sagittal projection. The axes of successive transforms are geo-



Fig. 6. Biorthogonal grids for the transformation from the artificially gracilized australopithecine outline (below) to *Homo sapiens*.

metrically homologous. The dilatations along axis 1-5 presumably increase the space available for the forebrain at the same time the jaw is shrinking. The dilatations along axis 2-4 represent constant expansion of the hind braincase in the direction causing the least increase in moment about the cranial base. Axis 3-6 seems aligned closely with the main axis of the temporalis muscle in modern man; it may represent the preservation of a fairly constant mechanical advantage for that muscle. As the jaw shortens and the back of the head lengthens, the constancy of this axis ensures the constant relation of temporalis pull to the condyle, mandibular notch, and temporomandibular joint (9).

This analysis cannot prove that the forms I have invoked are in the hominid line. It shows only the rigorous geometric consistency of such a sequence, but it does not explain how the axes are maintained by selection. It is possible that there exist only a few axes along which evolutionary change, specifically size allometry and neoteny, can take place, so that change of form itself is canalized.

Further research with biorthogonal grids should include (i) certain computational improvements-better treatment of singularities, inclusion of data inside the boundaries, extension to solid forms; (ii) application to morphology and systematics in other suitable taxa; and (iii) application to problems of growing form in embryology, orthodontics, and the like. The advantage of the method proposed is great. Measurement of shape change independent of shape itself allows us to construct just those curves along which shape is most significantly varying, instead of having to guess at the appropriate morphometric index in advance.

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References and Notes

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Press, Chicago, ed. 2, 1964), pp. 176–177], who wrote, "The representation of the genus Austra-lopithecus is based on a skull found at Sterkfon-tein in South Africa, Homo erectus on a skull cap and portions of jaws found in Java." The H. sapiens skull is labeled "Modern European" but is otherwise unattributed otherwise unattributed.

- The chimpanzee outline is traced from a photo-graph of the skull of an adult female [figure 79, below, in A. Delattre and R. Fenart, L'Hominisation du Crâne (Centre National de la Recherche Scientifique, Paris, 1960)]
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17 February 1977; revised 9 May 1977

Liquid Chromatographic Analysis of Endogenous Catecholamine

Released from Brain Slices

Abstract. A simple new liquid chromatographic technique has been applied to transmitter release studies in brain slice preparations. This method, which gives direct readings of picomoles of endogenous transmitter released, has been shown to yield reliable results with a variety of brain slice manipulations.

Brain slices in oxygenated physiological buffers retain the metabolic and electrical characteristics of neuronal tissue (1, 2), and such preparations are widely used to study in vitro release of neurotransmitters (3-6). Traditionally, to obtain the requisite sensitivity for release studies, the slices are loaded by incubation with radiolabeled transmitter. We now report an extremely sensitive and simple method for quantitatively determining the release of endogenous catecholamine transmitters and their metabolites from brain slices. The new technique, by measuring endogenous release, avoids one of the sources of uncertainty in radiolabeling methodsnamely, redistribution. For instance, in tissues which contain several transmitter systems, such as hypothalamus, uptake of labeled amines may not be specific to a single neuron type. It is unlikely that endogenous amines redistribute, and hence the new technique may be more specific.

The essence of the method is to utilize a cell slice chamber of small volume, 1 ml or less, and to couple this with the extreme sensitivity of high-performance liquid chromatography (LC) with electrochemical detection. The latter requires only 5- to 10-µl samples of the physiological buffer for analyses. The tissue is equilibrated in the buffer chamber, and then micro portions are removed to give a measure of spontaneous release. Drugs are next added in a 5- to 10- μ l volume, or electrical stimulation is applied. After sufficient release time, portions of the fluid are again removed for analysis of induced (stimulated) release. All samples are injected directly

on the LC column, and no pretreatment is necessary. Quantitative results are obtained by comparison with standard calibration plots. A complete description of the LC equipment and an assay for norepinephrine (NE) and dopamine (DA) with quantitative results in the picomole region have recently appeared (7). [None of the sample manipulations for brain tissue described for the assay in (7) are required in the usage described here; direct injection of samples is sufficient.]

Tissue slices were taken from Sprague-Dawley rats weighing approximately 350 g. After the rats were decapitated the brain was removed, rinsed with cold Yamamoto (8) or Krebs-Ringer bicarbonate (8) buffer, and placed on its dorsal surface on a glass plate over ice. Specific sections were removed bv standard dissection procedures, weighed, and cut with a sharp razor blade into slices about 0.5 to 1.0 mm thick. The average weights of the hypothalamus and a single striatum were 43.7 and 42.1 mg, respectively.

Any style cell slice chamber may be used, although the volume must be altered to accommodate 1 ml or less of solution. In the work described here, a volume of 200 μ l was used in a glass micro test tube with a built-in oxygen bubbler and platinum stimulating electrodes. The cell was immersed in a water bath at 37°C. A convenient chamber for simultaneous electrophysiological and chemical studies has been described by Spencer et al. (9) and could be miniaturized for LC sampling.

The minced tissue was transferred to the chamber and allowed to equilibrate. After 15 minutes, duplicate or triplicate

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