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Evolution in Morphometric Traits in North American Collignoniceratinae (Ammonoidea, Cephalopoda)

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Abstract: Eight species and one subspecies of two genera of Collignoniceratinae, *Collignoniceras* and *Prionocyclus*, are analysed with respect to standard distance measures and rib-frequencies methods of multivariate statistical analysis, including canonical variate ordination, principal components and generalized distances. It was found that the biostratigraphically inferred evolutionary sequence is upheld in detail for the *Collignoniceras* data. The 'nearest -neighbour' relationships between the *Prionocyclus* part of the sequence is less complete, although links in main branches are supported. The other aspect given consideration, that of gracile and robust shells (based on visual inspection of the conch), yielded the result that the subjective assignation of shells to gross morphological type is largely, though not unequivocally, upheld by the statistical analysis.

Introduction

Ammonite taxonomy is perforce largely based on external morphology - mode of coiling, tuberculation, ribbing and carination. The diagnostic significance of the suture line seems to have been recognized as being of secondary importance, at least for many groups (cf. Pérez Claros, 1999). Reyment and Kennedy (1998) and Reyment and Minaka (2000) recorded and described polymorphism in ornamental properties of Cretaceous ammonites of the genus *Neogastroplites*. However, it is by no means a trivial matter to distinguish between true polymorphism, in the classical genetic sense of the property (Falconer, 1960), and the merging of ornamental types in ecophenotypic variation of the kind that seems to occur in the present material with respect to the categories referred to as being 'gracile' and 'robust'. The functional significance of such differentiation remains obscure.

The primary aim of the present study is directed towards ascertaining to what degree the stratigraphically supported phylogeny within a subfamily of ammonites arrived at by the traditional methods can be recognized by the quantitative analysis of external morphological characteristics (excluding sutures); that is, mainly distance measures on the shape of the shell, but also ribbing density. With such information available, it should become possible to extrapolate to other groups and to work towards stabilizing phylogenetic relationships on less subjective grounds than are yielded by purely descriptive procedures. As far as is known to us, there have been no studies devoted to ascertaining to what extent, if any, wholly distance-related

variables are correlated with evolutionary status in ammonites (and, by extension, whether such

differentiation can represent a relationship between form and function). The work accounted for in this note shows, with reasonable clarity, that such is indeed the case, at least in the evolution of the Collignoniceratinae. There is, moreover, a more far-reaching consequence to our project. Gross morphology, such as is expressed in coiling and whorl-shape, has not been attributed importance of the first order in many evolutionary and taxonomical studies known to us. As we demonstrate in this note, there is information of evolutionary significance in characters of this kind, but that it can only be effectively extracted by means of appropriate quantitative procedures.

The Material Analysed

Members of the subfamily Collignoniceratinae that inhabited the Cretaceous Western Interior seaway of the United States first appeared in the Lower Turonian and ranged into the Upper Turonian. On a mondial scale, the subfamily arose in the uppermost Cenomanian and died out in the Coniacian. The analysis reported here is based on data to be presented elsewhere in Kennedy, Cobban and Landman (in preparation), to which monograph reference is made for details of provenance and stratigraphy. Owing to the scarcity of available specimens of some of the species concerned, the phylogenetic study is somewhat less complete than we should have liked it to be. Hence, the conclusions put forward here are necessarily of a preliminary nature.

The earliest Collignoniceratinae of the preserved sequence considered here is the monospecific genus *Cibolaites* Cobban and Hook 1983, of which neither its whence nor its whither seem to be known with any certainty. The genus is distinguished throughout most of its ontogeny by the presence of umbilical, ventrolateral and siphonal tubercles. Its mature body chamber is flat-sided, with progressively weakening tubercles and ribs (Cobban and Hook, 1983, pp. 16-18, pl. 2, figs. 1-9; pl. 3, figs 3-8; pl. 8, figs 6-8; pl. 13, figs 1-5; pl. 14, fig. 14).

Collignoniceras woollgari (Mantell, 1822) is believed to have descended from *Cibolaites*. It is thought to have given rise to several contemporaneous species in western Europe. In the region under consideration, four successive species seem to have derived from it (presumably via its subspecies *C. w. regulare* Haas, 1946, although the ensuing multivariate study leaves this undecided with respect to the actual route that may have been followed), of which one is considered in the present analysis, to wit, *C. praecox* Haas, 1946; the other three are not available in sufficient numbers for study. *C. praecox* differs from *C. woollgari woollgari* and *C. woollgari regulare* by the persistence of long and short ribs with ventrolateral tubercles outnumbering the umbilical, and a near-continuous siphonal keel. As will soon become apparent from the results of the morpho-evolutionary analysis, the inferred stratigraphically relationships between successive species may be a simplification of the actual evolutionary sequence of events.

The later Turonian history of the Collignoniceratinae in the Western Interior USA is considered to be marked by the evolution from *Collignoniceras praecox* of species of *Prionocyclus*. Juveniles of species of the two genera can be distinguished in that the keel of *Collignoniceras*

has siphonal clavi equal in number to the ventrolateral tubercles, whereas in *Prionocyclus* Meek,

1872, the serrations outnumber the ribs. It is significant that *Prionocyclus hyatti* Stanton, 1894, an early representative of the genus, is morphometrically closely allied to *Collignoniceras woollgari regulare* and somewhat less so with its putative ancestor, *C. praecox*.

In general terms, there is semi-quantitatively manifested intraspecific variation in the strength of the ornament of most of the species of the Western Interior Collignoniceratinae, a 'gracile' category and a 'robust' one. Testing the soundness of this interpretation of morphological variability forms an integral part of the analysis presented in the following.

Methods

Photographs of the specimens passing muster for statistical study were scanned and the coordinates of seven sites (Fig. 1) considered diagnostic were recorded, using the digitization program *TpsDig* written by F. James Rohlf (SUNY at Stony Brook, USA). The required distances were computed from these coordinates by simple geometry. This is freely admitted to be an arbitrary manoeuvre and we have desisted from confusing the issue by not calling the coordinate pairs thus obtained "landmarks". In any event, they cannot be equated to the landmarks used by Johnston *et al.* (1991) in their analysis of spiral growth in gastropods. The resulting data, suitably corrected for slight differences in magnification from specimen to specimen, were studied by standard multivariate analyses made on the distance- measures between adjacent sites and the maximum breadth of the last whorl. The factor of ornamental complexity was introduced into the analysis by appending rib-counts to the data-matrix. This latter addition accounts adequately for the morphological categories gracile/robust.

The multivariate statistical methods most useful for our study were found to be (1) principal component analysis of the distances (six in all) and the breadth, maximum directly observed diameter and ribbing density, (2) principal coordinate analysis of the coordinate data, and (3) canonical variate analysis of the distance measures in "ordination mode". Unless otherwise stated, the measures were logarithmically transformed. The use of this transformation tends to stabilize the multivariate distribution of the data. Accounts of these procedures applied in like situations are to be found, for example, in Reyment and Savazzi (1999), including examples of the computational procedures applied here and exemplified by ammonite data. Additionally, comparisons between species were made by standard procedures of generalized statistical distance analysis (for the larger samples), backed up by one-way univariate analysis of variance.

The links indicated by the superimposed minimum spanning tree on the plots are certainly not infallible statements of fact. For this reason, relationships between species have been further illuminated by means of pair-wise contrasts between latent vectors (principal components) of the logarithmic covariance matrices of the individual samples. Almost all multivariate "variability" in samples is located to the first latent root. For the most part, the smallest latent roots are almost zero and hence the associated latent vector may be considered as representing an almost invariant linear relationship between variables, as was suggested by Gower (1967).

Findings

Ordination of canonical variate means

A useful phylogenetic tool is often provided by the minimum spanning tree imposed on the plot of the canonical variate means. This gives the standard ordination of multivariate means a nearest-neighbour categorization. A partial analogy with stars in the firmament serves to illustrate this - stars that to the unaided eye seem to be close to each other, can actually lie at extremely great distances from each other in the third dimension. The analyses accounted for in this section are designed to see how well morphometric and morphological characters can reproduce the inferred phylogeny of the lineage.

The first set of means was obtained from the canonical variate extraction in covariance space of the logarithms of the distances between seven sites and nine samples, augmented by directly measured maximum breadth of the shell and ribbing frequency counts in relation to directly measured diameter. How well then is the inferred evolutionary succession mirrored in the coiling and ornamental properties of the species of the lineage? In Fig. 2, the canonical variate means are seen to divide into two branches. The sequence shown in Fig. 2 indicates implied relationships with respect to form within the collignoniceratinid lineage. The minimum spanning tree for the means is superimposed on both plots. It is seen that *C. molenaari* is markedly separated from all other species, as is reflected in its being a monospecific genus established by traditional criteria. This observation accords with the supposition that the morphological passage from *Cibolaites* to *Collignoniceras* was abrupt ('punctuated' as it were). The ordinated linkage order goes from *C. w. woollgari* to *C. w. regulare* to *P. hyatti*, on one branch, and from *regulare* to *C. praecox* to *P. macombi* Meek, 1876, to *P. wyomingensis* Meek, 1876, on the second branch. However, we shall see in the following that in some relationships, *P. hyatti* tends to behave as though it were a *Collignoniceras,* a peculiarity it does not share with the other representatives of the genus included in our study, and which may reflect its middle-of-the-road evolutionary and morphological status between *Collignoniceras* and *Prionocyclus.*

A spanning tree cannot be expected to provide a mirror-image of an inferred phylogenetic sequence. What it is designed to seek is morphometric nearness relationships free of any obligatory time constraint. It is therefore interesting to be able to record that the multivariate analytically obtained results reflect rather well the phylogenetic indications based in part on biostratigraphical context. Many of the samples are small and it is encouraging that the results yielded by this analysis are so clearly manifested. In general, it seems clear that the observed stratigraphical ordering of the species is upheld, grosso modo, by the morphometric ordination. We note that, excluding the small samples (to wit, *woollgari woollgari, praecox, wyomingensis*) all generalized statistical distances between samples are highly significantly different.

In order to test the reliability of results obtained for such small samples, an alternative canonical variate model was used. Here, all values were reduced to standard size by division of them by the maximum diameter of the shell. This standardization has a subsidiary effect, notably, that it transforms the data into compositions, and, consequently, the variables to parts. This change in properties necessitates a methodology appropriate to (constrained) simplex space (Aitchison, 1986). The multivariate analysis was therefore made on the log-ratio covariances (which involves the loss of one dimension due to the division by one of them). The ordination illustrated in Fig. 3 differs in several respects from the foregoing (full-space) version in that *P.*

germari (Reuss, 1845) is quite out of place in relation to the evolutionary succession. The

morpho-evolutionary passage from *molenaari* through the two subspecies of *C. woollgari* is, however, maintained. We note that *P. hyatti* is now relegated to a branch of its own. Sidestepping the anomalously located *P. germari*, there is a branch that runs from *C. woollgari* s. l. through *C. praecox*, *P. macombi, P. wyomingensis* and *P. novimexicanus*(Marcou, 1858), the latter being registered as a branch-off from *P. macombi.* Apart from the anomalous location of *P. germari*, the result illustrated in Fig. 3 is in many respects more closely compatible with the conventional succession of species than Fig. 2. The main point to be heeded is, however, that the linkages are essentially the same in both representations, notably the *Cibolaites-Collignoniceras* sequence and the *C. praecox-P. macombi-P. wyomingensis* passage.

Results obtained by the principal component analysis of the distances

For the purposes of this part of the analysis, two latent vectors turned out to be of special interest. The latent root attached to the first latent vector is overwhelmingly large in relation to the other roots. The smallest latent root is virtually zero and hence may be considered to be an expression of an invariant linear relationship between the variables (Gower, 1967). Such an invariant relationship is of special taxonomic and hence phylogenetic interest. The species studied in this connexion are: *C. woollgari woollgari* and subspecies *C. w. regulare, C. praecox, P. hyatti, P. novimexicanus, P. macombi* and *P. germari*. We wish to make it clear that the method of comparison of angles (Blackith and Reyment, 1971) is not a statistical technique, being rather a procedure appropriate to *ad hoc* data-analysis. Nonetheless, it has proven itself to be useful in many taxonometric studies.

The first principal component

This section is concerned with examining how divergent succeeding species in the evolutionary succession are from each other. The angles between pairs of first latent vectors and sixth latent vectors, respectively, are listed in Table 1. The angles for the first latent vector for the comparisons of *C. molenaari* and *C. w. woollgari*, respectively *C. w. regulare* are almost identical (21.33° , respectively, 21.88°). This interesting result indicates not only that the ancestral species is separated by a strongly expressed morphological jump from its descendants, but also that the angle between ancestor and descendant subspecies is identical and that the two subspecies of *C. woollgari* are morphologically close to each other. This observation is supported by the small angle between these two subspecies, namely, 2.21° . The species next in the stratigraphical hierarchy is *C. praecox*, the angle between its first latent vector and both subspecies of *C. woollgari* being the same, to wit, 9.56°. The angle between *C. praecox* and *P. hyatti* is quite small, being 4.82° , whereas that between *P. hyatti* and *P. macombi* is 6.24°. The next passage from *P. macombi* to *P. wyomingensis* is connected with a small angular difference, notably, 3.18° . There is a notable leap in the angle between the first latent vector of *P. wyomingensis* and its descendant *P. novimexicanus,* namely 11.24°. The final link, from *P. novimexicanus* to *P. germari* is accompanied by an angular divergence of 7.73°. It is significant

that the angular divergences between latent vectors of the *Prionocyclus* sequence are mostly of

the same order of magnitude.

Comparisons made for the 'smallest' latent vectors are all noticeably greater. This could conceivably indicate that intrinsic morphometric specific differences are to be found in the invariant principal component, granted that the first latent vectors, which are all connected to more than 98% of the total variability, are so similar. The more interesting relationships are:

1. *Cibolaites molenaari-Collignoniceras woollgari* subspecies. The angles for vector I are here almost identical, as reported above. The values for vector VI differ strongly, with the angle between the vectors for *molenaari-C. woollgari woollgari* being almost a right angle, whereas that for the comparison with *regulare* is a relatively low 38.75°.

2. *Collignoniceras praecox-C. woollgari* subspecies. The angular differences for vector VI are large, being essentially greater for the comparison with *C. woollgari woollgari*. The angular differences for the comparisons between first vectors are small, and smallest for the latter subspecies.

3. *C. praecox-P. hyatti.* The result yielded here is noteworthy. The first latent vectors are almost collinear, which hardly accords with the linkage in Fig. 3 yielded by the minimum spanning tree. However, the value for vector VI places these vectors exactly at right angles to each other. We are inclined to accept this result as indicating support for the view that the invariant latent vector of distances harbours taxonomically relevant information.

4. The plot in Fig. 3 shows *regulare* and *germari* to be located near to each other, but the linkage sequence does not indicate these two taxa to be close. Comparison of the smallest latent vectors yields a relatively large angle, namely 48.23°.

5. *C. w. regulare-P. hyatti.* The biostratigraphical scheme leads one to expect that *C. praecox* would be more like *P. hyatti* than *C. w. regulare*, granted that it has been put forward as the logical ancestor of the former, and this is indeed implied by the angle between the first latent vectors, being the smallest of the entire set of values reported in Table 1 and, in effect, denoting collinearity. However, the angle between vector VI for these two taxa is by far the smallest of all and it seems that it is this relationship that is reflected in the minimum spanning tree (Fig. 2).

6. Anomalously large angular differences occur for the pairings *macombi-wyomingensis* and *wyomingensis-novimexicanus*, probably due to the small sample sizes involved. We note that the sample size for *P. wyomingensis* is beneath the level for a resolvable covariance matrix.

Robust vs gracile shells

The routine taxonomic appraisal of the material suggested that there are two classes of ornamental categories in the species of the genera considered here, to wit, robustly ornamented shells and finely ornamented shells (the gracile shell-type). Only three species occur in sufficient numbers to permit statistical appraisal of these categories- *P. hyatti, P. macombi* and

P. germari. The same suite of methods as were used for the full set of observations were applied

to the reduced set, noting that there are now 6 groups for 6 distance measures. In Fig. 4, the canonical variate means for the two ornamental categories for these three species are plotted and linked by the superimposed minimum spanning tree. The most notable feature of the plot is that robust and gracile shell-types for each species, respectively, are linked, and that their means do not coincide, or almost coincide in location. Hence, differences in multivariate means of the subjectively identified categories are tangible, but not so great as to confuse taxonomic issues. In Fig. 4, we show the plot of the individual points in the plane of the first two canonical variate axes (i.e. the canonical variate scores on the first two axes). The points for the six categories group naturally with gracile and robust forms for each species being nearest neighbours. Links between species are the union of robust *germari* to robust *macombi* and robust *germari* to gracile *hyatti.*

Comparisons of the first and sixth principal components lead to interesting consequences (Table 2). All angles between various comparisons of first latent vectors of the logarithmic covariance matrix are low. Note particularly the values for *germari* and *macombi*, 1.99° and 1.87° respectively. The angles for the sixth latent vectors are large and generally of the same order of magnitude as found for the complete data-set, but with one striking exception, notably, the comparison between gracile individuals of *germari* and *macombi*, 7.91°. This would seem to point to a close morphological relationship between the two species, which is possibly of taxonomical significance.

Doubtlessly, the gracile/robust subsamples yield a more structured analysis than do the full samples. Granted that the taxonomic integrity of the subsamples was not infringed upon by the partitioning, it may be suggested that the qualitatively arrived att subdivision into two morphological types is largely justifiable.

The question now arises as to how morphometrically similar are the two categories *robust* and *gracile*? The material is not sufficiently comprehensive to allow categoric assertions. However, the data for *P. germari* may be taken to serve as a guideline. Robust *germari* links to robust *macombi*, thus implying a certain degree of ornamental homogeneity, whereas robust *germari* links to gracile *hyatti*. Fig. 4 intimates also that *germari* and *macombi* are morphometrically more alike than either is with *hyatti*. This observation adds further evidence with respect to the borderline evolutionary status of *Prionocyclus hyatti*, which in many aspects displays morphometrical properties of *Collignoniceras* type.

Conclusions

The multivariate-morphometrical analysis of a sequence of Collignoniceratinae from the Turonian of the Western Interior U. S. has brought to light several features of general interest for the study of evolution in ammonites with respect to the property of coiling . This result is somewhat unexpected, granted that coiling in shell-bearing cephalopods is under the rigid constraint imposed by the logarithmic growth bio-mechanism. These are:

1. The species of *Collignoniceras* align in accordance with biostratigraphical observations, thus

preserving generic integrity and evolutionary status. The passage from *Cibolaites* to *Collignoniceras* is abrupt, a saltation as it were.

2. The passage to *Prionocyclus* is slightly less well manifested in that there is a dichotomy in the relationship implied by the minimum spanning tree with *P.hyatti* occupying, jointly with respect to linkage (but naturally not time), an evolutionary position on a par with *C. praecox*. In this respect, the former species behaves in some cases as though it were a *Collignoniceras*. The dichotomous impression is further strengthened by the passage of *praecox* to *macombi* which in turn, links to *wyomingensis* (in agreement with the biostratigraphical inference - cf. Table 3).

3. The second branch in Fig. 2 lets *hyatti* link directly to *germari* and *novimexicanus*. In Fig. 3, *hyatti* is located on a separate branch. This result accords with the transitional status of this species, as indicated by the results of the present study.

Finally, the qualitative observations leading to the recognition of robust and gracile shell forms in all species can be upheld in part, as far as can be judged from those samples comprising sufficient material for statistical calculations. Also here, the ambiguous evolutionary status of *P. hyatti* is manifested. The possible functional significance of the two shell types would seem to be worth detailed study.

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FIGURES

Fig. 1.   Locations of the points measured on the shells superimposed on a gracile specimen of *Prionocyclus macombi* Meek, 1876.

Fig. 2. Minimum spanning tree superimposed on the plot of the first two canonical variate means for 7 distance measures (6 coordinate-based and maximum breadth of the conch), one frequency (ribbing) and 9 groups (the species and subspecies). Analysis made on the covariances of the logarithmically transformed data.

Fig. 3. Minimum spanning tree superimposed on the plot of the first two canonical variate means for the same set of data as in Fig. 2, but standardized with respect to size. Analysis made on the log-ratio covariances (cf. Aitchison, 1986).

Fig. 4. Minimum spanning tree superimposed on the canonical variate means for robust and gracile categories of three species of *Prionocyclus,* based on 6 distance measures and 6 groups (three "robust" classifications and 3 "fragile" classifications).

Table 1

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Angles between first latent vectors (covariance matrix of logarithmically transformed variables) for critical pairings.

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Comparison between	Angle for vector I	Angle for vector VI
Ci. molenaari/Co. woollgari woollgari*	21.33	87.80
Ci. molenaari/Co. woollgari regulare*	21.88	38.75
Co. woollgari woollgari/Co. praecox*	2.24	81.53
Co. woollgari woollgari/Co.regulare	5.38	67.31
Co. woollgari regulare/Co. praecox	5.82	59.54
Co. woollgari regulare/P. hyatti	6.71	20.53
Co. w. regulare/P. germari	3.29	48.23
P. hyatti/P. germari	3.58	33.92
Co. praecox/P. hyatti	1.26	90.00
Co. praecox/P. macombi	5.45	54.06
P. macombi/P. wyomingensis*	7.79	88.10
P. novimexicanus/P. germari	5.12	46.06

  The asterisk denotes comparisons made on very small sample sizes.
Co = *Collignoniceras*, Ci = *Cibolaites*, P. = *Prionocyclus.*

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Table 2

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Angles between first and sixth latent vectors for the robust/gracile data for critical pairings of three species of *Prionocyclus.*

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Comparison between	Angles for vector I	Angles for vector VI

germari G/germari R	1.99	41.07
macombi G/germari R	1.87	85.40
germari G/hyatti G	2.21	55.62
germari G/macombi G	3.35	7.91
hyatti G/macombi G	5.22	56.69

R denotes the robust morphological category, G the gracile one.

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Table 3. The biostratigraphical sequence for the species included in the analysis

Substage	**Species**
	Prionocyclus germari*
UPPER TURONIAN	*Prionocyclus novimexicanus*
	Prionocyclus wyomingensis

Prionocyclus macombi*

	Prionocyclus hyatti *
MIDDLE TURONIAN	*Collignoniceras praecox* *
	Collignoniceras woollgari *

LATE
LOWER   *Cibolaites molenaari* *
TURONIAN

The asterisks denote species currently used as zonal indices in the Turonian sequence of the Western Interior USA.