THE USE OF LANDMARKS TO DESCRIBE AMMONITE SHAPE

Examples from the Harpoceratinae

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Abstract

The use of landmarks and geometrical morphometric techniques is illustrated with examples from the Harpoceratinae (Ammonitina). This approach is useful in analysing morphological variations of characters such as rib pattern or ventral shape on the scale of the genus or species. It can be used to map forms so that similarities and dissimilarities between organisms can be read and quantified directly.

1. INTRODUCTION

The simplicity of construction of an ammonite shell (a spiral tube) suggests that such morphology should be easy to quantify. However, the detailed morphology is extremely complex, especially because of ornamental variations (ribs, keel), often making precise quantification difficult. Two types of biometric methods are traditionally used and are gradually superseding qualitative descriptions which provide observations that are difficult to interpret, especially in the context of the biological concept of species (implying analysis of shape variations).

The most common biometric method is based on the measurement of linear dimensions (e.g. diameter, whorl thickness), which are then processed either two-by-two (bivariate analysis) or simultaneously (multivariate analysis). This method has proved effective for analysing growth allometries. It allows forms to be distinguished by type of coiling and overall geometry. The other biometric method is based on mathematical equations (calculated from linear

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dimensions) whose graphical plots are analogous to the organism's morphology. Raup (1966) thus defined four parameters which are sufficient to describe the general shape of a tube and its mode of coiling (W: whorl expansion rate, D: relative distance between the generating curve and the axis of coiling, S: shape of the generating curve, and T: rate of translation with respect to the centre of the generating curve). Other parameters based on the same approach have been defined by other workers (e.g. Okamoto, 1988; Ackerly, 1989). This approach is particularly informative for analyses involving a broad spectrum of morphological variation (and therefore with high taxonomic ranks). These two methods, based on a linear dimension type descriptor, become less informative to account for complex morphologies such as rib pattern, whorl-section shape or ventral-keel shape. These are characteristics which are frequently used as taxonomic criteria of species or genera. The biometric methods listed above are therefore partly ineffective for telling species apart. In such cases, qualitative analysis is the most widely used method despite its inherent inaccuracy (see above).

There is, however, one method for quantifying shape (developed in particular by F.L. Bookstein) suitable for complex biological morphologies. It is based (1) on the recognition of landmarks on the organism and (2) on comparison of the relative positions of these points between organisms by geometrical morphometric methods. These methods then allow morphological distances between the shapes being compared to be mapped and the morphological distances between the organisms can be read and quantified directly. The concepts and terminology of this method can be found in abundant literature (e.g. Sneath, 1967; Bookstein *et al.*, 1985; Rohlf and Bookstein, 1990; Rohlf and Slice, 1990; Bookstein, 1991).

The objective of the analysis presented here is to describe the main stages, illustrated by examples from the early Harpoceratinae.

2. MATERIAL

The morphologies of several species of the genera *Fuciniceras* and *Protogrammoceras* (Harpoceratinae, Lower Jurassic) are analysed. The diagnostic characters of the species are (1) more or less falcoid rib pattern, and (2) raised monocarinate to flat tricarinate ventral shape. For most workers *Protogrammoceras* has a monocarinate venter and clearly falcoid ribs, whereas *Fuciniceras* has a tricarinate venter and slightly falcoid ribs. A recent study (Neige and Dommergues, 1995) has shown that the two genera are not phyletically meaningful. They are used here in their morphological sense, as classically accepted by workers. In addition, the analyses set out here provide morphological results which cannot be directly interpreted in phyletic terms. Eight species are analysed (in stratigraphic order from earliest to most recent): *P. dilectum*, *P. volubile*, *F. lavinianum*, *F. isseli*, *P. marianii*, *P. celebratum*, *F. cornacaldense*, *P. curionii*. All are from the Central Apennines of Italy. The morphologies analysed correspond to the pre-adult growth stage (just before the adult living chamber). From five to twelve individuals per species were studied. For inter-species comparisons one mean individual was calculated to allow for intra-species variation.

3. METHOD OF SHAPE ANALYSIS

3.1. Landmark Location

The first stage consists in identifying landmarks on the organism for all of the individuals to be compared. Recognition of such homologies is generally based on compara-

tive anatomy. Much of the validity of the method therefore resides in the homological value of the landmarks selected. This is why Bookstein (1991) defines three types of points of supposedly different homological value: junctions between three structures, centres of centroids sufficiently small to be clearly located, or intersections of curves with a plane of symmetry of the organism (type 1); points located at maxima of curvature and sufficiently prominent not to be confused with type 3 points (type 2); points located at the extremities of the organism (type 3). With this nomenclature, the maximum of biological information is concentrated on type 1 points and the minimum on type 3 points. However, any homology remains hypothetical. When a homologous point (of whatever type) is selected, it may accordingly be used in the context of the homological assumptions accepted by the investigator.

3.2. Shape Comparison

The idea is to seek to characterise differences between shapes precisely rather than to define each of them. D'Arcy Thompson was the first to state and apply the principle (1992, p. 271, first published 1917): "In a very large part of morphology, our essential task lies in the comparison of related forms rather than in the precise definition of each [...]". Subsequently different works have conferred a quantitative and more applied dimension upon these methods. Those illustrated here are sometimes grouped together as the "Procrustes methods" (e.g. Sneath, 1967; Bookstein *et al.*, 1985; Bookstein, 1991). In addition, Van Valen (1993) has developed the principle of serial homology which is intra-individual homology. It supposes that several instances of the same character found in a single individual may be compared using the Procrustes methods. This type of homology is especially important for the analysis of ammonites where several repetitions (copies) of ornamental features (such as ribs) almost invariably occur (because of accretionary growth).

These Procrustes methods take on considerable importance in the analysis of living and fossil taxa (e.g. Laurin and David, 1990; Tabachnick and Bookstein, 1990; Johnston *et al.*, 1991; Zelditch *et al.*, 1992; Neige and Dommergues, 1995; El Hariri *et al.*, 1996). Two examples are illustrated in this paper.

3.2.1. Baseline. This fitting technique developed by Bookstein *et al.* (1985) and Bookstein (1991) consists in selecting two points from among the set of landmarks to form a reference segment (A and B, Figure 1). The coordinates of the two landmarks are

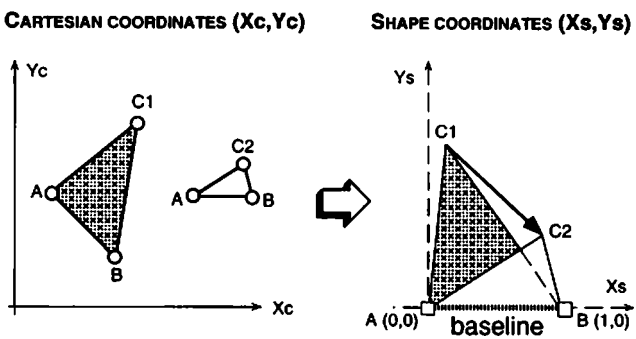


Figure 1. Theoretical comparison of two geometrical objects defined by landmarks and carried out by the baseline method.

then converted by translation, rotation and rescaling to (0,0) and (1,0) in a morphological coordinate system. The coordinates of the other landmarks (C1 and C2, Fig. 1) are recalculated taking these three operations into account. The vector joining the two points then indicates the morphological distance (regardless of size and orientation) between triangles (ABC1) and (ABC2). Their position relative to the baseline can then be quantified by parameters of relative length (expressed in baseline units) or of angle. Furthermore, the choice of points forming the baseline does not affect results (see Bookstein, 1991, p. 204). Baseline-type adjustments are carried out here using Statview 4 software following the procedure of Bookstein (1991, p. 130).

3.2.2. LSTRA. This adjustment technique (Least Square Theta Rho Analysis) consists of superimposing, with the best possible fit, the set of points of one shape with their homologue of the other shape (Sneath, 1967; Bookstein, 1991). It is based on three operations: translation, rotation and rescaling (Figure 2). The remaining differences are then characterised by a vector field extending from each point of one shape to its homologue on the other shape. The distance between the two shapes may also be expressed arithmetically (in standard deviation units): the sum of vector lengths ($\Sigma\Delta$). The set of such distances between all the taxa taken two-by-two, forms the distance matrix. LSTRA adjustments are carried out using Procrustes software (David and Laurin, 1992).

3.3. Morphological Maps

Morphological differences may be visualised graphically on "morphological" maps. The simplest method is to plot the homologous points (after Procrustes adjustment) in a system of morphological coordinates. With the LSTRA technique, the distance matrix may be converted into phenetic trees. These trees allow the morphologically closest taxa to be grouped together. They are calculated here with the Fitch algorithm of Phylip software (Felsenstein, 1990). This algorithm seeks out the non-rooted tree and estimates the length of the branches providing the closest fit with the distance matrix. Notice that this method provides an estimate of the overall morphological distance between organisms regardless of the apomorphic, plesiomorphic or homoplasic nature of the characters. It cannot be used to reconstruct the evolutionary history of taxa. The nodes obtained between taxa do not represent ancestral states but merely degrees of morphological similarity.

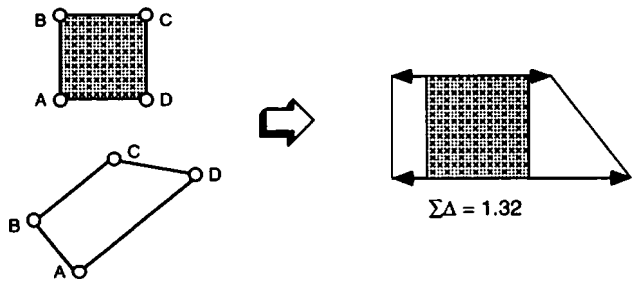


Figure 2. Theoretical comparison of two geometrical objects defined by landmarks and carried out by the LSTRA method.

4. EXAMPLES FROM THE HARPOCERATINAE

4.1. Landmark Location

In the Harpoceratinae four points (R1–R4) already recognised or investigated by several workers (Spath, 1913; Gabilly, 1976; Braga Alarcon, 1983; Dommergues *et al.*, 1990) are used to describe the rib pattern (Figure 3A): R1 is the beginning of the rib close to the umbilical seam; R4 is the end of the rib towards the ventral area. Between these two points, a sinusoidal pattern is formed. Two landmarks are defined to characterise it. The first R2 is the point where the tangent through the protoconch (P) touches the lower bend. The second R3 is the point where the tangent parallel to the line P-R2 touches the upper bend. As the studied Harpoceratinae are planispiral with rather flat sides, the problem of three-dimensional projection can be ignored and we may consider the whorl sides to be a two-dimensional plane. For the morphology of the whorl section (Fig. 3B) including the ventral keel, nine points are selected (S1 to S9): S1 is the apex of the ventral keel; S2 and S3 are located at the points of contact of tangents through S1 to the top of the lateral keels. S4 and S5 lie at the points of contact of tangents to the inter-keel area drawn parallel to the previous tangents; S6 and S7 are the points of greatest whorl width; and, the final two landmarks, S8 and S9, lie on the umbilical seam.

4.2. Shape Comparison

4.2.1. Baseline. Segment R2–R3 is chosen as the baseline, mainly because the criteria used by earlier workers to identify the species studied are the length and angle of the rib on the ventral and umbilical parts of the side. This choice of baseline focuses the analysis on these features. This morphological adjustment technique allows the differences of shape between the species compared to be clearly located. For example, (Figure 4A) *F. lavinianum* is characterised by shorter ventral and umbilical rib segments (relative to the baseline) than *P. curionii*, making the ribs of the latter appear more sinuous.

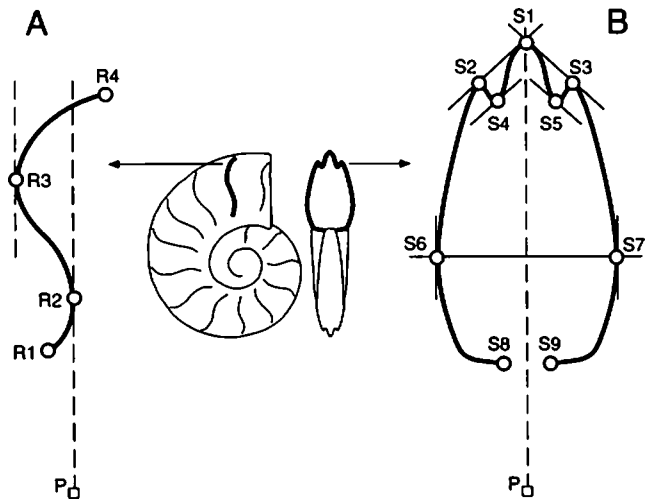


Figure 3. Landmark location depicting rib shape (A) and whorl section (B).

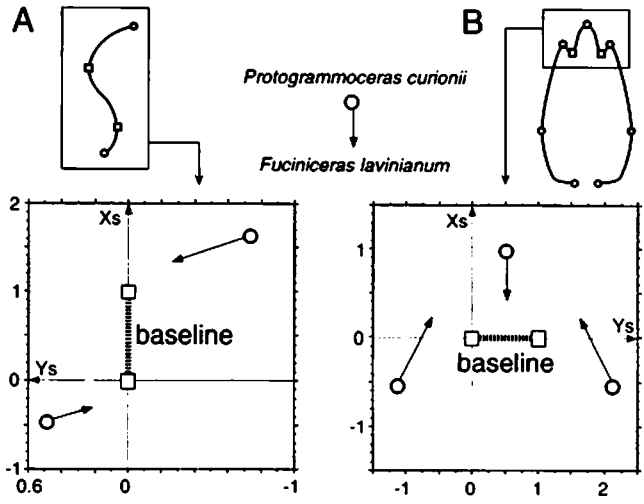


Figure 4. Comparison of the morphology of two species by the baseline method. (A) rib pattern. (B) ventral area. The vectors show the purely morphological differences (regardless of size and orientation) between the two species.

For the ventral area, the baseline chosen is segment S4-S5, chiefly for graphical convenience, but also to provide a clear picture of the modifications at the tops of the lateral and ventral keels. Points S6 to S9 are not considered, so as to focus the analysis on the ventral area. For the same two species as previously, the change in the ventral area is marked by an uplift of the two lateral keels in *F. lavinianum*, together with a fall in the central keel (Fig. 4B). This analysis indicates the transition from a monocarinate venter to a tricarinate venter is not merely the result of uplift of the lateral keels but also involves lowering of the ventral keel.

4.2.2. LSTRA. This method allows us to visualise and quantify overall differences in shape between species. The same two species as before are illustrated (Figure 5). The differences already highlighted are found. The sum of vector lengths provides a measurement of the morphological distance between the two species ($\Sigma\Delta = 0.80$ for the ribs, $\Sigma\Delta = 1.42$

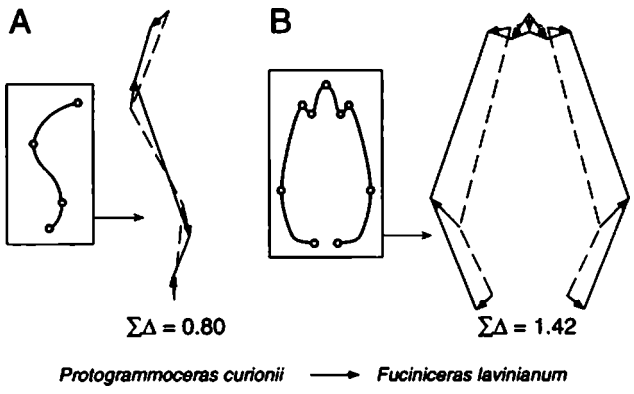


Figure 5. Comparison of the morphology of two species by the LSTRA method. (A) rib pattern. (B) ventral area. The vectors show the purely morphological differences (regardless of size and orientation) between the two species.

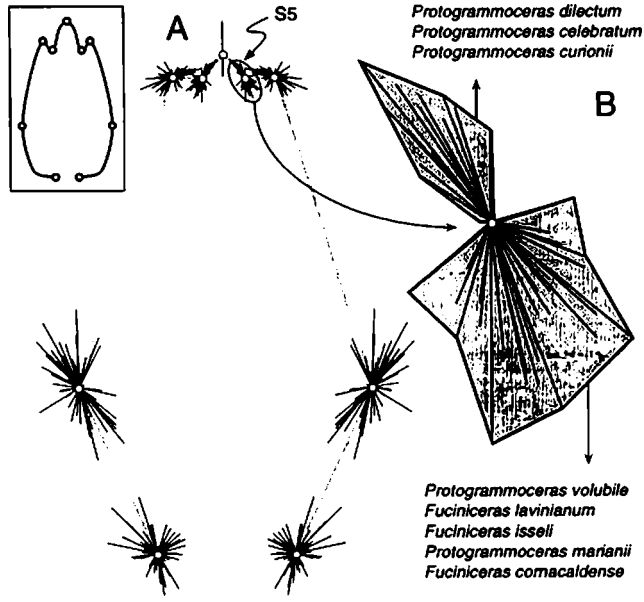


Figure 6. Comparison of the whorl section shape for 60 specimens belonging to eight species by the LSTRA method. (A) Each segment links one landmark on one individual to the homologous point on the mean consensus individual calculated from the entire population. This representation shows the morphological variation on the scale of the eight species. (B) Detail of landmark S5.

for the whorl section). These two measurements cannot be compared with one another as the analysis does not concern the same number of points nor the same morphological character. However, measurements between species are perfectly comparable if the same character is described by the same number of landmarks (see below).

Analysis of all the individuals of the eight species allows us to visualise the set of morphologies expressed. This is done using the generalised least square technique (GLS, Bookstein, 1991) and is illustrated here for the shape of the whorl section (Figure 6). In this case the difference between each individual and the mean consensus individual (calculated from the whole population) is represented by a straight line (Fig. 6A). The shape of the segment cloud indicates whether there are any preferential changes on the scale of the population. For points S4 and S5, for instance, the cloud is strongly anisotropic (Fig. 6B), probably due to shell construction constraints. In addition, the direction of changes in this region allows the two groups of species to be separated: *P. dilectum*, *P. celebratum* and *P. curionii* (clearly sharp monocarinate venter) versus *P. volubile*, *F. lavinianum*, *F. isseli*, *P. marianii*, *F. cornacaldense* (shouldered to tricarinate venter).

4.3. Morphological Maps

4.3.1. Baseline. Rib shape only is discussed here. The set of landmarks of the eight species (after processing by the baseline method) may be plotted on the same morphological space, where differences in shape can be read directly (Figure 7). There is a clear segregation between the two morphological genera for the ventral segment: shorter and more acute angle (relative to the baseline) in *Fuciniceras* than in *Protogrammoceras*. The latter is found, however, in two morphological states with the species *P. celebratum* and *P. curionii* characterised by a particularly long segment (relative to the baseline). Conversely, this segregation between the two genera is not found for the umbilical segment. On the contrary, a morphological trend is noticeable: the angle (a) of the segment varies from closed to open, paralleling the stratigraphic position of the species, a feature which had not been reported until now.

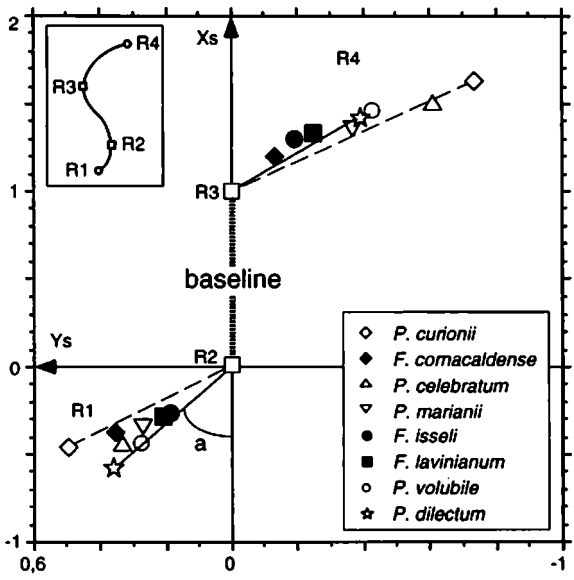


Figure 7. Comparison between species using the baseline method for ribs. a: angle between the umbilical segment of the rib and the baseline.

4.3.2. LSTRA. The fit of eight species taken two-by-two can be used to construct a distance matrix for the rib pattern and for the whorl section (Table 1). The phenetic trees calculated from these matrices are not congruent with respect to these two characters (Figure 8). For the ribs, the two morphological genera are segregated, whereas for the whorl section, *P. marianii* is located in the morphological space of *Fuciniceras*. These still preliminary findings require complete analysis on the scale of the Harpoceratinae subfamily before they can be really interpreted, in particular to understand any biomechanical relations between the two characters.

Table 1. Matrix of the arithmetic differences between species (ΣΔ), calculated by the LSTRA method. (A) for ribs, (B) for whorl sections

ΣΔ	#1	#2	#3	#4	#5	#6	#7
A (ribs)							
P. dilectum (#1)							
P. volubile (#2)	0.20						
F. lavinianum (#3)	0.40	0.34					
F. isseli (#4)	0.44	0.38	0.06				
P. marianii (#5)	0.26	0.12	0.25	0.30			
P. celebratum (#6)	0.38	0.22	0.51	0.56	0.28		
F. cornacaldense (#7)	0.55	0.59	0.44	0.41	0.55	0.78	
P. curionii (#8)	0.40	0.46	0.80	0.83	0.57	0.33	0.92
B (whorl sections)							
P. dilectum (#1)							
P. volubile (#2)	0.75						
F. lavinianum (#3)	1.20	0.58					
F. isseli (#4)	0.93	0.59	0.40				
P. marianii (#5)	0.98	0.68	0.44	0.21			
P. celebratum (#6)	0.50	0.88	1.43	1.24	1.34		
F. cornacaldense (#7)	0.83	0.40	0.50	0.33	0.48	1.04	
P. curionii (#8)	0.56	0.88	1.42	1.24	1.34	0.29	1.02

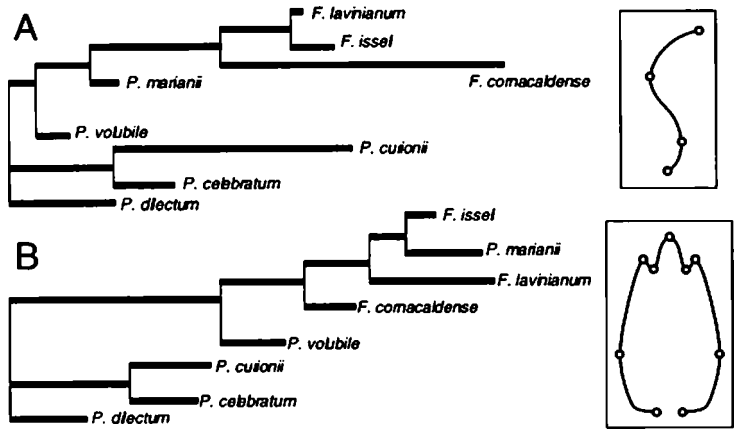


Figure 8. Phenetic trees computed from rib pattern data (A) and from whorl section shape data (B). Only the horizontal bars show morphological distances between species.

5. CONCLUSIONS

This analysis shows the value of the landmark technique and the Procrustes method when applied to ammonites. These methods provide a clear picture of morphological changes between organisms or species and, above all, allow such changes to be quantified for morphological maps to be drawn up for biological characters of complex shape (e.g. ribs or ventral keel). They reveal, for example, as yet unrecognised morphological patterns in the Harpoceratinae, such as the preferential direction of raising or lowering of the groove between the lateral and ventral keels (Fig. 6B). In a more general framework, these methods are the logical follow up to comparative anatomy, pin-pointing and quantifying the morphological differences between individuals with the same bauplan. Furthermore, they provide pointers to possible constraints on shell construction, and therefore on the interdependence of morphological characters commonly used in taxonomy. In return, this reflection on the nature of characters will make it possible to reconsider their use for, say, phylogenetic purposes.

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