



Disparity of Beaks and Statoliths of Some Coleoids: A Morphometric Approach to Depict Shape Differentiation

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6 Text-Figures and 3 Tables

Cephalopods
Beaks
Statoliths
Morphometry

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Unterschiede der Schnäbel und Statolithen einiger Coleoiden: Eine morphometrische Annäherung an Gestaltdifferenzierung

Zusammenfassung

Die Morphologien des Schnabels und der Statolithen repräsentativer Proben von Arten des Kladus Coleoidea wurden verglichen und zueinander in Beziehung gesetzt. Unterschiede zwischen den Spezies wurden mit Hilfe einer Näherungsmethode quantifiziert, die auf einem Markierungssystem beruht. Die erhaltenen Stammbäume wurden als morphologische Karten betrachtet, mit deren Hilfe die morphologische Ungleichheit analysiert werden kann. Die Resultate zeigen

- 1) große Unterschiede zwischen Octopoda und anderen Formen,
- 2) gute Übereinstimmung innerhalb des Kladus Oegopsida, dessen Spezies nicht unterscheidbar beisammen liegen und
- 3) eine doppeldeutige Position der Sepioliden, die mit Sepiiden (oberer Schnabel) oder Myopsiden (unterer Schnabel) zusammengefasst werden könnten oder aufgrund der Statolithen in zwei getrennte Cluster gesplittet werden könnten.

Abstract

Beak and statolith morphologies of representative samples of species belonging to the coleoid clade are compared and contrasted. Differences between species are quantified by a landmark-based approach. The phenetic trees computed are considered to be morphological maps from which to analyze morphological disparity. The results indicate

- 1) large differences in shape between the octopods and other forms,
- 2) good coherence of the oegopsid clade whose species are invariably clustered together, and
- 3) an ambiguous position for the sepiolids which may be clustered with sepiids (upper beak), myopsids (lower beak), or split into two separate clusters (statoliths).

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1. Introduction

The concept of morphological space is especially useful for understanding how the disparity (morphological expression of differences) of a set of organisms is structured and consequently for interpreting shape changes in terms of evolution or adaptation: disparity is the measure of how fundamentally different organisms are (RAFF, 1996). It is considered here to be a complement to the traditional analysis of taxonomic diversity. To be as useful as possible, the morphological space (representing disparity) must be based on quantification of the shape differences among the taxa under study. The result is a description in terms of morphological diversity metrics that is different from the strictly taxonomic description or from phylogenetic diversity metrics (ROY & FOOTE, 1997). This concept is illustrated here by exploring the disparity of some coleoid beaks and statoliths. Statoliths are calcareous particles whose shape is suspected to depend little on function but very much on evolutionary relationships (CLARKE & MADDOCK, 1988). Statoliths are involved in detecting gravity and in linear acceleration. Beak shape might be expected to be related principally to feeding habit, and less to evolutionary relationships. However, as suggested by CLARKE & MADDOCK (1988), there do not seem to be sufficient differences in the food of the cephalopods (at least for their sample) to account for shape differences of the beaks. They reached the conclusion that lower beak shape could be a very useful pointer to relationships among the living coleoids.

The present study quantifies similarities and differences in shape of these two features. Three morphospaces are computed for:

- 1) upper beak (lateral side),
- 2) lower beak (lateral side) and
- 3) statolith (anterior side).

These three morphospaces are then compared and contrasted, their differences discussed and placed in the context of phylogenetic relationships within the coleoid clade.

2. Material

Our analysis covers 13 genera, four belonging to the Sepioidea, seven to the Teuthoidea and two to the Octopoda (Table 1). This sample covers a wide range of coleoids including many taxa recently studied by molecular methods (BONNAUD et al., 1996, 1997; BOUCHER-RODONI & BONNAUD, 1996). Two different sets of the 13 genera (n1 and n2 in Table 1) are used in the two analyses (respectively statoliths and beaks) depending on the state of preservation of the material. However, sufficient overlap occurs to allow comparisons between beak and statolith disparity. All the specimens were caught in the area of Banyuls-sur-Mer (Western Mediterranean).

3. Method of Quantification

Methods of geometric morphometry (Procrustes analysis) have proved interesting on theoretical grounds (BOOKSTEIN, 1991; ROHLF & MARCUS, 1993) and effective in their applications to various zoological groups (e.g. see NEIGE & DOMMERGUES, 1995; EL HARIRI et al., 1996; NEIGE & BOLETZKY, 1997; NEIGE, 1999, for examples on cephalopods). These methods are based on the utilization of anatomically conspicuous points (landmarks sensu SNEATH, 1967; BOOKSTEIN et al., 1985; BOOKSTEIN, 1991). A given set of landmarks serves as a morphological descriptor. By comparing the relative positions of these landmarks it is possible to localize and quantify morphological differences between ontogenetic stages, individuals or taxa. Such a representation is termed a morphospace (NEIGE et al., 1997; ROY & FOOTE, 1997). Landmarks are localized on drawings of the specimens, and their coordinates determined in a two-dimensional reference system.

In the present work, the LSTRA technique (Least Square Theta Rho Analysis) was applied using MacMorpho/Consensus software (DAVID & LAURIN, 1996). The technique consists in superimposing, with the best possible fit, the set of points of one shape over homologous points of the

Table 1. Classification of the studied taxa (after MANGOLD & PORTMANN, 1989), and number of individuals used for analysis (n1 for statoliths and n2 for beaks).

ORDER	SUBORDER	FAMILY	SUBFAMILY		n1	n2		
Sepioidea		Sepiidae		<i>Sepia officinalis</i>	11	03		
				<i>Sepia elegans</i>	11	03		
				<i>Sepia orbignyana</i>	11	03		
		Sepiolidae		Rossiinae	<i>Rossia macrosoma</i>	03		
				Sepiolinae	<i>Sepietta neglecta</i>	05	01	
					<i>Sepietta oweniana</i>	07		
					<i>Sepiola sp</i>	01		
				Teuthoidea	Myopsida	Loliginidae		<i>Alloteuthis media</i>
<i>Loligo vulgaris</i>	32	13						
<i>Abralia verany</i>	01							
Oegopsida	Enoploteuthidae	Illicinae	<i>Illex coindetii</i>		09	06		
			<i>Todaropsis eblanae</i>		02			
	Omnastrephidae		Todarodinae		<i>Todarodes sagittatus</i>			01
					<i>Histioteuthis sp</i>			01
	Histioteuthidae							
Octopoda	Incirrata	Octopodidae		<i>Octopus vulgaris</i>		02		
				<i>Eledone cirrhosa</i>		02		

other shape, regardless of size and orientation (SNEATH, 1967; BOOKSTEIN, 1991). The remaining differences are then characterized by a vector field extending from each point of one shape to the homologous point of the other shape. The distance between the two shapes may also be expressed arithmetically (in standard deviation units) as the sum of vector lengths ($\Sigma\Delta$). The set of such distances between all the taxa taken two-by-two forms the distance matrix. The distance matrices can be converted into phenetic trees, allowing the morphologically closest taxa to be grouped together. Phenetic trees were calculated here with the Fitch2 algorithm of Phylip2 software (FELSENSTEIN, 1995). This algorithm seeks out the non-rooted tree and estimates the length of the branches providing the closest fit with the distance matrix. The nodes obtained between taxa do not represent ancestral states but merely degrees of morphological similarity.

Supplementing the computation of phenetic trees, simultaneous analysis of all individuals makes it possible to visualize the set of morphologies expressed. This was done using the generalized least square technique (GLS, BOOKSTEIN, 1991) computed with the GLS option of MacMorpho/Consensus software (DAVID & LAURIN, 1996). Here the difference between each individual and the mean consensus individual (calculated from the entire population) is represented by a straight bar. The shape of the bar cloud at each landmark indicates whether there are

any preferential shape changes at the scale of the population.

4. Results

4.1. Beaks

4.1.1. Data Acquisition

Following CLARKE (1986), a strict laboratory examination of samples was made. Beaks were extracted from fresh or thawed specimens, and then stored with the remainder of the specimen in alcohol. Camera lucida drawings were used for the analysis. Specimens were attributed to genera and species based on classical characters (e.g. general shape, tentacular club organization) excluding beaks.

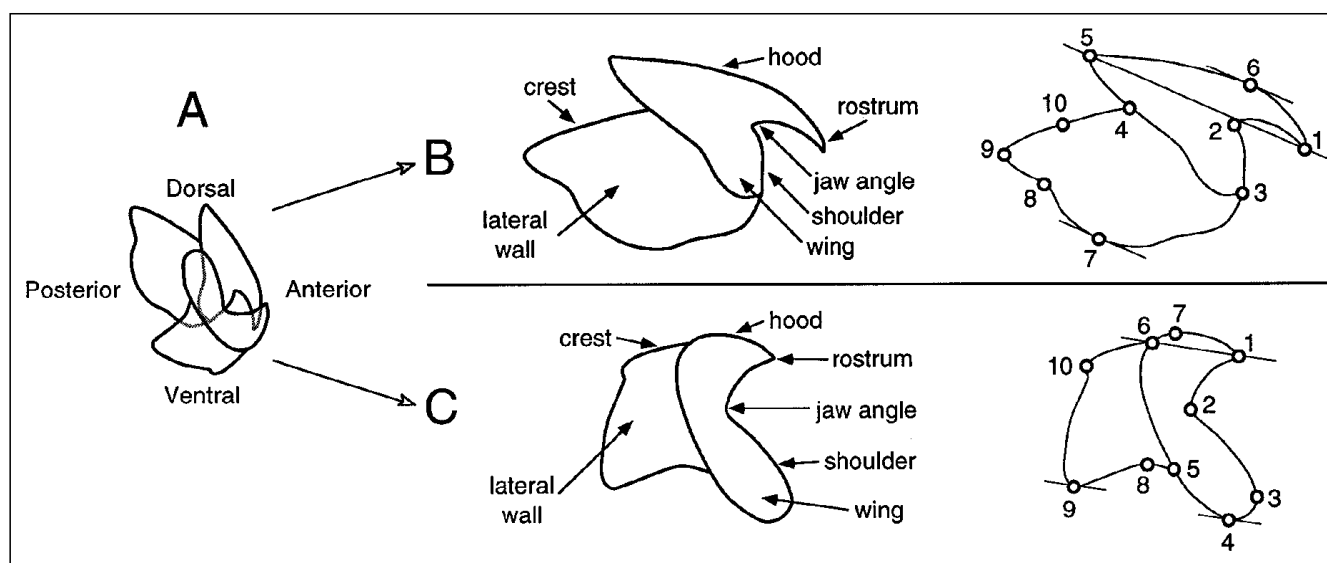
The recommendations of CLARKE (1986) were followed, namely, using the same axis of projection for all the drawings, and constantly wetting the beak with water to prevent major distortions when drawing (see CLARKE, 1986: Fig. 5). However, we did not follow CLARKE (1986: 9) with regard to the statement that

“... in most instances it is only necessary to identify and measure either the upper or the lower beak since they will give the same information.”

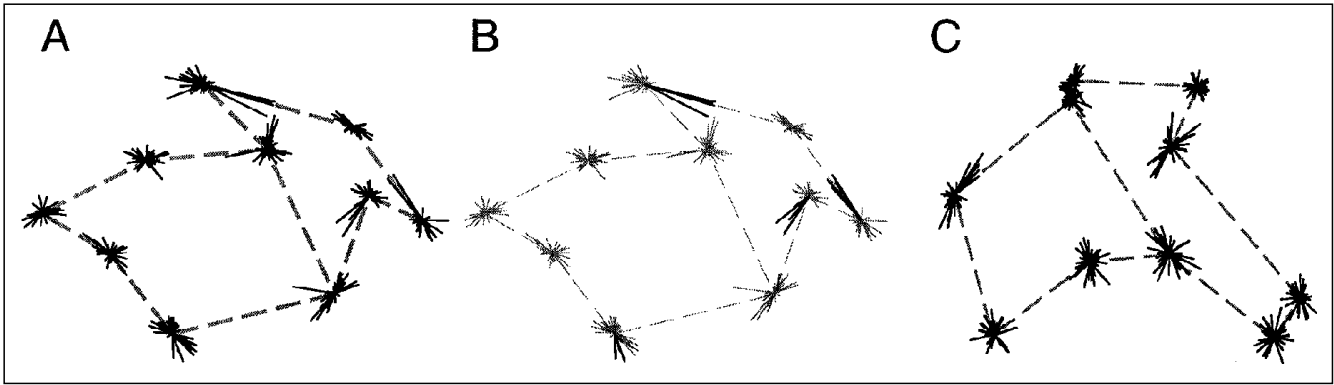
On the contrary, we constructed two independent morphospaces for the upper and lower beak so CLARKE'S claim could be tested.

Table 2.
Description of landmarks defining beak shape.

UPPER BEAK		LOWER BEAK	
Point	Description	Point	Description
1	Anterior tip of rostrum	1	Anterior tip of rostrum
2	Position of jaw angle	2	Position of jaw angle
3	Anterior contact wing/lateral wall	3	Maximal curvature of shoulder
4	Dorsal contact wing/lateral wall	4	Dorsalmost point of wing
5	Posterior end of hood	5	Dorsal contact wing/lateral wall
6	Tangent point (anterior) on hood to the axis 1-5	6	Ventral contact wing/lateral wall
7	Tangent point (posterior) on lateral wall to the axis 1-5	7	Tangent point (ventral) on hood to the axis 1-6
8	Maximal depression between points 7 and 9	8	Maximal depression between points 5 and 9
9	Posterior end of lateral wall	9	Tangent point (posterior) on lateral wall to the axis 1-6
10	Maximal curvature of the crest	10	Posterior end of lateral wall



Text-Fig. 1.
Beak morphology in lateral view (A) and location of upper (B) and lower (C) beak landmarks.



Text-Fig. 2. Comparison of the upper (A & B) and lower (C) beaks for the entire population. Very differently shaped octopod beaks produce the long vectors for upper beaks illustrated in B: black vectors for octopods, grey for others.

The landmarks selected to describe beaks are depicted in Text-Fig. 1, and described in Table 2. This description adopts the conventional morphology used by earlier workers (e.g. NAEF, 1923; CLARKE, 1962, 1986).

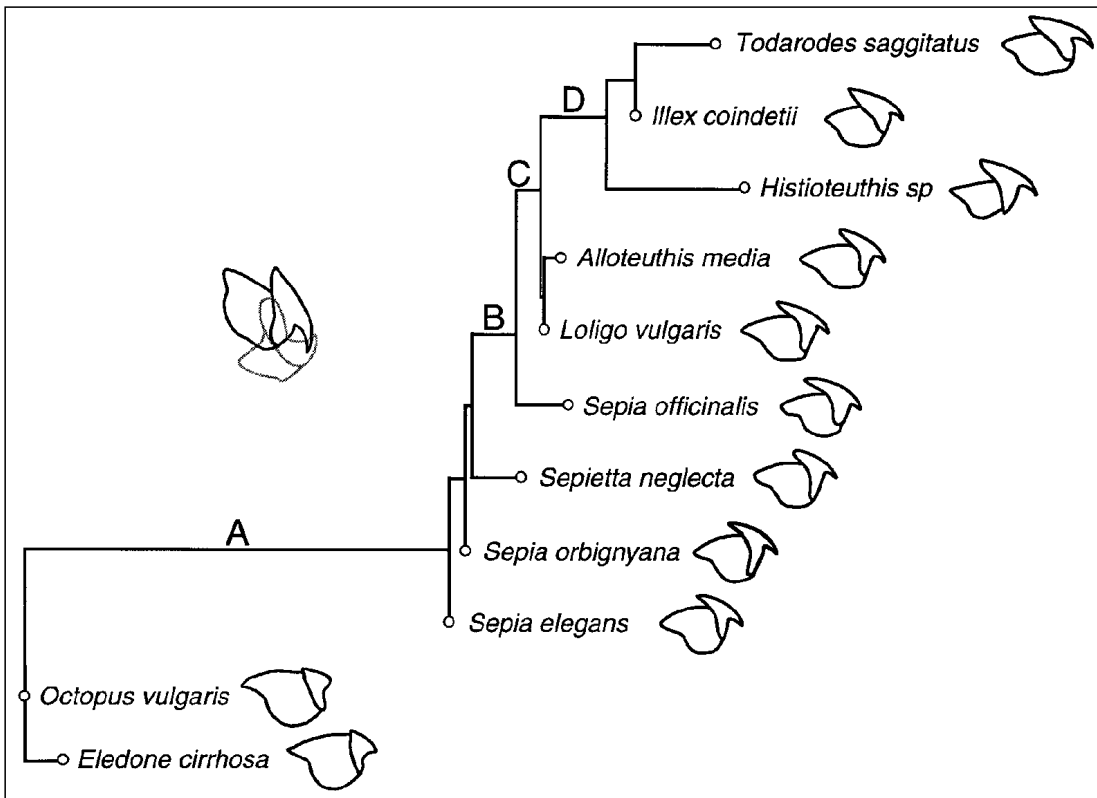
4.1.2. Morphospace

As a first step, a generalized least square (GLS) analysis was performed in order to explore the structure of the data. This computation allows all the individuals of a same morphospace to be compared (Text-Fig. 2). Each line represents the distance after adjustment between the mean individual (first target calculated from all individuals) and each individual (second target). These lines represent vectors of deformations at each point between the two targets. The longest vectors are for upper beaks (specifically for points 1 and 5), yielding an anisotropic distribution of vectors for some points (e.g. points 1, 2, 3, 5, 6, 7). The distribution of vectors for points on lower beaks seems comparatively isotropic (i.e. well distributed around mean shape), suggesting only slight differences of

shape within the sample. Comparison of upper and lower beak morphospaces therefore suggests a better structuration of shape for the former. The longer vectors are generally associated with the large differences in shape between octopod and decapod clades. This is illustrated for four points of the upper beak (Text-Fig. 2). *Octopus* and *Eledone* beaks are distinguishable from decapod beaks in having a short rostrum and hood.

The next step was to detect intraspecific variability for species represented by several individuals (see Table 1). No clear ontogenetic or sexual pattern was discovered for the range of size under study. Thus for interspecific comparisons, a mean shape was calculated for each species (GLS procedure) represented by more than one specimen. For others, the single specimen was considered to be representative of the shape of the species.

After computing the distance (the sum of vector lengths) between all species two by two (LSTRA procedure) for upper and lower beaks, two phenetic trees were constructed.



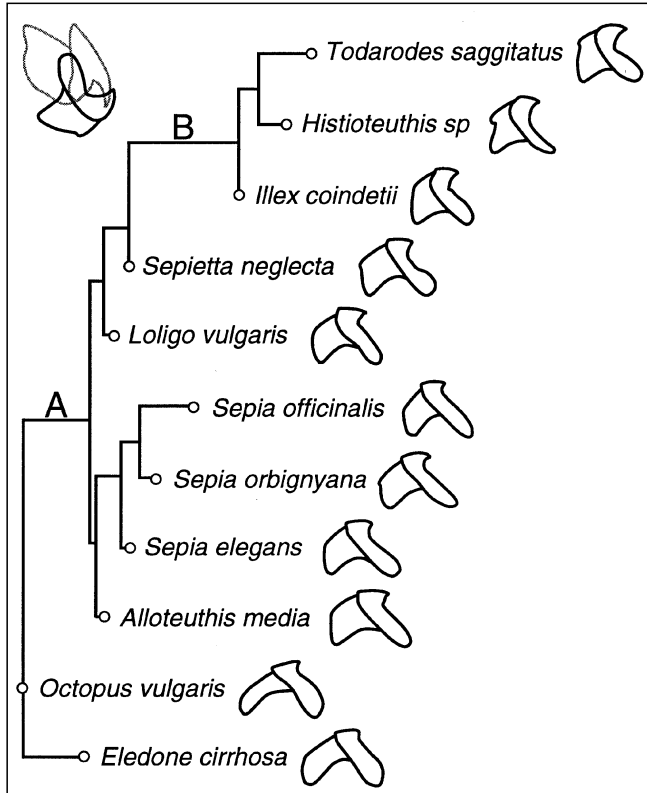
Text-Fig. 3. Phenetic tree computed for upper beaks. The horizontal bars show morphological distances between species.

The upper beak tree (Text-Fig. 3) confirms the large difference between the octopods (*Octopus vulgaris*, *Eledone cirrhosa*) and the decapods (see length of bar A, Text-Fig. 3). In short, shape modification from octopods to oegopsids is marked by increases in the rostrum, hood and wing to the detriment of the lateral wall. Within the decapods, a complex pattern can be seen, despite the general arrangement into Sepioidea – Myopsida – Oegopsida. The difference in shape seems to be greater between the latter and the two former (compare length of bars C and D, Text-Fig. 3). Although the nodes reflect the differentiation between these three main groups, there is still a large distance between *Sepia elegans*, *Sepia orbignyana* and *Sepietta neglecta* on the one hand and *Sepia officinalis*, *Loligo vulgaris* and *Alloteuthis media* on the other hand.

The phenetic tree for the lower beak is less informative (Text-Fig. 4). The arrangement is slightly disrupted, with an exchange of position in the tree between *Alloteuthis media* and *Sepietta neglecta*. Consequently three main groups occur: octopods, sepioids plus myopsids, and oegopsids, separated by a relatively long bar (see bars A and B, Text-Fig. 4). Shape alteration from octopods to oegopsids is marked by modification of lateral wall shape (long and narrow for the former, short and wide for the latter), and by modification of jaw angle (indistinct and near the rostrum for the former, pronounced and distant from the rostrum for the latter). The fact that upper and lower beaks do not yield exactly the same trees suggests that each provides complementary information and warrants individual study, contrary to the assertion of CLARKE (1986).

4.2. Statoliths

Disparity of statoliths has been studied in detail elsewhere (DOMMERS et al., 2000). Only the general results will be reported here for guidance.



Text-Fig. 4.
Phenetic tree computed for lower beaks.
The horizontal bars show morphological distances between species.

Table 3.
Description of landmarks defining statolith shape.

STATOLITHS	
Point	Description
1	Medialmost point of wing spur
2	Medialmost point of wing fissure
3	Dorsalmost point of wing shelf
4	Ventralmost point of wing shelf
5	Medial contact of ventral rostrum and wing
6	Lateralmost point of wing ventral indentation
7	Medialmost point of main spur
8	Lateralmost point of wing dorsal indentation
9	Intersection of a line parallel to the axis 5-10 and rostrum medial edge
10	Ventralmost point of ventral rostrum
11	Intersection of a line parallel to the axis 10-12 and ventral rostrum
12	Lateral contact of lateral dome and ventral rostrum
13	Intersection of a line parallel to the axis 12-14 and lateral dome
14	Lateralmost point of lateral dome
15	Intersection of a line parallel to the axis 14-18 and lateral dome
16	Medialmost point of lateral dome
17	Maximum swelling of lateral dome
18	Dorsalmost point of dorsal dome

4.2.1. Data Acquisition

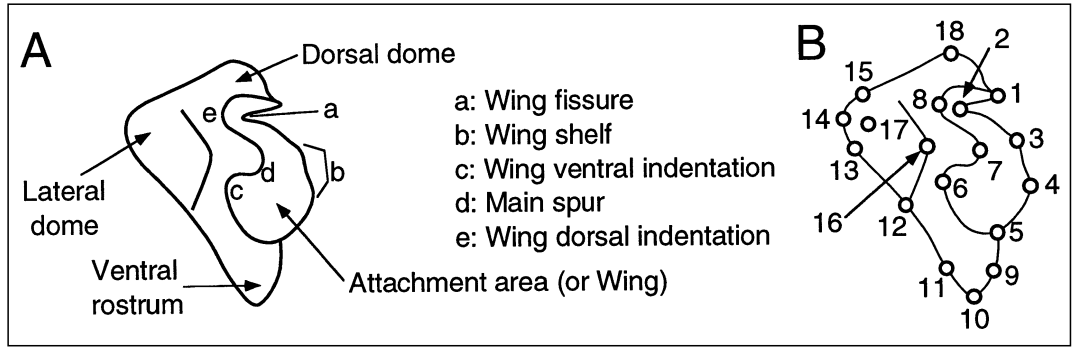
In this study, the anterior side of the statolith was analyzed. This side has the advantage of showing a clear partitioning, meaning a large number of homologous points can be identified. The locations of the 18 landmarks adopted in this study are shown in Text-Fig. 5, with descriptions in Table 3. As with the beaks, the chosen points take into account traditional morphology as described by earlier workers (e.g. CLARKE, 1978; CLARKE & MADDOCK, 1988). Because octopod statoliths are shaped very differently (see CLARKE, 1998: Fig. 2), this clade is omitted here.

4.2.2. Morphospace

A similar approach to the foregoing one was used, the main difference being that an ontogenetic pattern was found for *Sepia officinalis* and *Loligo vulgaris*. These two species were therefore included twice in the subsequent analysis (one shape for small and another for large specimens). The phenetic tree obtained (Text-Fig. 6) reflects overall many of the traditionally accepted taxonomic divisions. The separation between myopsids and oegopsids stands out clearly (see bar C, Text-Fig. 6). Sepiids are clustered together and stand closer to myopsids than to oegopsids. By contrast, the Sepiolidae are not clustered. While *Rossia macrosoma* occurs in an intermediary position between sepiids and myopsids, the Sepiolinae (*Sepietta*, *Sepioloa*) are clustered near the oegopsids. This reflects the ambiguous position of members of the Sepiolidae and questions the validity of the Sepioidea order (grouping Sepiidae plus Sepiolidae), already discussed by several authors (see BOLETZKY, 1995). Shape differences between sepiids and oegopsids are marked by

Text-Fig 5. Statolith morphology in anterior view (A) and location of landmarks (B).

- 1) a drastic modification of the lateral dome (bulbous for the sepiids, less marked for oegopsids),
- 2) development of the attachment area, ventrally, and
- 3) a change in the relative position of the attachment area compared with the remainder of the statolith.



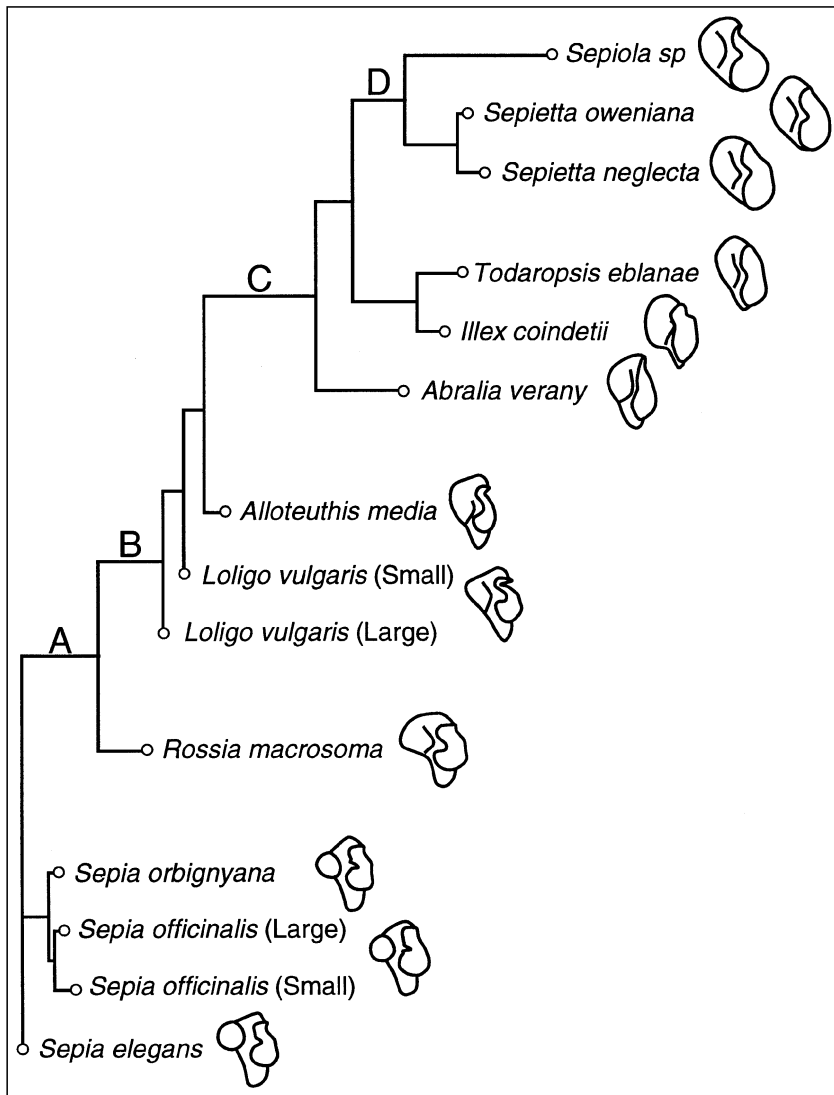
5. Conclusion

Similarities can be recognized in the patterns of the three phenetic trees. First is the split between Octopoda and the other orders (Sepioidea and Teuthoidea). This split is quantified here for beaks only. However, the fact that it was not possible to find homologous points for the statoliths of these two groups emphasizes their wide differences. Second is the consistently close clustering of the oegopsids reflecting similarity within the group and

distinctiveness from other species. Third is a varying degree of mixing between species representing Sepioidea and Myopsida. This is particularly the case for the Sepiolidae, which are clustered with sepiids (upper beak), myopsids (lower beak) or split into two separate clusters when the sample of species is larger (statoliths). This analysis therefore suggests, on the basis of two different characters, that sepiolids do not constitute a coherent morphological group. This was also observed by HEALY (1990) from spermatozoa shape. Genetic data also produce different sepiolid clustering depending on the species under study (BOUCHER-RODONI & BONNAUD, 1996; BONNAUD et al., 1997).

Finally, the present study suggests systematic diversity and morphological disparity approaches are complementary. The former establish coherent sets of clades to be grouped (e.g. on the basis of morphological, ecological or geographical data) whereas the latter analyze similarities and differences of shape for common features and authorize comparisons with external data (e.g. shape versus genetics) and also within morphological data (comparison of different features within the same set of species).

We now consider that the time has come to combine complementary investigations of the coleoid clade with the same dataset of species (as done by OGDEN et al. [1998] for octopodids). A first interesting focus could be the position of sepiolids which is clearly ambiguous in traditional systematics. A combined use of comparative anatomy and shape disparity analysis in the context of adult and ontogenetic variation would be particularly valuable in exploring the process of differentiation within clades (e.g. heterochronic). Subsequent comparison with phylogenetic relationships inferred from molecular studies would authorize investigation of the patterns of differentiation.



Text-Fig. 6. Phenetic tree computed for statoliths. The horizontal bars show morphological distances between species.

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