COMBINING DISPARITY WITH DIVERSITY TO STUDY THE BIOGEOGRAPHIC PATTERN OF SEPIIDAE

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ABSTRACT

Diversity and disparity metrics of recent cuttlefishes are studied at the macroevolutionary scale to establish the geographical biodiversity patterns of these cephalopods at species level and to explore the relationship between these two metrics. One hundred and eleven species distributed in 17 biogeographic areas serve as basic units to explore these complementary biodiversity metrics in space. Landmarks describe cuttlebones; differences between shapes are quantified using relative warp analyses. Relative warps are used as the morphological axis to construct morphospaces whose characteristics are described with total variance as a disparity index. Disparity is analysed and then compared with diversity (i.e. species richness). Results show the peculiarity of southern African coasts (high disparity level with low or high species richness) and the low disparity level of the "East Indies" area associated with high species richness. The particular pattern of southern Africa may have been caused by paleogeographical changes since the Eocene whereas that of the "East Indies" may indicate that this area could have acted as a centre of origin. The number of species in a given area does not predict the level of disparity, which suggests the need for both diversity and disparity metrics to be explored when studying biogeography.

INTRODUCTION

Disparity is a measure of how fundamentally different organisms are (Raff 1996). While applied first to the study of differences at the bauplan scale (see Gould 1991), this concept is now widely used at lineage scale to quantify differences in shape (Foote 1993, Dommergues *et al.* 1996, Wills *et al.* 1996). This measure of biodiversity is viewed as a complement to the most common one — diversity — which uses number of elements in a given taxonomic rank as the elementary quantification system. One of the most efficient measurements of the latter is species richness, while the former may be computed by detecting changes in morphospace occupation patterns (see Ciampaglio *et al.* 2001). If applied to the complete clade, each of these biodiversity metrics leads to the discovery of macroevolutionary patterns. The comparison between the two metrics offers an opportunity to search for evolutionary mechanisms at macroevolutionary scale (Foote 1993, Jablonski 2000). This biodiversity exploration has been widely used for time studies but more rarely for biogeographic distribution studies of living species (e.g. Roy *et al.* 2001). The aims of the present paper are to explore the diversity – disparity relationship and to expose a first set of results applied to the study of cuttlefishes (Cephalopoda: Sepiida) at the global scale. This study is now possible mainly because several studies have been published over the past 10 years on Sepiidae zoogeography (see Khromov 1998, Khromov *et al.* 1998, Lu 1998, Reid 2000). These papers offer a world-wide framework for the biogeographic spread of these animals.

MATERIAL AND METHODS

A database of occurrences of Sepiidae is set up from a bibliographic analysis which covers almost all published papers and monographs up to Reid (2000), the most recent study to be taken into account. From this bibliographic analysis, 111 species have been considered valid here, which are arranged in the genera *Metasepia* Hoyle, 1885, *Sepia* Linnaeus, 1758 and *Sepiella* Gray, 1849, in accordence with Khromov *et al.* (1998), Lu (1998), Reid and Lu (1998), and Reid (2000). Some attempts have been made to clarify the taxonomic status of the genus *Sepia* (see Khromov *et al.* 1998). These authors propose a subdivision of the genus *Sepia*, as a basically typological "open system" of six species complexes, which are not to be viewed as phylogenetic entities, since they represent a pragmatic subdivision that may help in the analysis of the genus. These species complexes have here been used to explore morphospace structuration of *Sepia*. For cuttlebone disparity analysis, 102 species were selected covering virtually the entire worldwide array of cuttlebones at the species scale. The difference between this last set of species and the previous one (n = 111) is explained by the removal of a number of species whose cuttlebones are poorly known. Each of these 102 species is represented, for the purpose of the present study, by a single cuttlebone adult shape which is considered to be the average specimen representative of the species. Sepiidae were arranged in biogeographic units following Khromov (1998) but with some modifications according to recent Australian studies (e.g. Lu & Reid 1997, Reid 2000). The latter author used (species range) boundary compression to indicate biogeographic boundaries. A total of 17 biogeographic units were established, labeled A-Q (Fig. 1). Intraspecific and ontogenetic variations are not reviewed here. Although these variations may be of interest in the context of disparity analysis, at the scale of the present study they might produce variability around the specific mean point that could be considered as noise (for further details about ontogenetic and intraspecific variations, see Neige & Boletzky 1997).
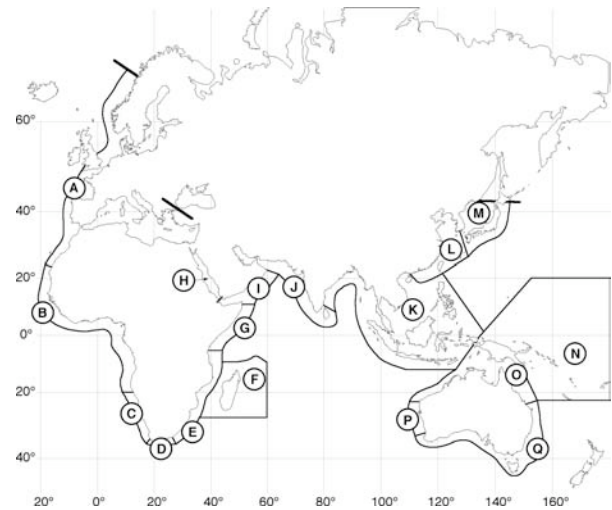

Fig. 1 Sepiid geographical distribution and biogeographic units selected for this study

Cuttlebone shape

The function of the cuttlebone is to ensure neutral buoyancy for the animal throughout life by cameral liquid and gas adjustment relative to the external environment (Denton & Gilpin-Brown 1961a, b). Its shape — bilaterally symmetrical — derived from the juxtaposition of four parts (see Hoyle 1886, Adam & Rees 1966, Roeleveld 1972, Bandel & Boletzky 1979, Khromov *et al.* 1998): outer cone, inner cone, phragmocone and spine (Fig. 2a). Moreover, some species display additional features such as ribs and furrows, pustules and keels. The outer cone gives the cuttlebone its general shape. The inner cone is consistently present near the protoconch and is partly fused with the outer cone. Its anterior extensions (limbs) may be flat and fused to the outer cone or to the phragmocone or form a rounded, cap-like cavity over the protoconch. The inner cone may also be reduced to a small fork. Two parts may be distinguished on the phragmocone ventral surface: the striated zone and the last loculus, the latter being the last septum. The phragmocone generally bulges ventrally but is sometimes slightly concave. The spine (or rostrum) at the posterior tip may be well developed, marked merely by a cone-shaped knob, or completely absent.

From cuttlebones to landmarks

The method used here to depict cuttlebone shape is landmark-based geometric morphometrics (Bookstein
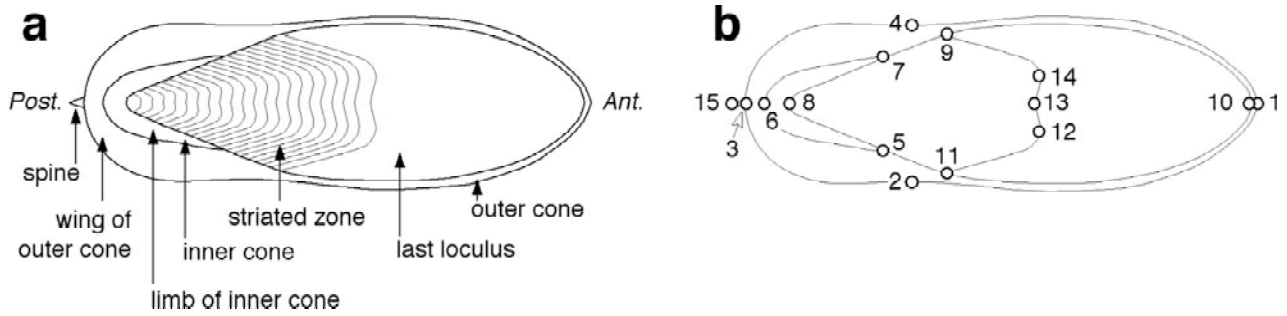
Fig. 2 a Cuttlebone morphology in ventral view. **b** Landmark location. Number and description of landmarks: 1, anterior end of outer cone (on sagittal plane); 2-4, anterior rupture of outer cone wings; 3, posterior end of outer cone (on sagittal plane); 5-7, anterior end of inner cone (contact with striated zone); 6, posterior end of inner cone (on sagittal plane); 8, position of the protoconch (which corresponds to the posterior end of the striated zone); 9-11, posterior contact between striated zone and last loculus; 10, anterior end of last loculus (on sagittal plane); 12-14, maximal curvature of the anterior end of striated zone; 13, contact between striated zone and last loculus in the plane of symmetry; 15, posterior end of the spine

1991). Landmarks are here considered to be the most efficient descriptors of a cuttlebone shape. This is mainly because this shape is a combination of different anatomical parts (e.g. outer cone, inner cone, striated zone) that may vary independently. An earlier study (Neige & Boletzky 1997) concerning only the three Mediterranean cuttlefish species validated this method to describe cuttlebone shapes in the context of ontogenetic, intraspecific and interspecific variations. First, 15 landmarks are chosen to describe the geometry of the different parts of the cuttlebones (Fig. 2). These points describe the relative position of the four parts of the cuttlebone and its general shape. Only the ventral view is analyzed here since it reflects the distinct elongation along the sagittal plane, and provides geometric information about the different component parts. When the spine is completely absent in a species, point 15 (posterior end of the spine) coincides with point 8 (position of the protoconch), which is the location of the spine at the very beginning of its development.

From landmarks to morphospaces

Relative warp analysis method (see Bookstein 1991, Rohlf 1993 for details) is used here to explore the disparity pattern of cuttlebones. Its main interests are (1) to compare and contrast all cuttlebone shapes and (2) to map the geometric transformations from a given configuration of landmarks (generally the mean of a sample) to each specimen (see Rohlf & Marcus 1993). These transformations can be computed in different ways depending on the relative weight attributed to large and small-scale shape changes. In our case, no particular scale of variation is considered to be of prime importance, so that the relative warp analysis used here corresponds to a principal component analysis among all pairs of forms of the Procrustes distances (i.e. size-free distances among two configurations of landmarks). The software applied was tpsRelw version 1.22 (Rohlf 1994). The analysis included the following steps:

— computation of a consensus shape (a mean shape) by a generalised least square adjustment (i.e. finding the mean shape by use of the complete data matrix);

— mapping the consensus on an orthogonal grid;

— calculation of the deformations between the consensus and all shapes of the initial data matrix. This step leads to the calculation of parameters that describe the deformation of the grid (by finding the thin-plate spline transformation that maps the mean configuration of landmarks onto each specimen or along axes, see Rohlf 1993);

— use of the deformation parameters in a multivariate analysis. The analysis produces some new axes (the so-called relative warp axes: RW) that concentrate a more or less extensive information content in the initial matrix. Relative warp analysis allows visualisation of deformation along an axis; computation of a morphospace using some relative warps (e.g. the first factorial plane: RW1 versus RW2), that generally concentrates a large amount of variance and illustrates the gross distribution pattern of shapes.
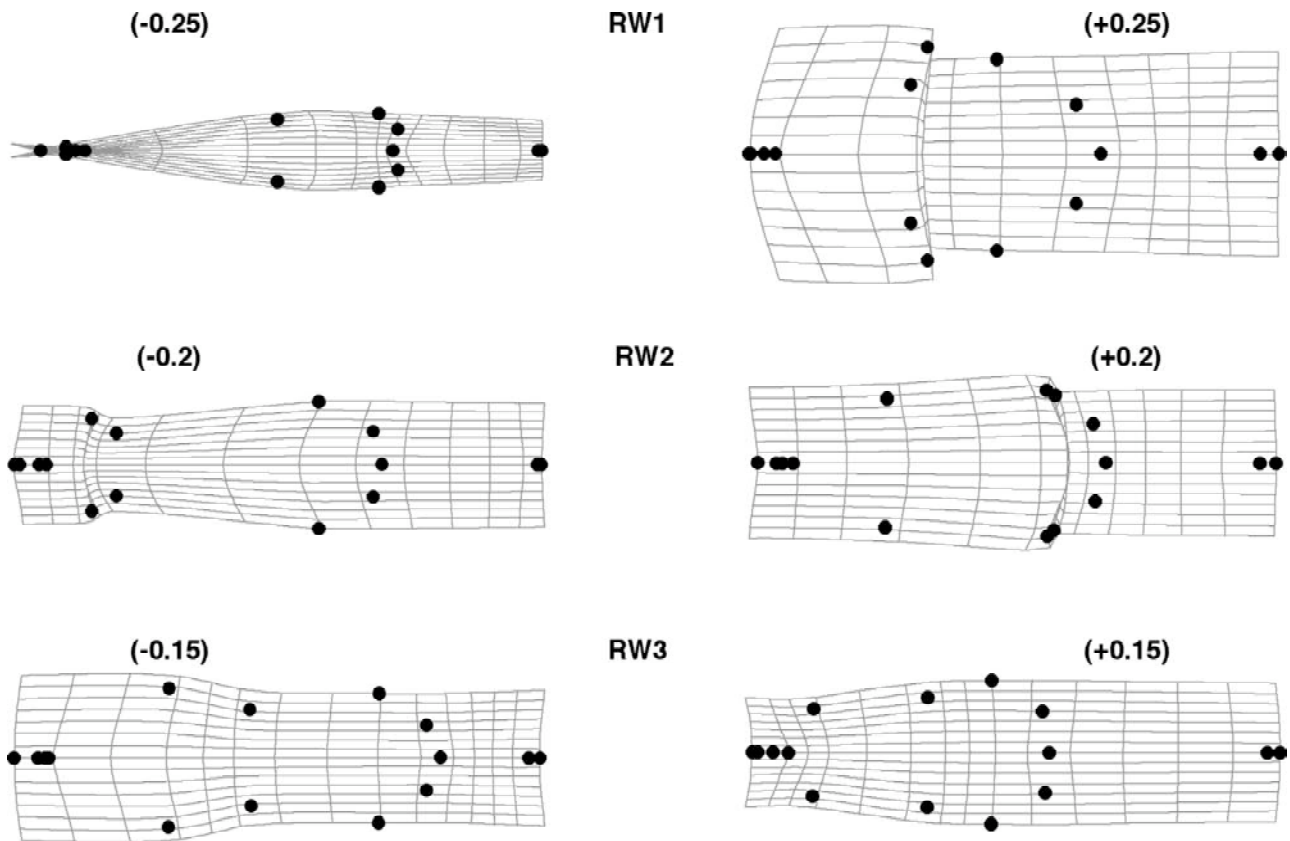
Fig. 3 Plot of the first three relative warps shown as thin-plate splines, for positive and negative displacement along the axis

From morphospaces to disparity

Coordinates of species on the multivariate morphospace could also be used as variables to assess disparity of a particular set of species. Parameters that quantify the distribution of a selected set of species of the morphospace have then to be computed. Several parameters are found in the literature (e.g. Foote 1993, Dommergues *et al.* 1996, Wills *et al.* 1994, Ciampaglio *et al.* 2001). Only one measure of disparity is used here: the average dissimilarity that is given by the total variance (the sum of variances for selected RW axes); this parameter is size sample free and is considered to be robust (Foote 1993). Error bars are calculated using a bootstrap process: taxa were resampled randomly with replacement 500 times. Resampling produces a different matrix each time (or similar ones by chance), and then also produces a different total variance index. Results are given here as mean and standard deviation of total variance calculated from the 500 different matrices. Bootstrap and morphospace parameters are computed using the MDA package (Navarro 2001).

RESULTS

Sepiidae disparity

The first relative warp (RW1) describes gross morphology of the sepion (Fig. 3): positive values are for a broad one associated with large wings, whereas negative values are for a narrow one associated with tiny wings. The second relative warp (RW2) explains the shape of the inner cone: long (positive values) or short (negative ones), regardless of general shape. The third one (RW3) focuses on the relative length of the striated zone. In the present case, percentages explained for relative warps are 53.02, 20.66, 11.49, 5.47, and 3.96, respectively, for the first five axes selected for subsequent analysis (other axes are not retained as their contribution is below the mean).

The family Sepiidae displays a wide range of shapes as shown on the morphospace (Fig. 4) which corresponds to the first factorial plane (RW1 vs. RW2) and thus quantifies global cuttlebone shape. The genus *Sepiella* occupies a very small portion of the morphospace (Fig. 4): with medium values on RW1 and rather negative values on RW2 (corresponding to
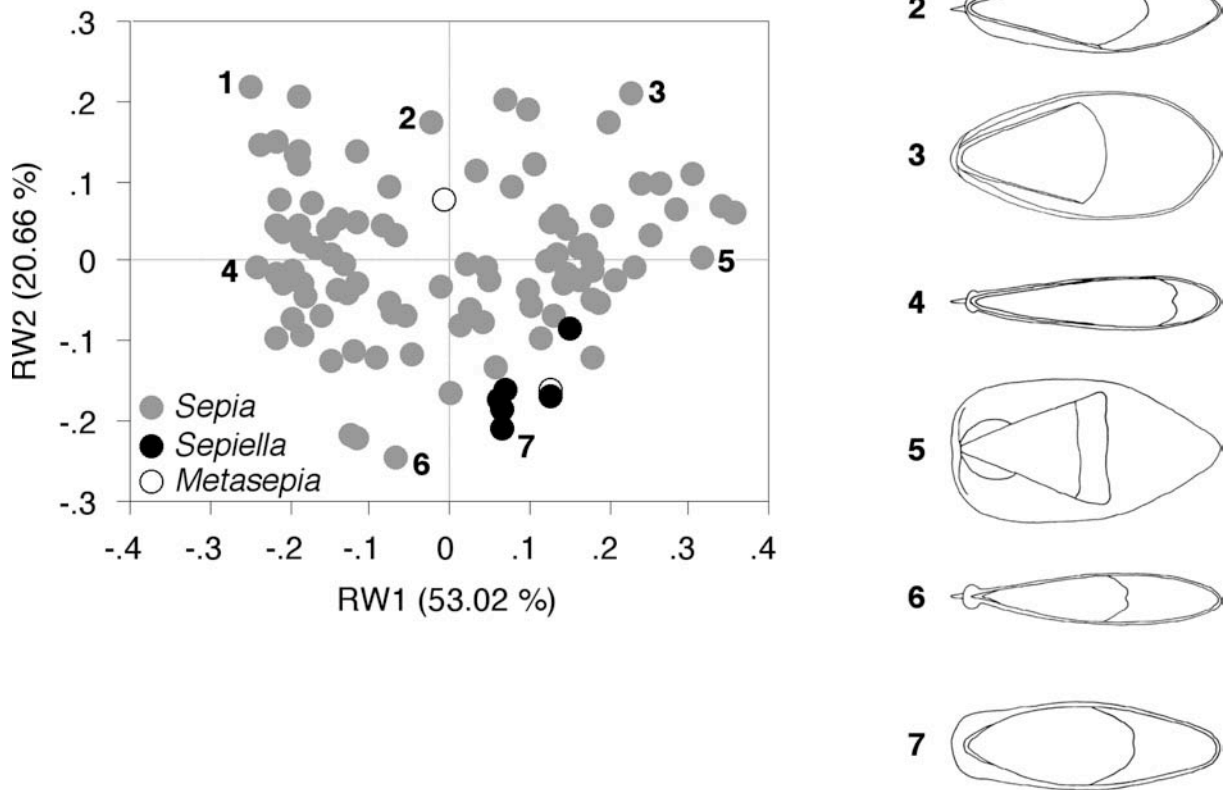
Fig. 4 Overall morphospace (RW1 vs. RW2) of sepiid cuttlebones for the three selected genera (*Sepia*, *Metasepia*, *Sepiella*). Drawings illustrate extreme shapes along the first two relative warps. 1, *Sepia aureomaculata* Okutani and Horikawa, 1987; 2, *Sepia rex* (Iredale 1926); 3, *Sepia senta* Lu and Reid, 1997; 4, *Sepia vercoi* Adam, 1979; 5, *Sepia typica* (Steenstrup, 1875); 6, *Sepia tokioensis* Ortmann, 1888; 7, *Sepiella cyanea* Robson, 1924

the very short inner cone). The two species of the genus *Metasepia* are not localised close together on the morphospace, mainly due to a difference in inner cone relative size. In contrast to *Sepiella*, *Sepia* covers nearly all shape possibilities (see Fig. 4). This is mainly because the latter genus is composed of many different species. "*Hemisepius*" and "*Anomalosepia*" species complexes display non-homogeneous spread of species on the morphospace (Fig. 5). The other species complexes display constrained spreads (Fig. 5). Such is the case for the "*Doratosepion*" species complex, which includes nearly all species with negative values on RW1. By contrast, this species complex displays very diverse values on RW2. This pattern corresponds to narrow cuttlebones with more or less long inner cones.

Sepiid disparity and diversity through space

The disparity level is clearly different between biogeographic units (Fig. 6). Three of the 17 units (A, B and N) show a particularly low level of total variance; this may be related to (1) the low number of species they contain, and (2) the morphological similarity of the species. The three units with the highest total variance (C, D and E) are those situated in the southern part of Africa. Total variance in other units gives intermediate values. Interestingly, unit K, corresponding partly to the "East Indies" Triangle of Briggs and recognised as a species concentration zone (Briggs 1999), displays a comparatively low disparity level. This is mainly due to the presence of morphologically close species.

Counts of species numbers (i.e. diversity metric) by area reveal marked differences (Fig. 6). A marked
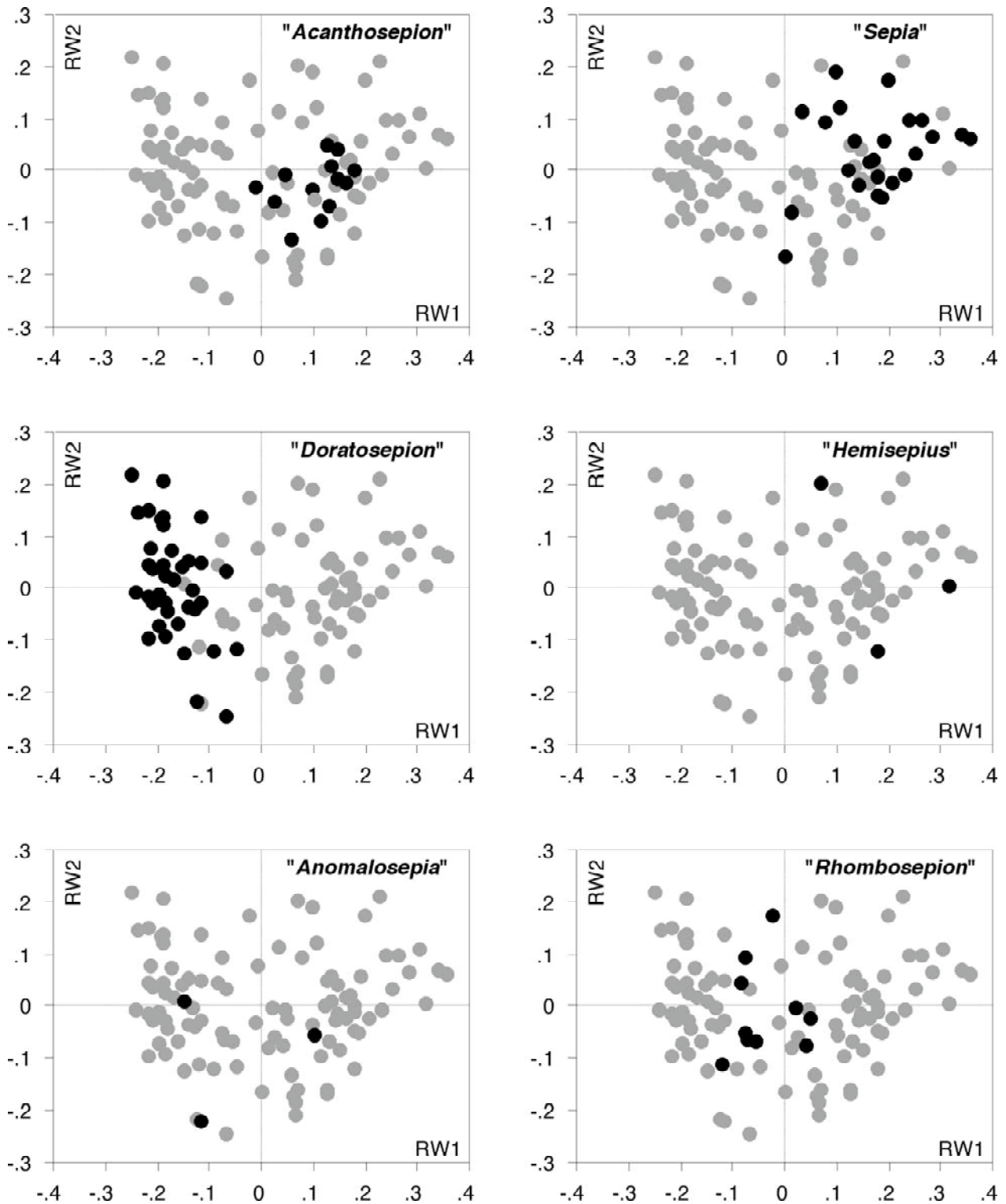
Fig. 5 Morphospaces of sepiid cuttlebones in each of the 6 main species complexes of the genus *Sepia* (see text). Black circles indicate the shapes present for a given species complex. Grey circles indicate the overall morphospace

diversity "hotspot" appears for the coast of SE Africa (unit E) with 20 different recorded species. A large area extending from eastern India to Japan and including Indonesia and the north coast of Australia (units K, L, M, and O) also displays a broad diversity level (with 23, 18, 21, and 25 species, respectively).

## DISCUSSION

Disparity versus diversity

As suggested by Foote (1993) the comparison between disparity, i.e. the morphological metrics of biodiversity, and diversity, i.e. the taxonomic metrics of biodiversity, is one of the ways of exploring macroevolutionary patterns and processes. The different relationships between diversity and disparity found here are worth some comments (Figs 6, 7).

1. The analogous relationship between diversity and disparity for units A plus B, on the one hand, and N on the other (crosses in Fig. 7) may be related to the relatively feeble species richness associated with a similar disparity level. This could be due to the marginal geographic location of these units: West side of Sepiidae range for units A & B and East side for unit N.

2. A drastic change in disparity level is observed along African coasts between units B and C, although both units contain the same species richness (n = 6).

3. A particularly high disparity level on southern African coasts (C, D and E) for very different species richness, respectively 6, 11 and 20 (open circles in Fig. 7) indicates a marginal position of such species within the morphospace (well marked at least for C and D). This high disparity level for a very different species richness may be caused by the coexistence of two independent phylogenetic clusters of species, one from the Atlantic Ocean and the other from the Indian Ocean. This distribution pattern could be explained using paleogeographical data. In the Eocene the Tethyan sea was still open at its eastern end and provided connection between Europe on the one hand and the Indian Ocean and East African coasts on the other (see Butterlin *et al.* 1993). At the end of the Eocene, this eastern corridor between the Mediterranean Sea and western India disappeared, leading to completely different ways of range extension for Sepiidae. The mixing of these two clusters in southern Africa may have produced the observed pattern.

4. A globally homogeneous and medium disparity level for other areas, F to Q except N (solid circles and squares in Fig. 7) is associated with various species richness (9 to 23 species). The disparity level is low
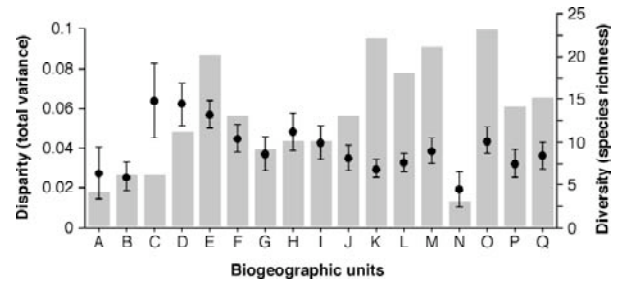
Fig. 6 Pattern of morphological disparity (black circles and error bars) and of taxonomic diversity (grey bars) for the Sepiidae in the 17 biogeographic units (see labels in Fig. 1). Morphological disparity is measured by total variance for the first five relative warps. Taxonomic diversity by species richness. Bootstrapping (500 replicates) generates error bars
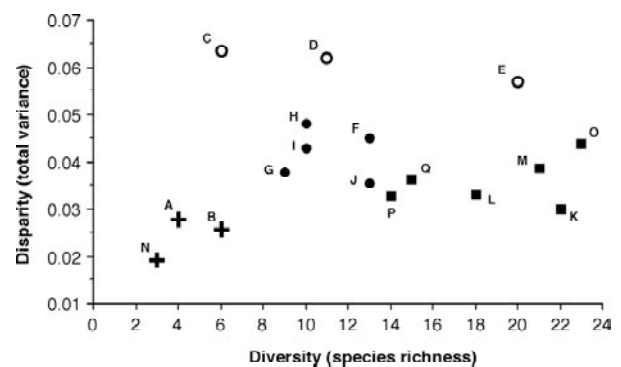
Fig. 7 The relationship between diversity (species richness) and disparity (total variance) in each of the 17 biogeographic units (letters refer to biogeographic units, see Fig. 1)

compared to species richness. This reflects the fact that this area and particularly unit K contains numerous species with a similar cuttlebone shape. This confirms that the "East Indies" Triangle is a particularly rich area in terms of number of species (see Briggs 1999) although the disparity metric highlights a low level of morphological diversity. The significance of this speciose area is the subject of much debate (see Briggs 1995), and different theories compete to explain this pattern, going from the "native" point of view (species are numerous because this area produces new species) to the "accumulative" one (species are numerous because this area accumulates species formed elsewhere). In the case of Sepiidae, the observed pattern supports the "native" theory. The "accumulative" one would certainly have produced a pattern associating a high disparity level (because species belong to different phyletic clusters, arriving from different areas and accumulating in the new area) with a high species richness. These results indicate that

the "East Indies" area represents a centre of origin for Sepiidae. Another point of view is given by Khromov (1998) who, when analysing geographical distribution of both recent and past sepiids, supposed a Tethyan origin for this group during the Oligocene. These times correspond to the closure of the Tethyan Sea due to the collision between Asia and Arabia (Lorenz *et al.* 1993) isolating the Mediterranean Sea to the west and the Indian Ocean to the east. For Khromov (1998) Sepiidae that were able to leave the Mediterranean Sea radiated first on the northern part of the Indian Ocean, and then in southeast Asia. We obviously need new data (namely a phylogenetic framework) to confront and properly test these two different points of view.

5. At the global scale, the relationship between diversity and disparity is clearly not linear (Fig. 7) and no simple adjustment models seem to fit (r = 0.15, *P* = 0.57). The conclusion is that the number of species in a given area does not predict its disparity level. This was found for other taxa (e.g. Roy *et al.* 2001).

Finally, as previously seen, the absence of a clear phylogenetic hypothesis for Sepiidae is a major gap, which prevents the present study from reaching a thorough comprehension of the observed patterns. The next step of the analysis will therefore be to propose a phylogeny of Sepiidae and to link it to present observed patterns.

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