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MORPHOMETRICS OF HARD STRUCTURES IN CUTTLEFISH

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ABSTRACT. Cuttlefishes exhibit several hard structures that have been characterised using morphometric analysis. Most of these data come from cuttlebones, although statoliths and beaks are also used. It appears that morphometric techniques are mainly used for taxonomic purposes. However, some analyses have emphasised functional morphology and macroevolution. Morphological features (including the inner shell) of cuttlefishes and their availability for study (numerous specimens, culture in the laboratory) make them a first rank model for numerous studies in life sciences that require morphometrics, and especially in the field of evolutionary biology.

CEPHALOPODS, CUTTLEFISH, MORPHOMETRICS, TAXONOMY, DISPARITY, EVOLUTIONARY BIOLOGY

INTRODUCTION

Morphometrics, as any other scientific field, has its own celebrities, who have greatly increased our knowledge. Among them is D'Arcy Thompson and his famous book *On Growth and Form* (1917). The basic idea of Thompson was to link numerical precision with biological science. Applied to the field of form comparison, he proposed to define the *Science of Form* as resulting from a two step process: “*The study of form may be descriptive merely, or it may become analytical. We begin by describing the shape of an object in the simple words of common speech: we end by defining it in the precise language of mathematics; and the one method tends to follow the other in strict scientific order and historical continuity*” (Thompson 1917). It is well known that D'Arcy Thompson was interested in cephalopods, as suggested by a famous photograph of him observing a shell section of a *Nautilus*. However, it is interesting to note that he used the words of common speech, and not the precise language of mathematics to discuss the shape of cuttlefishes. This was published in a short paper (Thompson 1928) devoted to explaining how to catch a cuttlefish, and included reports by classic authors (including Aristotle).

Morphometrics, a term that D'Arcy Thompson did not use, corresponds to the second step of his *Science of Form*. A modern and operational definition may be found in Rohlf & Marcus (1993, p. 129): “*The field of morphometrics is concerned with methods for the description and statistical analysis of shape variation within and among samples of organisms and of the analysis of shape change as a result of growth, experimental treatment or evolution. Morphometric methods are needed whenever one needs to describe and to*

compare shapes of organisms or of particular structures. The samples may represent geographic localities, developmental stages, genetic effects, environmental effects, etc”. Methods to describe and compare shapes are understood here as quantitative, based for example on dimensional measurements. Statistical analyses are mainly a multivariate exploration of data: the analysis at one time of many descriptors on many observations. In a broader sense, morphometrics may be applied to any biological shape. In practice, it is generally restricted to hard structures, mainly because these are not subject to deformations during analysis (e.g. storage, desiccation, dissection) but also because their shape represents a long process of growth and thus supposedly reflects some basic biological information (for example to explore taxonomy or phylogeny). However, we cannot exclude soft parts from the field of morphometry, although morphometric studies are then much more difficult to manage, when considering post-mortem shape deformation e.g.

During the last two decades, progress in morphometrics has greatly increased the field of the *Science of Form* (see Adams *et al.* 2003), but progress in this field will convey nothing unless applied to some biological models, whatever the biological perspective covered: fundamental or applied. In this context, cuttlefishes have a special place within the cephalopods, largely due to their well-developed hard structures, and particularly when considering their inner shell.

This paper reviews what has been done and what could be done when using morphometrics to describe and quantify cuttlefish hard structures. It focuses primarily on *Sepia officinalis*, although it is not restricted to this species, since a discussion of such important fields as species comparisons and macroevolution is useful.

Hard structures in cuttlefish

In theory, four cuttlefish hard structures may be studied using morphometric techniques: (1) the inner shell (Fig. 1 A), or cuttlebone, whose function is to control buoyancy of the organism, (2) the statoliths (Fig. 1 B), which participate in the detection of gravity and linear acceleration, (3) the beaks (Fig. 1 C) and (4) the radula (Fig. 1 D), both being part of the digestive system. Although considered here as hard structures, their respective composition is quite different: aragonite for inner shells and statoliths, chitin for beaks and radula. To my knowledge, only three of the four have been extensively studied using morphometric tools: inner shell, beaks and statoliths.

A basic description of morphometric techniques

The following brief presentation of morphometric techniques is based in part on works of Rohlf & Marcus (1993) and Lestrel (2000). Only those who have been applied to cuttlefish hard structures are considered here. Complementary and up-to-date information of any kind about morphometrics may be found at the following reference web site:

<http://life.bio.sunysb.edu/morph/index.html>.

Traditional Morphometrics

Traditional Morphometrics uses quantitative features such as linear dimensions, perimeters, surfaces or angles as basic raw data (variables), and compares them using statistical approaches. In

practice, variables usually correspond to distances measured on the organisms (Fig. 2). Therefore, statistical methods used can be mathematically very simple or more complex; examples vary from ratio calculations (i.e. the calculation of the proportion of a given character to total length of an organism or a given anatomical structure) to the calculation of new variables using multivariate statistics. The aim of these multivariate statistics is to reduce the number of variables under study. *Traditional Morphometrics* is now widely and routinely applied to cephalopod studies (e.g. Kassahn *et al.* 2003 for an application in *Sepia apama*, and Natsukari *et al.* 1991 in *S. esculenta*).

Coordinate Morphometrics

Coordinate Morphometrics emphasises the recognition of homologous landmarks (Fig. 2): points which have to convey a biological meaning, for example a point at the intersection of two structures. The basic idea is to compare and quantify geometrical differences between sets of landmark configurations (reflecting sets of organisms or species) rather than to quantify shape itself. This approach is relatively recent (starting in the eighties: Bookstein *et al.* 1985, Bookstein 1991), thus applications on sepiids are still relatively sparse (Neige & Boletzky 1997, Dommergues *et al.* 2000, Neige & Dommergues 2002, & Neige 2003a, 2003b). *Coordinate Morphometrics* offers interesting advantages (Rohlf & Marcus 1993): (1) movement of one structure relative to another one is easily located and quantified, (2) it is easy to separate affine shape changes from non-affine or local transforma-

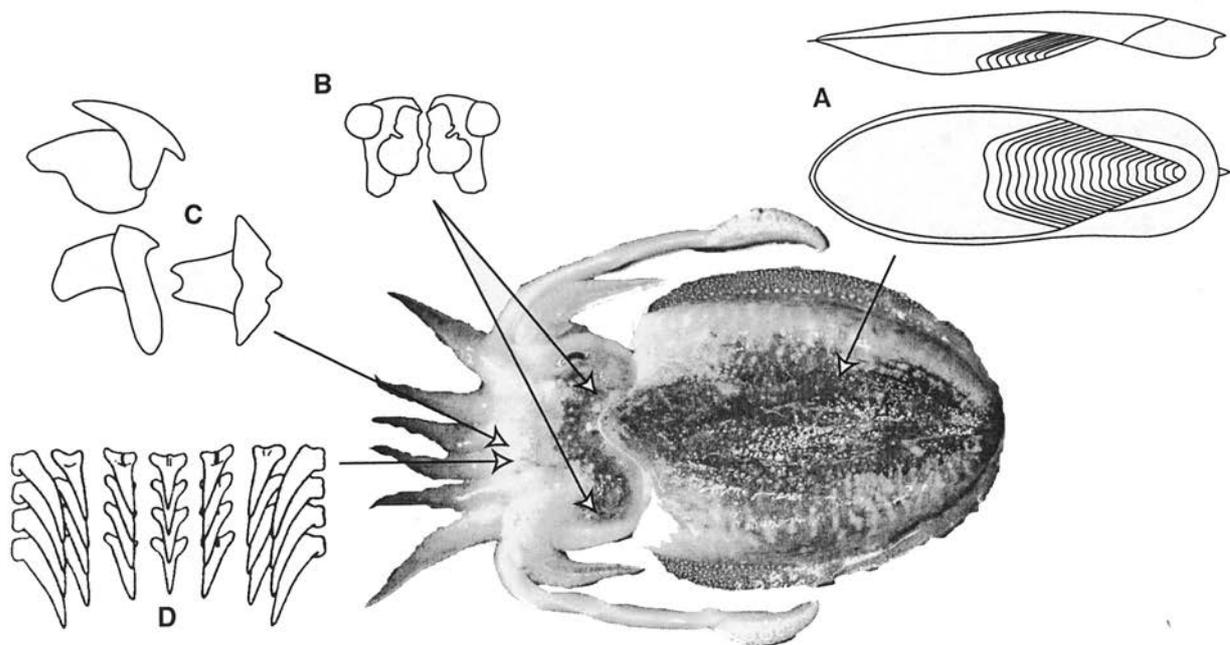


Fig. 1. – *Sepia officinalis* and its main hard structures. A, cuttlebone. B, statoliths. C, beaks. D, radula. Only the first three structures have been studied using morphometric techniques.

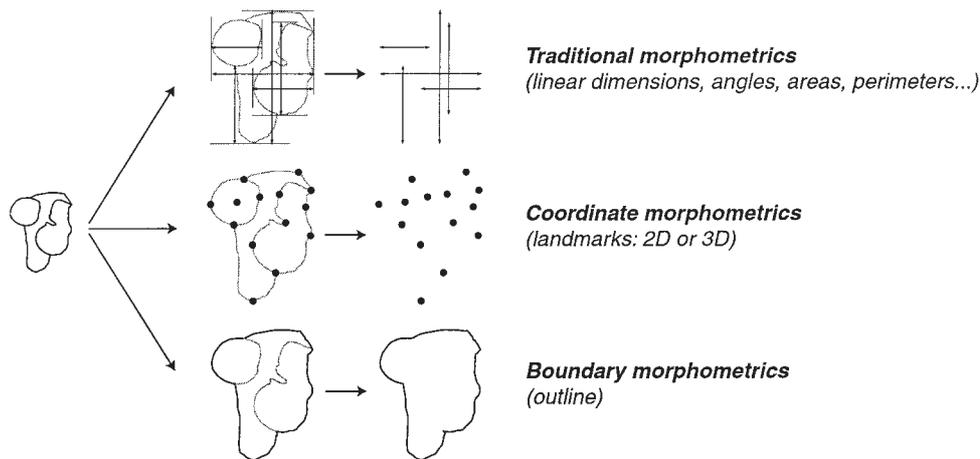


Fig. 2. – The three main morphometric techniques applied to cuttlefish hard structures, exemplified here on a statolith. Note that they fundamentally differ by the nature of data they are based on (see text).

tion, (3) graphical outputs allow identification and location of shape modifications precisely from one shape to another one, using vector fields, for example.

Boundary Morphometrics

Boundary Morphometrics uses the general outline of an organism or a part of an organism as the shape proxy (Fig. 2). This technique is used when the biological information of interest is confined to the outline (Lestrel 2000). The first step defines points located on the outline, and the second step uses Fourier analysis (or an equivalent technique) to transform spatial configuration (the position of the points on the outline) into frequency components (amplitude and phase). It is important to note that amplitudes may be used thereafter in multivariate statistical analysis. An important advantage of *Boundary Morphometrics* is that the frequency component transformation is reversible, allowing outlines to be geometrically reconstructed using frequency information. Application of this approach is still very rare with cephalopods. Thus far, only one work has attempted such an analysis on sepiids (Lombarte *et al.* 1997), exploring intraspecific statolith variability in *S. officinalis*.

Usefulness of morphometrics for species identification and comparison

Morphometrics of the Cuttlebone

Scientists working on cuttlefish taxonomy have traditionally used cuttlebone features as a proxy for species identification. Many of them described the shape with basic terminology, while others attempted to characterise shape by measurements. Whatever the mode of description, quantitative or

not, it has been noted, following Lu (1998), that utilising cuttlebone shape alone is certainly not significant when attempting to define a species. This is due in part to large cuttlebone shape variations, which occur in a species, due to growth, sexual dimorphism or geographical position. However, (1) several species were described based only on the cuttlebone (e.g. *Sepia elegans* and *S. orbignaya*), and (2) cuttlebone shape in turn (i.e. when species have been formally described, using soft and hard structures), is a good proxy when a species should be recognized from a specimen.

The first attempt to quantify cuttlebone shape is found in the work of Hoyle (1886, p. 123). He defined the locular index as the length occupied by the last loculus (the last septum) when compared to the cuttlebone length. The use of cuttlebone measurement ratios – i.e. ratios removing a part of size effects, another part (the allometric one) being still present – is now standard for taxonomic purposes (e.g. Roeleveld 1972, Reid 2000). For example, Guerra *et al.* (2001) used several cuttlebone shape parameters to compare *S. officinalis* and *S. hierredda*. Their results show some differences between the two species, which are congruent with genetic differences.

Some workers have used a landmark based approach to explore cuttlebone shape at the species level (Neige & Boletzky 1997). For *S. officinalis*, no sexual dimorphism and no ontogenetic growth allometry exist (for total cuttlebone sizes ranging from 62 to 256 mm). However, in the same analysis it is demonstrated that underfed individuals that were reared in the aquarium (Boletzky 1974) are morphologically different from wild specimens, the former possessing a relatively broader anterior part. Note that the absence of sexual dimorphism and ontogenetic growth allometry are in contradiction with some other studies (e.g. Bello 2001).

These opposite results may be due to the relatively low number of specimens used for the landmark based approach.

Morphometrics of Statoliths

Many studies have focused on statoliths because of their ageing potential (Bettencourt & Guerra 2001 for a study on *S. officinalis*). Some others have considered the shape of statoliths for their taxonomic value and evolutionary significance. Among them, Clarke (see Clarke 2003 for a bibliographic list) explored this potential essentially using morphometric methods. Using *Traditional Morphometrics*, he demonstrates that the shape of statoliths is not only related to functional aspects, but shows much about relationships between genera and species.

Statolith shape analysis has benefited from various modes of quantification. In an exploratory analysis, Lombarte *et al.* (1997) quantified statolith shapes with two methods. One method uses linear measurements of several parts of statoliths, the other uses their outline to define points on the shape and subsequently uses Fourier analysis to explore shape differences. Lombarte *et al.* (1997) finally used a hierarchical classification based on 20 first Fourier parameters to evaluate shape variability for three species (including *S. officinalis*). Their final result is that statoliths show a high degree of intraspecific shape homogeneity (in the case of *S. officinalis*, for mantle lengths ranging from 40 to 210 mm). Dommergues *et al.* (2000) recognise 18 landmarks to depict statolith shape for several Mediterranean coleoid species including the three cuttlefishes *S. officinalis*, *S. orbignyana* and *S. elegans*. The different landmark topologies are compared and overall dissimilarities combined into phenetic trees. They conclude (1) that the three sepiid species have morphologically similar statolith shapes, compared to other coleoids (always with a distinctive lateral dome), and (2) that *S. officinalis* exhibits ontogenetic shape variations (mantle lengths ranging from 48 to 191 mm). Differences between the two results (intraspecific homogeneity *vs* ontogenetic variation) may essentially be due to the fact that the morphological aspects of statoliths under study are not identical depending on the morphometric technique used: the outline for Fourier based approach *vs* a part of the outline plus some points located at the connexion between the parts of the statolith for landmarks based approach.

Morphometrics of Beaks

In his handbook for identification of cephalopod beaks, Clarke (1986) defines some principal measurements to quantify and describe the beak (also see Clarke 1962). Most of them are linear measurements, one is an angle. Clarke's proposal is to calculate some ratios, which may serve for taxonomic

identification (lower beaks only). Finally, qualitative and quantitative descriptions are gathered in a series of keys for the identification of families and genera. Quantitative description of beak shapes using landmarks (for upper and lower beaks), of different coleoids including *S. officinalis*, *S. orbignyana* and *S. elegans*, has been attempted by Neige & Dommergues (2002). They conclude that both the upper and lower beaks do not indicate the same interspecific pattern, shape differences being much more marked for upper beaks.

Usefulness of morphometrics to explore functional morphology of the shell

Based on ratio calculations (cuttlebone width/length and thickness/width ratios), Sherrard (2000) attempts to correlate the cuttlebone's general shape among various species with their actual maximum habitation or capture depths. It appears that relative cuttlebone width is larger in specimens of shallow water species, with relative thickness not differing significantly among species. Ward (2000) also reaches a quite similar conclusion. However, depth limits within cuttlefishes are in a large part a function of the microstructure of the shell (e.g. angle between septa and the dorsal shield, septal thickness and density and morphology of pillar structures, see Bandel & Boletzky 1979). These must be extensively studied before one can identify anatomical factors that cause depth limits in cuttlefishes.

Morphometrics and macroevolutionary studies

During the last decade, macroevolutionary studies have seen some new developments thanks to the use of morphometric techniques. The general aim of these studies is to observe changes in biodiversity at large scales (in time and space) and then to establish which factors are responsible for these changes (Jablonski 2000). For example, a novel idea is that taxonomic diversity and morphological disparity can become complementary biodiversity indices. Although they share common data, it is generally considered that comparing the two offers an opportunity to infer macro-evolutionary processes (Foote 1993).

The case of sepiids has been studied by Neige (2003a, 2003b). In this example, the number of species is used as a taxonomic diversity index whereas dissimilarities within cuttlebone shape are used as a morphological disparity index. Cuttlebone shape is characterised using 15 landmarks, then relative warp analysis method is used (Bookstein 1991) to explore dissimilarities between shapes. This method produces some new axes (the so-called relative warp axes: RW axes)

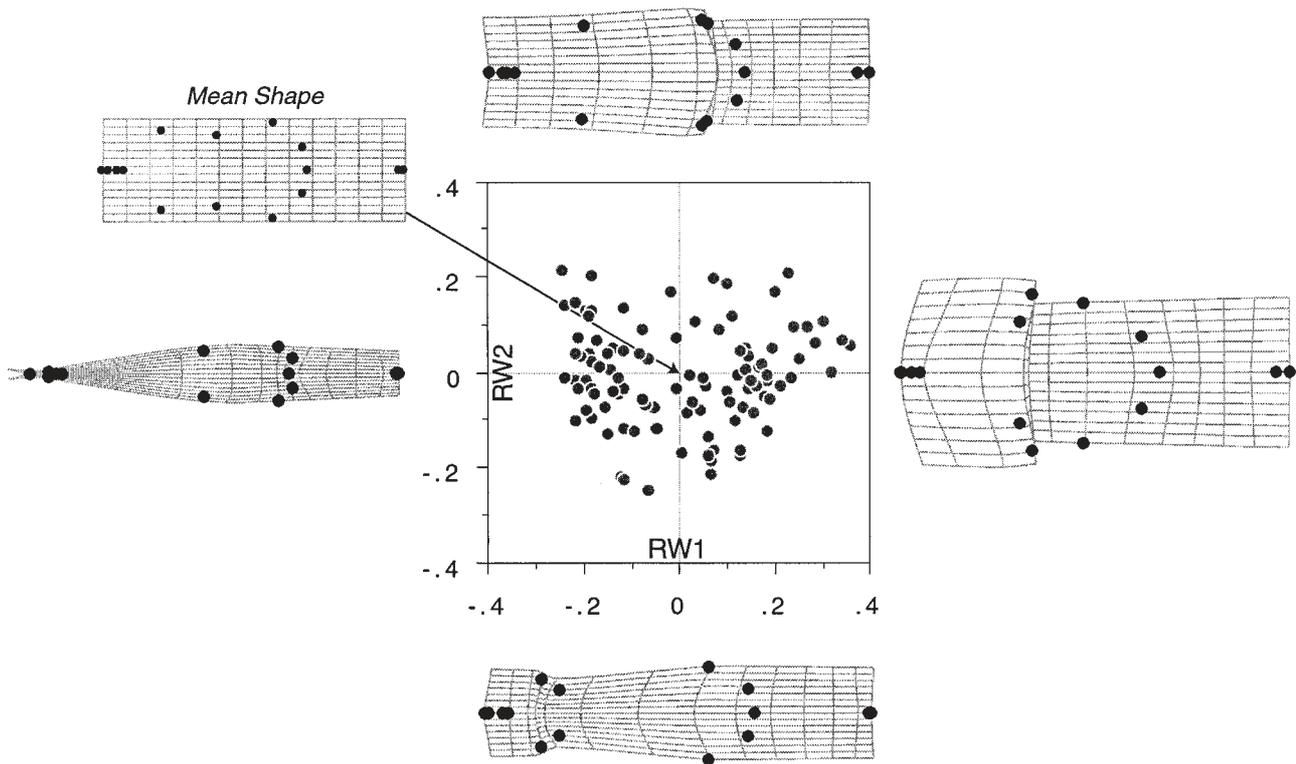


Fig. 3. – Overall morphospace (RW1 vs. RW2) of sepiid cuttlebones, and a plot of the first two relative warps shown as thin-plate splines, for positive and negative displacement along the axis. Mean shape is calculated from all shapes of the initial data matrix (covering all sepiid species known at present) (after Neige 2003a, modified).

that concentrate information contained within the initial matrix, and allows visualisation of deformation along an axis (Fig. 3). A morphospace is constructed using these relative warp axes (here RW1 vs. RW2). It concentrates a large amount of variance and illustrates the gross distribution pattern of cuttlebone shapes. It is possible to construct a morphospace for 17 chosen biogeographical units, because biogeographic distributions are known for the different sepiid species (see Fig. 4 for biogeographic limits). The total variance (the sum of variances for selected RW axes calculated on the points of the morphospace) is used here as a measure of morphological disparity for each of the 17 morphospaces (corresponding to the 17 biogeographical units). High values indicate that a given biogeographical unit comprises species with very different cuttlebones; low values indicate that cuttlebones are morphologically close to one another. Results in Figure 4 are plotted with one bar for taxonomic diversity (left light bar in Fig. 4), and one bar for morphological disparity (right dark bar in Fig. 4) for each of the 17 biogeographical units. The initial result is that the number of species does not predict morphological disparity (i.e. couples of bars on Fig. 4 display very distinctive patterns). This indicates that morphological disparity is a measurement of biodiversity that expresses



Fig. 4. – Comparison of taxonomic diversity (left light bar) and morphological disparity (right dark bar) for each of the 17 biogeographical units for the complete cuttlefish clade. Note an intriguing geographical reverse pattern between West (few species with high disparity level) and East (many species with a relatively low disparity level).

complementary biological information to standard taxonomic diversity. A secondary result is the apparent contrast between the western diversity/disparity pattern (from Norway to the Gulf of Aden) and the eastern diversity/disparity pattern (Fig. 4). The western part associates few species with high disparity level (with one exception), while the eastern part associates an inverse pattern (with one exception). This intriguing geographical reverse pattern may have been, at least in part, a product of the history of the clade as a whole, and could reveal a complex biogeographical history (see Neige 2003a for details).

CONCLUSIONS

As reviewed here, the use of morphometrics on cuttlefish hard structures has allowed us to describe shape in a quantitative way. Several techniques have been employed, some traditional (i.e. *Traditional Morphometrics*), others more recently used for biological applications (i.e. *Coordinate Morphometrics*, *Boundary Morphometrics*). In the case of cuttlefishes, the main and traditional application of morphometrics is obviously concerned with taxonomic identification. But many other domains may also require morphometrics, for example functional morphology or biogeography, as demonstrated in the present paper. Some new techniques, such as *Structural Morphometrics* (Lestrel 2000), have not been attempted on sepiids yet, but it should be noted that their application for biological purposes is still very rare. These new techniques may open new perspectives to characterise texture or surface patterning, an interesting technique to quantify namely the shape of cuttlebone dorsal shield surfaces. These new morphometric tools have recently been explored for otolith characterisation (Parisi-Baradad *et al* 2005). Fourier analysis has traditionally been used to represent otolith image. However, it is difficult to locate the contour's singularities from this spectrum. As an alternative, wavelet transform and curvature scale space representation allow to quantify the irregularities of the contour and to determine its precise position (Parisi-Baradad *et al.* 2005).

Finally one might ask why cuttlefish should be a model within cephalopods, for the specific field of morphometric studies. This question may be answered if shape is seen not only as a static property but also as the result of a dynamic process of growth. In fact, description of shapes says nothing on the related processes that have generated them. These processes have to be viewed as a complex association of genetic and environmental factors. One very recent conceptual development that may be explored using morphometric tools is to affirm (or to reaffirm) that the shape of an organism and

of its individual structures is a composite of many constituent parts: the so-called modules. Module partitioning and integration are genetically controlled (Raff & Sly 2000, Klingenberg *et al.* 2003). Their recognition can be based on partitions of configuration of landmarks. This emerging field of research is promising, because it opens the opportunity to understand shape in depth, and not only to mathematically characterise it. A consequence is that any scientific field that uses shape (e.g. taxonomy, phylogeny, biogeography) is potentially affected by these reinterpretations of morphology. For such studies, structures of organisms suspected to be arranged in modules are needed. Additionally specimens of different ontogenetic stages are needed in order to explore the variability at different taxonomic levels. Thus, cuttlebone is obviously the structure to be studied in this context. Existence of modules within the cuttlebone has already been pointed out by some authors, although they were not using this terminology, and did it in a qualitative way (Adam & Rees 1966, Roeleveld 1972, Lu 1998). Specimens are available from different species, at different ontogenetic stages, and possibly under different controlled conditions of growth if reared in the aquarium. Cuttlefish could therefore become a model even outside the study of cephalopods in this particular field of evolutionary biology.

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