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Review

The study of morphological variation in the hominid fossil record: biology, landmarks and geometry

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ABSTRACT

This review considers some recent advances in shape analysis based on landmark data, and focuses on the application of these methods to the study of skeletal evolution in primates. These advances have provoked some controversy. The major aims of this review are to put these debates in context and to provide an overview for the nonmathematician. The purpose of morphometric studies is considered, together with issues relating to the nature, significance and identification of landmarks before turning to a review of available technologies for the analysis of morphological variation. These are considered in terms of underlying models and assumptions in order to clarify when each is appropriate. To illustrate the application of these methods, 3 example studies are presented. The first examines differences amongst ancient and modern adult human crania using 2-dimensional data. The second illustrates the extension of these methods into 3 dimensions in a study of facial growth in monkeys. The third presents an application to the analysis of the form of the hominoid talus. The review ends with an account of available software resources for shape analysis.

Key words: Geometric morphometrics; shape analysis; facial variation; talus; sexual dimorphism.

INTRODUCTION

This review considers new quantitative approaches for the analysis of morphological variation. The methods are described in the context of primate and especially human skeletal morphology but they can be applied to the analysis of variability in diverse areas of biomedicine including diagnostic imaging (Bookstein, 1996) and developmental biology. In describing modern and more established approaches to the analysis of morphological variation some terms will, inevitably be frequently used and so are defined early to avoid confusion. The focus of the methods to be reviewed here is landmark data. Landmarks in this context are recognisable 'equivalent' points on the objects under comparison. Sets of landmarks occupy 2 or 3 dimensions and the term 'form' is used to describe the configuration of a set of landmarks. The field of geometric morphometrics deals with methods for the analysis of such configurations in which their full geometry is preserved throughout and which operate in a specific shape space (Kendall's shape space; Rohlf, 1999; and see later in this review). These methods allow for the visualisation of group and individual differences, sample variation, and other results in the space of the original specimens. The term 'shape' is used to refer to the aspects of form remaining with size removed. Size is a loose term with different meanings under different circumstances but in geometric morphometric studies 'centroid size' (see below) is a natural size measure. The issues surrounding the definition of size variables are discussed more fully in Hills & Wood (1984), O'Higgins (1997) and O'Higgins & Jones (1998).

The quantification of form is self evidently of importance in studies of variation in size and shape. Landmark coordinates or measurements derived from them underpin many such studies (for the simple reason that landmarks record equivalences or homologies in a way that outline, or surface tracings, do

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not; see below). To many readers it will seem surprising therefore that the issue of how best to deal with landmark coordinate data has only recently been resolved to any satisfactory degree. Many issues have impeded progress in such analyses. These include difficulties relating to visualisation of results, superimposition of forms and description of deformations. In addition there have been major issues with respect to statistical models and assumptions that have required resolution. This review therefore begins with a consideration of some established and more recent approaches to the analysis of form variations. This allows issues relating to the analysis of form variability to be explored. Following this, the review will consider, in a modern light, the purpose of morphometric studies of form, summarise recent advances in understanding of the significance of landmarks together with models, assumptions, statistical shape spaces and suitable methods for their analysis. This review of methodology is followed by some illustrative examples.

ISSUES ARISING IN THE ANALYSIS OF LANDMARK DATA USING ESTABLISHED AND SOME MORE RECENT APPROACHES

A classical use of landmark data for the study of biological form is within craniometry in which linear dimensions, and indices constructed from dimensions, are used to examine morphological differences within and between samples of skulls. Examples of 'standard' craniometric measurements are given by Martin (1928) and Brothwell & Trevor (1964). Typically univariate and multivariate analyses are undertaken to investigate patterns of morphological variation. Examples include a comprehensive and classic study of craniometric variation in humans (Howells, 1973), and more circumscribed studies of cranial variation and sexual dimorphism in hominoids (for example Wood, 1976; Van Vark, 1984; Bilsborough & Wood, 1986; O'Higgins, 1989; O'Higgins et al. 1990). Multivariate analysis of postcranial hominoid material is also well established, with examples coming from the study of morphological variation in foot bones (Lisowski, 1967; Day & Wood, 1968; Oxnard, 1972; Kidd et al. 1996). The results of multivariate studies are often presented as plots of specimens on canonical axes, or principal components, that summarise major aspects of variability in the original measurements, or as matrices of interspecimen distances that express overall differences.

These approaches lead to precise mathematical descriptions of patterns of covariance between (often disconnected) variables but they do not generate simple, readily-interpretable, spatially-integrated analyses of the size and shape differences under study. This is because, in classic craniometry (or indeed morphometric analysis of any series of forms), using interlandmark distances, the measurements are frequently taken in such a way that the geometry of the full landmark configuration is lost. The analyses are therefore not able to generate pictorial representations of mean forms or variability about mean forms. Rather the interpretation of the meaning of canonical or principal component axes depends on assessment of loadings of variables on these axes with subsequent interpretation of such loadings in terms of major contributing variables to the patterns of covariance revealed by each. In the extreme these interpretations tend to be abstract and mathematical rather than pictorial and anatomical.

For this reason configurations of cartesian coordinates of landmarks are increasingly preferred as the basis for comparison (that is without reference to distances between the landmarks; e.g. Creel & Preuschoft, 1971). Coordinate data retain the full geometry of the landmarks, but have proved more difficult to compare statistically than linear dimensions. The reason for this is the problem of registration. With coordinate data the differences in landmark locations observed between specimens are entirely dependent on how they are aligned and scaled with respect to each other ('registered'; see, for example, Bookstein, 1978). The perceived displacement of any particular landmark from one specimen to another depends upon the way in which the specimens are scaled, reflected, rotated and translated with respect to each other. Different registrations will generate different impressions of the shape transformations and regions close to the registration points will appear to change less than those more distant. This difficulty has encouraged the development of methods that preserve the geometry of the full landmark configuration whilst using interlandmark distances or angles that avoid registration problems (e.g. Lele, 1993; Rao & Suryawanshi, 1996, 1998). However, these alternatives suffer from their own peculiar and less obvious pitfalls that will be described later in this review.

A further possible approach is to use coordinate data but to dispense with the issue of registration by describing differences between coordinate sets in terms of deformations rather than absolute movements. The best known representation of deformation is in the form of a 'transformation grid' (Thompson, 1917)

whose distortions represent one possible deformation of the (2 or 3-D) space in the vicinity of the reference specimen required to take its landmarks exactly into those in the target specimen. Since deformation methods describe stretchings and contractions of space required to match landmarks between specimens rather than differences in absolute landmark locations they are unaffected by registration. Deformation methods can either operate on subsets of landmark configurations known as finite elements or on the configuration as a whole. The finite element approach suffers from the potential difficulties that different subdivisions of the whole landmark configuration (different element designs) can generate different impressions of the deformation, and that the deformation as a whole will show marked discontinuities at element boundaries. Where deformations of complicated elements or whole configurations are analysed then the results depend critically on the choice of method ('homology function') for matching internal points (other than landmarks). These issues are reconsidered later in this review.

Recent advances in the analysis of landmark data

Thus, until recently it has been a difficult task to gather and carry out sophisticated computations on full 3-D data from adequate samples. The classes of methods described above were developed as best they could, given the state of knowledge of shape spaces and computational technologies of the time. Statistical models, assumptions and methods most appropriate to the analysis of form variability through landmark data have only become well understood in the last few years. It is the purpose of this review to describe these latest theoretical developments, to consider the current state of statistical shape analysis using landmark data and to provide practical examples of the use of appropriate methods in studies of primate and human variation. The consideration of recent advances begins with an assessment of the purpose of morphometric studies before going on to consider more carefully the biological significance of landmarks and appropriate statistical models, assumptions and methods for their analysis.

THE PURPOSE OF MORPHOMETRIC STUDIES

This review focuses on the description of form in terms of landmark configurations but in other studies the interest may be in curves, areas, volumes etc. (see O'Higgins (1997) for commentary on theoretical and practical aspects of such approaches). It is essential that the description of form used is appropriate in terms of the biological hypothesis being addressed and that it is adequate to enable this hypothesis to be tested.

In general the aim of a morphometric study is to generate reports of variations within a collection of specimens. Note that the specimens themselves are not completely analysed in every detail of morphology; instead quantitative descriptions of aspects of their morphology are the subject of analysis. These descriptions are abstract representations (e.g. configurations of sets of landmarks) of the specimens under study. Different representations of specimens are therefore to be expected to generate results that differ to some degree. The generated reports must, however, have certain properties; they should be biologically plausible (i.e. relate in a biologically meaningful way to the variations of form under study), they should be suggestive (i.e. lead to biological insights) and they should have some statistical authority. Of major interest to the biologist studying a collection of complex forms are: estimates of mean form, localisation of form differences (i.e. the ability to locate regions which differ most), description of patterns of form variation, and importantly reports of the relationships between any patterns of size and shape variation and external factors. Bookstein (1991) put it elegantly in asking 2 questions: Is there evidence for covariance between form and some factor? What is the nature of this covariance? Thus morphometrics is the exploration of the relationship between extrinsic (e.g. geography, species, sex, etc.) and intrinsic (e.g. growth) factors, and patterns of form variation. It also concerns itself with the localisation and characterisation of such form differences.

QUANTIFYING MORPHOLOGY: WHAT ARE LANDMARKS?

Landmarks provide one way of sampling form. They are chosen so that they can be located and are in some way equivalent on all specimens. In effect, they sample the 'map' of 'equivalences' between specimens. There are, however, numerous practical and philosophical issues surrounding the identification and nature of equivalent landmarks. Principal amongst the latter is the issue of homology.

In biology a special type of equivalence, homology, forms the basis of many studies (Hall, 1994, provides a recent review). In evolutionary studies the term

'homology' relates to the matching of parts between organisms according to common evolutionary origin. In developmental studies, however, 'homology' is used in a different sense; to refer to the matching of structures through ontogenetic time, or shared process. This matching is not necessarily physical since growth phenomena (e.g. bony remodelling, shifting muscle insertions) may result in replacement of material between different ages such that structures that appear equivalent in terms of their local relations need not necessarily reflect the locations of the same material. Despite this replacement of material, structural identity is sometimes maintained. Wagner (1994) commented that this requires the action of 'morphostatic' mechanisms and, as such, although structures may not be equivalent in the sense of material, they may be equivalent in terms of the continuity of such mechanisms. Developmental equivalence may therefore be considered to equate to homology in the sense of Van Valen (1982); 'correspondence caused by continuity of information'. This is an homology of the processes giving rise to structure.

This concept of correspondence through continuity of information begs the question of how such homologies might be identified. The pragmatic answer is that they are identified on the basis of prior knowledge of the processes underpinning morphogenesis. For the skeleton such knowledge is patchy and incomplete at finer levels of morphological detail. Does this mean homologies can never be identified? That frontal bones of humans and apes are homologous (in the sense of Van Valen) is almost certainly true. Difficulties arise however in matching finer details of frontal morphology and, at some point, the finest details cannot be convincingly matched in purely biological terms. The more distinct the morphologies being compared the less likely perfect correspondence (in whatever sense) can be achieved between all parts. The consequence is that the sampling of the map of homologies will be incomplete at some level of detail. This will bring with it limits to the questions that can be reasonably asked in the absence of further information about process.

The definition of the homology map depends entirely on biological rather than mathematical or geometric criteria. The identification of landmarks on the homology map may, however, depend on the geometric features that result through homologous processes. The practical difficulties in identifying landmarks are recognised in a commonly quoted taxonomy of landmarks that is designed to encourage critical appraisal (Bookstein, 1991; Marcus et al. 1996). They can be summarised and are modified slightly as follows. (1) *Type I landmarks* whose homology from case to case is supported by the strongest (local) evidence (meeting of structures or tissues; local unusual histology etc.). (2) *Type II landmarks* whose claimed homology from case to case is supported by geometric (tooth tip etc.), not local or histological evidence. Type II landmarks include landmarks which are not homologous in a developmental or evolutionary sense but which are equivalent functionally such as wing tips. (3) *Type III landmarks* have at least one deficient coordinate (which means that they can be reliably located to an outline or surface but not at a specific location, e.g. tip of a rounded bump).

In terms of the homology map most confidence can be placed in landmarks of type I and least in landmarks of type III. This should not necessarily preclude the use of all types of landmarks but it should lead to the expectation of greater (possibly directional) variation due to error alone in data based on type III rather than type I landmarks when interpreting results.

ACQUIRING LANDMARK DATA

The collection of 2-D coordinates from 2-D specimens or images is a relatively straightforward matter using graph paper, planimeters or digitising tablets. In studies of 3-D objects, for which x, y and z coordinates of landmarks are of interest the matter of data acquisition is more problematic since three dimensional digitisers have tended, until recently, to be bulky, slow and expensive. Recently modern electromagnetic pointing devices and mechanical arms have become available and offer substantial benefits over the older technology. Furthermore, modern imaging modalities such as laser scanning, MRI and CT coupled with 3-D reconstruction permit the recovery of landmark coordinates from computer generated images using software probes (Spoor et al. 2000). Advances in software and hardware are also making possible lightweight stereophotogrammetric devices using digital cameras directly linked to portable computers. Information on specific devices and approaches can be found at the web sites and bulletin boards listed at the end of this review.

HOW TO ANALYSE LANDMARK DATA

The analytical tools employed in any morphometric study should be capable of producing insights into biological phenomena. It was noted earlier that in analysing variations amongst landmark data the issue

of registration is of great importance. Much debate in the morphometric literature has focused on the relative merits of 'registration free' approaches to morphometrics vs 'registration dependent' (e.g. Bookstein, 1978, 1991; Lele, 1993; Richtsmeier et al. 1993*a*, *b*; Dryden & Mardia, 1998, p. 286). The arguments often seem overly complicated to non-statisticians with the result that biological workers might be discouraged from carrying out studies using perfectly appropriate methodologies. For this reason it is worth rehearsing the basic models and assumptions underpinning morphometric studies in order to identify those methods that are useful and appropriate for particular biological questions. This rehearsal is specifically aimed at the biologist rather than the statistician and so avoids mathematical formulae except where straightforward.

MODELS

In considering how landmark configurations vary between specimens an appropriate mathematical/statistical model of biological form variability is the starting point for choosing appropriate statistical methods. The basic model underlying most statistical studies of shape variation is simply that landmarks are perturbed about a mean form. Other models are possible, such as the log-normal model for inter-landmark distances deriving from the work of Mosimann (1970), and which has recently been applied specifically in relation to the analysis of form variations by Rao & Suryawanshi (1996) and Mardia et al. (1996). Inference under this model may be carried out using standard multivariate methods (Rao & Suryawanshi, 1996). In general, however, under this model, the estimation of mean forms is not straightforward (Lele, 1993) and the distance metric between specimens has highly undesirable properties for certain kinds of shape analysis, namely that this metric depends on the mean shape (Rohlf, 2000*a*); see 'shape space for interlandmark distance', below). For this reason most analyses of shape variability take some variant of the perturbation model as their basis.

Under the perturbation model alone there are limits to what can be estimated. Thus the 'mean reflection size and shape' (i.e. ignoring reflections; Dryden & Mardia, 1998, p. 281) can be estimated using interlandmark distances. Alternatively, Dryden & Mardia (1991), use general covariance matrices which are rather more complex to deal with mathematically. Mean reflection size and shape can also be estimated under the perturbation model through euclidean distance matrix analysis (EDMA: Lele, 1993).

EUCLIDEAN DISTANCE MATRIX ANALYSIS

In EDMA, form is expressed as a matrix of all possible interlandmark distances (the form distance matrix). The mean is expressed as a matrix of mean interlandmark distances calculated after Lele (1993). Using interlandmark distances alone it is not possible to estimate the relative movements of landmarks since this calls for certain additional assumptions with respect to registration. EDMA does, however, allow some aspects (excluding direction) of the variability of landmarks to be estimated. EDMA enables the examination of form differences through the calculation of a form difference matrix (FDM: the ratios of equivalent pairs of all possible interlandmark distances from each). Examination of this matrix (which for k landmarks is $k(k-1)/2$ in size; it becomes very large rapidly as the number of landmarks increases) can indicate which landmarks are most changed but, not relative movement (without making assumptions in relation to registration). EDMA can also be used to assess the significance of differences in reflection mean size and shape between 2 groups. Lele & Richtsmeier (1991), Lele & Cole (1995) and Dryden & Mardia (1998, p. 284) discuss aspects of such testing. Recent work by Rohlf (2000*b*) seems to indicate that there are considerable statistical issues yet to be resolved in relation to the assessment of differences between means using EDMA. These are such that the methods are not suitable for the testing of differences between all possible forms and, in consequence, methods depending on additional assumptions offer more reliable approaches.

ADDITIONAL ASSUMPTIONS: INDEPENDENT ISOTROPIC DISTRIBUTIONS

Particular variants of the perturbation model may assume specific distributions of landmark perturbations, such as isotropic independent distribution (iid) at each landmark in which each landmark is able to vary ('randomly') in location independent of the other landmarks. An alternative would be dependence between landmarks, in which movements at landmarks are assumed a priori to be correlated. If the additional assumption is made that the landmarks are independently and isotropically distributed about the mean (iid) it is possible to estimate mean shape consistently but not mean size-shape using Procrustes superimposition techniques (see later, and Kent & Mardia, 1997). The bias (leading to errors) in mean size estimation is small, however, for small variations and the shape part of the estimate is consistent. Shape

and size and shape can be estimated consistently under gaussian iid models (offset normal distributions; Mardia & Dryden, 1989). These models can be generalised to non-iid perturbations but the procedure is complicated (Dryden & Mardia, 1991). Alternatively the complex Bingham distribution (Kent, 1994) is often a reasonable model inference.

In summary then, minimal assumptions allow us to estimate mean size and shape using a variety of approaches. These estimates will differ slightly when variations are large (to the biologist such variations would appear immense in most applications and would probably not require statistical analysis in any case). In biology, however, the estimation of mean shape is only of passing interest in most applications, for the mean provides no information about variability and covariations with form. To be useful we generally need methods which allow us to compare means and describe patterns of form variation. In order to do so certain (entirely reasonable in the vast majority of biological studies) further assumptions need to be made.

LOCALISATION AND CHARACTERISATION OF FORM DIFFERENCES

Two basic approaches exist for the localisation of form differences using coordinates. One takes each form, superimposes it with respect to the other (registration) and then describes differences in terms of landmark displacements relative to this registration. Clearly, if the relative displacements of landmarks are to be examined then assumptions need to be made in relation to the superimposition of forms.

The other approach describes differences between landmark configurations in terms of deformation, i.e. mapping of one form into another and/or stretchings and compressions at points in one form (commonly called the reference form) so that its landmarks exactly fit those of another form (commonly called the target form). The deformation can be expressed as a deformed grid (the mapping of the space in the region of the reference to that in the region of the target) after Thompson (1917), or as the principal strains (rates of deformation in the direction of minimum and maximum deformation) of a finite element analysis. If the deformation of one form into another is of interest assumptions must be made about the way in which deformations occur. Issues relating to finite element approaches in the description of deformations have been raised earlier in this review. They will be considered in more detail below, after superimposition methods and shape spaces have been reviewed.

SUPERIMPOSITION

For the analysis of relative landmark displacements it is essential that forms are registered with respect to each other. In biology it is nearly always impossible to carry out such a registration in an unequivocal way (i.e. in a way that exactly mimics biological truth; Lele, 1991). One reason is that many structures do not have a 'natural' register with each other (e.g. skulls where, in some sense, all bones move away from each other). Note that even if registration between 2 diagrams were certainly wrong it would still be possible to make useful descriptions of shape differences. For example, in the case of 2 skulls, one having a larger face than the other, superimposed first over the occiput and then over the maxilla we would conclude from both analyses that the face is relatively larger in one. Arrows drawn over landmarks do not indicate the 'true' differences in landmarks, rather, the relative differences given the particular registration.

Several practical possibilities for registration arise but 3 have received particular attention (Dryden & Mardia, 1998). One might register (i.e. translate, rotate and scale) to a common baseline (e.g. Bookstein 2-point registration; Bookstein, 1984); register so that most points fit well (robust or resistant fit; Siegel & Benson, 1982) or register by minimising the sum of squared distances between the equivalent landmarks of forms (Generalised Procrustes Analysis; GPA). GPA of n specimens, each represented by a $k \times m$ matrix of landmark coordinates, X_i, $i = 1, \ldots, n$ results in registered specimens denoted, X_i', for which the sum of squared differences, d_F^2, between them is minimised.

$$d_F^2 = \sum_{i=1}^{n} \sum_{j=i+1}^{n} (X_i' - X_j')^2$$

Scaling is according to centroid size (the square root of the sum of squared euclidean distances from each landmark to the centroid which is the mean of landmark coordinates).

SHAPE SPACES FOR REGISTERED LANDMARKS

Once registration is carried out, each shape (scaled form) can be represented as a point in a 'shape space'. The space with a distance (see above) resulting from generalised Procrustes analysis (Kendall's shape space; Kendall, 1984), has the desirable property that independent isotropic distributions (iid) of landmarks result in isotropic distributions of points representing specimens in the shape space (e.g. Kent, 1994; Dryden

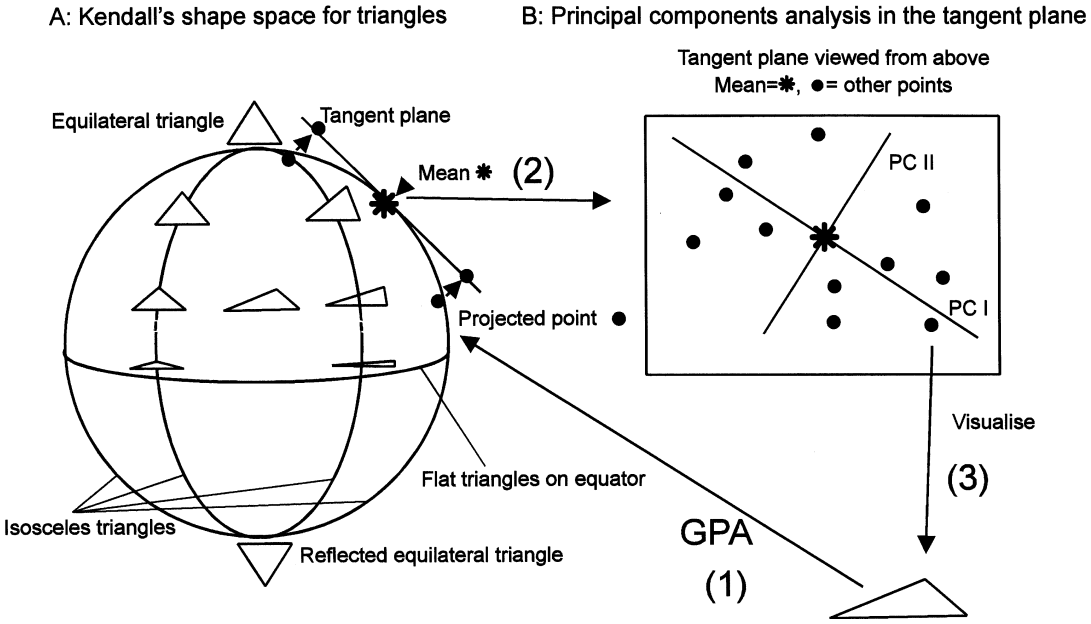

Fig. 1. (*A*) Representation of Kendall's shape space for triangles. Equilateral triangles lie at the poles; the southern hemisphere is a reflection of the northern. The sphere is divided into 12 equal half lunes (6 in each hemisphere); if the apices of the triangles are unlabelled and reflections are ignored all triangles lie in one half lune. Isosceles triangles lie along the lines dividing lunes and flat triangles at the equator. (*B*) A schematic indicating the projection of points representing triangles in Kendall's shape space into a space tangent to the mean triangle (arrows) and the principal components of shape variability (PC I, PC II) in this tangent space. The steps involved in the analyses used in this study are (1) generalised Procrustes analysis (GPA) to register figures, that are then represented as points in the shape space; (2) projection of points into a space tangent to the mean and the principal components (PCs) of shape variation in this space are extracted; (3) visualisation of the shape variability represented by PCs is achieved by reconstructing figures.

& Mardia, 1998, p. 137; Rohlf, 1999, 2000*a*). This means that if we assume this superimposition is adequate in terms of biology, and if landmarks vary in location isotropically, we can expect to find an isotropic distribution of specimens in the shape space. Conversely, deviations from iid landmark variations will lead to a nonisotropic distribution of specimens in the shape space. Such distributions of specimens in the shape space can be of biological interest since the principal directions of variation might be related to interesting biological variables such as age, 'size', sex, species etc. The shape spaces with distances resulting from Bookstein 2-point registration and from robust fitting are such that they approximate Kendall's shape space only when variations are small (Dryden & Mardia, 1998, p. 33).

With registration it is therefore of considerable interest to consider the adequacy of the superimposition method in relation to the resultant shape space. Different registrations will lead to different distributions of specimens in the shape space (different variance-covariance matrices) and so possibly to different biological conclusions. If variations are small, however (in relation to Procrustes distance, not in relation to a vague notion of biological variation), then all registrations will yield approximately similar results (Kent, 1994). Thus we can reasonably undertake studies of landmark displacement vectors. Dryden & Mardia (1998, p. 287) suggest that 'if the data lie within full Procrustes distance of about $d_F = 0.2$ of an average shape then methods give very similar conclusions'. Increasing experience of the use of Procrustes methods indicates that this proposal is more stringent than it need be. Larger variations yield useful biological insights and, in many circumstances, as the number of landmarks increases the approach is increasingly robust. It seems that no biological data set has yet been published that violates these assumptions to the extent that erroneous biological conclusions are reached.

Statistical inference in Kendall's shape space is not straightforward since this space is non-euclidean (i.e. it is curved; Rohlf, 1999, provides a clear account). For triangles the space is equivalent to the surface of a sphere of unit diameter (Fig. 1*a*) but for more than 3 landmarks (k landmarks in m dimensions) the space is high dimensional and more complex. Because of this, great care is needed in carrying out statistical analyses. One particularly appealing approach that naturally allows the study of allometry (the way in which relative proportions of specimens change with overall size; Hills & Wood, 1984), is to carry out principal components analysis (PCA) in the tangent plane to Kendall's shape space (Kent, 1994; Dryden

& Mardia, 1993). For triangles we take the scatter of points on the spherical shape space representing variation within our sample and project it into a euclidean tangent plane in exactly the same way as a cartographer might project a map from a globe onto a flat sheet of paper (Fig. 1*b*). The coordinates of the points representing specimens are no longer given in terms of the sphere, but rather as coordinates in the plane. As long as the projection has not resulted in excess distortion (as might occur if the projection encompasses a large proportion of the sphere) we can carry out useful analyses in this plane. For higher dimensions the tangent space to the shape space can be imagined as a space of $km-m-m(m-1)/2-1$ dimensions.

Procrustes tangent coordinates can be estimated using the partial Procrustes tangent space projection given by Dryden & Mardia (1993; see also Rohlf, 2000*a*). This projection results in a $(k-1)m$ vector of tangent space shape coordinates with respect to the mean for each specimen. Both of these vectors of tangent space coordinates are of rank $km-m-m(m-1)/2-1$. Principal components analysis can be carried out using tangent space coordinates to extract $km-m-m(m-1)/2-1$ eigenvectors; which are the principal components of variation of shape (Fig. 1*b*).

In studies where growth changes in shape are the major source of variation it is reasonable to expect that the first few principal components will serve as an adequate representation of allometric (i.e. size-related) shape changes. Note that, since Procrustes analysis eliminates scaling, the variations we examine through PCA are shape rather than form variations. If we wish to examine the relationship between size and shape we can do this by examining plots and correlations or regressions of principal component (PC) scores vs centroid size for the significant principal components. It is possible to visualise variations in shape represented by the principal components by simply 'warping' ('morphing') the mean shape along each PC of interest. This is achieved by adding to the mean coordinates the product of the eigenvectors (for the PC of interest) and the score on that PC (Kent, 1994). If the PCA is based on tangent space coordinates, a projection of the values for the hypothetical specimen into the space of the original specimens is also carried out.

SHAPE SPACE FOR INTERLANDMARK DISTANCES

Corruccini (1988) investigated the differences between the results of a multivariate study of cranial morphology using cartesian coordinate data and one using linear dimensions taken from the same landmarks. His study indicated that similarities are found between analyses using input data in the form of chords and coordinates, but that these were not necessarily identical. It is only recently that the reasons for these discrepancies have been understood. They relate to the method of superimposition used for landmarks, the way in which means are calculated for interlandmark distances and, importantly, to differences in the distributional properties of the shape space in each approach.

PCA of the complete set of scaled interlandmark distances (ilds) is an extension of the log-distance approach to the estimation of mean reflection size and shape (Mardia et al. 1996; Rao and Suryawanshi, 1996) in which ilds are scaled to their geometric mean. Coordinate representations of figures can be generated through multidimensional scaling (Mardia et al. 1979). There are difficulties, however, with such an approach. For triangles, when the coordinates of the vertices are ild perturbed (see above), the distribution of points representing these triangles within the shape space depends on the shape of the original triangle. The consequence is that results of analyses of shape variation (through, for instance, the extraction of principal components) depend on mean shape. The space also becomes much more complicated as the number of landmarks increases (Rohlf, 2000*a*). Additionally whilst other assumptions about form perturbations might yield more satisfactory distributions around one particular mean triangle, they will yield different distributions around another. It seems therefore that present knowledge of the shape space for interlandmark distances does not allow sensible analyses of patterns of variation amongst specimens. Similar issues probably apply to shape spaces based on angles (Rao & Suryawanshi, 1998), but further exploration of their behaviour is required.

DEFORMATION

A completely different class of morphometric methods attempts to describe form differences in terms of the deformation of the space in the vicinity of a reference specimen into that in the vicinity of a target specimen. Early attempts to produce mathematically defined, reproducible visualisations of deformation (e.g. De Coster, 1939; Moorees & Lebret, 1962; Sneath, 1967) were impeded by as yet unresolved practical and theoretical issues. More successful were applications of the methods of Finite Element Analysis and Finite Element Scaling Analysis (FEA, FESA: Lewis et al. 1980; Cheverud et al. 1983; Cheverud & Richtsmeier,

1986; Richtsmeier, 1989; O'Higgins & Dryden, 1993). In the latter methods, forms are divided into finite elements (triangles, tetrahedra, hexahedra, octahedra, etc.) whose interior is deformed between reference and target. The deformation can be expressed in terms of the mapping of internal points (such as the nodes of a regular cartesian grid) between the elements of the reference and those of the target (using mathematical functions often termed 'homology functions' which match points in the vicinity of one form to that of the other). Alternatively the principal strains arising when deforming the elements between reference and target can be calculated at equivalent points within the elements.

These methods assume several things. For the simplest elements (triangles in 2-D and tetrahedra in 3-D) only one set of principal strains (representing the principal magnitudes and directions of deformation) need be drawn. The underlying assumption is that the interiors of the finite elements deform uniformly in relation to the landmarks defining the element. For more complex elements ($k > 3$ in 2-D and $k > 4$ in 3-D) inhomogeneity of deformation is allowed; several principal strains can be drawn at 'homologised' (using the chosen 'homology function') internal points. Here additional assumptions are made that relate to the way in which the chosen homology function matches points between target and reference elements. With all finite element methods a further problem arises because the principal directions and magnitudes of deformation or the matching of points between target and reference can show a marked change at element of boundaries. Different element designs can therefore result in widely different pictures of deformation.

Alternative approaches to the study of deformations use homology functions derived from the deformation of the whole configuration of reference landmark coordinates into target coordinates. Such functions can be used to draw cartesian transformation grids that resemble those first proposed by Thompson (1917). By 'homologising' the space in the vicinity of the reference form to that in the vicinity of the target it is a simple procedure to map the nodes of a regular grid over the reference into those of a deformed grid over the target. Sneath (1967) used cubic splines as the homology function. More recently the Thin Plate Spline has come to be commonly used (TPS; Bookstein, 1989; Marcus et al. 1996; Dryden & Mardia, 1998). This function minimises the bending energy of the deformation and so results in minimal local variation of grid elements with respect to their neighbours.

The resulting grids do not suffer from the problems of element design and discontinuity between elements encountered in FESA since they are derived from a smooth mathematical function applied to the whole landmark configuration. The grids can be interpreted as indicating how the space in the region of a reference shape might be deformed into that in the region of the target such that landmarks in the reference map exactly into those of the target. The basic assumption of the thin plate spline method is that this deformation involves minimum bending. The statistical and graphical models of shape transformations resulting from these approaches are readily interpretable and are highly visual (e.g. Bookstein, 1978, 1989; Marcus et al. 1986; O'Higgins & Dryden, 1992). Care should be taken, however, in balancing their visual appeal against the underlying assumptions in their construction. From a biological perspective it is important to bear in mind that this mapping is purely mathematical and it is based only on the locations of a few important points (the original landmarks) whose homology or equivalence is known a priori from biological arguments.

One issue concerning the use of transformation grids is that they are difficult to interpret objectively. Descriptions of grids tend to be rather subjectively based on the observed deformations and major features of the deformations can easily be overlooked. Bookstein (2000) has recently addressed this issue and has developed a method for extracting spatially discrete, localised features of transformation grids. This he does by extrapolating the deformation of the grid until one or more folds, termed 'creases' appear. The parameters of the creases are properties of the original thin plate spline thus the extrapolation does not create the creases, it simply makes them visually obvious. The creases are spatially discrete and localised and, as such, they emphasise the important features of transformation grids; local extremes of relative expansion or compression (see Fig. 2*c* for an example). In this simple method lies a straightforward route to the generation of more objective accounts of deformations. Bookstein (2000) extended the use of creases through rotations of the grid to generate objective data on direction and magnitude and gives an algorithm for their computation. The method of creases is new but looks set to become a further useful addition to the morphometric toolkit enabling objective description and quantitative comparison of transformations. The fact that creases point to localised and discrete features of deformation means that they may have value in identifying shape 'characters' that differ between specimens. As such

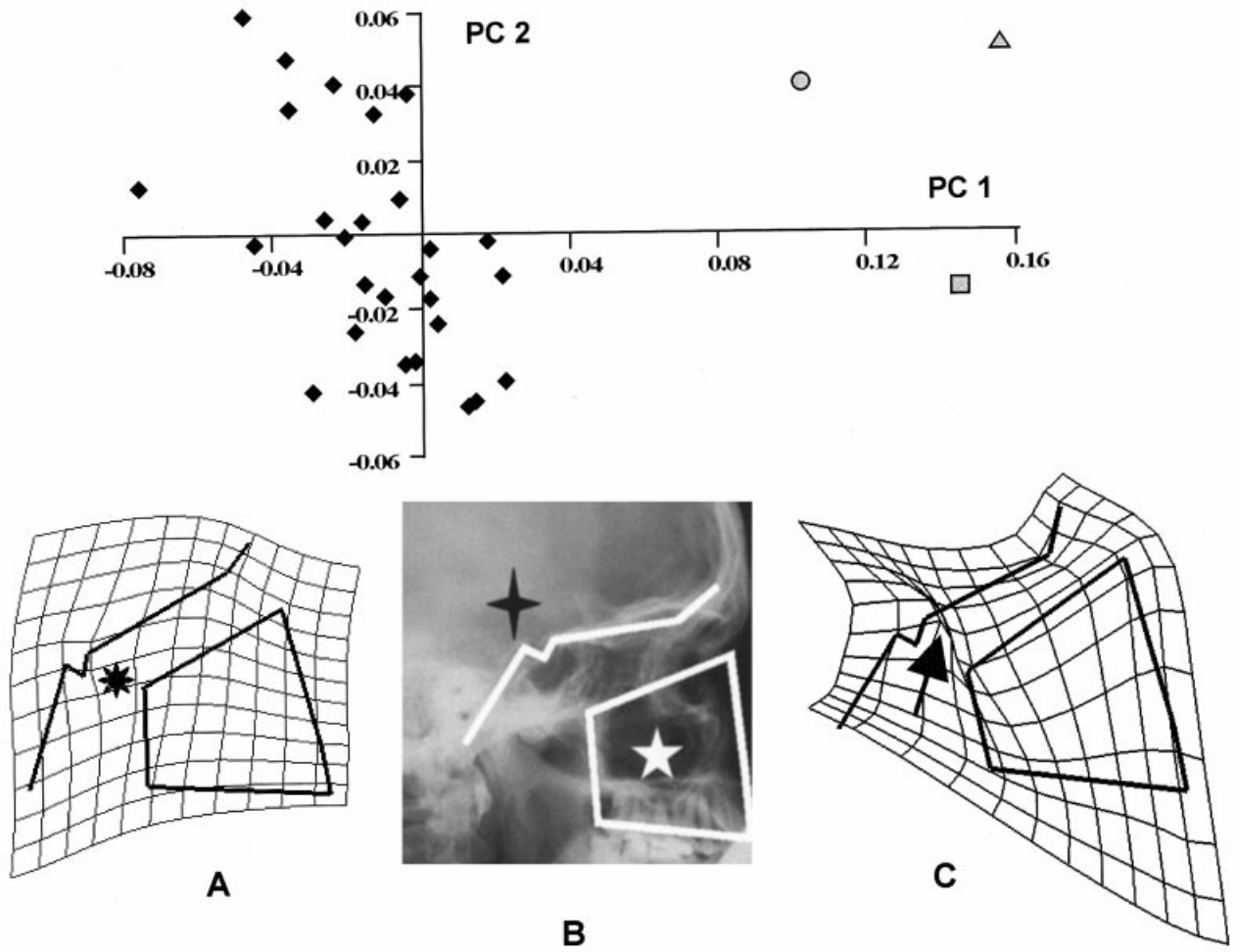

Fig. 2. A study of lateral radiographs in fossil and modern *Homo*. The size and shape of the 'face' and midline cranial base is represented by a series of landmarks connected as shown over the radiograph of a modern human in inset *B*. The 5-pointed white star in *B* overlies the 'facial block' whilst the 4-pointed black star is sited just above the lines representing the midline cranial base. In the top frame the first 2 principal components of shape variation are shown. Black diamonds, modern humans; grey circle, Gibraltar 1 Neanderthal; grey triangle, Monte Circeo 1 Neanderthal; grey rectangle, Kabwe 1 archaic *Homo sapiens*. Modern and fossil specimens are completely separated on PC 1 (38% total variance) and show no separation on any other PC. The shape variability represented by PC 2 accounts for 13.5% of the total variance. Shape variability along PC I is illustrated by the inset diagrams *A* and *C* (not to scale). In *A* the overall mean shape warped along PC 1 to a score of -0.02 ($\sim$ modern mean) is drawn with a deformed transformation grid superimposed. The transformation grid is calculated between fossil and modern group means on PC 1, it is relatively expanded in the region of the sphenoid (black star) and contracted over the face. In *C* the overall mean shape warped along PC 1 to a score of 0.13 ($\sim$ mean fossil score) is drawn with a superimposed grid representing the differences between modern and fossil groups (the reverse transformation to that shown in *A*). The deformation of the grid is multiplied by a factor of $\sim \times 2$ and shows a crease (arrowed) oriented superoinferiorly in an oblique anterior direction indicating compression on either side in the region of the sphenoid. The radiographs and landmark data for fossils were provided by Professor M. C. Dean and Dr F. Spoor. See text for discussion.

they may represent the beginnings of an integration between morphometric studies of shape variability and cladistic studies of evolutionary branchings based on morphology.

MORPHOMETRICS: MODELS, ASSUMPTIONS AND BIOLOGY

The foregoing discussion has considered several commonly applied models, assumptions and methods for the study of form variation. It is clear that each of the methods depends on a basic model of shape variation and often on some assumptions about shape variability. For the practical biologist it is important to have an appreciation of how these models and assumptions might influence statistical results and visual representations of shape variability. Such appreciation is beneficial in avoiding major pitfalls and in reaching reasonable biological conclusions.

If there are doubts about the validity of models and assumptions and so about the statistical and geometric findings of a study, the robustness of any findings can be assessed through the use of diverse approaches with different underlying assumptions (e.g. TPS or

FEA and superimposition), different sets of landmarks, different finite elements etc. Furthermore, where possible, independent testing of assumptions should be considered. Such independent tests might include studies of bone remodelling or vital staining in analyses of growth and evolutionary divergence in growth.

APPLICATIONS AND EXAMPLES

Three examples of the analysis of skeletal variation in primates are now presented in order to illustrate the application of the methods based on Procrustes distance and Thin Plate Splines. These methods are chosen because, as indicated in the review above, the underlying models and assumptions are reasonable in most biological studies. Unlike approaches based on interlandmark distances, Procrustes methods have desirable properties with regard to shape spaces and TPS whilst being a reasonable choice of homology function offers advantages over FEA methods with respect to issues concerning element design. Thus, when variations are small, this combination of methods (GPA/TPS) allows adequate estimation of mean shape, study of covariances, localisation and visualisation of shape differences. The first example study examines differences in the relationship between the face and cranial base in modern and fossil *Homo*. It uses 2-D data. The second illustrates the extension of these approaches into 3 dimensions in a study of facial growth of the living mangabey, the monkey *Cercocebus torquatus*. The third demonstrates an application of these methods in the postcranium and examines variations in the talus amongst living apes and humans.

STUDY 1: HOW DOES THE FACE VARY IN RELATION TO THE CRANIAL BASE AMONGST LIVING AND FOSSIL HUMANS?

In modern humans relative to archaic varieties of *Homo* a major difference seems to be that the face is tucked under the anterior neurocranium (Lieberman, 1998). The consequence is that in modern humans, browridges are small, the face flat and vertical, and the frontal bone bulging. One possible causative explanation for this modern human morphology was considered by Lieberman (1998). He suggested that these anatomical differences from archaic forms might be attributed to a shortened anterior sphenoid allowing the facial skeleton to tuck further below the frontal. Detailed analysis (Spoor et al. 1999), failed to confirm any absolute shortening of the anterior sphenoid but a geometric morphometric analysis did point to some clear differences between archaic and modern humans.

In order to illustrate the use of geometric morphometric methods, I have here extended those earlier analyses and the study is summarised in Figure 2. In Figure 2*B* a lateral radiograph is shown in which the facial skeleton is represented by a white box (containing a white star) connecting landmarks on the face. The anterior part of this box is defined by the landmarks: nasion, anterior nasal spine, prosthion and the posterior part by the posterior maxillary plane (Lieberman, 1998). The cranial base in the midline is represented by a line connecting the most anterior part of the anterior cranial fossa, foramen caecum, most anterior, deepest and most posterior points on the pituitary fossa and basion (below the 4 point black star, Fig. 2*B*).

The landmarks described above were registered through Generalised Procrustes Analysis (GPA) and the tangent space coordinates submitted to Principal Components Analysis (PCA). The first 2 principal components of this analysis are shown in the upper frame of Figure 2. The first (horizontal) principal component (PC 1) accounts for 38% of the total variance and it is the only component on which modern and fossil crania are separated. The pattern of shape variability represented by this PC is visualised by reconstructing the mean shape warped to the fossil (Fig. 2*C*) and modern human (Fig. 2*A*) mean positions on PC 1. In order to aid interpretation of the difference between these warped images a cartesian transformation grid (Fig. 2*A*) is drawn taking the fossil mean as the reference (Fig. 2*C*; for description of the grid overlying this see legend and below) and the modern human mean as the target.

Spoor et al. (1999) noted in their analysis that the anterior sphenoid is not shortened (anteroposterior length) in modern humans relative to that of the fossil sample. Thus, what anatomical changes result in the modern face being tucked under the anterior cranial base relative to the fossils? The geometric analysis presented by Spoor et al. (1999) and modified here indicates that this is mainly due to general reduction in relative facial size, for the transformation grid in Figure 2*A* indicates relative vertical compression in the anterior face in modern humans with less reduction in the posterior part of the face. Additionally the upper part of the face appears to be relatively reduced along an oblique anteroposterior axis as indicated by the posterior bending of the grid lines over nasion and relatively inferiorly displaced (downward curvature of grid lines).

An important finding of this geometric analysis is therefore that, in modern humans, the upper face is repositioned and reduced relative to the upper base. This generalised change in the face is to a considerable degree responsible for the tucking of the anterior face under the anterior cranial fossa with concomitant loss of the characteristic sloping forehead and large brow ridges found in fossils. These are both features of the outer table of the frontal bone and are due, at least in part, to the outer table accommodating the 'step' between upper face and anterior cranial fossa in fossils.

It is interesting to note that, in addition to the face being relatively smaller in general with upper face repositioned in relation to the anterior cranial base, there is one prominent local difference in that the region of the anterior sphenoid appears relatively expanded. The black star in Figure 2*A* overlies this region and it can be seen that here the grid squares become relatively expanded. The transformation grid drawn over the fossil mean in Figure 2*C* presents the reverse transformation: modern human to archaic human means. This deformation of the transformation grid has been multiplied by a factor of ~ 2 and at this point a crease appears in the grid. The crease is indicated by an arrow, it lies within the anterior sphenoid and it can be seen to lie supero-inferiorly in an oblique anterior direction. The crease is such that it indicates that in the comparison of modern with archaic humans the major localised feature of the grid is relative compression of the regions either side of the crease. Conversely the crease signifies a local maximum of expansion, archaic to modern, aligned precisely along the sphenoid. Thus archaics differ from modern humans in having a relatively shortened anterior sphenoid and conversely, that of modern humans is relatively lengthened when compared with archaic *Homo*. Since the anterior sphenoid does not differ much between modern and archaic forms in absolute horizontal length (Spoor et al. 1999) care should be taken to interpret these findings correctly. The crease (Fig. 2*C*) or relative expansion (Fig. 2*A*) overlying the anterior sphenoid actually indicates a localised region that is particularly stable in comparison with the whole landmark configuration.

This simple study serves to illustrate how the visualisation of shape differences using geometric morphometric techniques can aid in interpreting differences between forms. This visualisation, and especially the crease, is a valuable adjunct to the numerical results of morphometric studies. The geometric analysis itself excludes size however and thus great care must be taken in distinguishing relative from absolute differences. Size is readily dealt with independently. In the next example study an approach to the integrated study of size and shape variability in 3-D is presented.

STUDY 2: HOW DOES THE FACE VARY DURING GROWTH WITHIN A SINGLE PRIMATE SPECIES?

In this next example (O'Higgins et al. 1991; O'Higgins & Jones, 1998) studies of facial growth in *Cercocebus torquatus* are reviewed with the aim of illustrating how geometric morphometric methods can be extended into 3 dimensions. This study also illustrates how size information can be incorporated into such a study to address allometric growth.

Each face from a growth series of *Cercocebus torquatus* is described by a series of 31 landmarks (detailed in O'Higgins & Jones, 1998). These landmarks are used to generate representations of the faces as shown in Figure 3. Variability in these faces is then explored using PCA of tangent space coordinates derived from GPA of the original coordinates. Variability among specimens on the first 2 principal components from this analysis is pictured in Figure 4. PC 1 summarises 52% of the total variance and so describes an aspect of shape variability of considerable importance in explaining the whole. In order to visualise the aspect of shape variability described by this component the rendered mean face is warped to the extremes of this component. The effects of this warping are illustrated by the 2 rendered, warped, mean faces, shown at the left and rightmost extremes of PC 1 in Figure 4. The leftmost face possesses relatively large orbits and a relatively orthognathic, relatively small midface whilst the rightmost face possesses relatively small orbits and a prognathic, relatively large midface. These differences are consistent with what might be expected of the shape changes occurring during growth.

This growth related aspect is explored further in Figure 5 where scores on PC 1 are plotted against centroid size. It can be seen from the upper frame of Figure 5 that these variables show an almost perfect, tight, linear relationship with a correlation of 0.95 ($P < 0.001$). Thus it can be concluded that variability along PC 1 relates to shape changes with increasing size, one aspect of growth (others being the relationship between size or shape with time; but absolute age data are not available). The lower images in Figure 5 indicate the deformation of 1 plane of a cartesian transformation grid from the mean of 'small' specimens (left; regular, planar, grid) to the mean of 'large' specimens (right; distorted grid). This

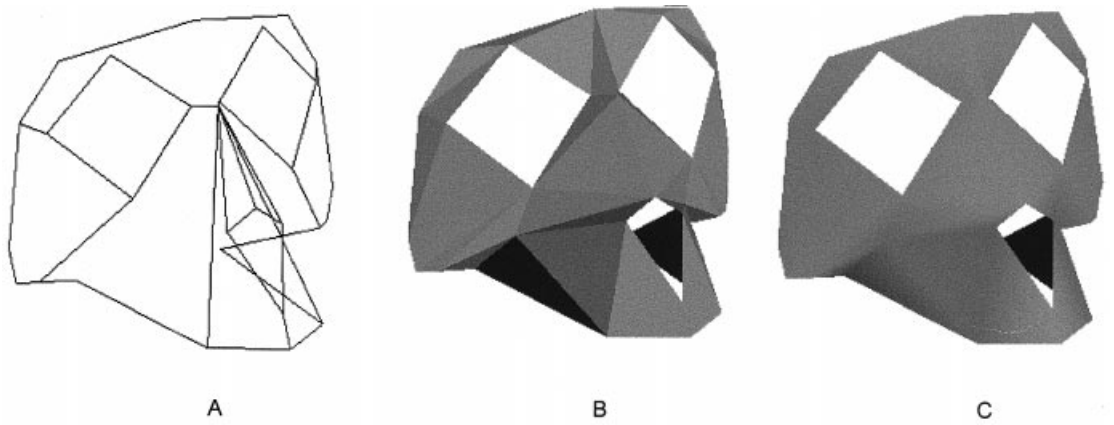

Fig. 3. Mean *Cercocebus torquatus* face, (*A*) wireframe delineating sutural boundaries and limits of facial landmarks; (*B*) flat surface rendering; (*C*) smooth surface rendering.

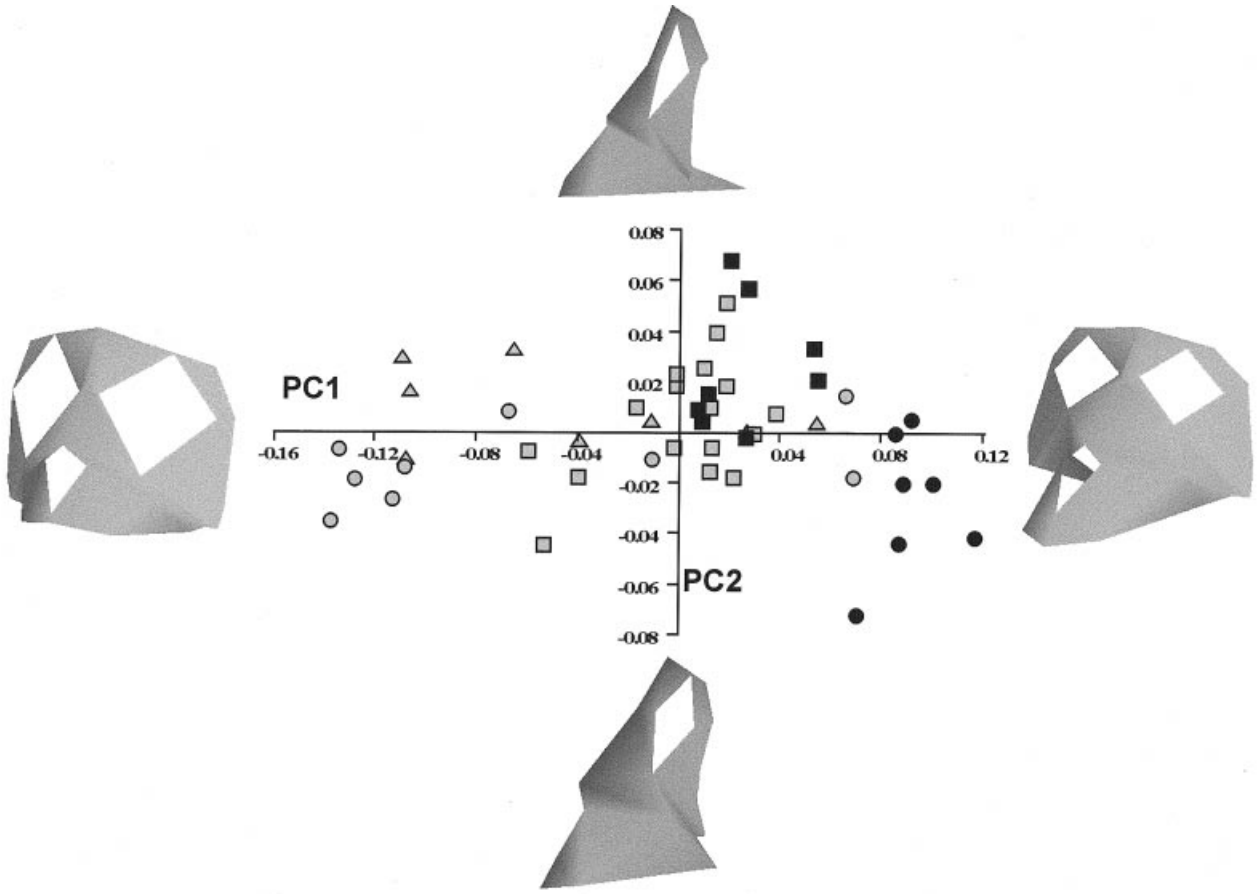

Fig. 4. Plot of the first 2 principal components from the analysis of the *Cercocebus torquatus* growth series. Horizontal axis, PC 1–52 % total variance; vertical axis, PC 2–8 % of total variance. Circles, males; squares, females; black, adult; grey, subadult. The pattern and magnitude of shape variability represented by each principal component is indicated by the rendered faces drawn at each extreme. Thus, far left, the mean after warping to the negative extreme of PC 1; far right, mean warped to positive extreme of PC 1. Similarly top and bottom rendered faces with respect to PC 2. See text for discussion.

serves to emphasise the development of greater relative prognathism during growth and to point to the subnasal region as being particularly important in this regard.

Of interest is the potential for such approaches to enable readily interpretable studies of comparative facial growth among related species. Such studies have the potential to identify the contribution of growth to interspecific facial variations. These approaches can also help in understanding the ontogenetic basis of intraspecific differences such as those due to sex. Thus Figures 4 and 5 impart

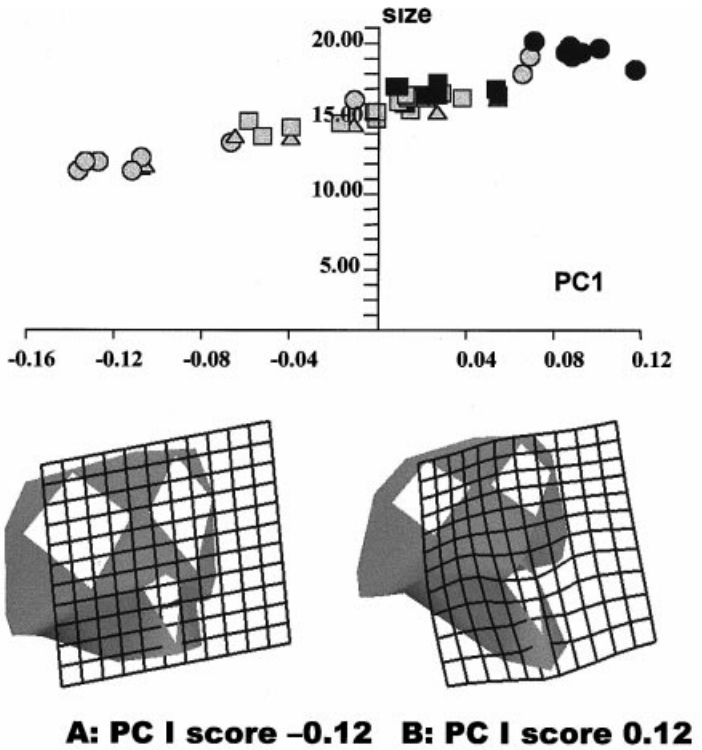

Fig. 5. Plot of centroid size (vertical axis) vs PC 1 score for the *Cercocebus torquatus* growth series. Circles, males; squares, females; black, adult; grey, subadult. Correlation between centroid size and PC 1, $r = 0.95$, $P < 0.001$. Shape variation along PC 1 is visualised with a transformation grid calculated using a triplet of thin plate splines. (*A*) a square grid in the vicinity of the shape represented by a score of -0.12 on the first principal component and 0.0 on all other PCs is deformed in (*B*) to that in the vicinity of the shape represented by a score of 0.12 on PC 2. See text for discussion.

information relating to the ontogeny of sexual differences. From Figure 5 it is clear that a part of the difference between adults of different sexes can be explained in terms of relative extension of the common growth vector into larger size ranges in males. From Figure 4, however, it is also evident that adult males and females are distinguished by their scores on PC 2 (a *t* test indicates adult male and female means on PC 2 are different; $P < 0.003$), which shows no correlation with size over the whole sample. In Figure 4 the upper (lateral) face drawn above the positive extreme of PC 2 indicates the shape of the mean warped to this extreme whilst that at the opposite extreme of PC 2 represents the opposite warping of the mean.

Given that males have lower scores on PC 2 than females, these diagrams indicate that males, compared with females, have a different set of the midface with respect to the upper face; with male muzzles being relatively expanded under the upper face. This is accompanied by a relative downward rotation of the upper nasal region with respect to the lower orbital. Note however that the range of scores on PC 2 represented by the warped means drawn at its extremes in Figure 4 is approximately twice the difference in scores between male and female adult means. Thus the impression of difference between adults of each sex on this axis is exaggerated by a factor of 2.

In any case this finding is of considerable interest since sexual dimorphism is currently thought to arise in the main through relative extension of facial growth in the male (reviewed by O'Higgins & Jones, 1998). These findings indicate, however, that sexual dimorphism in this species arises in part through extension of a common growth vector in males and in part through dissociation of male and female growth vectors in the later stages of growth. Thus existing models of the ontogeny of sexual dimorphism in the primate face may require re-examination.

STUDY 3: VARIATION IN THE POSTCRANIAL SKELETON

The example studies outlined above have focused on variations in the primate and hominin face. The geometric morphometric tools the studies employed are, however, equally applicable to the postcranial skeleton. In this third example study the methods are applied to an analysis of variation among hominoid tali.

The hominoid talus has been the focus of some

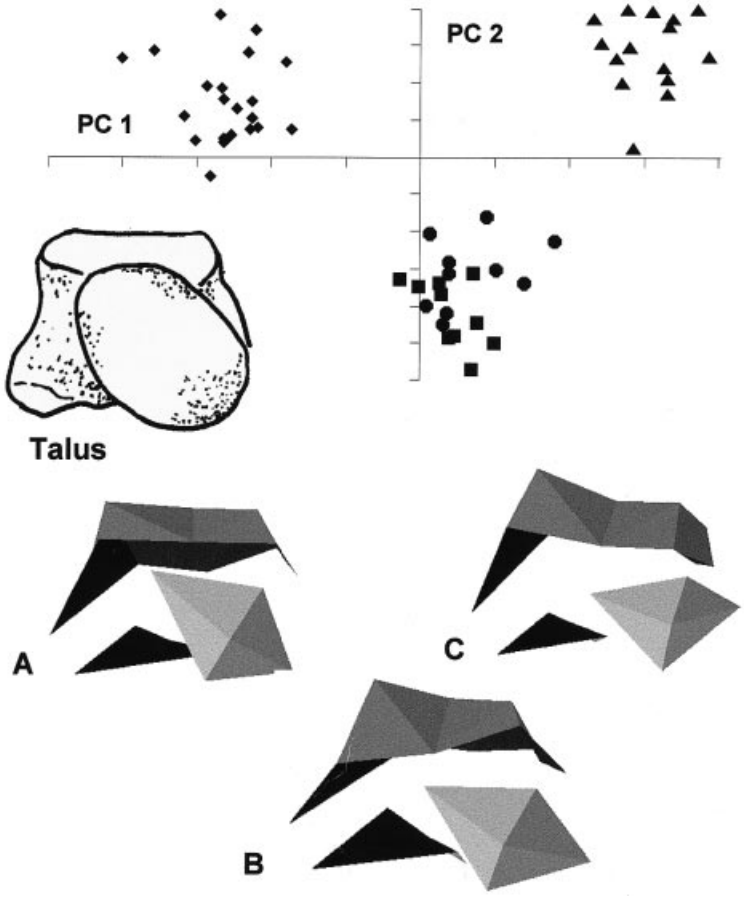

Fig. 6. Variations in talar shape. 24 landmarks describing the size and shape of the talus are submitted to PCA after Procrustes registration and tangent space projection. PC 1 (36% total variance) and PC 2 (15% total variance) separate modern human tali (black diamonds) from orangutans (black diamonds) and African apes (common chimpanzee, black circles; lowland gorilla, black squares). The rendered reconstructions of the warped mean (*A*, *B*, *C*: humans, orangutans and African apes, respectively) illustrate the aspects of shape variability represented by the combination of PC 1 and PC 2. The inset view of the human distal talus serves to aid interpretation of these rendered images since it is drawn in the same orientation. Thus the upper rendered surface in each represents the superior medial and lateral talar articular surfaces; the diamond shaped surface represents the talar head and the dark, lower surface, the subtalar joint. The rendered reconstructions (*A–C*) are drawn in the same relative position as the clusters they represent in the PC plot. PC 4 (4.7% total variance) is not shown but the African apes are completely separated from each other on this vector.

interest in human evolutionary studies because it is a principal bone in the foot, modern humans being uniquely bipedal among living primates, and because fossil tali are relatively well known in the fossil record. Previous studies have used either standard osteometric approaches to the analysis of the morphology of this bone (Lisowski, 1967; Day & Wood, 1968; Oxnard, 1972; Kidd et al. 1996) or they have relied on visual appraisal and functional analysis (Lewis, 1980; Clarke & Tobias, 1995). These studies have resulted in hypotheses about the possible functional adaptations of fossil tali but have failed to generate readily interpretable, integrated accounts of variation in this complex bone. This third example (Brisco, Aiello & O'Higgins, unpublished) aims to explore how morphological variations in the form of the hominoid talus might be interpreted using geometric morphometric techniques. Figure 6 summarises this study.

In Figure 6 a human talus is drawn in distal view (marked 'talus'). The superior articular surface of the body of the talus rises above the joint surface of the talar head, whilst the lateral and medial facets of the talar contribution to the ankle joint, and the subtalar articular surfaces are not visible. The picture labelled A in Figure 6 illustrates the same view of the rendered 'mean' (explained below) human talus, this rendering being based on the coordinates of 24 landmarks taken on the joint surfaces and limits of these surfaces. The talonavicular joint surface is foremost, the superior, medial and lateral articular surfaces are uppermost and the subtalar joint (viewed from above) is lowermost. This rendering was purposefully designed so as to show the joint surfaces as well as their relationship to each other.

In the upper frame of Figure 6, PC 1 is plotted against PC 2 from the analysis of tangent coordinates

derived from landmarks following GPA. These 2 components show interesting distinctions amongst the hominoid tali and together account for 51% of the total variance in the whole sample. Tali form 3 tight clusters; from right to left along PC 1 these are (1) bipedal *Homo*, (2) knuckle-walking *Pan* and *Gorilla* and (3) arboreal *Pongo*.

The lower frame of Figure 6 shows the effect of warping the overall mean shape to the centres (= 'means') of each of these 3 clusters. These warped means are shown in the lower frame of PC 6 in the same relative locations as they occupy in the plot of PC 1 vs PC 2. It is of interest to consider what morphological features distinguish these tali. As the mean is warped along PC 1 (A to B to C, lower frame) the talonavicular joint surface comes to lie more horizontally and the head more medially. Variations on PC 2 represent changes in the proportions of the superior talar articular surface and mediolateral orientation of the talar head not readily visible in this view together with flaring of the lateral facet of the ankle joint that can be discerned in this view.

These visualisations together with the tight clustering of locomotor groups on the first 2 PCs suggest that this approach is worth pursuing in future analyses of foot bone evolution and adaptation in primates. Of particular interest will be the results of studies that include fossil foot bones since these ought to facilitate objective functional interpretation. Indeed it may eventually be possible to carry out biomechanical analyses (e.g. Oxnard, 1991) using computer modelling (i.e. strain distributions following loading) on reconstructed mean forms and hypothetical intermediates.

PROSPECTS

The aim of this review has been to provide a concise but accessible account of the techniques of geometric morphometrics, and indicate their possible applications to the study of the hominid and primate skeleton. The methods are sensitive to subtle changes in form and lead to a cogent integration of abstract statistical findings and concrete variations in shape.

The first study examined the relationship between cranial base and face architecture in 2 dimensions using radiographs. Modern imaging techniques will allow these methods to be extended to 3 dimensions. The second study focused on a study of facial ontogeny (from cross-sectional rather than longitudinal data) using 3-D landmarks from the external surface. It presages comparative studies of facial growth, which, as imaging technologies become cheaper and more available could well be longitudinal in nature. The third example focuses on the postcranial skeleton and serves to indicate that in such studies there is potential to enhance biomechanical interpretation. Future studies of fossils should be of considerable interest.

It was noted in the Introduction that these methods are much more widely applicable and it is expected that, in future, they will begin to play a significant role in other areas of research where morphological variation is of interest. It is only during this decade that these methods have reached maturity and it is likely that during the next decade they will be gradually taken up in other fields. Critical to this will be the arrival of readily useable software and mensurational tools. Already, however, several such resources are available; this review ends therefore with suggestions as to where they may be found. The most important source of information and software is the world wide web and e-mail special interest lists. The web site maintained by F. J. Rohlf at the State University of New York is by far the most comprehensive (and original) source of software, information and links. It can be accessed at http://life.bio.sunysb.edu/morph/. Another useful resource is the morphometrics bulletin board maintained by L. Marcus of the American Museum of Natural History and Queens College of CUNY. This bulletin board is described fully at the above address. A program named 'Morpheus et al.' that provides a comprehensive, cross-platform environment for morphometric data analysis can be downloaded from http://life.bio.sunysb.edu/morph/morpheus/.

Other sites of interest include http://www.cpod.com/monoweb/aps/ from which a software suite 'APS' for the analysis of covariances with shape can be downloaded; http://www.amsta.leeds.ac.uk/Statistics/softwarenew.html provides much specialised statistical software in the S plus language. Finally http://evolution.anat.ucl.ac.uk/morph/helphtmls/morph.html provides access to the *morphologika* web site. This program is being developed by myself and my colleague Nicholas Jones to enable straightforward geometric morphometric analyses in a PC environment; *morphologika* was used in all of the analyses presented in this paper.

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