Geometric Morphometrics in Primatology: Craniofacial Variation in *Homo sapiens* and *Pan troglodytes*

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**Key Words**
Morphometrics · Size · Shape · Thin-plate spline · Chimpanzee · Man · Procrustes · Allometry

**Abstract**
Traditionally, morphometric studies have relied on statistical analysis of distances, angles or ratios to investigate morphometric variation among taxa. Recently, geometric techniques have been developed for the direct analysis of landmark data. In this paper, we offer a summary (with examples) of three of these newer techniques, namely shape coordinate, thin-plate spline and relative warp analyses. Shape coordinate analysis detected significant craniofacial variation between 4 modern human populations, with African and Australian Aboriginal specimens being relatively prognathous compared with their Eurasian counterparts. In addition, the Australian specimens exhibited greater basicranial flexion than all other samples. The observed relationships between size and craniofacial shape were weak. The decomposition of shape variation into affine and non-affine components is illustrated via a thin-plate spline analysis of *Homo* and *Pan* cranial landmarks. We note differences between *Homo* and *Pan* in the degree of prognathism and basicranial flexion and the position and orientation of the foramen magnum. We compare these results with previous studies of these features in higher primates and discuss the utility of geometric morphometrics as a tool in primatology and physical anthropology. We conclude that many studies of morphological variation, both within and between taxa, would benefit from the graphical nature of these techniques.
Introduction

The morphology of the vertebrate skull has been an active area of study for more than 200 years. During this period, this field has progressed from the classical descriptive and comparative studies of Owen and Huxley to statistical examinations of size and shape variation within and between taxa [1]. Explicitly quantitative studies of human craniofacial morphology have become more prevalent and increasingly statistically sophisticated over the years [2]. This trend (which is not confined to morphometry [3]) no doubt results in part from the increased availability of computer processing power and statistical software packages. However, from a purely methodological point of view, it is arguable that the development of morphometrics also arises from the recognition that the statistical study of cranial variation has proven a prerequisite for the formulation and testing of hypotheses regarding the evolution of hominid craniofacial form [4].

Morphometrics — the description and statistical analysis of shape variation and its covariates [5] — is itself currently undergoing what has been termed by some a ‘revolution’ in its methodology [6, 7]. Traditionally, morphometrics has been based on the univariate and multivariate analysis of linear distances, angles, ratios and areas [8]. While there has been some debate as to the relative suitability of uni- and multivariate methodology [9–11], it has been generally realized that multivariate methods offer many advantages to the researcher. These kinds of analysis, while proving empirically useful, were somewhat undermined by their lack of ability to depict graphically the shape differences between forms. For example, it is difficult to picture the actual shape change from principal-component coefficients. Studies of morphology using techniques such as canonical variate analysis routinely lack illustrations depicting the shape differences between groups of specimens (e.g. many of the examples given in Albrecht and Miller [12]). Among primatologists, Oxnard [13] has long advocated the advantages of the visual component in data analysis. However, because of their relative complexity, his ideas have not been adopted by many other researchers. After outlining some new developments in morphometrics, we would like to outline briefly the results of a previous ‘traditional’ morphometric study, the specimens from which form the source of the data for our study. It should be noted that our aim is not to invalidate the results of this original study but to show that developments in the statistics of size and shape offer more intuitive, and indeed more graphical, methods with which to study biological form.

D'Arcy Thompson, Geometry and Morphology

An early attempt to produce a system of geometric shape comparison was that of D'Arcy Wentworth Thompson [14], who developed a method to produce transformation grids in which a square grid is drawn over one form and smoothly deformed to produce the second form. The pattern of grid deformation describes the shape change. However, Thompson failed to state his methodology explicitly and quantitatively. This did not prevent attempts to duplicate his methods [15]. Resulting problems and inconsistencies led Medawar [16] to declare the method 'analytically unwieldy'. Dating from early work on biorthogonal grids [15], statistical techniques have been developed which allow the explicit depiction of the geometry of a given form and the rigorous testing of differences between forms [5, 17]. These techniques have shifted the analytical framework from linear distances to cartesian (i.e. XY) landmark data, thus pre-
serving all aspects of the size and shape of the form under study and allowing depiction of shape change.

Landmark-based techniques have received some use in primatology and physical anthropology. Biorthogonal grid analysis has been used to examine orthogenesis in hominids [18] and sexual dimorphism in macaques [19]. However, this technique has been superceded by newer approaches. One of these, finite element scaling analysis (FESA) [20], has been used widely, despite statistical objections to this usage [21]. FESA is the inverse of a form of analysis widely used in engineering to study strain in materials under loads. Landmarks are connected to form series of discrete finite elements that unite to model the form being studied. For applications in biological morphometry, these units are assumed to have biological meaning. Cheverud and his co-workers have applied this technique to the study of variation in a number of primate species [22–26]. A further analytical method, euclidean distance matrix analysis (EDMA), has been used to study growth patterns in a number of species [27, 28] and has also been used (along with FESA) to examine facial morphology in the Nariokotome Homo erectus specimen [29]. EDMA analyses shape differences between forms by examining all possible distances between landmarks. Further details are given elsewhere in this paper.

Recently Fred L. Bookstein has developed a group of techniques (namely, shape coordinate, thin-plate spline and relative warp analyses) which have generally escaped the attention of the biological community. Reports of these methods have remained in the specialist statistical and biomedical literature [30, 31] and a rather technical monograph [5], with as yet few published applications relevant to the field of anthropology [32–34]. Accordingly, in this paper we review these methods and illustrate their utility with an examination of (a) craniofacial variation in 4 populations of modern Homo sapiens, (b) relationships between size and shape in these samples and (c) differences between Homo and Pan troglodytes. Prior to reporting our study, we provide a brief introduction to what is understood here by ‘size’, ‘shape’ and how one quantifies shape differences between forms. We describe how these components are treated (and partitioned) by the methods of geometric morphometrics.

Statistical Analysis of Landmark Data

Centroid Size. There is much confusion about the exact definition of ‘size’ and ‘shape’ in morphometric analyses in general. Bookstein [35] provides an illuminating discussion of some of the various definitions used in the past, though it should be noted that the very decomposition of form into the sum of size and shape has been questioned [36]. Centroid size, the summed-squared distance of all the landmarks about their centroid, exhibits all the desirable properties of a size variable, in particular that of being uncorrelated with shape under a null hypothesis of zero allometry [37]. It should be noted that centroid size is a geometric measure of size and, while having valuable mathematical properties, may not be the best biological measure.

Shape Coordinates. Given this size variable, how does one quantify shape? Shape can be defined as those properties of a figure that are invariant to changes in position, orientation or geometric scale [5]. To quantify shape for group comparisons or studies of correlations of shape, a number of statisticians [5, 38] recommend the study of triangles of landmarks. Two landmarks are chosen as a ‘baseline’ and are assigned coordinates (0,0) and (1,0), respectively. The remaining n – 2 non-baseline landmarks are then assigned new coordinates relative to this axis using formulae given in Bookstein

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These new coordinates are termed 'shape coordinates'. Note that these variables are essentially identical to the 'Bookstein shape variables' of Mardia and Dryden [38] and the 'Bookstein coordinates' of Goodall [39], though these authors center the baseline at (0,0), giving the two baseline landmarks coordinates of (0,0) and (0,0). All formulations can be easily transformed to Kendall's spherical shape variables [40]. Bookstein [5] reviews the properties of these new derived shape variables. Of particular importance is the fact that, combined over the triangles of a rigid truss, they encompass all possible shape variables (ratios, angles, areas, etc.) that can be derived from the interlandmark distances. The particular choice of baseline is for graphical convenience and analyses of shape coordinates are independent of the choice of baseline, in such a way that for small variation in shape, all analyses result in virtually identical multivariate statistics.

Shape coordinates may be plotted and mean forms calculated (for the purposes of intersample comparison) by simple averaging. In addition, they can be used as variables in many standard analyses (e.g. Manova, clustering and canonical variate analysis). Note, however, that shape coordinate pairs should be analysed together (e.g. by Manova rather than Anova, and multiple rather than bivariate regression) and that one cannot interpret the component axes resulting from a principal-component analysis of shape coordinates (although the technique can be used for ordination of samples in space of reduced dimension). A principal-component analysis approach to the study of variation is provided by the technique of relative warp analysis [41].

Shape coordinates are a measure of geometric shape (sensu Mosiman [37]) as opposed to allometric shape. Allometry can be tested using multiple regression of shape coordinate pairs on centroid size. The proper test for a general effect of varying size on organismal shape is the F test for the equation

\[ S = \alpha + \beta_1 X_1 + \beta_2 Y_1 + \beta_3 X_2 + \beta_4 Y_2 + \cdots + \beta_{2n-1} X_n + \beta_{2n} Y_n, \]

where \( S \) is centroid size, \( X_i, Y_i \) are shape coordinate pairs (\( n \) in number), \( \alpha \) is the intercept and \( \beta \), the slope. Note that this is the inverse of the usual allometric equation (size is here being regressed on shape, rather than vice versa). Bookstein [5] has pointed out that the coefficients of this multiple regression (\( \beta_1 \) to \( \beta_{2n} \)) do not necessarily describe any significant allometry thus detected, and the intercept is meaningless. Examination of relationships of the form \( S = \alpha + \beta_1 X_1 + \beta_2 Y_1 \) allows one to describe the allometry that occurs at a given landmark 'i'.

**Affine and Non-Affine Components of Shape Difference.** The shape difference between any two forms or mean forms can be decomposed into a uniform and a non-uniform component. The uniform (also called linear or affine) component is that part of the shape change that keeps parallel lines parallel (for example, the change from a square to a parallelogram). This uniform component represents global shape change, i.e. change that occurs equally across all landmarks. The non-uniform component represents the remaining change (for example, the change from a square to a kite) and is landmark specific. This decomposition allows the researcher to identify changes localised to specific areas on the form under study. Thus three versions of shape space can be considered – the full shape space, the uniform subspace and the non-uniform subspace. For a sample of forms, the uniform components of variation from the grand mean form can be estimated for each specimen using the formulae given in Bookstein [42]. Like the shape coordinates, all tests on these components should be multivariate. Any deviation of these affine components from circularity (e.g. correlation or differ-
ing variance between the x and y components) indicates a within-sample factor (e.g. sexual dimorphism) which may need explanation. A significant relationship with centroid size (as detected by multiple regression) is evidence for allometry (see above).

In this spirit of Thompson and building on the approach of Sneath [43], Bookstein [44] developed thin-plate spline analysis. Similar to the methods of Thompson, thin-plate spline analysis allows the deformation of a reference form onto another form, resulting in a grid that demonstrates how homologous landmarks on one form are mapped onto the other. The non-affine components of a deformation can be further decomposed to reveal more local or regional scales of landmark change (deformation). In the parlance of thin-plate spline analysis, the component elements of the non-affine deformation are known as 'partial warps'. These are the coefficients for the so-called 'principal warps' (i.e. the potential form change) of the reference form and they give magnitude and direction to the shift in position of landmarks that maps a given form onto the reference. A shape-space metric known as 'bending energy' expresses the level of deformation required in meeting the target form: affine deformation requires zero bending energy, whereas the non-affine components of change require successively larger amounts of bending energy at successively smaller, more local scales of deformation (it takes more energy to move two landmarks that are close to each other than to move two landmarks that are relatively separated). As a basis for thus decomposing any deformation of the average shape, the partial warps use only information about that average. They are not necessarily aligned with important features of the shape change under study. Any rotation of these features might be equally useful for reporting empirical phenomena. Nevertheless, this particular decomposition is often suggestive in craniofacial applications.

Further details of the thin-plate spline and its use in morphometrics are given in Bookstein [5]. It is important to note the difference between deformation-based and superimposition-based methods. Deformation models are characterised by the depiction of the form of one organism as a continuous deformation of another (reference) organism. Superimposition methods (e.g. the Procrustes procedure used in this paper to examine digitisation error) differ in that the homologous landmarks of one organism are superimposed on those of another so as to optimise some measure of goodness of fit [45].

**Within-Sample Shape Variation: Relative Warp Analysis.** Relative warp analysis consists of fitting a thin-plate spline to the deformation of a given reference configuration (e.g. overall sample mean) to each specimen in a sample. Variation among the specimens is described in terms of the variance in the parameters of the spline function, expressed relative to the bending energy or Procrustes distance matrices. Relative warps are principal components of this space and describe the major trends in shape variation within the overall sample [41]. Various forms of relative warp analysis can be obtained by varying the exponential weight for the bending energy metric (β) between -1 and 1. A full exposition of the mathematics behind relative warps is given on pages 136–140 of Rohlf's paper [41]. A value of $\alpha = 1$ corresponds to the relative warp analysis of Bookstein [5]. This results in large-scale features being weighed more heavily than relatively small-scale features and is suitable for searching for growth gradients of the classical Huxleyan type [45]. A value of $\alpha = 0$ corresponds to a principal-component analysis of shape in the Procrustes geometry of shape space. Lastly, a value of $\alpha = -1$ corresponds to a principal coordinate analysis of bending energy itself and is appropriate if the researcher is primarily interested in small-scale phenomena [46].
A 'Traditional' Morphometric Study: Craniofacial Variation in Homo

Luboga and Wood [47] have examined variation in foramen magnum position and prognathism within 4 samples of modern Homo (African, Australian Aboriginal, Chinese and Romano-British). Linear measurements, and calculated ratios thereof, were taken from lateral radiographs in order to examine foramen magnum position and its relationship with cranial size (taken as the geometric mean of 41 linear measurements). No statistically significant differences in foramen magnum position were found between the 4 samples, although they note that the foramen magnum is consistently located more anteriorly in the Romano-British sample. Larger crania were found to have a more posteriorly located foramen magnum. In addition, basicranial flexion was measured using the angle BS-S-FC (fig. 1), while prognathism was estimated using the angles S-FC-AL and S-FC-SN. No significant differences in basicranial flexion were noted, while there was significant relative prognathism in the Australian and African samples.

In this paper we re-examine the dataset of Luboga and Wood [47] using geometric morphometric techniques. We illustrate how the new morphometric methods are of greater utility than the analysis of linear distances and derived indices in the examination of craniofacial variation in Homo, given their ability to allow visualisation of the differences between samples. In addition, we examine variation between modern
Table 1. Landmarks used in the study. Figure 1 gives their location

<table>
<thead>
<tr>
<th>Landmark</th>
<th>Abbreviation</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>Glabella</td>
<td>GL</td>
<td>The most prominent point between the supraorbital arches in the sagittal plane</td>
</tr>
<tr>
<td>Nasion</td>
<td>NA</td>
<td>The junction of the internasal suture with the nasofrontal suture</td>
</tr>
<tr>
<td>Foramen caecum</td>
<td>FC</td>
<td>The anterior limit of the cribiform plate of the ethmoid bone, immediately in front of the crista galli</td>
</tr>
<tr>
<td>Sella</td>
<td>S</td>
<td>The geometric centre of the sella turcica: the estimated intersection of the anteroposterior and supero-inferior diameters</td>
</tr>
<tr>
<td>Subnasospinale</td>
<td>SN</td>
<td>The point at which the tangent to the lower margins of the nasal apertures intersects with the midline (i.e. the deepest point in the fossa immediately below the anterior nasal spine)</td>
</tr>
<tr>
<td>Alveolaris</td>
<td>AL</td>
<td>The lowest point on the alveolar process between the sockets of the two upper central incisors</td>
</tr>
<tr>
<td>Opisthocranion</td>
<td>OPN</td>
<td>The most prominent point on the posterior aspect of the cranial vault in the sagittal plane</td>
</tr>
<tr>
<td>Opisthion</td>
<td>OP</td>
<td>The point at which the internal and external surfaces of the occipital bone meet, on the posterior margin of the foramen magnum, in the sagittal plane</td>
</tr>
<tr>
<td>Basion</td>
<td>RS</td>
<td>The lowest point at which the internal and external surfaces of the occipital bone meet, on the anterior margin of the foramen magnum, in the sagittal plane</td>
</tr>
</tbody>
</table>

human populations and the allometry of cranial shape. Lastly, we illustrate the decomposition of size and shape variation, via thin-plate spline analysis, with a description of craniofacial differences between modern humans and the common chimpanzee. We note at this point that our choice of specimens and analysis (Homo and Pan) do not stem from any particular research agenda but instead are chosen for their heuristic value.

**Materials and Methods**

The following analyses are based on two-dimensional landmark data extracted from 232 lateral radiographs of modern *H. sapiens* and 2 such radiographs of *P. troglodytes*. Details of samples are given in Table 2 and in Luboga and Wood [47]. The African Homo specimens date from recent times (after 1947), the Australian Aboriginal sample dates from the late 1800s, the Chinese sample from between 1823 and 1930, and the Romano-British sample from between the first and third centuries AD [48]. All specimens were judged to be adult on the basis of alveolar eruption of the third molar and fusion of the sphen-occipital synchondrosis. As over half of the material was unsexed, sexes were pooled for all analyses, although it should be noted that there is slight sexual dimorphism in both the African and Romano-British samples [49]. Only 2 chimpanzee radiographs were available for study. However, such is the magnitude of differences in craniofacial form between *Pan* and *Homo* that the comparison of shape differences using the thin-plate spline has a useful illustrative value. The cartesian coordinates of the same 9 landmarks analysed by Luboga and Wood (Table 1; fig. 1) were obtained from the radiographs using a GRAF/BAR® Mark II sonic digitising tablet and the DS-DIGIT program [50]. The appendix provides further details of all public domain programs used in this paper.

Repeatability of data collection was examined using the following procedures: 1 radiograph was chosen at random from each of the 4 *Homo* samples. These were digitised 10 times (twice a day,
Table 2. Crania used in the study, by sample and sex

<table>
<thead>
<tr>
<th>Sample</th>
<th>Code</th>
<th>Male</th>
<th>Female</th>
<th>Unsexed</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>African</td>
<td>AFR</td>
<td>26</td>
<td>27</td>
<td>13</td>
<td>67</td>
</tr>
<tr>
<td>Chinese</td>
<td>CHI</td>
<td>50</td>
<td></td>
<td>50</td>
<td></td>
</tr>
<tr>
<td>Australian Aboriginal</td>
<td>AUS</td>
<td>54</td>
<td></td>
<td>54</td>
<td></td>
</tr>
<tr>
<td>Romano-British</td>
<td>ROB</td>
<td>28</td>
<td>19</td>
<td>14</td>
<td>61</td>
</tr>
</tbody>
</table>

Table 3. Results of examination of possible measurement error

<table>
<thead>
<tr>
<th>Dataset</th>
<th>ε</th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>AFR</td>
<td>CHI</td>
<td>AUS</td>
<td>ROB</td>
<td>mean</td>
</tr>
<tr>
<td>Experienced user (n = 10)</td>
<td>0.003</td>
<td>0.011</td>
<td>0.008</td>
<td>0.012</td>
<td>0.009</td>
</tr>
<tr>
<td>Inexperienced user (n = 10)</td>
<td>0.030</td>
<td>0.096</td>
<td>0.049</td>
<td>0.091</td>
<td>0.066</td>
</tr>
<tr>
<td>All data (n = 67, 50, 54 and 61)</td>
<td>0.020</td>
<td>0.026</td>
<td>0.018</td>
<td>0.022</td>
<td>0.022</td>
</tr>
<tr>
<td>Total data (n = 232)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.032</td>
</tr>
</tbody>
</table>

Error (ε) values represent the mean residual (over the 9 landmarks and n individuals) for a generalised resistant fit analysis for each dataset. See main text for further details; for codes, see table 2.

for 5 days), once by one of us and once by a person inexperienced with the use of a digitising tablet. For each of the 8 trials (4 specimens by 2 observers), the 10 replicates were overlaid on each other using generalised least squares superimposition [51]. All superimpositions were obtained using the program GRF-ND [52]. We constructed a measure of error (ε) according to the equation

\[ \varepsilon = \frac{1}{n} \sum_{i=1}^{n} \sum_{l=1}^{o} d_{l,i}^2 \]

where \( d_{l,i} \) represents the Procrustes distance for a given landmark \( l \) and individual \( i \) from the average configuration, and \( n \) the total number of specimens (or replicates) in the analysis. Values of \( \varepsilon \) were calculated for each of the 8 samples detailed above (\( n = 10 \) in each case), for an analysis of the 4 total samples (\( n = 67, 50, 54 \) or 61) and for the total sample of 232 crania.

Repeatability of the measurement system was found to be satisfactory for present purposes. Examination of the error (ε) values in table 3 gives a mean value of 0.009 units for the experienced user over all 4 trials. A value of zero would indicate perfect repeatability of coordinates. By contrast, the value for the inexperienced user was 0.066 units. This value exceeds that for within-population variability (0.022) and that for total variation in the pooled sample (0.032). Thus, while inexperience greatly increases the potential error in data capture, the error for an experienced user is less than within-sample variation, and well below between-sample variation. We can therefore place confidence in the ability of these data to reflect true differences between samples if, as here, the data are collected by a single experienced individual.

Shape coordinates were calculated for all specimens using the baseline OPN-GL (fig. 1). In all cases, shape coordinates and centroid size were calculated using the program XY [53]. Relative warps and uniform components (\( X_{uni} \) and \( Y_{uni} \)) of variation were calculated from these shape coordinates using the program TPSRW [54] with the grand mean as the reference configuration. A weighting metric (\( \alpha \)) of zero was used. A preliminary analysis included the uniform component of variation. How-
ever, as removal of this subspace had little effect on the results, this component was excluded in the analysis reported here.

Three major analyses were carried out. The first examined variation among the 4 modern *Homo* samples. Differences in skull size were tested for using Anova of centroid size scores, differences in craniofacial shape between the groups using Manova of the 7 non-baseline shape coordinate pairs, and Mancova with centroid size as the covariate. In addition, canonical variate analysis was used both as an ordination technique to show the groups in space of reduced dimension and also to examine the degree of total shape variation between groups. For the second analysis, craniofacial allometry was examined by regression of shape coordinate pairs and relative warps on log centroid size. The final analysis examined the differences in craniofacial form between *Homo* and *Pan* by a thin-plate spline analysis of the mean Romano-British and chimpanzee shape coordinate forms. Thin-plate spline analysis was carried out with the TPSPLINE [55] and VECTOR [56] programs; the former can be used to show shape differences in the manner of a D'Arcy Thompson transformation grid, while the latter program enables partial warps to be displayed as displacement vectors at individual landmarks.

**Results**

*Variation between the Groups of Extant Homo*

Cranial size (as measured by centroid size) varied significantly between the 4 samples \((F = 4.23; \text{d.f.} = 3, 228; p < 0.01)\) with the Australian Aboriginal specimens having significantly larger crania than all other groups (Tukey's honestly significant difference range test; \(p = 0.05\)). The 2 uniform components \((X_{um} \text{ and } Y_{um})\) differed slightly (but significantly) between groups (fig. 2; Manova; Wilks' \(\Lambda = 0.537; \text{d.f.} = 6, 452; p < 0.0001\)). Univariate range tests showed the Romano-British and Chinese material to differ in uniform components from the other 2 samples which, in turn, were indistinguishable from each other (Tukey's honestly significant difference range test; \(p = 0.05\)). These uniform components were not correlated with each other but were
weakly correlated with centroid size ($r = 0.218; F = 5.71; p < 0.005$) according to the equation

$$S = 0.998 + 0.002 X_{{\text{cent}}} - 0.008 Y_{{\text{uni}}}.$$  

Thus, size allometry is associated mainly with a vertical dilation to the chosen baseline.

All 7 shape coordinate pairs varied significantly among the 4 samples, with values for Wilks’ $\Lambda$ ranging between 0.380 and 0.631 (all were significant at $p < 0.0001$; d.f. = 6, 454). Thus, the overall separation between samples was highly significant (Wilks’ $\Lambda = 0.058; F = 26.30$; d.f. = 42, 641; $p < 0.0001$). This separation remained highly significant when the effects of centroid size were removed via Manova (Wilks’ $\Lambda = 0.060; F = 23.95$; d.f. = 42, 635.59; $p < 0.0001$). Figure 3 superimposes mean shape coordinate forms for all 4 samples. The African and Australian samples can be clearly seen to be relatively more prognathous (relative to this baseline) than their Chinese and Romano-British counterparts. In addition, the position of the foramen magnum varies between samples, with the Australian crania being characterised by a relatively low basion and opisthion (fig. 3).

A canonical variate analysis of the 7 shape coordinate pairs resulted in 3 (out of a possible 3) statistically significant variates ($p < 0.0001$). The first variate (accounting for 50% of the between-sample variation) separated the Australian material from all others (fig. 4). The second variate (37% of the variation) separated the African material, while the third variate (13%) separated the Chinese and Romano-British material from each other. The shape differences between the groups have been discussed in the preceding paragraph. The first canonical variate was weakly correlated with cranial size ($r = -0.22; p < 0.01$). The remaining 2 variates were uncorrelated with cranial size.

Discriminant functions derived from the shape coordinates allowed 90% of the specimens to be correctly re-allocated to their sample of origin (table 4).
**Fig. 4.** Scatter of the 4 *Homo* subsamples based on the first two variates derived from a canonical variate analysis of the 7 shape coordinates. ● = African; ○ = Australian; + = Chinese; Δ = Romano-British. Error bars encompass 95% of the specimens within each group.

**Table 4.** A posteriori re-allocation results for 4 *Homo* samples, based on a canonical variate analysis of the 7 shape coordinate pairs

<table>
<thead>
<tr>
<th></th>
<th>AFR</th>
<th>AUS</th>
<th>CHI</th>
<th>ROB</th>
<th>Correct, %</th>
</tr>
</thead>
<tbody>
<tr>
<td>AFR</td>
<td>62</td>
<td>1</td>
<td>3</td>
<td>1</td>
<td>92.54</td>
</tr>
<tr>
<td>AUS</td>
<td>0</td>
<td>53</td>
<td>0</td>
<td>1</td>
<td>98.15</td>
</tr>
<tr>
<td>CHI</td>
<td>5</td>
<td>2</td>
<td>41</td>
<td>2</td>
<td>82.00</td>
</tr>
<tr>
<td>ROB</td>
<td>2</td>
<td>0</td>
<td>6</td>
<td>53</td>
<td>86.89</td>
</tr>
</tbody>
</table>

The overall percentage correctly re-allocated to their sample of origin was over 90%. For codes, see table 2.

**Table 5.** Morphological (unbiased Mahalanobis, lower, and Procrustes, upper) distances between the 4 *Homo* samples

<table>
<thead>
<tr>
<th></th>
<th>AFR</th>
<th>AUS</th>
<th>CHI</th>
<th>ROB</th>
</tr>
</thead>
<tbody>
<tr>
<td>AFR</td>
<td></td>
<td>4.23</td>
<td>4.89</td>
<td>5.23</td>
</tr>
<tr>
<td>AUS</td>
<td>15.8</td>
<td></td>
<td>5.55</td>
<td>6.92</td>
</tr>
<tr>
<td>CHI</td>
<td>12.0</td>
<td>13.2</td>
<td></td>
<td>3.13</td>
</tr>
<tr>
<td>ROB</td>
<td>12.1</td>
<td>19.5</td>
<td>6.46</td>
<td></td>
</tr>
</tbody>
</table>

All Mahalanobis distances are significant at p < 0.0001. All Procrustes distances are multiplied by 100.

was significantly different from the values obtained from 100 randomised analyses (mean of 38.7%; p < 0.01). Table 5 gives the unbiased (i.e. corrected for unequal sample size) Mahalanobis $D^2$ distance between samples. All distances are statistically significant (p < 0.0001). The greatest similarity was between the Chinese and Romano-British samples ($D^2 = 6.46$), while the greatest dissimilarity was between the Australian and Romano-British samples ($D^2 = 19.50$).
In an attempt to explicitly recreate the traditional indices of foramen magnum position and prognathism used by Luboga and Wood [47], shape coordinate pairs were recalculated using the baseline S-FC (fig. 1). A Manova of these coordinates for the basion, subnasospinale and alveolare all revealed statistically significant variation between the samples (Wilks' $\Lambda$ = 0.789, 0.649 and 0.525, respectively; d.f. = 6, 454 and $p < 0.0001$). This implies that there is significant variation in basicranial flexion, and maxillary alveolar and basal prognathism between the 4 samples. The nature of this variation can be seen by examining plots of mean shape coordinates (fig. 5). Basicranial flexion is greatest in the Australian sample (fig. 5a), while maxillary alveolar and basal prognathism are greatest in the African and Australian samples (fig. 5b, c).
Table 6. Relationships between shape coordinate pairs and centroid size

<table>
<thead>
<tr>
<th></th>
<th>R</th>
<th>F</th>
<th>p</th>
<th>α</th>
<th>βx</th>
<th>βy</th>
</tr>
</thead>
<tbody>
<tr>
<td>OP</td>
<td>0.17</td>
<td>3.46</td>
<td>0.05</td>
<td>25.42</td>
<td>2.47</td>
<td>-5.25*</td>
</tr>
<tr>
<td>BS</td>
<td>0.26</td>
<td>8.05</td>
<td>0.001</td>
<td>29.25</td>
<td>3.18</td>
<td>-10.41*</td>
</tr>
<tr>
<td>S</td>
<td>0.26</td>
<td>7.73</td>
<td>0.001</td>
<td>31.43</td>
<td>5.17</td>
<td>-12.43*</td>
</tr>
<tr>
<td>FC</td>
<td>0.36</td>
<td>17.40</td>
<td>0.0001</td>
<td>36.73</td>
<td>11.88*</td>
<td>-14.39*</td>
</tr>
<tr>
<td>NA</td>
<td>0.45</td>
<td>28.70</td>
<td>0.0001</td>
<td>68.12</td>
<td>23.00*</td>
<td>-14.66*</td>
</tr>
<tr>
<td>SN</td>
<td>0.14</td>
<td>2.21</td>
<td>n.s.</td>
<td>25.86</td>
<td>5.34*</td>
<td>-0.98</td>
</tr>
<tr>
<td>AL</td>
<td>0.08</td>
<td>0.79</td>
<td>n.s.</td>
<td>22.58</td>
<td>1.82</td>
<td>1.26</td>
</tr>
</tbody>
</table>

R, F and p are the multiple correlation coefficient, F ratio and significance level for the individual multiple regressions. α is the intercept and βx and βy, the slopes for the relationship. *p < 0.05: significant slopes; all intercepts were significantly different from zero. Degrees of freedom were 2 and 229.

Craniofacial Allometry in Homo

Multiple regression of shape coordinates on centroid size suggests that there is a significant but minor relationship between craniofacial size and shape (R = 0.386; F_{14, 217} = 2.71; p < 0.001). Thus, 14.9% of variation in shape can be 'explained' by size variation. Five of the 7 shape coordinates show a significant relationship with size (p between 0.05 and 0.0001), although it should be noted that the explanatory power of these relationships is slight (r varying between 0.17 and 0.45; table 6). This result is borne out when derived relative warps are correlated with centroid size (table 7). While relative warp I allows some separation of the African and Australian specimens...
Fig. 6. Thin-plate spline analysis of the differences between Homo and *Pan*. Panel a depicts the affine deformation, while panel b shows the non-affine deformation.

from their Romano-British and Chinese counterparts (being a measure of prognathism), overall the resulting allometries, though in some cases significant, are of low explanatory power. We thus conclude that, although there is significant shape variation between the 4 populations examined here, little of this variation can be explained by simple linear size effects.

**Differences between Homo and Pan**

The transformation of *Homo* (Romano-British mean) to *Pan* is illustrated in figure 6. This transformation can be partitioned into affine and non-affine components using the TPSPLINE software. The affine component (fig. 6a) is characterised as:

\[
X_{\text{pan}} = +0.949 \, X_{\text{homo}} - 0.044 \, Y_{\text{homo}} \quad \text{and} \\
Y_{\text{pan}} = -0.201 \, X_{\text{homo}} + 1.032 \, Y_{\text{homo}}
\]
Table 7. Relationships (represented by Pearson’s correlation coefficients) between derived relative warps (RW) and cranial size (as measured by centroid size)

<table>
<thead>
<tr>
<th>RW</th>
<th>All</th>
<th>AFR</th>
<th>AUS</th>
<th>CHI</th>
<th>ROB</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>-0.17</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>2</td>
<td>+0.16</td>
<td>+0.30</td>
<td>-</td>
<td>-</td>
<td>-0.38</td>
</tr>
<tr>
<td>3</td>
<td>-0.24</td>
<td>-</td>
<td>-0.29</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>4</td>
<td>-</td>
<td>-0.26</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>5</td>
<td>+0.19</td>
<td>+0.43</td>
<td>+0.29</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>6</td>
<td>-</td>
<td>+0.30</td>
<td>+0.51</td>
<td>+0.33</td>
<td>-</td>
</tr>
<tr>
<td>7</td>
<td>+0.31</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>8</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

Only relative warps showing a significant correlation at the 5% level (7 of 12) are shown. All refers to analysis of the total sample. AFR, AUS etc. refer to analyses of the subsamples. For codes, see table 2.

Table 8. Principal warps for the thin-plate spline analysis of Pan and Homo

<table>
<thead>
<tr>
<th>Landmark</th>
<th>Principal warp</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1</td>
</tr>
<tr>
<td>OPN</td>
<td>+0.005</td>
</tr>
<tr>
<td>GL</td>
<td>-0.507</td>
</tr>
<tr>
<td>OP</td>
<td>-0.009</td>
</tr>
<tr>
<td>BS</td>
<td>-0.015</td>
</tr>
<tr>
<td>S</td>
<td>+0.058</td>
</tr>
<tr>
<td>FC</td>
<td>-0.267</td>
</tr>
<tr>
<td>NA</td>
<td>+0.801</td>
</tr>
<tr>
<td>SN</td>
<td>-0.144</td>
</tr>
<tr>
<td>AL</td>
<td>+0.079</td>
</tr>
</tbody>
</table>

See text for further details and table 1 for abbreviations.

an expansion in the sella-alveolar axis. The non-affine component (fig. 6b) clearly depicts the increased relative prognathism of Pan, along with the movement of the foramen magnum back (and up) along the cranium. Figure 6b also shows a difference in degree of basicranial flexion (FC-S-BS) between the human and chimpanzee forms.

This non-affine transformation can be further decomposed into partial warps. These describe the difference between the two forms in terms of the possible ways that the initial form (in this case, Homo) can be deformed. These possible deformations are the principal warps for the Romano-British mean cranial form and are presented in table 8. Principal warp 1 represents a relatively small-scale change (which requires a large amount of bending energy: 0.1083 units). For Homo this primarily corresponds to movement of the glabella (coefficient of -0.507) and nasion (coefficient of +0.801) in opposite directions. By contrast, principal warp 6 corresponds to a large-scale change, with many coefficients of similar magnitude (table 8).

Given these principal warps, we can now describe the actual deformation from Homo to Pan – the sum of the partial warps presented in table 9. 'X' and 'Y' in table 9 are the weights for each partial warp to create the total deformation. Thus, for the glabella, we obtain:
Table 9. Partial warps for the thin-plate spline analysis of *Pan* and *Homo*

<table>
<thead>
<tr>
<th>Partial warp</th>
<th>Magnitude</th>
<th>X</th>
<th>Y</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0.218</td>
<td>+0.337</td>
<td>−0.323</td>
</tr>
<tr>
<td>2</td>
<td>0.334</td>
<td>+0.509</td>
<td>−0.274</td>
</tr>
<tr>
<td>3</td>
<td>0.841</td>
<td>+0.914</td>
<td>−0.069</td>
</tr>
<tr>
<td>4</td>
<td>0.355</td>
<td>−0.557</td>
<td>−0.212</td>
</tr>
<tr>
<td>5</td>
<td>4.711</td>
<td>−1.626</td>
<td>+1.437</td>
</tr>
<tr>
<td>6</td>
<td>9.459</td>
<td>+3.074</td>
<td>+0.086</td>
</tr>
</tbody>
</table>

See text for further details.

\[
X_{\text{par}} = -0.507 (+0.337) X_{\text{homo}} \quad \text{and} \\
Y_{\text{par}} = -0.507 (-0.323) Y_{\text{homo}}.
\]

By contrast, the contribution of the nasion to the first partial warp can be seen to be:

\[
X_{\text{par}} = +0.801 (+0.337) X_{\text{homo}} \quad \text{and} \\
Y_{\text{par}} = +0.801 (-0.323) Y_{\text{homo}}.
\]

The landmarks nasion and glabella clearly ‘move’ in opposite directions (+0.801 vs. −0.507), and the changes in x and y coordinate are almost equal but also in opposite direction (+0.337 vs. −0.323). Therefore, whereas the principal warp coefficients (table 8) provide the relative direction and magnitude of possible landmark movement, the partial warp scores (table 9) provide the x and y vectors of this movement for all landmarks.

Table 9 presents weights for all 6 partial warps. As one proceeds from partial warp 1 through to 6, the localisation of the warp decreases while the magnitude (a measure of the importance of the warp to the total deformation) increases. Note that for any given partial warp, the movement of landmarks is parallel (all landmarks share the same partial warp weights) but of different magnitude (landmarks have different principal warp coefficients). As will be discussed later, these partial warp weights can form the basis for further analyses.

The change at the landmarks in the deformation of *Homo* to *Pan* mean forms is illustrated as displacement vectors in figure 7. The salient features of the landmark displacements in partial warps 1–6 are as follows:

**Partial Warp 1** (fig. 7a). This warp displays the most localised change. The nasion is displaced anteriorly and inferiorly (upper facial prognathism) so that the glabella and the foramen caecum are displaced posteriorly relative to this antero-inferior shift of the upper face.

**Partial Warp 2** (fig. 7b). Here the alveolare and subnasospinale move apart, the former anteriorly, the latter posteriorly. Thus, partial warp 2 may be said to show the increased length of the chimpanzee naso-alveolar clivus (subnasal prognathism).

**Partial Warp 3** (fig. 7c). This warp illustrates the prominent glabella in *Pan*. Along with partial warp 6, it illustrates the ‘opening out’ of the chimpanzee cranial base (i.e. lesser basicranial flexion than in *Homo*) and a shorter anterior cranial fossa (dimension FS-C) housing the relatively smaller chimpanzee frontal lobes.

**Partial Warp 4** (fig. 7d). This warp chiefly illustrates the anteroposteriorly narrower foramen magnum in *Pan* compared with that in *Homo*. The opisthion and basion converge.
Fig. 7. Partial warps for the thin-plate spline analysis of the superimposition of *Homo* on *Pan*. Note that arrow lengths on the last partial warp (f) are scaled one fifth compared to those on the other 5 warps.
Partial Warp 5 (fig. 7c). This warp may be termed the ‘prognathism warp’ since it best shows the overall anterior migration of the midfacial region at the alveolare and subnasospinale, along with the relocation of the cranial base at the sella. Such is the dramatic nature of this midfacial regional difference that positions of the upper face as represented by the glabella and nasion adopt a relatively posterior location. We may also note the change in angulation of the foramen magnum (at the opisthion) from the horizontal in Homo to a more vertically inclined position in Pan.

Partial Warp 6 (fig. 7f). Landmark displacements are effectively confined to an anteroposterior direction in this, the most global of the partial warps. This warp shows the posterior retreat of the foramen magnum position in Pan relative to that in Homo.

Overall, the partial warps illustrate the following three major differences between Pan and Homo: (1) an increase in midfacial and subnasal/maxillary prognathism in Pan; (2) a decrease in basi-craniy kyphosis in Pan; (3) a more posteriorly located and obliquely oriented foramen magnum in Pan.

Discussion

The purpose of this paper has been to introduce the use of a number of geometric morphometric techniques for the study of anthropometric variation. We have used shape coordinates and relative warps in the examination of the covariance of size, shape and origin in 4 populations of modern humans and have applied a thin-plate spline analysis to the decomposition of shape differences between Homo and Pan crania. By choosing the dataset from a previously published study, we are in a position to assess the relative merits of newer and more traditional techniques. We begin the discussion by comparing our findings with those of Luboga and Wood [47], showing where our two sets of results concur and where they differ, and we address how the biological interpretations of these two studies are affected accordingly. Finally, we briefly consider further methods not used in this study and suggest areas for future research to which their application would be particularly well suited.

Comparison of Findings: Craniofacial Variation in Homo

Craniofacial Allometry. Under the present definition of allometry we find little indication that the variation in relative landmark positions among the four groups of modern humans is strongly size related, despite the significant group differences in cranial size (as measured by centroid size). Although the highest correlation coefficients we obtain (0.36 and 0.45 for foramen caecum and nasion, respectively) are also the highest noted by Luboga and Wood [47] (their table 4), our results (table 6) suggest that the size-related changes in relative landmark position are more in evidence at the foramen caecum and nasion than at the basion (r = 0.26). In other words, Luboga and Wood’s two variables (BS-FC and BS-NA) may in fact measure change at the foramen caecum and nasion as much as they do that at the basion. If we take these two points as approximate representations of the inner and outer tables of the frontal bone, respectively, it may be that the allometric effects detected in the localised region of the foramen caecum and nasion reflect changes in the thickness of the frontal bone and the development of the frontal sinus in the larger Australian skull [57]. It is worth noting that the regression coefficients obtained by the present study and those reported in Luboga and Wood [47] are not directly comparable. The latter coefficients are of
major axis bivariate regressions on log-log data, with the independent variable the geometric mean of a number of linear measurements of the cranium. This measure of overall cranial size is likely to contain some redundancy and autocorrelation.

**Basicranial Flexion.** Luboga and Wood report no significant differences in basicranial flexion (angle BS-S-FC) between the 4 human samples, although they do note that ‘the estimates of lower facial prognathism were consistently correlated with larger cranial base angles, thus indicating more prognathic faces in the Australian and African subsamples’ [47, p. 72]. In contrast, we found a significant variation in the shape coordinates from baseline S-FC (fig. 6), but no consistent association of basicranial flexion with measures of prognathism. Although the measures are not directly comparable, the study of Ross and Ravosa [58] on the correlates of basicranial flexion in haplorhine and strepsirhine primates suggest that the more likely relationship with basicranial flexion is with brain size relative to basicranial length rather than with facial orientation [see 58, 59 for reviews of the postulated functional and morphological correlates with basicranial flexion].

**Prognathism.** Our findings concur with those of Luboga and Wood [47] that the African and Australian groups are the more prognathous (see above). Their measures of prognathism were the angles S-FC-AL and S-FC-SN. These angular measures, however, provide no information about the relative locations of the subnasospinale and alveolar with respect to the rest of the face and cranium, since in both cases the three points which measure the angle are themselves free to rotate around their centre (foramen caecum) while the position of each triangle of points itself is not known in relation to the rest of the cranium (in fact, each triangle can rotate about any of its three vertices).

**Position and Orientation of Foramen magnum.** Luboga and Wood [47] interpret their results to imply that ‘within modern human crania there is an allometric trend such that larger crania have a relatively more posteriorly located foramen magnum’ (p. 73) since their linear dimensions from the basin to the foramen caecum, nasion and subnasospinale increase at a rate greater than isometry when regressed on their measure of overall cranial size. However, as noted before, this linear dimension could equally well show that the foramen caecum, nasion and subnasospinale are positioned relatively further anteriorly as opposed to the basin being positioned further posteriorly with increasing cranial size. This is because this variable contains no information about the location of either the basin or any of the three terminal points with respect to the rest of the cranium.

Both the present study and that of Luboga and Wood [47] explore foramen magnum position in the sagittal plane. However, as Dean and Wood [59, 60] have pointed out, this takes no account of the position of the foramen magnum in relation to the bilateral structures of the cranial base such as the petrous axes and bitympanic line.

**Differences between Pan and Homo**

Dean and Wood [59] have noted that the basicranium is compressed anteroposteriorly in *H. sapiens* compared with the condition in pongids. This observation is also borne out in the present study by the most global of the partial warps (No. 6). In *H. sapiens*, the anterior margin of the foramen magnum (basion) reaches the bitympanic line, while in the pongids *Pan, Gorilla* and *Pongo*, the basion is positioned posterior to this coronal axis [see 59, their fig. 2]. This relative compression is thought to be related to a reduction in the angle of the petrous axis, a reduction in the length of the sphenoid bone and a rotation of the face beneath the neurocranium [59]. Although the longer
Fongid cranial base results from an increase in growth rate along with a prolongation of growth compared with that in humans, Dean and Wood [61] note that 'no single heterochronic change underlies the differences' (p. 178) between pongids and humans so that the differences cannot be attributed simply to neotony in humans.

**Further Methods and Prospects for Future Research**

We hope that, by this stage, we have demonstrated the utility of the geometric methods presented herein. This 'new morphometrics' is a synthesis of biology, geometry and statistics which has two separate aspects which we believe to be important. Firstly, it allows graphical depiction of variation between two or more forms and, secondly, rigorous statistical testing of aspects of this variation. It is important to note that, in many cases, the results (e.g. re-allocation rates from discriminant analyses, Mahalanobis distance matrices from canonical variate analyses) of geometric analyses will be similar to those of more traditional studies [Lynch, pers. obs.]. However, we are more likely to find differences as we are sampling all possible ratios, linear distances and angles that can be obtained from our set of landmarks [5]. Secondly, our ability to visualise the differences obtained (via splines and shape coordinate plots) is greatly increased.

The techniques of EDMA and FESA have received considerable attention from primatologists and physical anthropologists (see Introduction). While these techniques, and others [62], all form valuable parts of the current morphometric canon, there appears to be some controversy over their relative utility when compared to the spline-based methodologies. Rieunoi et al. [63] outline a number of problems they see in the application of thin-plate splines to morphometrics. They note that bending energy is a non-symmetric function – thus, the bending energy for the transformation of A to B does not equal that from B to A. This is of little significance as the bending energy metric is of limited use in analysis, offering solely a means to decompose the total deformation into its partial warps. In addition, their problems with the visualisation of the results of spline analyses of three-dimensional data appear to be unfounded. Lele has presented EDMA as a cure for what he believes to be a problem with 'coordinate-based' techniques (such as shape coordinate, Procrustes and TPS analyses), in that EDMA is a 'coordinate-free' method, being based solely on distances between landmarks and is thus invariant to translation and rotation. As Rohlf and Marcus [6] note, this is also a property of thin-plate spline, Procrustes and shape coordinate analyses. In addition, graphical reconstruction of forms after an EDMA is only possible using a statistical procedure similar to that used to unfold trusses which thus introduces often substantial error into the resulting depictions [64]. As shown by Bookstein [5], EDMA is of lower efficiency than the core of the new geometric methods for most applications. EDMA results in relatively large numbers \(n(n-1)/2\) of variables for analysis, compared to the \(2n-4\) variables that are utilised in a shape coordinate analysis. Lastly, EDMA can only be used in the comparison of two forms or two groups (in this respect it is somewhat similar to thin-plate spline analysis). There is no EDMA equivalent to relative warp analysis or canonical analysis of shape coordinates. We thus suspect that the technique of EDMA may be of limited use in the majority of problems faced by systematic morphologists. It should however be noted that there have been no published studies contrasting these competing techniques. We are currently contrasting EDMA and spline-based analyses in the examination of variation among primates.

The analyses presented here were confined to a two-dimensional dataset. However, the techniques of geometric morphometrics are equally as applicable to three-
dimensional data, although in many cases the software is still under development. Shape coordinate analysis in three dimensions is a simple extension of the two-dimensional case and is illustrated in Bookstein’s 1991 monograph [5]. Anthropometric spline-based analyses of three-dimensional curves and surfaces have already been attempted [65]. In addition, the statistical theory of ‘edgels’ (features incorporating information about edge direction at landmarks) will soon allow full coverage of two- and three-dimensional form [66]. We can only hope that these statistical tools will soon become available to the research community at large.

In many studies (particularly those utilising fossil specimens), incomplete preservation of specimens results in missing landmarks on individuals. As multivariate procedures (as used in classical and geometric analyses) require complete datasets, these missing landmarks must be supplied by estimation. Traditionally, linear distances could be supplied by multiple linear regression or by direct substitution of the grand mean. Geometric techniques allow a number of ways in which landmark position can be estimated. Shape coordinates can be directly estimated as with the traditional methods mentioned above, i.e. interpolation of the missing ‘x’ and ‘y’ values using regression equations developed from perfect specimens. In addition, landmark positions could be directly estimated using the spline interpolation function.

As alluded to earlier, partial warp scores can form part of additional analyses. Deformations (and thus warp scores) can be obtained for all specimens in a study with reference to a single reference specimen. These partial warp scores can then be plotted (one plot for each warp, one observation for each specimen) and plots examined for clusters, trends etc. This is the approach taken by Yaroch [67] in her study of Neanderthal crania and of Swiderski [68] in his study of squirrel scapulae. Indeed, Swiderski’s approach to studying character transformations along a cladogram would appear to offer an excellent framework for future primatological studies. However, a word of warning is in order. There may be a temptation to use these warp scores in phylogenetic analyses (i.e. analysis via gap-coding and cladistic methodologies). As Bookstein [69] points out, there are difficulties with this approach stemming from the definition of, and requirement for, homology among characters. Although researchers are currently attempting to use partial warp scores in this manner [70–72], we feel that, until extensive simulation studies are undertaken, researchers should limit themselves to using the thin-plate spline to study character change along the branches of an independently derived cladogram, rather than to derive the phylogeny using these techniques. Indeed, preliminary results indicate a number of undesirable properties of partial warp weights as cladistic characters [73].

We believe that the development of geometric morphometric techniques has heralded a paradigm shift in the way form can be quantified. The philosophical basis for many of the techniques can be traced to work in the early part of this century – for example, thin-plate spline analysis to the work of D’Arcy Thompson [14] and shape coordinate analysis to Galton’s attempts to quantify facial outlines [69]. Thus, what we are experiencing is more a gradual evolution than the ‘revolution’ suggested by some [6]. Thanks to the work of software developers such as Rohlf and Slice, applications of geometric techniques have begun to appear in the fields of systematic botany [74, 75], zoology [68, 76] and palaeobiology [77, 78]. The future is likely to see increased interaction between the ‘tool makers’ and ‘tool users’, interaction which is likely to further application of these exciting techniques to the field of primatology and evolutionary biology.
Acknowledgments

We are grateful to Fred Bookstein for answering our questions about geometric morphometrics and his very helpful comments on a number of versions of this manuscript. Linda Nelson and Lucia Yarooh helped with various stages of this project, while Gavin Naylor, F. James Rohlf, Bernard Wood and Gabrielle Macho provided critical reviews of the manuscript. We are grateful to Les Marcus and the other organizers of the 1993 NATO Advanced Study Institute on geometric morphometrics for providing the impetus for this work. This research was conducted while C.G.W. was in receipt of grants from NERC.

Appendix

The public domain morphometric software mentioned in this paper is available via anonymous FTP from LIFE.BIO.SUNYSB.EDU in the subdirectory MORPHMET. All programs are for IBM compatible PCs and use the same input file format. Regular upgrades of these programs are announced on the biological morphometrics bulletin board MORPHMET. To subscribe, send a message with the line ‘Subscribe morphmet “your name”’ to LISTSERV@CUNYVM.BITNET. Readers with World Wide Web access should set their WWW programs to ‘http://life.bio.sunysb.edu/morph/morph.html’ for further details on all of the above.

**DS-Digit** was written by D. Slice (State University of New York, Stony Brook) and is a generic digitiser interface for the collection of two- and three-dimensional coordinate data from most makes of digitising tablet.

**GRF-ND** was written by D. Slice (State University of New York, Stony Brook) and carries out Procrustes analysis of two- and three-dimensional data in accordance with the algorithms presented in Rohlf and Slice [51]. Among other features, the program allows calculation of shape coordinates, eigenanalysis of variation and animation of the patterns of variation.

**TPSPLINE** is written by F. James Rohlf (State University of New York, Stony Brook) and allows decomposition of a deformation into affine and non-affine components, along with calculation of principal and partial warps. A Windows® version is now available at the site mentioned above.

**TPSRW** computes relative warps and uniform components of variation for a sample. It allows the user to vary a number of parameters including the a metric and the reference form and was written by F. James Rohlf (State University of New York, Stony Brook). A Windows® version is also available.

**VECTOR** is a Windows® program written by Julian Humphries of Cornell University. It is similar to Rohlf’s TPSPLINE program, except that it allows depiction of warps as vector diagrams (this ability has been added to Rohlf’s newer spline program).

**XY** by Michel Baylouc of the Musée d’Histoire Naturelle in Paris, allows calculation of shape coordinates, centroid size, interlandmark distances and allometric coefficients for landmark data.

References


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