Morphological links in an evolutionary sequence of the Cretaceous ammonite genus *Metoicoceras* Hyatt

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Species of the ammonite genus *Metoicoceras* are not generally strongly differentiated with respect to coiling and ornament. The present study addresses the problem of how well purely visual (subjective) identification succeeds in identifying taxonomically and hence evolutionarily relevant differences between forms. Multivariate statistical analysis, based on coiling, standard dimensions of the conch and ornamental properties, indicates that quantitative procedures reproduce traditional methods to a conspicuous degree, with the added advantage of objective repeatability. Additionally, uncertain phylogenetic relationships could be resolved by appropriate methods of multivariate statistical analysis and possible new information on dimorphism in the conch was obtained. © 2000 Academic Press

1. Introduction*Metoicoceras* Hyatt, 1903 (type species: *Ammonites swallovi* Shumard, 1860) encompasses involute, compressed and ribbed ammonites of small to medium size, species of which occur in the middle and upper Cenomanian, principally in the USA, but also sporadically elsewhere in Europe, northern and western Africa, Madagascar, Israel, Iran, southern India, Peru and Brazil towards the top of the range of the genus. One of the earliest species of *Metoicoceras to appear, M. praecox* Haas, 1949, is relatively widely distributed in the Western Interior USA, but has only recently been adequately monographed (Cobban and Kennedy, 1991).

Phylogenetic connexions among the species of the genus have posed a problem to specialists for many years, partly because of disjunct geographic occurrences of presumably important links and partly because of unresolved time-relationships and the lack of continuous biostratigraphical information. This, we believe, is the first published attempt at analysing the problem.

The aim of our statistical analysis is to attempt an objective, morphometrically oriented classification of the North American species with the end in view of unveiling diagnostic morphological features of use for future work and for developing a methodology for more general use in the analysis of, and search for, evolutionary links in ammonites. An ever-present issue in palaeontological systematics concerns the consistency of taxonomical conclusions allowing that conventional methods are highly prone to arbitrary interpretation. It is therefore desirable that this discretionary aspect be curtailed to as great an extent as possible. This is one of the classical aims of numerical taxonomy; however, that line is not adopted in this note.

2. Taxonomic overview

Species of *Metoicoceras* are generally characterized by their compressed, involute shells, ornamented with primary and secondary ribs, umbilical bullae, inner and outer ventrolateral tubercles and feeble siphonal tubercles making a fleeting appearance in the ontogeny of older species. This morphology was invoked by Cooper (1998) as grounds for erecting a genus *Praemetoicoceras*. However, we note in passing that the present study has not produced support for this step. Species attributed to the genus *Metoicoceras* are generally similar in appearance, but ornamental polymorphism is not a major source of confusion in identifying

species. At least two species of the genus are known to be dimorphic, although the present study suggests that this property may extend to *Metoicoceras praecox* Haas. This latter species arose early in the preserved lineage. It lacks inner ventrolateral tubercles on mature whorls and it is less involute than the norm for the genus. *Metoiceras latoventer* Stephenson, 1953, has a squarish whorl section and hence a broad venter; it resembles *M. swallovi* (Shumard). *Metoiceras frontierense* Cobban, 1988, possesses persistent inner ventrolateral tubercles that set if off from other forms. *Metoiceras mosbyense* Cobban, 1953, differs from earlier species with respect to the morphology of its ribbing pattern and its relatively well-defined dimorphism with macroconchs being larger, more slender and more weakly ornamented (with or without umbilical bullae) than microconchs. *Metoiceras geslinianum* (d'Orbigny, 1850) is believed by one of us (WJK) to have evolved from *M. mosbyense*. It is the youngest species in the Western Interior; it is also dimorphic. Differential diagnoses of North American species of *Metoicoceras* are given in Cobban and Kennedy (1991).

3. Material and methods

Published photographs of species of *Metoicoceras* and *Nannometoiceras* were used for obtaining the measurements, in addition to standard measures on the shell for *M. praecox* given in Cobban and Kennedy (1991). Museum references to the original specimens are given in that monograph. The amount of data available is not great, which has the consequence that the results presented here can do no more than serve as a tentative indication aspects of the morphological relationships between taxa.

The measurements used for analysis were obtained by direct mensuration (breadth, maximum diameter) and by digitizing eight diagnostically located sites on the conch in lateral aspect so as to highlight coiling. Distances between sites were then computed (thus yielding seven distances). In order to 'standardize' the observations to a common scale of reference, the data were divided by the maximum diameter obtained by direct measurement. This has the effect of standardizing for size differences, but introduces a constraint (the constant-sum constraint for compositions) in the data (Aitchison, 1986). This manipulation has several consequences for the ensuing multivariate statistical analysis in that the elements of the data-matrix are no longer variables in the statistical sense, but parts, inextricably bound to each other by the relationship that each row of the data-matrix (composed of D parts) of positive proportions sums to a constant. The

appropriate sample space for such vector data is the d-dimensional unit simplex, where $d=D-1$. The problem is far from new, having been recognized in the Galton-Pearson spurious correlation paradox (Pearson, 1897). Strangely, and unfortunately, the implications of spurious covariances between data consisting of parts have been glossed over, even by professional statisticians. It was not until Aitchison (e.g., 1986, 1997) devoted attention to the problem that a wherewithal for rigorously analysing such data was firmly established.

The statistical properties of the simplex S^d, the relevant space for by compositions, are radically different from R^d, that is, everyday space, which imports that standard methods of multivariate analysis that ignore the constrained nature of the compositional vector (or row-sum of the data-matrix) are not mathematically valid. Failure to take this into account leads invariably to analyses flawed by misinterpretations of the compositional variability. The standardization of these data has the consequence that the sizes of the individual specimens are irrelevant. Aitchison (1986) showed that any meaningful, scale-invariant function of a composition can be expressed in terms of ratios of the components of the composition. For many purposes of statistical analytical procedures, log-contrasts have been found to perform well (Aitchison, 1997; Reyment and Savazzi, 1999).

The appropriately constructed multivariate methods employed in the following are: constrained canonical variate analysis and constrained principal component analysis. It is important to note that both techniques are only available in the covariance mode, inasmuch as the correlation coefficient is not coherently defined in simplex space and is, therefore, not legitimately available for multivariate purposes (Aitchison, 1997). For more detailed descriptions of these methods, we refer the reader to Reyment and Savazzi (1999).

4. Findings

The points plotted in Figure 1 are constrained (log-ratio) canonical variate means linked by the minimum spanning tree. The linkage pattern does not necessarily encompass information on time-relationships, although this aspect is conveyed to a certain degree in the figure. The links between *M. praecox, M. frontierense* and *M. mosbyense* accord with the currently accepted views on phylogeny and ammonite systematics (cf. Kennedy, 1988). The location of *M. geslinianum* is not in agreement with that opinion, although it is located parallel to *M. mosbyense* in a stratigraphically reasonable position. The position occupied by
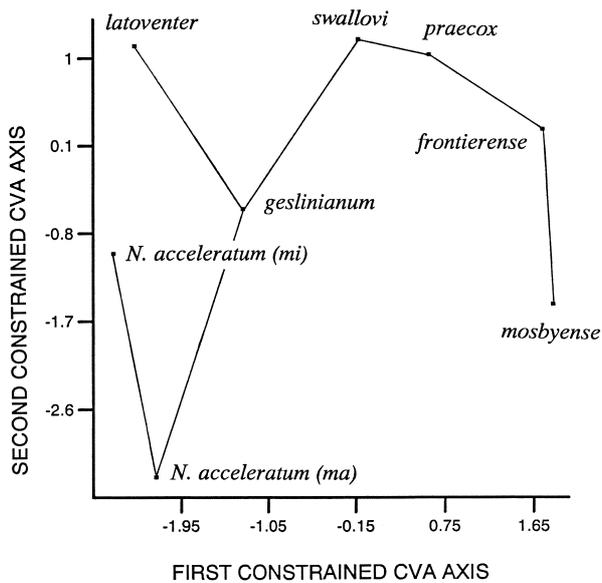
Figure 1. Plot of the constrained canonical variate means for *Metoicoceras* and *Nannometoiceras* with the minimum spanning tree (cf. Reyment and Savazzi, 1999) superimposed.

M. swallovi cannot be defended since it has not been inserted into any standard biostratigraphical sequence currently available. The same applies for *M. latoventer*. The link from *M. geslinianum* to *Nannometoiceras acceleratum* (Hyatt, 1903) is in harmony with the phylogeny recognized by Kennedy (1988). An interesting feature of this linkage is that it proceeds from *M. geslinianum* via the macroconchs of *N. acceleratum* to the microconchs of the latter species. The link uniting *M. geslinianum* with *N. acceleratum* is in accord with current opinion (Kennedy, 1988; Kennedy and Cobban, 1991). It may be significant that the generalized statistical distance in Figure 1 *M. geslinianum* and *N. acceleratum* is somewhat greater than distances between any pairs of adjacent species of *Metoicoceras* in the linkage pattern (Table 1). Larger samples would be required, however, in order to permit a definite conclusion on the significance of this observation.

Inspection of the canonical variate loadings (Table 2) provides an approximate guideline for understanding how the differentiation expressed in Figure 1 is being produced, albeit on a very tentative basis (reification of canonical variate coefficients is not a recommended statistical procedure). Remembering that these coefficients are actually ratios produced by division with the maximum diameter of the conch, we see that for the first vector (50.77% of the variability) most of the work of differentiation is due to the second, third and eighth elements; that is, the distance from the proximal whorl-margin to the umbilicus, the distance from the umbilicus to the distal whorl-margin (the venter) and the standardized ribbing density. The second vector (26.6% of the variability) is mainly an indication of input by components 3 and 7, with a lesser contribution from component six and thus also reflects the role of the distance from the umbilicus to the distal whorl margin, the breadth of the conch, and the distance between the proximal whorl margins over the umbilicus. The third canonical root is also statistically significant. It encompasses about 20% of the total variability and reiterates the contributions of parts 3 and 5.

Table 1. Mahalanobis squared generalized distance (D^2) between adjacent species as located in Figure 1.

Adjacent pairs	D^2
M. mosbyense–M. frontierense	7.94
M. frontierense–M. praecox	5.23
M. praecox–M. swallovi	3.62
M. swallovi–M. geslinianum	7.06
M. geslinianum–M. latoventer	5.50
M. geslinianum–N. acceleratum	13.47

Dimorphism

Dimorphism has been reported to occur in some species of *Metoicoceras* (see above). The present analysis seems to have uncovered a further example, thus suggesting that the condition of dimorphism in the genus may be more widely developed than hitherto suspected. We underscore that the results presented here are to be regarded as provisional inasmuch as the sample-sizes available are small. The data used for

Table 2. Log-ratio loadings for the first two canonical variate vectors; see text for the definition of the parts.

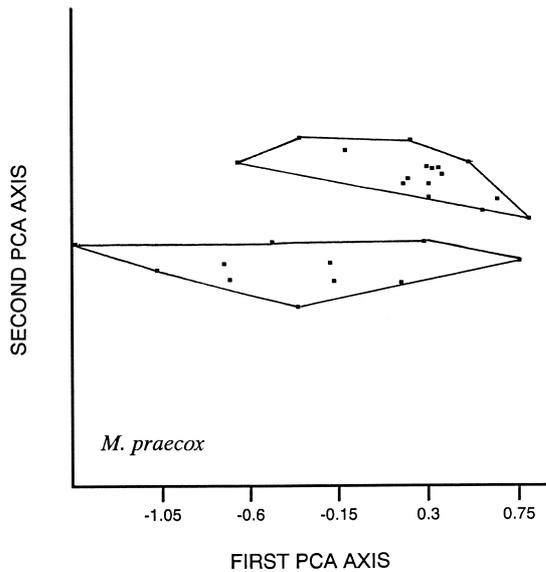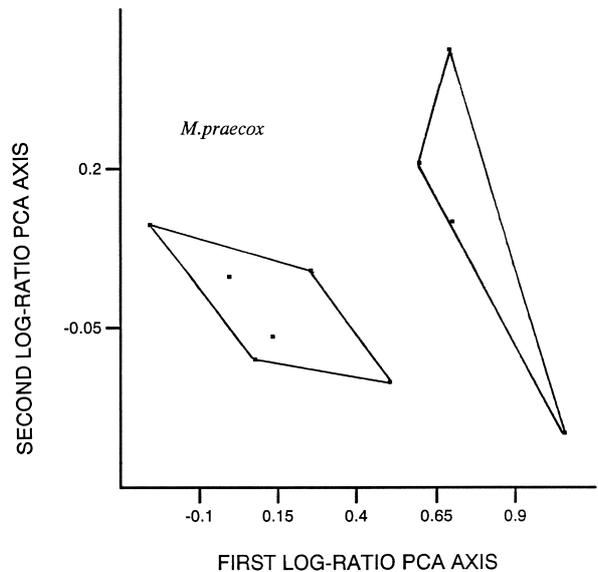| Parts							
1	2	3	4	5	6	7	8
First vector							
−1.681	3.917	−9.359	1.238	2.312	−1.898	1.440	5.130
Second vector							
1.278	−0.657	6.485	0.690	−1.361	4.033	−8.394	−1.973

Figure 2. Presumed dimorphism in shell-measures for *Metoicoceras praecox* as disclosed by the plot of the scores of the principal component analysis for the logarithmically transformed data for the five distance measures: maximum diameter, maximum whorl-breadth, whorl-height, diameter of the umbilicus and the breadth of the shell at the base of the body chamber. Convex hulls outline the two constellations of points

Figure 3. Plot of the scores for the compositional principal component analysis of *Metoicoceras praecox*. The clustering displayed plot indicates the possible existence of sexual dimorphism in the characters considered.

these analyses derive partly from the observations used in the foregoing canonical variate analysis and partly from table 1 in Cobban and Kennedy (1991). The method of principal component analysis was used for obtaining the ordinations. In the case of Figure 2, the data are of the normal or 'open' kind and were therefore analysed by the usual method (full-space principal components). The data in Figure 3 derive from the compositional data-matrix, which necessitated the use of log-contrast principal component analysis (Aitchison, 1986; Reyment and Savazzi, 1999). Figure 2 shows the plot of the 27 scores for the principal component analysis of *M. praecox*, for five logarithmically transformed variables: maximum diameter, whorl-breadth, whorl-height, umbilical diameter, and diameter at the base of the body chamber. There is a clear grouping of the points into two constellations (outlined by convex hulls). This figure may be pointing to the existence of dimorphism as expressed by the characters measured. It should be noted that inasmuch as the data are logarithmically transformed, the influence of size is repressed.

Figure 3 displays the plot for the species *M. praecox* obtained by log-contrast principal component analysis, using the data consisting of nine parts and the centred log-ratio covariance matrix (Aitchison, 1986). The feature of interest here is that there is an indica-

tion of differentiation into two groups. This result supports the notion that *M. praecox* displays dimorphism in the characters considered here and fits in with the ordination obtained for a different set of observations (Figure 2).

5. Concluding remarks

The analysis briefly accounted for here has demonstrated how the application of standard multivariate statistical methods to distance-measures on species of *Metoicoceras* provides a useful tool in the study of morpho-evolutionary changes in a lineage. The quantitative results agree well with the available biostratigraphical evidence for this group of ammonites, which implies that consistency in the direction of morphological change in the conch may well exist. The analysis has been able to add to our knowledge of dimorphism in Upper Cretaceous ammonites and to bring to light a further case in *Metoicoceras praecox*.

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