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Morphometrics and phenetic versus cladistic analysis of the early Harpoceratinae (Pliensbachian ammonites)

By

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With 11 figures and 2 tables in the text

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Abstract: A faunal sequence of Mediterranean Harpoceratinae belonging to the genera *Protogrammoceras* and *Fuciniceras* (Middle Carixian to Middle Domerian) is analysed. Ammonite shell shape and ornamentation are described in entirely quantitative terms. Phenetic and cladistic trees are proposed. The results lead to the conclusion that (1) the two genera considered are meaningful entities in a morphological sense but not in terms of phylogeny; (2) the species considered fit into a clade where the morphologies of the two genera occur independently twice over.

Zusammenfassung: Eine Faunensequenz von mediterranen Harpoceratinae, die zu den Gattungen *Protogrammoceras* und *Fuciniceras* (Mittel-Carixian bis Mittel-Domerian) gehört, wird analysiert. Schalenform und Ornamentierung werden ausschließlich quantitativ charakterisiert und als Grundlage von phenetischen und cladistischen Diagrammen verwendet. Die Diagramme zeigen: (1) die beiden Gattungen sind lediglich im morphologischen, nicht aber im phylogenetischen Sinne brauchbare Einheiten; (2) die untersuchten Arten bilden einen Clade, in dem die Merkmalskombinationen beider Gattungen zweimal iterativ entstehen.

I. Introduction

The Harpoceratinae was a world-wide subfamily that originated in the Pliensbachian and reached its fullest extension during the Toarcian. Here we have selected the early sequence of species which inhabited the Mediterranean province of the Western Tethysian realm and lived from the Middle Carixian to the Middle Domerian. In the literature, these species are usually ascribed to the genera *Protogrammoceras* Spath, 1913 or *Fuciniceras* Haas, 1913. A variety of phylogenetic hypotheses have been proposed for these genera (e. g. Cantaluppi 1970, Wiedenmayer 1980, Braga 1983, Dommergues et al. 1990, Ferretti 1991). One major reason for there being several conflicting hypotheses is that the definition of the two genera is ambiguous. For most workers

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Protogrammoceras bears a single ventral keel and clearly falcoid ribs, whereas *Fuciniceras* bears a triple ventral keel and slightly falcoid ribs. The sheer number of species that exhibit both *Protogrammoceras* and *Fuciniceras* traits suggests that these classifications are probably artificial. Accordingly, the generic names are mainly of morphological significance and have no clear phylogenetic meaning. Thus, in this study, generic definitions are not used a priori, and investigations are based directly on the species, which are deemed to belong to a single monophyletic group. In the following study, to emphasise that these genera have only morphological significance, the names are placed in inverted commas (e.g. "*F.*" or "*Fuciniceras*", "*P.*" or "*Protogrammoceras*").

Another reason why phylogenetic assumptions are commonly conflicting is that, when diagnosing species, shape is defined in ordinal and subjective terms. In addition, shell construction and the relationships between shell features are usually overlooked. Consequently, it is difficult to identify just what is phylogenetic information and to decipher convergence and biomechanical links correctly.

In contrast to all earlier analyses, our aim in this study is to establish morphometric frameworks in which to characterise shape in an objective way, and to investigate morphological constraints before attempting any phylogenetic reconstruction. Such morphometric frameworks, based on the identification of landmarks, are computed by the fitting methods proposed by SNEATH (1967) and BOOKSTEIN et al. (1985). Once shape has been defined, relationships between species can be formalised using phenetic and cladistic methods. Finally, a cladistic tree is proposed as a starting point for a hypothesis about phylogenetic relationships.

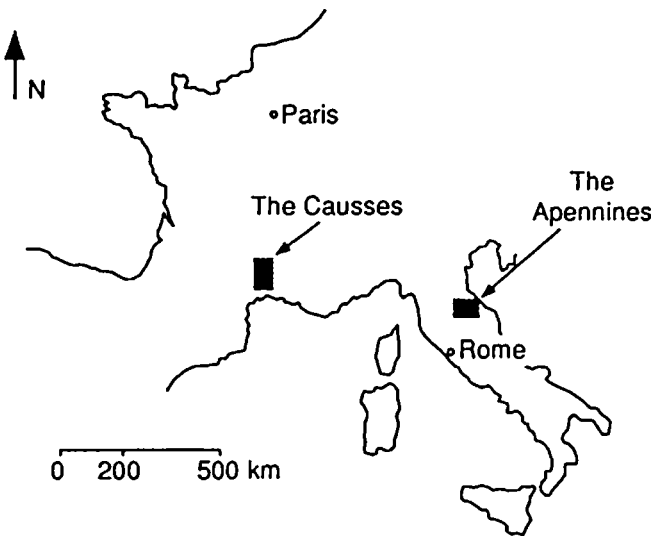


Fig. 1. Geographical location of the areas where the studied ammonites were collected.

II. Material

What are here termed "*Fuciniceras*" and "*Protogrammoceras*" belong to the early Harpoceratinae (Hildoceratáceae) and may be treated as a monophyletic group. The ammonites discussed in this paper came from the Central Apennines of Italy (Fig. 1), where two sections – Gola del Burano (DOMMERGUES et al. 1990, FERRETTI 1991) and Gorghe (FERRETTI 1991) – afford a bed-by-bed study of the faunal sequence. Successives beds may be grouped together if the fauna they contain display no obvious biometrical differences (see DOMMERGUES et al. 1990 for these amalgamations). This reconstruction allows us to propose a stratigraphic reference sequence comprising eight successive taxa, which are, from oldest to youngest: "*P.*" *dilectum* (FUCINI 1900), "*P. volubile* (FUCINI 1900),"*F.*" *gr. portisi* (FUCINI 1900) – *laevinianum* (FUCINI 1900), "*F.*" *gr. brevispiratum* (FUCINI 1900) – *isseli* (FUCINI 1900), "*P.*" *marianii* (FUCINI 1904), "*P.*" *celebratum* (FUCINI 1900), "*F.*" *cornacaldense* (TAUSCH 1890) and lastly "*P.*" *curionii* (MENEGHINI 1867-1881). The final species heralds the development of the Upper Domerian Harpoceratinae. Because of the scarcity of "*F.*" *cornacaldense* in the Apennine fossil record, a population of corresponding age belonging to "*F.*" *boscense* (REYNES 1868), a very close form (DOMMERGUES & MEISTER 1986) collected in the Causses (France) (Fig. 1), is added in this study. Situated in the southern part of the epicontinental NW European sea, the Causses were widely exposed to various Mediterranean influences (successive faunal ingressions) during the Domerian. In addition, plaster casts of some of the original ammonites figured by FUCINI (1899-1900) and collected in the Central Apennines, supplement the species "*P.*" *dilectum*, "*F.*" *gr. portisi-laevinianum*, "*F.*" *gr. brevispiratum-isseli* and "*P.*" *celebratum*. All told, 80 study specimens are used for morphological investigations of the seven evolutionary steps in question. To ensure standardisation in the morphometric analysis, all the selected specimens are internal moulds.

III. Method

For earlier workers (SPATH 1913, FUCINI 1899-1900, CANTALUPPI & BRAMBILLA 1968, FISCHER 1975, GÉCZY 1976, WIEDENMAYER 1980, BRAGA 1983, DOMMERGUES et al. 1990, FERRETTI 1991), the major distinguishing features for identifying the different species were the whorl section, the ventral area and the rib shape patterns. These features were evaluated as part of an ordinal approach by DOMMERGUES et al. (1990). These workers drew up a standardised chart using SPATH's terminology (SPATH 1913) to define four typical kinds of rib shape, respectively termed from less to more falcoïd: angulirursiradiate, subanguliradiate, subfalciradiate and falciradiate. DOMMERGUES et al. (1990) proposed a similar approach for the ventral area and for the whorl section, defining six typical morphologies ranging from a tricarinate to a monocarinate ventral shape. Because population studies yield a number of intermediate morphologies, the main problem with this kind of characterisation

is the difficulty of ascribing each ammonite to a standardised type morphology.

In contrast with this ordinal approach, we attempt in this paper to establish entirely quantitative morphometric frameworks for early Harpoceratinae morphology. To this end, morphology is characterised using pre-established homologous points. These points, known as landmarks (SNEATH 1967), are characteristic loci defined on the surface of the shell. They must be precisely recognisable on a given organism and must be reproducible from one specimen to another. These landmarks are used to characterise the rib pattern and whorl section shape around the ventral area. Besides, in the case of the morphometric framework for ribs, a repetitive homology occurs in each individual, meaning that the same feature (a rib) can be identified several times on the same ammonite. This so called "serial" homology (VAN VALEN 1993) occurs notably with organs that have been conformed by successive and continuous increments (e.g. mollusc shells). Such serial homology is known to be controlled in part by iteration of what is basically the same developmental program (VAN VALEN 1993), and was considered in other terms by D'ARCY THOMPSON (1992) in his chapter about the equiangular spiral:

"It has been conformed by successive and continuous increments; and each successive stage of growth, starting from the origin, remains as an integral and unchanging portion of the growing structure. We may go further, and see that horn and shell, though they belong to the living, are in no sense alive. They are by-products of the animal; they consist of 'formed material', as it is sometimes called; their growth is not of their own doing, but comes of living cells beneath them or around. The many structures which display the logarithmic spiral increase, or accumulate, rather than grow".

IV. Morphometry

A. Shape parameters

Basic geometric parameters (RAUP 1967) are very convenient tools for describing general shell morphology. Moreover, because they are calculated by division of linear dimensions (Fig. 2A), they provide dimensionless results that are fully compatible with baseline or LSTRA analyses. The first two shape parameters were described by RAUP (1967): D is the relative distance between the generating curve and the axis of coiling (= c/d, Fig. 2A) and S is the aspect ratio of the generating curve (S = b/a, Fig. 2A). The other two Raup parameters are not used: T (whorl translation rate) because all the ammonites in this study have planispiral shells (therefore T = 0) and W (whorl expansion rate) because most of the shells are incomplete, so diameters cannot be measured. In addition to the D and S parameters, a new third one, here named TR (for triangulation), is calculated. TR is (b-f)/g (Fig. 2A) and provides information about the triangular versus quadrangular configuration of the whorl section.

B. Landmark location

As seen above, all the studied species are characterised by more or less falcoid ribbing. For our morphometric construction, a rib is defined by four landmarks: R1 to R4 (Fig. 2B). 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 forms. To characterise it, two landmarks are defined. The first, R2, is the point where the tangent drawn through the protoconch (P) touches the lower bend. The second, R3, is the point where the tangent parallel to the P-R2 line touches the upper bend. Once the four landmarks have been defined, ribs can be represented by a three-part line: umbilical segment (R1-R2), middle segment (R2-R3), and ventral segment (R3-R4). Because the studied Harpoceratinae are planispiral with rather flat sides, the problem of three-dimensional projection can be neglected, and we have considered the whorl sides as a two-dimensional plane.

Whorl section is characterised by a set of nine landmarks (Fig. 2C). The first one, S1, is the apex of the ventral keel. S2 and S3 are located at the points of

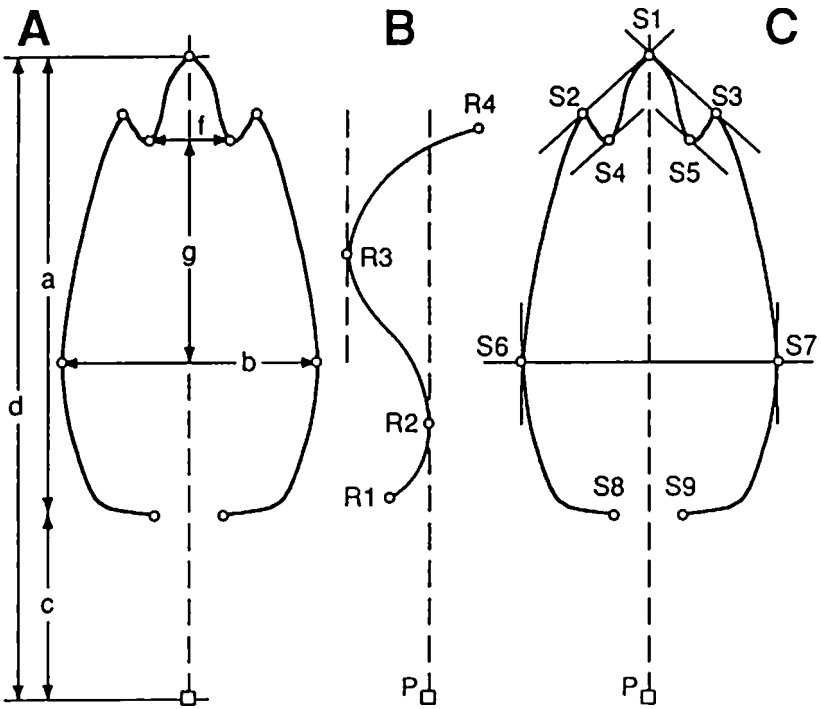


Fig. 2. Landmark location and linear dimensions depicting the shells. A – Linear dimensions on shells. B – Rib landmark location. C – Whorl section landmark location.

contact of tangents through S1 to the top of the lateral keels, or homologous locus. 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 the greatest whorl width. The final two landmarks, S8 and S9, lie on the umbilical seam.

The use of landmarks to determine shape reduces the discrepancy between a shape and its geometrical representation. By describing shapes in this way, we can seek out geometrical similarities and differences. Such similarities and differences can be determined by two different methods: the baseline procedure (Bookstein et al. 1985), or Least Square Tetha Rho Analysis (LSTRA, Sneath 1967), which is a geometrical fitting procedure that quantifies the overall difference between shapes. The main value of these two methods is that they completely exclude size and spatial position and focus on differences in shape alone.

C. Baseline method and applications

A set of landmarks delimiting a geometric shape, associated with their Cartesian coordinates, is used to describe each object (Fig. 3A). A sequence of translation, rescaling and rotation rearranges the network of landmarks so that there is a common baseline from a to b (Fig. 3B) with shape coordinates (0,0) and (1,0) respectively. Applying translation, rescaling and rotation to all the Cartesian coordinates of the other landmarks (c, c', c" and d, d', d") transforms them into shape coordinates (Fig. 3B). Thus, using such coordinates means pure geometrical shapes can be compared without size-related distortion.

The baseline method was developed by Bookstein et al. (1985), and by Bookstein (1991). It has been applied to organisms that exhibit spiral growth such as gastropods (Johnston et al. 1991) and foraminifera (Tabachnick & Bookstein 1990), as well as to rodent skulls (Zelditch et al. 1992). In this paper, the method is applied to ammonites, using ribs and the ventral area.

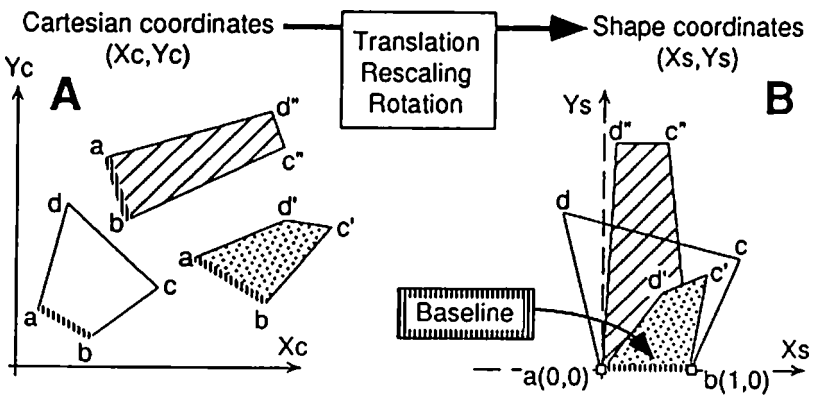


Fig. 3. Theoretical comparison of three geometrical objects defined by landmarks and carried out using the baseline method.

1. Application to rib pattern

A set of six to ten ribs in the same half whorl is measured for each specimen. So as to eliminate significant ontogenetic variations, all the chosen specimens are of roughly the same size close to the end of the phragmocone. This means that "consensus" individuals can be computed by averaging all the rib shape parameters from each individual. By averaging these consensus individuals a "consensus" species is constructed for use in the subsequent comparisons of species.

The R2-R3 segment is chosen as the baseline (Fig. 4A), chiefly because the criteria used by previous workers to identify the studied species are the length and the angle of the rib on the ventral and umbilical parts of the side. This choice of baseline focuses the analysis on these features. Moreover, if one compares the four landmarks, the coefficients of variation are smaller in the cases of R2 and R3 than in R1 and R4. In any event, the choice of the baseline does not produce any bias in the analysis of shape coordinates, as demonstrated by BOOKSTEIN (1991, Appendix 2). Using R2-R3 as a baseline means that the Cartesian coordinates of the two other landmarks (R1 and R4) must be transformed into shape coordinates using BOOKSTEIN's procedure (1991). These shape coordinates are used to calculate four non-sized parameters to describe the rib pattern (Fig. 4A). The first one is umbilical segment length (USL). It represents the proportion of this segment with respect to the baseline. Associated with USL, the second parameter is the umbilical segment angle to the baseline axis (USA). Similarly on the ventral area, the third parameter is the ventral segment length (VSL) and the fourth one is the ventral segment angle to the baseline axis (VSA).

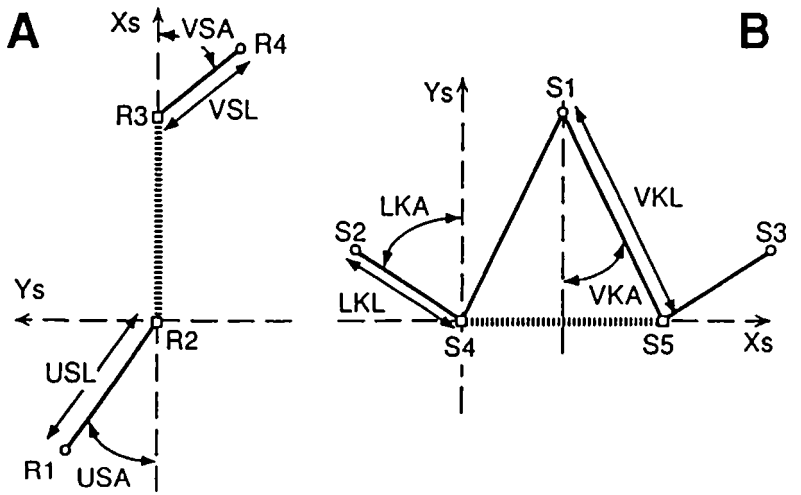


Fig. 4. Characters and morphometric parameters for ribs (A) and ventral area (B), using baseline computation.

2. Application to ventral area

The ventral area is analysed using a similar morphometric approach in an attempt to characterise both the ventral and the lateral keels. Measurements are made in axial view, and a single ventral section is analysed for each specimen. The shape of the ventral area for the different species is obtained by averaging all the individuals within each species.

The chosen baseline is the S4-S5 segment, chiefly for graphical convinience (Fig. 4B). From shape coordinates of S1, S2 and S3, four non-sized shape parameters are computed for the ventral and the lateral keels (Fig. 4B). The ventral keel is characterised by its length (VKL) and its angle relative to the mid-line of the ammonite (VKA). The lateral keel is characterised by its length (LKL) and its angle relative to the ammonite mid-line (LKA).

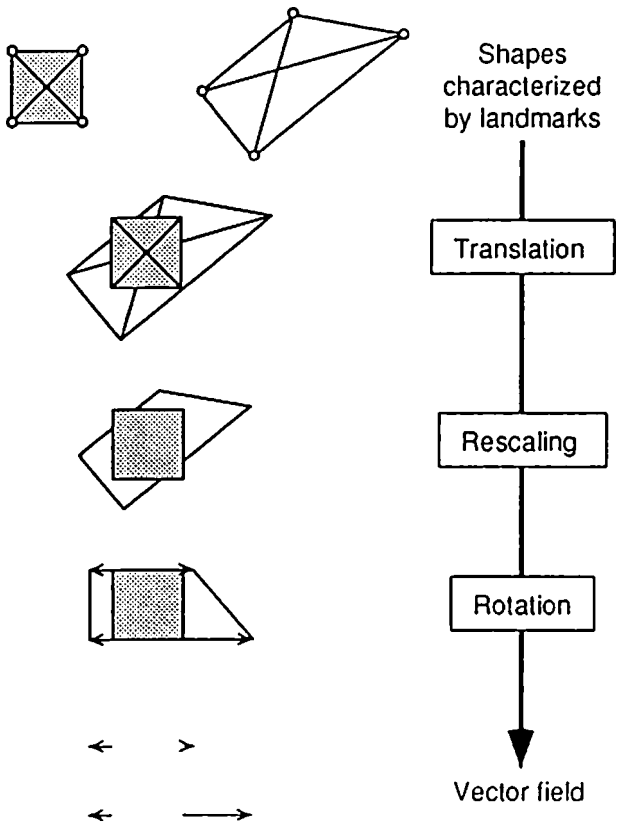


Fig. 5. Theoretical comparison of two geometrical objects defined by landmarks and performed by LSTRA fitting (from LAURIN & DAVID 1990).

D. LSTRA method and applications

In LSTRA, the differences in shape between two objects are represented by a set of vectors (Fig. 5). Each vector is drawn from a point on one object to its equivalent on another. The differences in shape of the two objects are calculated by minimising the overall vector field. This fitting technique involves computing a translation parameter, a rescaling factor, and a rotation angle (Fig. 5). The measurement of the morphological distance between two objects is thus given by the sum of the vector lengths: $\Sigma\Delta$ (Fig. 5) to go from one object to the other. This arithmetic distance ($\Sigma\Delta$) between two objects, calculated using the LSTRA method, is computed with the Procrustes package (David & Laurin 1992a). This method was first described by Sneath (1967) and has recently been applied to sea-urchins and brachiopods (Laurin & David 1990, David & Laurin 1992b) and to rodents (Din et al. 1993).

In this paper, thè method is used to compare whorl sections and ribs among ammonite species. Rib shape is determined from the four landmarks previously described (Fig. 6A). In the same way, whorl section shape is determined from the nine landmarks described above (Fig. 6B).

V. Results

A. Baseline

1. Rib pattern

– USL: three main groups of umbilical segment length (USL) can be subjectively recognised (Fig. 7A) determining three sets of species with respectively: (1) short segments for "*F.*" *gr. portisi-laevinianum* and "*F.* " *gr. brevispiratum-*

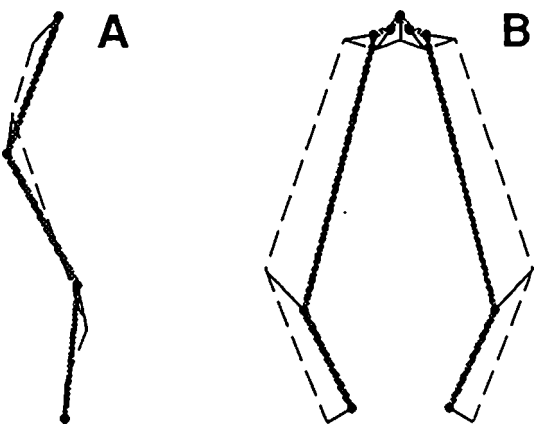


Fig. 6. Morphological changes using the LSTRA procedure: comparison of "*F.*" *portisi-laevinianum* (thick line) and "*P.*" *curionii* (dashed line) for ribs (A) and whorl section (B).

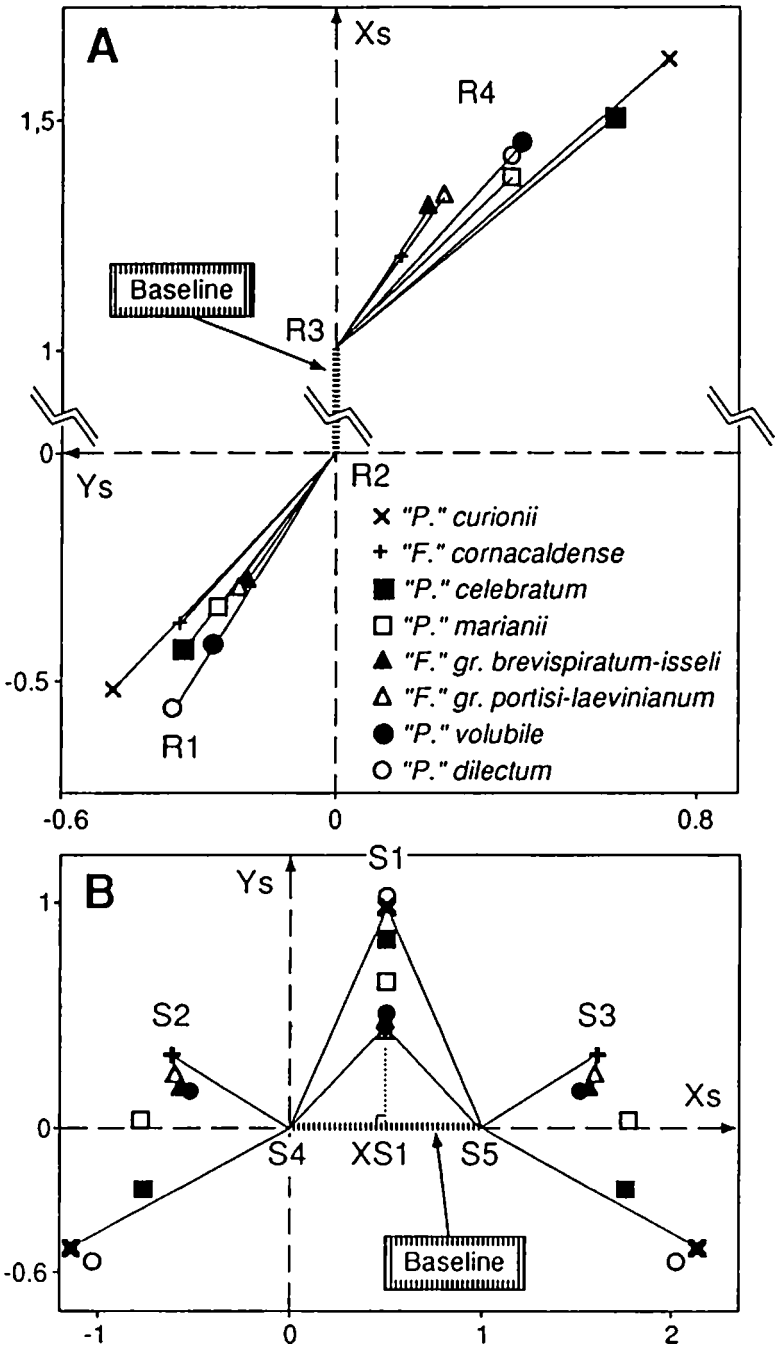


Fig. 7. Comparison between species using the baseline procedure in the shape plane (Xs-Ys). A – Ribs: plotting of landmarks R1 and R4, with R2-R3 segment as baseline. B – Ventral area: plotting of landmarks S1, S2 and S3 with S4-S5 segment as baseline (same species symbols as in A).

isseli, (2) intermediate length segments for "*P.*" *volubile*, "*F.*" *cornacaldense* and "*P.*" *celebratum*, and (3) long segments for "*P.*" *dilectum* and "*P.*" *curionii*. "*P.*" *marianii* is in an ambiguous position lying mid-way between the first and second groups.

– USA: umbilical segment angle (USA) distribution allows us to recognise subjectively three different sets of species (Fig. 7A): (1) closed angle grouping "*P.*" *dilectum*, "*P.*" *volubile*, "*F.*" *gr. portisi-laevinianum* and "*F.*" *gr. brevispiratum-isseli*, (2) intermediate angle grouping "*P.*" *marianii* and "*P.*" *celebratum*, and (3) open angle grouping "*F.*" *cornacaldense* and "*P.*" *curionii*. This parameter (USA) is particularly important because it exhibits a sustained trend from closed to open following the stratigraphic sequence of species.

– VSL and VSA: ventral segment length and angle (respectively VSL and VSA) distributions determine three sets of species. These groups of species are roughly the same for these two features: (1) a closed angle associated with a short segment for "*F.*" *gr. portisi-laevinianum*, "*F.*" *gr. brevispiratum-isseli* and "*F.*" *cornacaldense*, with a particularly short segment for the latter, (2) intermediate angle and segment length for "*P.* " *marianii*, "*P.*" *dilectum* and "*P.*" *volubile*, and (3) an open angle with a long segment for "*P.*" *celebratum* and "*P.*" *curionii*, with a particularly long segment for the latter.

2. Ventral area

– VKL, VKA and LKA: the relative length of ventral keel (VKL) provides indications on the relative elevation of the keel, which are exactly correlated to those given by the ventral keel angle (VKA). This correlation is due to the choice of the baseline, where XS1 (the X-ordinate projection of S1, Fig. 7B) is always 0.5. Thus, the triangle formed by XS1, S1 and S4 contains a right-angle at XS1, such that:

$$\sin(VKA) = 0.5 / (VKL)$$

This relation implies that VKL is a redundant parameter and is therefore excluded from the subsequent analysis, while VKA is retained. A further correlation occurs between the pairing VKA-VKL and LKA, but it is in this instance a biomechanical link and not a by-product of computation. This link stems from the fact that in nowhere among the taxa considered does a tricarinate ventral shape derive from a monocarinate ventral one by a simple raising of the ventrolateral edge. On the contrary, the tricarinate ventral shape is due to a raising of the ventrolateral edge and a correlative lowering of the ventral keel. Conversely, certain other Liassic groups display a raised ventral keel with high lateral keels (e. g. Arietitidae, *Caenisites*). Distribution of the species in the shape plane (Xshape-Yshape, Fig. 7B) for VKA, VKL and LKA is marked by two main sets of species separated by two intermediate species. A first group composed of "*P.*" *dilectum* and "*P.*" *curionii* exhibits a high ventral keel (keeled sensu Arkell et al. 1957), with no lateral keel defining a bent ventrolateral

edge (acute sensu ARKELL et al., 1957). An intermediate species close to this group is "*P.*" *celebratum*, with a similar but less pronounced pattern. The morphologically opposite group is composed of "*P.*" *volubile*, "*F.*" *gr. portisi-laevinianum*, "*F.*" *gr. brevispiratum-isseli* and "*F.*" *cornacaldense*, characterised by a tricarinate ventral area (tricarinate sensu ARKELL et al. 1957). An intermediate species between the keeled acute shape and the tricarinate one is "*P.*" *marianii*. This species has an average ventral keel with a shouldered ventro-lateral edge, but does not have marked lateral keels. This ventral area is then qualified as keeled-shouldered sensu ARKELL et al. (1957).

– LKL: three sets of lengths occurs for the lateral keel (LKL). Short sets "*P.*" *volubile*, "*F.*" *gr. portisi-laevinianum*, "*F.*" *gr. brevispiratum-isseli* and "*F.*" *cornacaldense*. Intermediate length sets "*P.*" *marianii* and "*P.*" *celebratum*, and long sets "*P.*" *dilectum* and "*P.*" *curionii*.

The major result of this morphometric analysis is that the species are gathered into different combinations depending on the considered parameter. Accordingly, because of these conflicting groupings, related to a mosaic distribution of features, it seems somewhat difficult to propose a phylogenetic framework on the strength of these results alone.

B. LSTRA

Another possible way to characterise similarities and differences between species is to analyse the two features (rib pattern and whorl section shape) in order to quantify the overall morphological differences between species. This is done using the LSTRA method previously explained. Examples of geometrical fitting are given for rib pattern and whorl section shape (Fig. 8) illustrating by a set of vectors the changes in shape from one species to another.

The pairwise distance matrix (Table 1) characterises the morphological difference between each pair of species by a single value for the two sorts of features. This arithmetic distance ($\Sigma\Delta$) does not consider the location of the differences. Because of this non-location of differences, two different pairs of comparisons might provide a similar measurement of $\Sigma\Delta$. Such computation could lead to differences being misinterpreted, notably when very different morphologies are compared. In our case, though, all of the phenotypes display a coherent morphological pattern, even if they range from monocarinate to tricarinate for the ventral area, and feature less or more falcoid ribbing.

The pairwise distance matrix is formed into a phenetic tree by running the Fitch algorithm (no constant rate of morphological change is assumed) in the Phylip package (FELSENSTEIN 1990). This method constructs trees from the overall similarities calculated between two species. Because results are based on overall similarities, it is obvious that such a tree covers all of the characters including apomorphies, plesiomorphies and homoplasies. Accordingly, the proposed phenetic trees group species on the basis of morphological similarities, which may equally well arise from true phylogenetic links or form

similar adaptive or biomechanical morphological responses. Thus, such trees do not indicate phylogenetic relationships directly, but can provide useful morphometric information for preparing cladistic analyses. Indeed, as DARLU & TASSY (1993) pointed out, in a phenetic tree, the nodes do not represent any ancestral states as in a cladistic tree, but the degree of morphological similarity of the species studied.

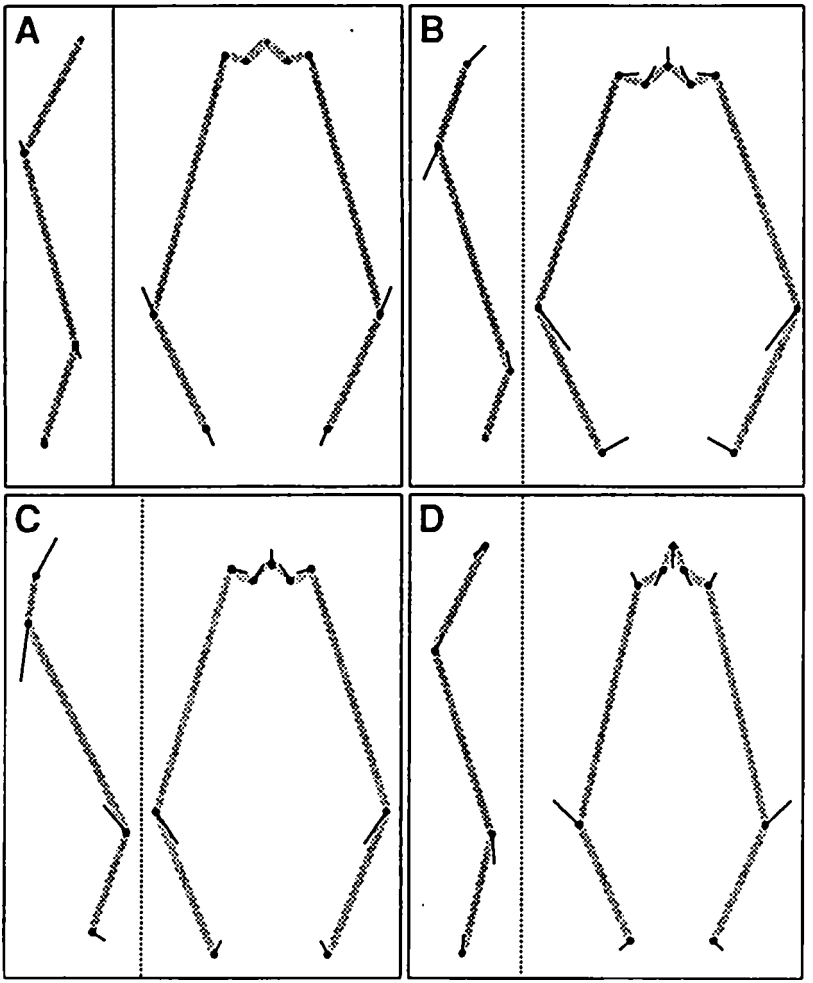


Fig. 8. Examples of morphological comparisons between taxa, computed by the LSTRA procedure. Note that the dashed line corresponding to the versus individual as figured on Figure 6 is removed so the vector field can be seen more easily. A – *"P." volubile* versus *"P." marianii*. B – *"F." gr. portisi-laevinianum* versus *"P." celebratum*. C – *"F." cornacaldense* versus *"P." curionii*. D – *"P." dilectum* versus *"F." gr. brevispiratum-isseli*.

Table 1. Matrix of the arithmetic difference between species (ΣΔ), calculated by the I.STRA method for ribs and whorl sections.

ΣΔ	*"P." dilectum*	*"P." volubile*	*"F." gr. portisi-laevinianum*	*"F." gr. brevi.-isseli*	*"P." marianii*	*"P." celebratum*	*"F." cornacaldense*
RIBS							
"P." volubile	0.20						
"F." gr. portisi-laevi.	0.40	0.34					
"F." gr. brevi.-isseli	0.44	0.38	0.06				
"P." marianii	0.26	0.12	0.25	0.30			
"P." celebratum	0.38	0.22	0.51	0.56	0.28		
"F." cornacaldense	0.55	0.59	0.44	0.41	0.55	0.78	
"P." curionii	0.40	0.46	0.80	0.83	0.57	0.33	0.92
WHORL SECTION							
"P." volubile	0.75						
"F." gr. portisi-laevi.	1.20	0.58					
"F." gr. brevi.-isseli	0.93	0.59	0.40				
"P." marianii	0.98	0.68	0.44	0.21			
"P." celebratum	0.50	0.88	1.43	1.24	1.34		
"F." cornacaldense	0.83	0.40	0.50	0.33	0.48	1.04	
"P." curionii	0.56	0.88	1.42	1.24	1.34	0.29	1.02

In our case two trees are proposed (Fig. 9), the first computed from the rib pattern matrix and the second from the whorl section shape one (Table 1). In such trees, as previously discussed, the nodes depend only of the degree of similarity between species. Indeed, the morphometric distance between species is represented by the sum of the length of all the horizontal segments from one species to another. The rib pattern tree (Fig. 9A) clearly separates the two different genera defined by earlier workers: a first group contains the three species usually attributed to "*Fuciniceras*": "*F.*" *gr. brevispiratum-isseli*, "*F.*" *gr. portisi-laevinianum* and "*F.*" *cornacaldense*, and the second one includes the five species generally ascribed to the "*Protogrammoceras*" genus: "*P.*" *dilectum*, "*P.*" *volubile*, "*P.*" *marianii*, "*P.*" *celebratum* and "*P.*" *curionii*. In contrast, the phenetic tree based on the whorl section challenges the traditional taxonomy by the inclusion of "*P.*" *marianii* in the "*Fuciniceras*" group, which underlines the ambiguous use of the two genera in the literature.

Once again, a phylogenetic reconstruction seems difficult to propose, because the two phenetic trees, based on two different kinds of features, fail

to provide similar results. Moreover, as seen above, phenetic trees cannot be treated as phylogenetic trees. Thus, the LSTRA and baseline analyses indicate that, for instance, an identical rib pattern between two species does not necessarily mean that the two species will exhibit the same whorl section shape, or vice versa. This sort of mosaic pattern suggests that the evolutionary history of the Harpoceratinae studied here is strewn with numerous homoplasies. So the previous morphometric analysis, however valuable for characterising shape, cannot serve as a basis for deciphering phylogenetic relationships. In fact, only a cladistic analysis is a valid way of reconstructing the phylogeny of the species studied. Such an analysis, based on the characterisation of shape established during the morphometric stage of this work, is now proposed.

VI. Cladistic reconstruction

A phylogenetic systematic (cladistic) analysis is carried out to propose a reconstruction of the relationships among the eight species under study. The concepts and terminology of this method can be found in abundant literature (e.g. Hennig 1965, Platnick 1977, Wiley 1981, Funk & Brooks 1990). The

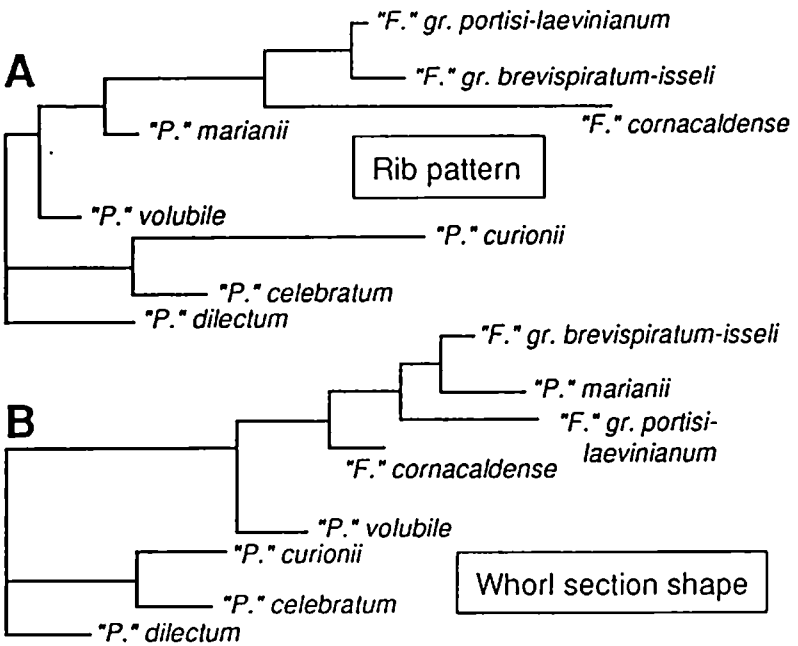


Fig. 9. Phenetic trees computed from rib pattern data (A) and from whorl section shape data (B).

cladistic method is the most convenient for determining phylogenetic relationships. Since it was developed, an increasing number of studies have based their phylogenetic hypotheses on cladistic logic. These cover a broad range of taxa: fossil and recent, animal and plant (e. g. Tassy & Darlu 1986, Funk & Brooks 1990, Carlson 1993, David 1993). Only a handful of published studies about cephalopods are available (Engeser & Bandel 1988, Landman 1989, Landman et al. 1991, Dommergues & Meister 1992, Landman & Waage 1993). In this work, cladistic trees are computed by running the PAUP package (Swofford 1991).

A. Neutral reading of character states

This first cladistic analysis, using a neutral reading of character states, is based on a statistical method for determining the different states, and no attempt is made to eliminate characters even if one can suspect that they may be linked by biomechanical constraints. Conversely, in instances where there is an obvious mathematical tie between characters (VKA and VKL), only one (VKA) is retained in the analysis. This procedure avoids artificial redundancy. The ten characters previously analysed are used: computed with the baseline method (USL, USA, VSL, VSA to describe ribbing, and VKA, LKL, LKA to describe the ventral area) or computed with the linear dimensions ratio (S, D, TR to describe overall shell shape).

1. Character states

Only multistate characters are recognised. Character states are coded on a purely morphometric basis, using analysis of variance. This method is valuable in that it tests differences between species' character states statistically, regardless of stratigraphic order.

An analysis of variance is computed for each of the ten characters. Two or more species have the same state, and so are ascribed the same code, if (1) no

Table 2. Matrix of the eight species versus the ten characters used for the cladistic analysis based on neutral reading of character states.

	USA	USL	VSA	VSL	VKA	LKA	LKL	TR	D	S
"P." curionii	2	4	3	7	1	3	2	1	0	2
"F." cornacaldense	2	2	1	0	4	0	0	1	3	2
"P." celebratum	1	2	4	6	0	3	1	1	2	1
"P." marianii	1	0	2	3	2	2	1	1	2	2
"F." gr. brevi.-isseli	0	0	0	1	4	1	0	2	2	3
"F." gr. portisi-laevi.	0	0	1	2	4	1	0	2	3	4
"P." volubile	0	1	2	5	3	1	0	1	3	3
"P." dilectum	0	3	3	4	0	4	3	0	1	0

significant differences (significance level of 95 %) occur between them for the considered character, and if (2) the species in question have the same type of relation (significant difference or no difference) with regard to all other species. If (n) sets of species are determined by this method, the codes of the multistate characters are incremented from 0 to (n-1). Table 2 shows the data matrix constructed from these ten successive analyses of variance, where the meanings of the codes are:

- USA: most closed angle coded 0, most open angle coded 4;
- USL: shortest segment coded 0, longest segment coded 4;
- VSA: most closed angle coded 0, most open angle coded 4;
- VSL: shortest segment coded 0, longest segment coded 7;
- VKA: most closed angle coded 0, most open angle coded 4;
- LKA: most closed angle coded 0, most open angle coded 4;
- LKL: shortest segments coded 0, longest segment coded 3;
- TR: most triangular section coded 0, most quadrangular section coded 2;
- D: most involute shell coded 0, most evolute shell coded 3;
- S: most compressed shell coded 0, widest shell coded 4.

For instance, "*P.*" *dilectum*, "*P.*" *volubile*,"*F.*" *gr. portisi-laevinianum* and "*F.*" *gr. brevispiratum-isseli* have the same code (0) for USA (Table 2), meaning that the analysis of variance of USA detects no significant difference between these four species, and meaning that they have the same type of relation with regard to the other four species: significant difference versus "*F.*" *cornacaldense* and "*P*" *curionii*, and no significant difference versus "*P.*" *marianii* and "*P.*" *celebratum*.

2. Determination of polarity

The choice of outgroup is a crucial step which determines (1) the polarisation of character state sequences, and (2) the computation of a rooted tree. In our analysis, "*P.*" *dilectum* is chosen as the outgroup, on two grounds. The first is that this primitive-looking species exhibits a closest morphology to the potential ancestor of the Harpoceratinae (Psiloceratacеae, Oxynoticeratidae ?, *Glevi-ceras* ?). The second ground is that "*P.*" *dilectum* has the lowest stratigraphic rank of the eight studied species, and is obviously the oldest taxon of the Harpo-ceratinae sub-family. Even if the stratigraphic criterion is not generally used to determine polarity (because the lowest fossils are not necessarily the most primitive), in our case, this choice seems the most straightforward, because no other obvious criteria are available (BRYANT 1991), and because stratigraphy concords with the morphological data. The use of a single outgroup implies that the ingroup should be considered as monophyletic.

For this first neutral cladistic computation, all character states are unordered, leading to the outgroup character states being implicitly considered as plesio-morphic, and all other character states of other species as being apomorphic. Moreover, all characters are presumed to be reversible and are weighted equally.

3. Results

The analysis yielded twelve equally most parsimonious cladograms, each of them 41 steps long and a consistency index of 0.902, which reveals the presence of homoplasies. These twelve cladograms are summarised in a strict consensus one (Fig. 10A). It is marked by a severe polytomy, grouping all of the species, except the outgroup, which is, by definition, rooted at the base of the cladogram. Such a strict consensus is unresolved, and so no phylogenetic assumption can be proposed. Another consensus tree can be computed based on the previous one, but keeping the nodes which occur in fifty percent or more of the set of the equally most parsimonious cladograms. This so called "fifty percent majority rule consensus cladogram" (sensu SWOFFORD 1991) is illustrated in Fig. 10B. This type of consensus cladogram provides a good illustration of the consistency of nodes. In our case, the second node implies a three group polytomy. The crown-group is composed of four species, and its topology can be written: ("*F.*" *cornacaldense* ("*P.*" *volubile* ("*F*". *gr. portisi-laevinianum*, "*F.*" *gr. bre-*

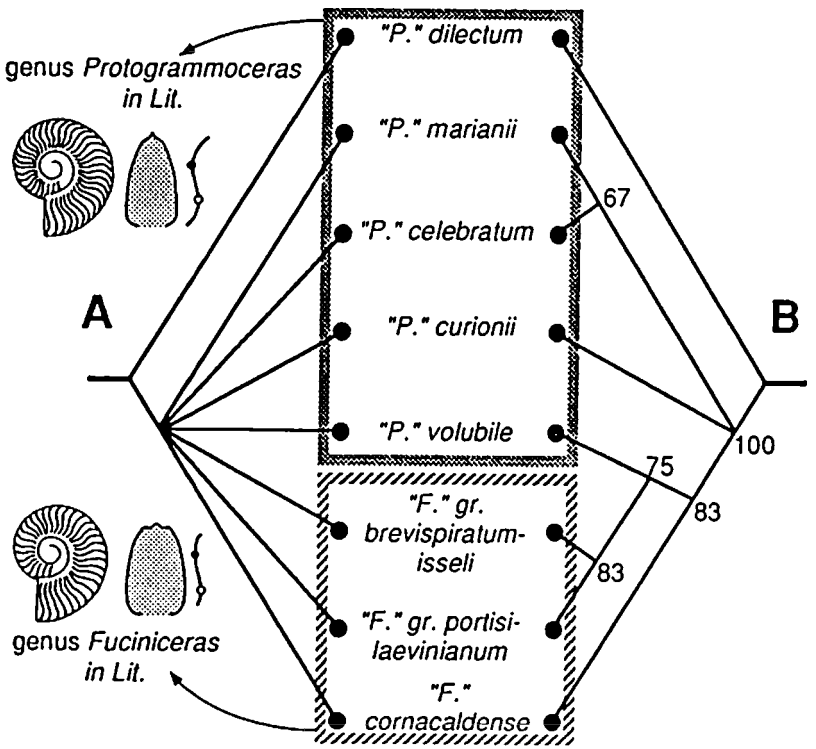


Fig. 10. Cladistic trees based on neutral reading of character states. A – Strict consensus tree. B – Fifty percent majority rule consensus tree.

vispiratum-isseli))). We note that no nodes within the crown-group are supported by more than ten trees out of twelve (83 %). Anyway, as no relevant criteria are available for choosing between the twelve trees, strict use of the cladistic method leads us to reject the use of nodes supported by less than 100 percent of data as a basis for a phylogenetic assumption.

This first neutral cladistic analysis highlights the difficulty of constructing a convincing phylogenetic hypothesis. Indeed, because of homoplasies, there is a severe conflict in the distribution of characters within the studied Harpoceratinae. One way to resolve these conflicts is to reconsider the way characters are interpreted and to review their state similarities with a view to improving the previously postulated assumptions about homologies.

B. Interpreted reading of character states

Faced with a situation of non cladistic resolution, we propose to make certain new assumptions founded on a revised set of homologies. These new assumptions, particularly as concerns the character states, are used to propose a new phylogenetic hypothesis by performing a new cladistic computation.

Idealy, characters used to formulate phylogenetic assumptions must not be subject to any homoplasies and/or, if the fossil record can be presumed good, must display constant evolution in keeping with a well-known stratigraphic sequence (e.g. a trend). In our analysis, the only character satisfying both these points is the umbilical segment angle (USA), and the changes in this character are assumed to match the true phylogeny. However, basing a phylogenetic assumption on this sort of morphostratigraphic argument implies that we believe the stratigraphic data to be reliable. In point of fact, the stratigraphic sequence of species admitted in this article is broadly accepted by workers in different areas (Cantaluppi & Montanari 1968, Braga 1983, Dommergues et al. 1983, Ferretti 1991, Meister et al. 1994). Thus, the simplest assumption is to consider that the stratigraphic data do reflect the true sequence of appearance and disappearance of the taxa. That will be our main assumption, backed by the following supporting argument. USA is protected against adaptative changes in ventral shape because of its umbilical position. Indeed, no biomechanical connection can be readily suspected between ventral area changes and USA, and this character, because of its umbilical position, is probably less affected than those of the ventral area by general shell shape changes brought about by ecological (hydrodynamic) transformations. So, because USA does not appear to be linked to any other characters, we may presume that it reflects the true phylogeny with no serious danger of homoplasies induced by simple ecological adaptations.

To conclude, as USA exhibits a sustained trend and as it is isolated from alternations of the hydrodynamic ventral area, it is here assumed to be the best guide to the reconstruction of phylogeny.

Apart from the two characters VKA and LKA that are suspected to be biomechanically linked being rolled into one, the second cladistic analysis is based on the nine characters previously computed using the baseline method or the linear dimensions ratio. VKA and LKA are combined as a new parameter termed VLKA (ventral and lateral keel angles) which quantify the type of ventral keel as well as the type of lateral keels.

1. Character states

The coding process is now based on the assumption discussed above and gives priority to the character USA. Thus, transformation steps of other characters, which do not conform with those of USA are viewed as homoplasies.

The different codes representing differences between species are directly determined for USA, USL, VSA, VSL, VLKA, LKL from the baseline results (see Fig. 7), and for TR, D and S from linear dimension ratio results. As in the previous cladistic analysis, "*P.*" *dilectum* is selected as the outgroup. But now, all multistate characters are considered to be ordered. All are equally weighted. Consequently, the outgroup state features are consistently assigned the code (0), which indicates plesiomorphy. The codes are indicated on the cladistic tree (Fig. 11) where:

- Character 1 (USA): progressive apomorphy from 0 (closed angle) to 2 (open angle);
- Character 2 (USL): progressive apomorphy from 0 (long) to 2 (short). 3 = first order reversion from short to long;
- Character 3 (VSA): progressive apomorphy from 0 (medium angle) to 1 (closed angle). 2 = first order reversion from closed to medium angle. 3 = second order reversion from medium to closed angle;
- Character 4 (VSL): progressive apomorphy from 0 (medium length) to 1 (short). 2 = first order reversion from short to medium length. 3 = second order reversion from medium length to short;
- Character 5 (VLKA): progressive apomorphy from 0 (keeled-acute) to 1 (tricarinate). 2-3 = first progressive order reversion from tricarinate to keeled-acute. 4 = second order reversion from keeled-acute to tricarinate;
- Character 6 (LKL): progressive apomorphy from 0 (long) to 1 (short). 2 = first order reversion from short to long. 3 = second order reversion from long to short;
- Character 7 (TR): progressive apomorphy from 0 (triangular section) to 2 (quadrangular section). 3 = first order reversion from quadrangular to triangular section;
- Character 8 (D): progressive apomorphy from 0 (closed umbilic) to 1 (open umbilic). 2 = first order reversion from open to closed umbilic;
- Character 9 (S): progressive apomorphy from 0 (compressed section) to 2 (depressed section). 3-4 = first progressive order reversion from depressed to compressed section.

2. Results

The analysis yielded a single most parsimonious cladogram (Fig. 11), 28 steps long. Unlike the previous cladistic tree, constructed from a neutral reading of character states, this tree is fully resolved. According to this result,

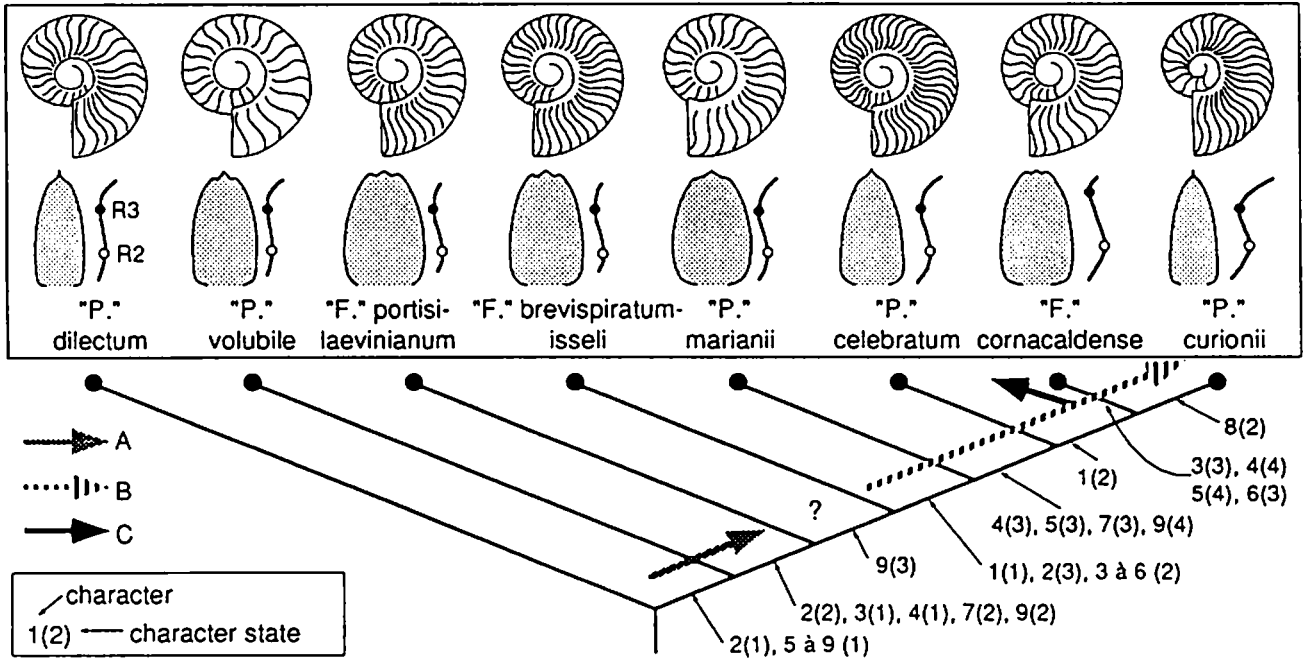


Fig. 11. Cladistic tree based on interpreted reading of character states. A – Transition from "*Protogrammoceras*" to "*Fuciniceras*" morphologies. B – First order reversion from "*Fuciniceras*" to "*Protogrammoceras*" morphologies. C – Second order reversion from "*Protogrammoceras*" to "*Fuciniceras*" morphologies.

based on previously coded reversions, the clade can be divided into three evolutionary sequences: (1) a transition from "*Protogrammoceras*" morphologies towards "*Fuciniceras*" morphologies (Fig. 11, arrow A), then (2) a first order reversion leading from "*Fuciniceras*" morphologies to "*Protogrammoceras*" ones (Fig. 11, arrow B), and (3) a second order reversion involving "*F.*" *cornacaldense* in an iteration of "*Fuciniceras*" morphology (Fig. 11, arrow C). So, the proposed phylogeny posts that the species are arranged in a clade in which the "*Protogrammoceras*" and "*Fuciniceras*" morphology occurs twice over.

VII. Discussion

1. The characterisation of ammonite shape: Background, method and implications

The development of biometric methods for depicting fossil shape transforms the description of ammonite morphology from an ordinal to a quantitative process. While a great deal has been made of this change in the way shape is characterised for shell outlines (Raup 1967, Okamoto 1988, Ackerly 1989), there is still scope for development with regard to the less prominent traits (e. g. ornament, whorl section and ventral area patterns). Until now, rib or ventral area patterns have been described in ordinal terms (Dommergues et al. 1990, Hohenegger & Tatzreiter 1992). However, some workers (Gabilly 1976, Braga 1983) have felt the need for an improved description of these features and have defined a number of well localised points which help to describe shape, although still as part of an ordinal approach. For rib patterns, no studies have gone further, and descriptions are still ordinal. No quantified studies have been proposed for the detailed morphology of the ventral area although some have been attempted for the whorl section (Raup 1967, Checa 1991). In fact, these quantifications provide an estimate of overall whorl section shape, but fail to describe particular whorl section features such as keels.

In line with these earlier studies, and based on the recent development of morphometric tools (Bookstein et al. 1985, Bookstein 1991), this paper seeks to quantify certain subtle ammonite features. To do this, rib and ventral area patterns are described using a set of landmarks. Morphometric tools (baseline method, LSTRA) are then used to eliminate size components, with a view to obtaining a pure shape statement of these features. A major improvement on the previous ordinal view is that quantification allows us to effectively explore the morphological space occupied by the different taxa.

For the Harpoceratinae reviewed here, analysis of the morphological space for rib pattern and ventral area allows us to identify distinct sets of species from various morphological traits. Depending on the parameter considered, these groupings of taxa do not gather the same species, revealing a mosaic distribution of features. This emphasises the need to consider and study these organisms as complex entities, combining numerous traits, whose fluctuations within a clade are not necessarily congruent.

Thus, as the rib shape and ventral area do not fluctuate on the same pattern, several species within the clade may display a combination of "*Protogrammoceras*" and "*Fuciniceras*" traits. This phenomenon underscores just how inoperative the usual definitions of these two genera are.

2. Biomechanical connections between features

There have been several attempts to analyse the biomechanical connections between features in ammonites (e. g. CHECA 1986a, CHECA 1986b, CHECA & WESTERMANN 1989, KORN 1992). These studies have shown the importance of being able to recognise traits that depend on others, especially within lineage studies. In such instances, the dependent characters must not be used as independent criteria to provide information about taxonomy or phylogeny.

In our study, a single example of a biomechanical connection has been demonstrated between the ventral keel angle (VKA) and the lateral keel angle (LKA), but others are strongly suspected (e. g. between the ventral part of the rib and the ventral area of the ammonite). Consequently, the influence of these different features should be reduced in any phylogenetic reconstruction. In this study, a first cladistic analysis was carried out without taking these biomechanical connections into account, while the second analysis did include them. The results of these two analyses demonstrate that it is impossible to construct a relevant phylogeny if biomechanical connections are not previously exposed. On the contrary, by fully taking into account these connections to specify the relative importance of the different characters, and by recognising the paramount importance of the USA, we are able to come up with a more satisfying phylogenetic reconstruction.

3. Relationships between the Harpoceratinae species under review

Various phylogenetic assumptions have already been made for the Harpoceratinae studied here. Some workers using typological conception of species (CANTALUPPI 1970, CANTALUPPI & MONTANARI 1973, BRAGA 1983) consider that the Mediterranean Harpoceratinae formed two distinct lineages from the Middle or Upper Carixian. They claim that these two lineages correspond to the two genera *Protogrammoceras* and *Fuciniceras* right from the time the family first appeared in the fossil record. Other authors taking in account the intraspecific variability (DOMMERGUES et al. 1983, MOUTERDE & FERRETTI 1986, DOMMERGUES et al. 1990) argue that the two genera *Protogrammoceras* and *Fuciniceras* are chiefly of morphological significance and lack any clear phylogenetic meaning. These workers suggest that the species belong to a single monophyletic group where the "*Protogrammoceras*" and "*Fuciniceras*" morphologies may iterate.

To test these two different assumptions, relationships among the species have been analysed here in two different ways, the first investigating the phenetic relationships, the second the phylogenetic ones.

Phenetic analysis leads to the construction of two phenetic trees, one for the rib pattern, and one for the whorl section. While the rib pattern tree fits in with the usual division of genera, the whorl section shape tree implies a conflict, and includes one "*Protogrammoceras*" species with the "*Fuciniceras*" ones. Moreover, the distances between taxa are clearly different between these two phenetic trees. Once again, the traditional definition of the two genera is hardly operative.

Cladistic analysis is first carried out in the context of a neutral reading of the character states. This produces a strongly unresolved cladistic tree. Accordingly the previously postulated set of homologies must be revisited and improved and the biomechanical connections between different features taken into account. Following this checking phase, a second cladistic analysis allows us to put forward a new phylogenetic assumption, where the studied Harpoceratinae species are distributed in a resolved cladogram which may be divided into three evolutionary sequences: (1) a sequence from "*P. dilectum*" to "*F. gr. portisi-laevinianum*" corresponding to a transition from "*Protogrammoceras*" to "*Fuciniceras*" morphologies; (2) a sequence from "*F. gr. brevispiratum-isseli*" to "*P. curionii*" corresponding to a first order reversion from "*Fuciniceras*" to "*Protogrammoceras*" morphologies; (3) a second order reversion for "*F. cornacaldense*" from "*Protogrammoceras*" to "*Fuciniceras*" morphologies. This cladistic analysis supports the assumption that the two genera are meaningful in terms of morphology rather than phylogeny.

4. Taxonomic consequences

This new phylogenetic assumption suggests that we should revise the current taxonomy for the early Harpoceratinae. However, this revision is still premature because this work is merely a first step towards a complete analysis of the family, which would need to include all the genera, including the Toarcian forms.

VIII. Conclusion

By using a quantitative mode of description based on the identification of landmarks for rib pattern, ventral area and whorl section, we are able to analyse changes that pertain to shape alone. When applied to the early Harpoceratinae, this means we can:

– (1) demonstrate the existence of biomechanical connections between features - manifestly between the ventral and lateral keels, and probably between the ventral part of the rib and the ventral area.

– (2) analyse relationships among taxa by both phenetic and cladistic means through a neutral reading of character state investigations. Both of these analyses point to homoplasies occurring in the clade;

– (3) decipher the homoplasies and carry out further cladistic analysis whereby the eight species under review are arranged in a resolved cladogram where the

two previously defined genera "*Protogrammoceras*" and "*Fuciniceras*" appear to be inoperative as phylogenetic entities. These genera do have morphological significance, though, and their diagnostic morphologies appear independently several times in the cladogram;

– (4) identify three episodes in the evolutionary history of the taxa under review: (a) a sequence from "*Protogrammoceras*" to "*Fuciniceras*" morphologies, (b) a first order reversion from "*Fuciniceras*" to "*Protogrammoceras*" morphologies, and (c) a second order reversion from a putative "*Protogrammoceras*" like ancestor of "*F.*" *cornacaldense* to a distinctive "*Fuciniceras*" morphology.

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