Coleoid cephalopods through time (Warnke K., Keupp H., Boletzky S. v., eds)

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TRENDS IN THE EVOLUTION OF THE DECABRACHIA

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ABSTRACT

The Phylogenetic Systematics of the Decabrachia is given. Relevant synapomorphies are worked out in some detail. Emphasis is placed on the evolution of the shell.

The Oegopsida possess a strongly reduced phragmoconus which must be derived from a normal belemnite-like structure.

The monophylum Uniductia, with its sister groups Spirulida and Myopsida, is characterised by the synapomorphy "loss of the right oviduct" (Berthold & Engeser 1987).

The Spirulida are characterised by the following major synapomorphies: total reduction of the proostracum and endogastric incurvation or coiling of the narrow phragmoconus. The fossil genera *Belemnosis*, *Belemnosella*, *Spirulirostra* and *Amerirostra* form the stem-lineage of *Spirula*. *Groenlandibelus*, *Naefia* and *Adygeya* are provisionally assigned to the stem-lineage of the Spirulida.

The monophylum Myopsida has a secondary bowl-shaped and asymmetrical protoconcha unlike the sphaeroidal initial chamber of the Spirulida. Other synapomorphic characters are the densely arranged septa and the considerably enlarged funnel-shaped septal necks. Especially the myopsid eye is a synapomorhic character of high rank.

Within the monophylum Myopsida, the Sepiolidae are more closely related to the Sepiidae than to the Loliginidae. The latter show several conspicuous autapomorphies and many more symplesiomorphic features than do the Sepiidae.

The shell of the fossil *Vasseuria* indicates that this genus belongs to the stem-lineage of the Loliginida. *Belosepia* has its systematic position in the stem-lineage of the Sepiida. The enigmatic *Belosepiella* is here interpreted as a stem-lineage representative of the Sepiolidae.

A model of the development of the sepiid shell type is proposed.

Keywords: Mollusca, Cephalopoda, Coleoidea, Decabrachia, Phylogenetic Systematics

INTRODUCTION

As a complement to my results on the evolutionary history of the Decabrachia (Haas 1997) I provide here some comments based on new observations and publications. The principal cladistic relations (Fig. 1) within the Decabrachia were established by Berthold and Engeser (1987) and later modified by Engeser (1990) and myself (Haas 1989a, 1989b, 1997). Young, Vecchione and Donovan (1998) came in some instances to other conclusions than I, as far as fossil representatives are concerned. Here I sketch the evolution of the ten-armed coleoids which may provide a clue for the reconstruction of the shape and related behaviour of the fossil forms.

DESCRIPTIONS AND DISCUSSIONS

The origin of the **Neocoleoidea** (Decabrachia and Octobrachia) is rather dubious. We have to imagine their predecessors as animals similar to the aulacoceratids. The Palaeocoleoidea (Belemnites), to which the latter belong, have as synapomorphy, paired armhooks and a closing membrane of the initial chamber. The Neocoleoidea (Octobrachia and Decabrachia) are the adelphotaxon of the Palaeocoleoidea. They must have retained the caecum

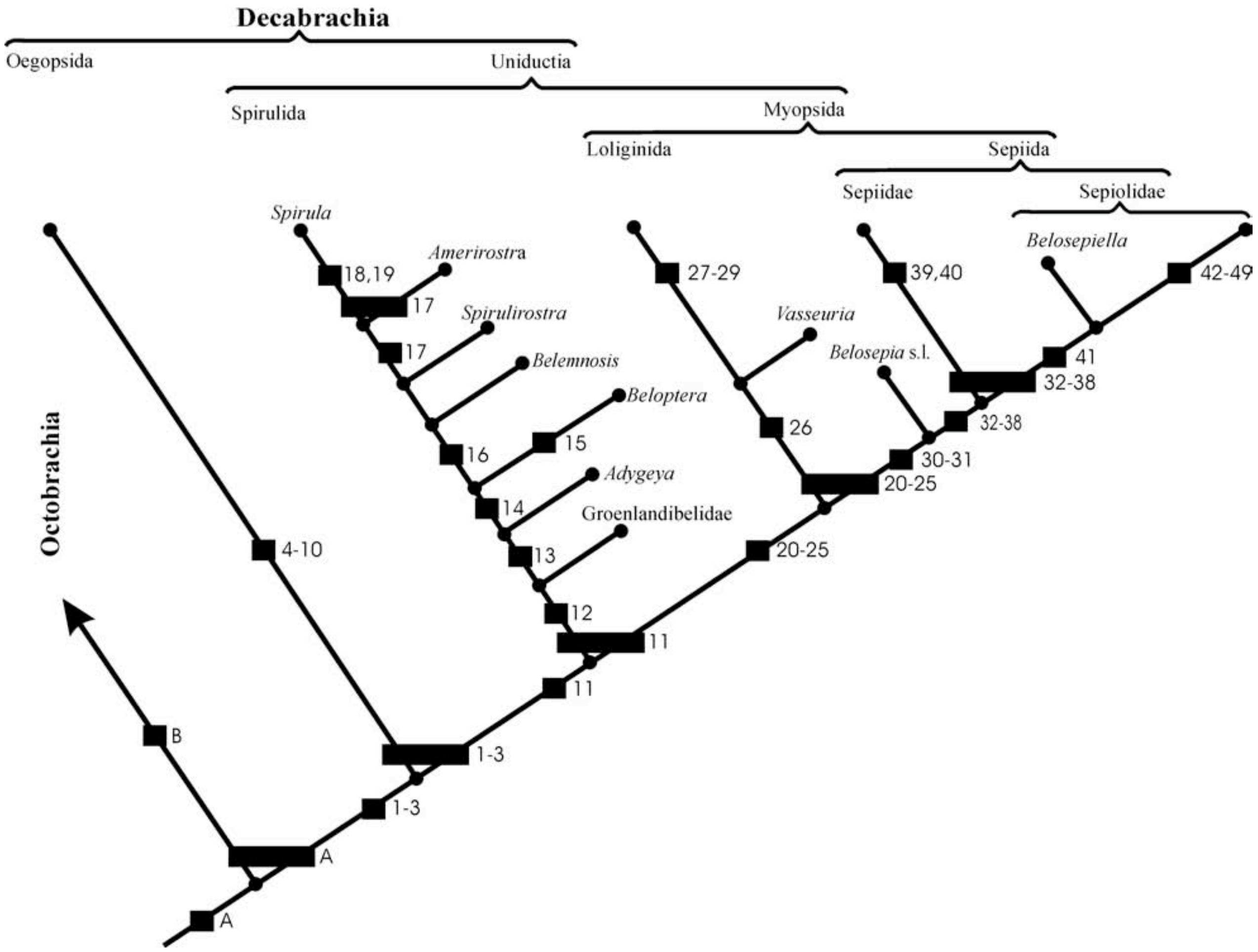

Fig. 1 Cladogram of the Neocoleoidea (after Haas 1997; altered). Explanation of the Apomorphies in Appendix 1

and an almost closed living chamber with only a rather flat proostracal arch as main plesiomorphic characters. Synapomorhies of the ancestor must include arms with primitive suckers and an ink sac. From this ancestor or stem-group-representative of the Neocoleoidea the Octobrachia have branched off rather early by opening the ventral wall of the living chamber and by considerably reducing the phragmoconus. Finally the Octobrachia have reduced their shell nearly completely. The evolutionary history of this has been described by Haas (2002). The reduction of an arm-pair was shown by J. Z. Young (1977) who suggested the second pair as lacking in the Octobrachia.

The stem-line-representatives of the **Decabrachia** evolved the suckers in their own way in producing the horn-ring-sucker (Haas 1989a) and the fourth arm-pair is converted into tentacles. Given the possession of these syanpomorphic characters all living Decabrachia are considered to be a monophylum. The early Decabrachia are considered to have had a ventrally almost completely closed living chamber because this stage of development is also present in the oldest representatives of their aldelphotaxon, the Octobrachia (see Bandel *et al.* 1983). At least the outline of the proostracum of the original Decabrachia must have been a rather low arch. Consequently the evolution of a proostracum, hence the reduction of the ventral side of the living chamber in favour of the muscular mantle in Belemnites, Octobrachia and Decabrachia must be convergent.

The systematic position of the **Oegopsida,** known only from recent faunas, is well established by their sister-group relation to the Uniductia and some autapomorphies. Nevertheless their symplesiomorphies prevail. The Oegopsida are extremely diversified and they provide a great deal of work for neontologists with little or no help from palaeontologists. As a result of the extreme reduction of the phragmoconus and the loss of calcareous secretion in the whole shell it is rather difficult to imagine the original morphology of the Oegopsida. Moreover, it will be rather difficult to identify early relatives of the Oegopsida as fossils because all the important group characters are based on soft parts. Thus only the stem-line-representative of the

Decabrachia, which can be reconstructed, is an animal somewhat similar in form and likely habit to *Groenlandibelus*, which in the author's opinion is a primordial spirulid. The calcareous theca of the primordial oegopsid possessed a compressed and straight phragmoconus and a broad proostracum. In addition, horn-ring suckers are a crucial character. The predecessor of the Oegopsida must have had at least a reduced calcareous phragmoconus. In further evolutionary steps the typical characters of the Oegopsida developed, such as the characteristic organic structure of the long proostracum and the short conus, which is the relict of the phragmoconus, and finally both form the gladius. In the conus (Fig. 2) the protoconcha is no longer demarcated. It can be shown that the axis of the conus follows that of the animal and is not curved (Toll 1982). Sometimes rudimentary septa can be identified in the form of organic pellicles. During larval development (Naef 1923, 1928) strong allometric growth of the dorsal wall of the gladius is observed whereas growth of the ventral wall is retarded. Because of this, the early-formed proostracum grows out to considerable length and in some taxa (i.a. *Illex*) displays rather complicated longitudinal strengthening ridges.

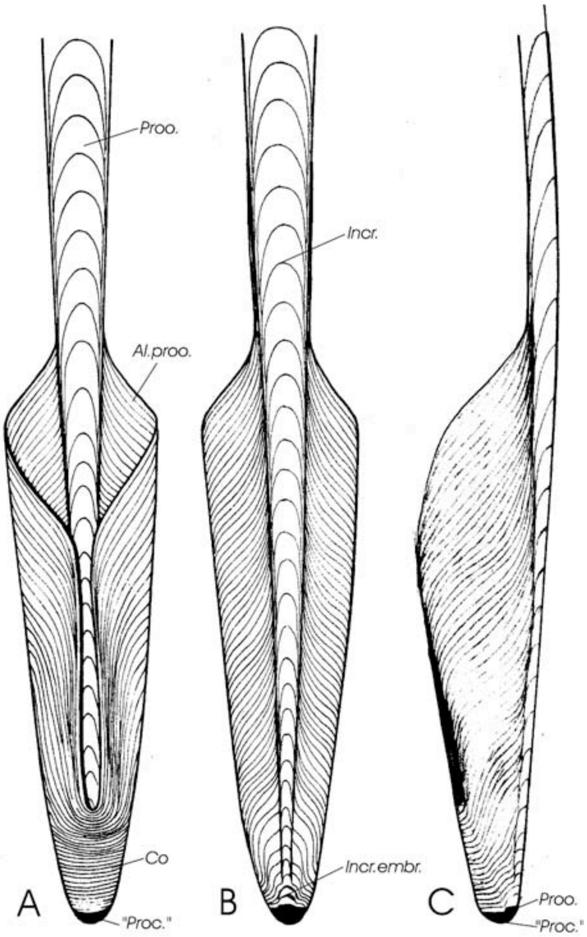

Fig. 2 Schematic diagram of the gladius of a young Oegopsid (*Gonatus*) to show the axis perpendicular to the degenerated protoconcha (*Proc.* marked in black) and the conus (*Co.*; symbols for the figure in Appendix 2). The growth increments of the embryonic part have been inserted from figures of Naef (1923/28). A rostrum-like organic tip of the shell has been omitted. The vanes of the proostracum form a secondary conus

We follow here the concept of **Uniductia** (Berthold & Engeser 1987, Haas 1997). This monophylum comprises the Spirulida, the Loliginida and the Sepiida. It is not unquestioned because there is only one single apomorphy, complete reduction of the right oviduct. In fossils this character is of no use. Furthermore it is not unambiguous. Thus in *Idiosepius*, which is in my opinion a simplified loliginid, has two oviducts but the right one is inactive (Nesis 1987). On the other hand, in the Pyroteuthinae, belonging to the Oegopsida, only the left oviduct is retained but this occurred after the Oegopsids had developed their typical autapomorphies. Another synapomorphy of the Uniductia, though not very sound either, can be seen in the tendency to curve the phragmoconus.

Among the living Cephalopods only **Spirula** has retained a spherical initial chamber. Unfortunately the ontogeny is virtually unknown. Thus all arguments on the evolution of the Coleoidea remain to a great deal hypothetical. It is almost certain that the Spirulida as well as all the other cephalopods with spherical initial chambers have inherited the spherical protoconcha from their precursors, leading as far back as to the Palaeozoic Sphaerorthoceratida. Thereafter a major change in ontogentic strategy occurred; supposedly there was a decrease in yolk content of the eggs. The shape and constriction of the protoconcha may have been caused by the contraction of the developing muscular mantle at this ontogenetic stage. In consequence the Oegopsida, which in cladisic terms are closest to the Spirulida, must be derived from ancestors with a spherical initial chamber which later, following an abbreviated ontogenesis, became reduced with the loss of the spherical shape of the protoconcha. In the course of the evolution towards the Spirulida s.s., the rudimentary spur-like proostracum seen in the Cretaceous *Groenlandibelus* and *Naefia* became

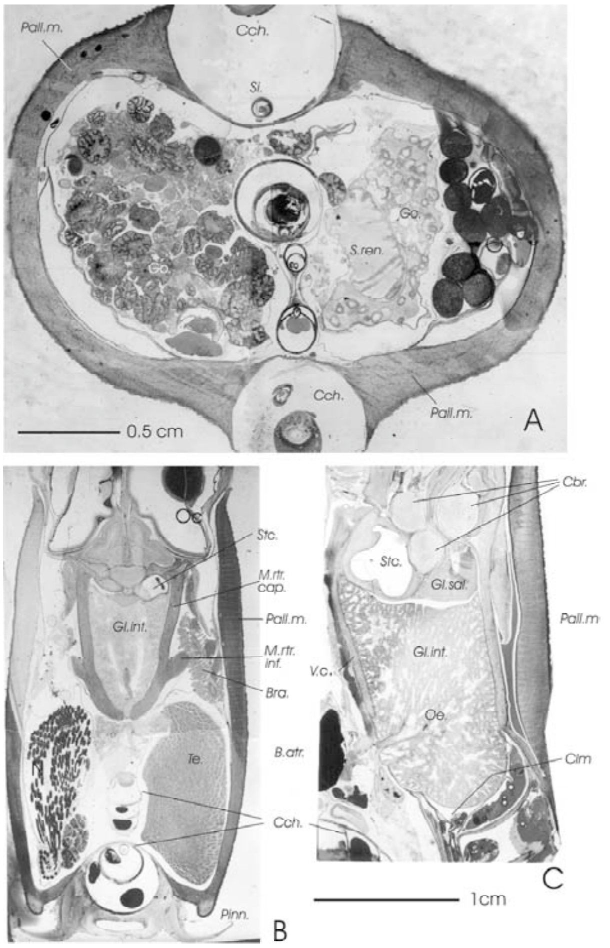

Fig. 3 *Spirula spirula* (L.). Semi-thin sections through shell and body to show the insertion of the muscular mantle at the concha and the saddle-like position of the viscera (especially of the sexual organs) in relation to the shell. Only the digestive gland remains within the terminal chamber. **A** Cross section. **B** Transverse Section. **C** Sagittal section

completely flattened out and only a short basal ring-like part of the living chamber, the cingulum camerae terminalis, remained. *Adygeya*, a spirulid from the Lower Cretaceous of the Caucasus described by Doguzhaeva (1996), shows that this event took place rather early. This fossil still possessed an only slightly cyrtocone shell but the terminal chamber already had a completely smooth edge like in *Spirula*. The numerous fossil forms have been split into too many genera. In Fig. 1 only some morhologically important forms are included. Their ranking is more or less typological. In Spirulida the edge of the last chamber as a site of insertion for the muscular mantle is no longer in use. It now only serves for the insertion of the retractor muscles. The muscular mantle has now been shifted far outside from the rim of the cingulum to a club- or bowl-shaped rostrum to which it is attached.

This development provides space for the viscera, especially for the gonad, which emigrated from the last chamber (Fig. 3). Only the posterior part of the digestive gland remains within the former living chamber. Along with this, an endogastric coiling of the longicone shell can be observed in the Spirulida. This can already be seen in the slight curvature of the apical part of the phragmoconus of primitive ancestors like *Groenlandibelus*, *Naefia and Adygeya*. Progressive stages of the above-mentioned descensus viscerum are demonstrated in our reconstructions of *Spirulirostra* (Fig. 4) and *Beloptera* (Fig. 5). Another example is *Amerirostra*. Here the theca has a higher degree of coiling than in *Spirulirostra* and there is an almost isolated dorsal plate originating from the epiconcha which is connected only by a narrow bridge with the epiconchal envelope of the theca (Jeletzky 1969). It must be assumed that the muscular mantle inserted at the edges of that dorsal plate.

In most of the Tertiary forms a heavy rostrum possibly served as a counterbalance for the phragmoconus to keep the animal in a more or less horizontal position. The shape of these creatures must have been rather plump. They can be imagined as highly manoeuvrable short distance swimmers living near the sea floor. In *Spirula* the rostrum is given up and only a thin epiconcha covering the spiral is left. With reduction of the heavy rostrum, *Spirula* changed from a benthic to a bathypelagic life style. In this context appear some of its autapomorphies: loss of the radula, terminal light organ and small circular fins positioned at the apical end of the body.

In summary, the longicone, almost tube-like shell follows the formula of an endogastrically coiled logarithmic spiral with loose whorls. The more primitive representatives show only curving of the apical part whereas growth of the proximal portion of the shell is tangential to that of the spiral. In later evolutionary steps the spiral portion increasingly took possession of the tangential part. In contrast to all other Decabrachia the Spirulida have altered their plan of construction in giving up the terminal chamber as a living chamber. There is only room for part of the digestive gland.

Together with the myopsid eye, the asymmetrical bowl-shaped initial chamber (median curvature of this bowl posteriorly stronger than anteriorly and therefore

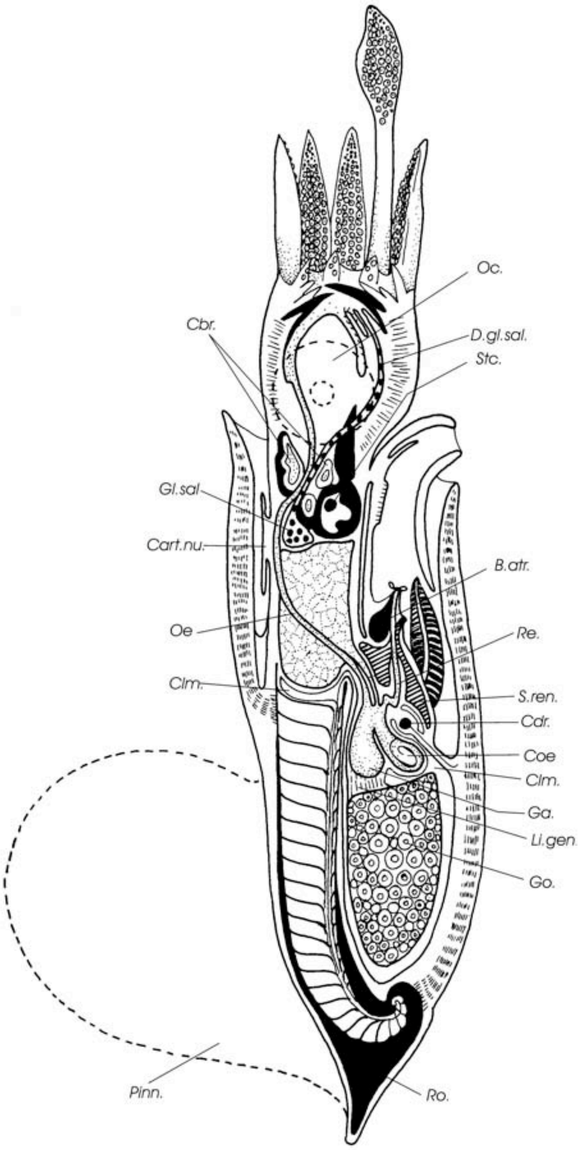

Fig. 4 *Spirulirostra*. Reconstruction, sagittal section. The descensus viscerum has already taken place. The muscular mantle inserts ventrally at the epiconcha and at the outer wall of the terminal chamber. Its sides are fixed at the wings of the rostrum (out of diagram). A salivary gland which is atrophied in *Spirula* is thought to be still present. Reconstruction of large fins which are located posteriorly. The plump animal is manoeuvrable for short distances and may have had an horizontal orientation in life

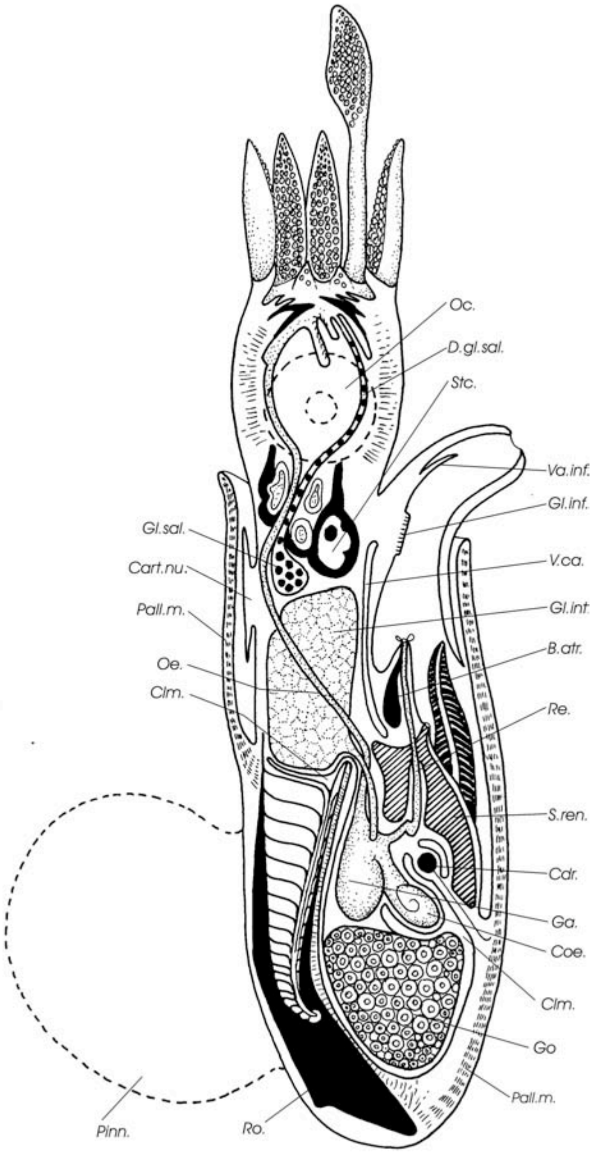

Fig. 5 *Beloptera*. Reconstruction, sagittal section. Descensus viscerum has taken place. Bulk of viscera embedded in the spoon-shaped rostrum. The muscular mantle inserts at the edges of the latter. The animal is thought to have been a vigorous short distance swimmer, which, as *Spirulirostra*, needed a salivary gland to kill prey of bigger size.

"asymmetrical") represent the most important synapomorphic characters of the **Myopsida**. The development of such an asymmetrical protoconcha may be associated with a change in the ontogenetic strategy and the considerable increase of the egg yolk and function of the inner yolk sac. Thus, the embryo remained for longer time within the egg. The asymmetry of the protoconcha is not yet fully understood. Cephalopod taxa with a small amount of yolk seem to form spherical initial chambers. Without question the Myopsida can be derived from the taxa with spherical protoconchae. Consequently their ontogeny is clearly secondary. On the other hand it is interesting that there are, as Boletzky (1988, 1989) remarked, many myopsid eggs poor in yolk, not much larger than oegopsid eggs but with the typical myopsid ontogenesis. Perhaps he is right in regarding the phylogenetic change in the phylogeny of the Myopsida

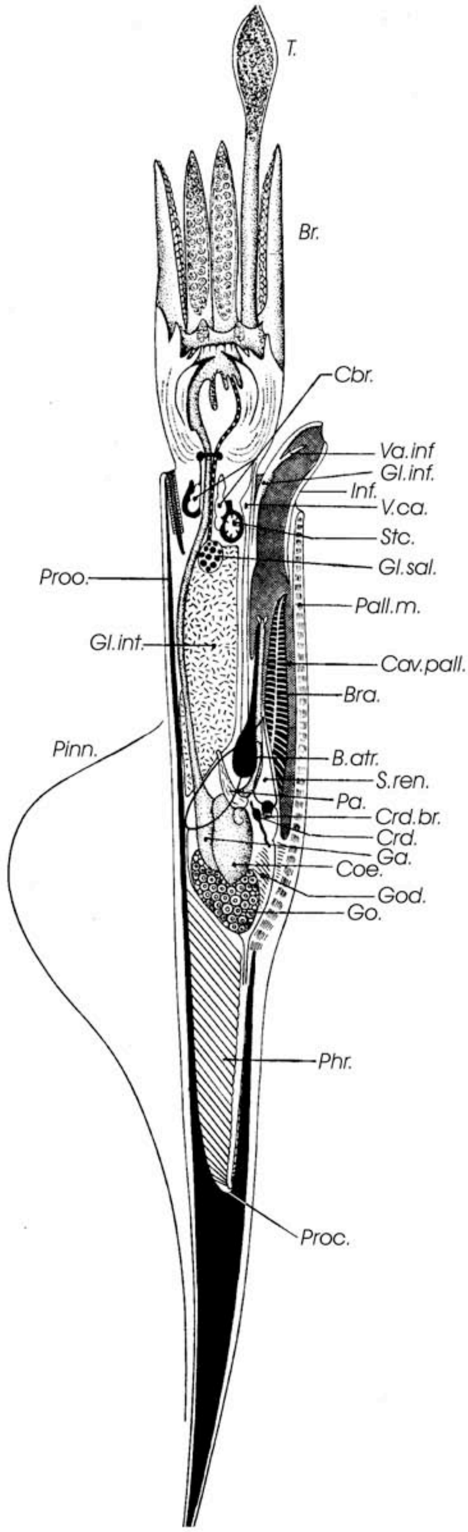

Fig. 6 *Vasseuria*. Reconstruction, sagittal section (after Haas 1997). The animal is shown with strong reminiscence to the loliginids. It retains many symplesiomorphic characters together with primitive sepiids. The very long proostracum of *Vasseuria* is taken into account in the reconstruction proposed here. The fins are inspired by those of *Alloteuthis*. Note the inclination of the septa and the resulting gain of space for the viscera and the muscular mantle. The latter inserts at the border of the theca as in loliginids and sepiids

as a change of the time table within the program of special ontogenetic steps. Such a genetic alteration in genetics could well have affected shell growth. In my view, the ontogeny of the Myopsida may reflect an abbreviated development of the initial shell. Thus, *Vasseuria*, which I regard a primitive representative of the Myopsida, shows that the sutural line of the first septum is already cut by the growth lines of the protoconcha in which a short proostracum is already developed. This means that only the first organic, so called primordial shell in *Sepia* embryos (Bandel & Boletzky 1979) would be the equivalent to the spherical protoconcha of *Spirula* or the Belemnoidea. The portion of the protoconcha distal to that primordial shell then is an equivalent of the conotheca. If all this obtains, it becomes intelligible that also in some forms with secondarily smaller eggs the program of the typical Myopsida shell formation cannot be cancelled.

As shown below, ***Vasseuria*** from the Eocene is an early representative of the Loliginida which shows many symplesiomorhies and thus is close to the stem-line of the Myopsida. The morphology of the shell (Haas 1997) can be reconstructed by thecal growth lines whose outlines are already considerably eccentric in the protoconcha, and this condition increases anteriorly forming an extremely long proostracum. The dorsal outline grows faster than the ventral one. Thus on the posterior end of the theca the dorsal side is markedly vaulted. Anteriorly, this arc becomes straighter as the theca grows. In terms of the vaulting of the posterior end the septa here are increasingly tilted to reach a constant position along the straight part of the theca. This has the effect of providing a larger surface of the muscular mantle and some more space for the viscera, especially the gonad (Fig. 6). In *Vasseuria* the phylogenetic novelty entails firstly the early ontogenetic part of the shell, whereas the later part follows the original plan. The rostrum, the siphuncular apparatus, the septa and the proostracum are general symplesiomorphic characters of the Decabrachia or even of the Coleoidea. This may also be true for the soft body that can be reconstructed like that of modern Loliginida of which *Vasseuria* is a stem-line-representative.

The **Loliginida** can be derived from a *Vasseuria*-like ancestor by further extending the already very long proostracum of the latter and reducing the

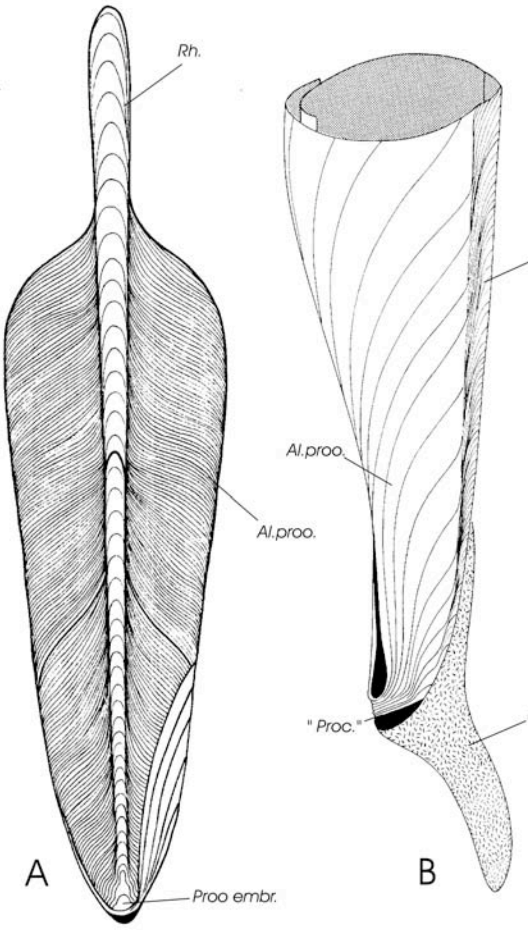

Fig. 7 Idealised gladii of loliginids. **A** *Loligo*. Asymmetric apical part forming an oblique conus. Growth increments of the embryonic shell *"proo.embr."* have been taken from SPIESS (1971). The wings of the gladius are interpreted here as parts of the proostracum and not of the conus. **B** *Alloteuthis subulata* (Lamarck). Apical part of the gladius with an organic spur (*"Ro."*) is the rudiment of the rostrum. The supposed secondary bowl-shaped and asymmetric protoconcha (*"Proc"*) is marked in black. The wings of the proostracum form a pseudoconus

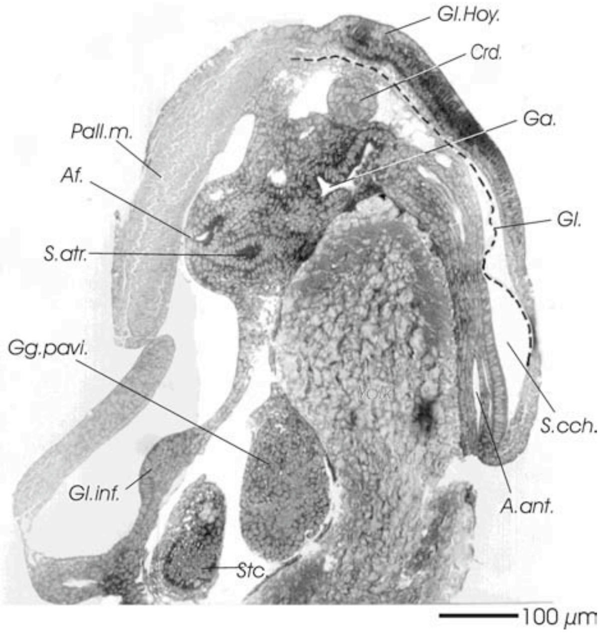

Fig. 8 *Loligo vulgaris* (Lamarck). Sagittal section through embryo in Naef´s stage XIII to show shell sac and gladius (dashed line) with an oblique curvature. Note that the posterior portion of the gladius and the shell sac correspond to the former protoconcha

phragmoconus so that only an organic gladius remains (Fig. 7A). In some taxa, e.g. *Alloteuthis*, though as in all loliginids the septarium is totally degenerated and the concha completely non-calcified, the apical portions still show the rudiment of a rostrum. The course of the growth lines (Spiess 1971) may be a reminiscence of calcareous loliginid forerunners (Fig. 7 B). The asymmetrically vaulted initial shell pellicle in loliginid embryos is similar to that of *Sepia* (Fig. 8). The transformation into an organic gladius results in a change of the constructional plan. The negative buoyancy must be compensated by a vigorous muscular mantle and large fins. The animals have developed into likely long distance swimmers.

The **Sepiida** together with their stem-line-representatives, the belosepiids, partly followed another path of evolution in which the muscular mantle is considerably dilated so that the visceral sac becomes very blunt. It is also supposed here that this started with a *Vasseuria*-like predecessor but with a shorter proostracum. In the course of the evolution of the Sepiida appeared a strong allometric growth of the visceral sac together with the theca. The latter together with the eccentric growth of shell and the extension of the visceral sac had caused, as already in the early stages of *Vasseuria*, an eccentric vaulting of the protoconcha which continues into the direction of the head. A proostracum proper cannot be observed in living sepiids. This may be the result of the strong widening and related geometrical flattening of the anterior arch of the mantle edge.

Some methods have been developed to model coiled invertebrate shells (Okamoto 1996, Raup 1966, Savazzi 1989). One is proposed by Okamoto (1996), a framework of different growth vectors being moved around a coiling-axis on the path of a logarithmic (equiangular) spiral. Normally the generating curve of such a shell model is a circle or ellipse with increasing diameters. A similar method as Okamoro´s "growing-

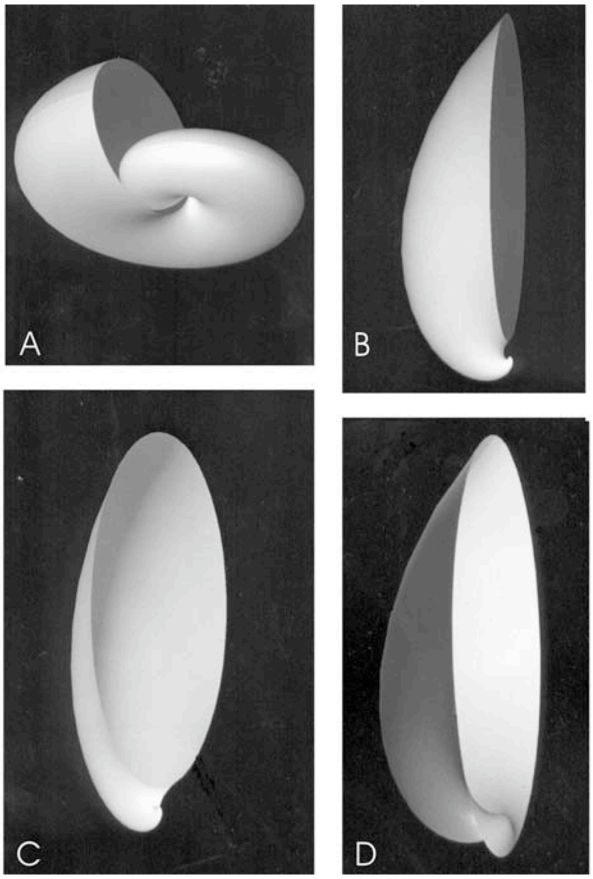

Fig. 9 Computer generated models of some planispirally coiled shells (produced by Dr. B. Siehl by means of the Program GRAPE of the University of Bonn). The ventral and dorsal outlines follow the formula of the logarithmic spiral. **A** Coiling with generating curves not growing eccentrically. This means that cross sections through the whorls are circular or elliptical. In this figure the ventral outline of a whorl is in contact with the dorsal outline of the preceding one. **B**, **C** Beginning of eccentric growth of the generating curve. Different views of the same model. The shell is not much different from the brachiopod or "bivalved" type proposed by Raup (1966). **D** Model with strongly eccentric generating curve. The aperture is turned over and a labrum appears. This model is a first approximation to the sepiid-like form

tube-model" has been employed here by Dr. B. Siehl who most kindly has produced the computer simulation for Fig. 9 using the program GRAPE (Graphics Programming Environment of the Institute for Applied Mathematics of the University of Bonn). Fig. 9 A is an ammonoid-like planispirally coiled tube with contacting whorls. In this case the generating curve is a circle or an ellipse. In Fig. 9 B, C the generating curve grows eccentrically stronger in anterior (dorsal) than in posterior (ventral) direction and thus results in an oval. In this figure the difference to Raup´s (1966) "bivalved " shell type, which can be found in brachiopods and which has isometric vectors of its generating curve, is not very significant. In Fig. 9 D the model shows considerable eccentric growth and narrow coiling and is similar to sepiid thecae. The shape of the labrum is simulated in first approximation as a consequence of an overturned aperture. In nature the further growth of the apical part of the shell, including the labrum, changes irregularly. The model allows for taking also the initial chamber into consideration. It is clear that the spiral growth of the shell does not begin at zero but in a certain initial growth stage of the protoconcha forming a cap before ending up in the originally spherical shape. In reality this cap equals the organic primordial shell described by Bandel & Boletzky (1979) in *Sepia officinalis*. From the circular outline of the aperture the progressively eccentric growth of the generating curve, described above, begins. We cannot discuss here all the biological implications of the eccentric growth model (they will follow in a special publication). The principal effect of that mode is to bring the phragmoconus as an hydrostatic apparatus onto the dorsal side of the animal, to gain more space for the viscera and to expand the muscular mantle. It can be easily imagined that the greater the eccentricity of the dorsal and the ventral outlines which form logarithmic spirals too, the flatter the cuttlebone becomes. Extremely eccentric spirally coiled shapes may be referred to as superspirals

With these considerations about the models of the coleoid shells in mind, we may return to *Vasseuria*, where the expression of spiral shell development with radial inclination of the septa can only be observed in the apical portion of the theca. In the anterior straight part the septa run parallel to each other and have the inclination of the last septum of the curved section. We can thus consider *Vasseuria* as the initial stage of coiling of the myopsid shell. Similar to the situation in the Spirulida this new character is established only in earlier ontogenetic stages, and during evolution it progresses more and more on the straight portion. It can be imagined that intermediary forms between *Vasseuria* and *Sepia* s.l. could be generated by our model but they have not yet been found in coleoids.

According to our model of an exponentially growing radius of a logarithmic spiral, the evolutionary trend of shell development in the sepiids s.l. extends from highly vaulted thecae to extremely eccentric and rather flat ones. This can be observed in *Belosepia* s.l.

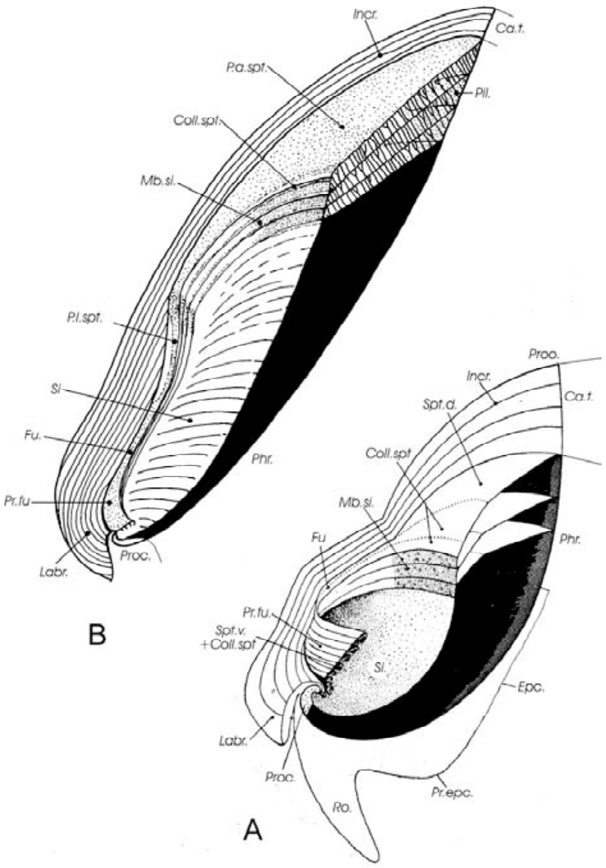

Fig. 10 Diagrams of apical parts of sepiid conchae to show insertion of the septa into the conotheca. **A** *Belosepia* (after Haas 1997). Curvature in comparison to *Sepia* rather high. A short and broad proostracum still present. Sipho rather wide but well demarcated. No pillar- or wall-structures to support the septa necessary. Furca and furcal process clearly preserve individual lateral and posterior parts of the septa. Furcal process rather high forming a transversal wall. **B** *Sepia*. Cuttlebone extremely extended forward. Septa strongly inclined, thus distance between each other small so that pillar- and wall-structures are necessary for stabilisation. Within furca and furcal process lateral and posterior septa lack individuality. Epiconcha omitted

(Paleocene - Eocene) (*Ceratisepia vanknippenbergi* Hewitt & Jagt 1999 from the Upper Cretaceous is probably *Conoteuthis* which belongs to the belemnoids according to Jeletzky 1966) via *Sepia* s.l. (Upper Eocene - Recent) to the extant sepiolids. ***Belosepia*** s.l. with its still highly curved theca has also a distinctly vaulted protoconcha (Fig. 10). Meyer (1989, 1993) indicates a spherical initial chamber in his schematic sections of *Ceratisepia elongata*, *Belosepia* and *Belocurta* but this is incorrect, hence also his inferred derivation of Sepiida from Spirulida. The cross section of the siphuncle in belosepiids is elliptical with the longest axis in median orientation. The septa are less inclined than they are in *Sepia* s.l. so that their posterior parts are well separated, even in the long processus furcae. Because of the posterior position of the most vaulted portion of the shell and the fact that the centre of buoyancy is at the rear of the animal, a heavy rostrum and an epiconchal process for balance are necessaray.

In the **Sepiida** the theca is considerably flatter than in *Belosepia*. This means that the radii of the logarithmic superspiral grow by far faster than with the latter. The biological advantage of this is to move the centre of buoyancy to the mid-point of the animal and thus to enable greater manoeuvrability on short distance. The extremely extended dorsal wall of the phragmoconus causes the septa to be strongly inclined and very closely spaced. To keep the thin septa apart, calcareous supporting pillars and wall structures are formed within the chambers. Similar supporting structures appear between the septal necks in *Belosepia* and this feature is known from many other coleoids. The strong eccentric growth of the theca has the result that in *Sepia* the proostracum, which in *Belosepia* still has a very short and broad outline, is totally smooth. The widening of the concha and the development of a broad labrum provides a large space for the viscera in both *Sepia* s.l. and *Belosepia* s.l. (Fig. 11, 12). In *Belosepia* s.l. and even more so in *Sepia* s.l., the posterior part of the phragmoconus cannot longer grow regularly. The insertion of the septa into the posterior end of the phragmoconus does not provide much space for their lateral and posterior parts. They are so closely stacked that they cannot be clearly distinguished. In certain parts of the concha, calcification ceases and only organic pellicles are secreted. The mode of insertion of the septarium into the theca is demonstrated in Fig. 13 for *Belosepia* s.l. and *Sepia* s.l. The lateral parts of the septa converge and constitute the furca. The posterior parts together with short rudiments of the internal shell layer form the furcal process. Especially in *Belosepia* s.l. but also in some species of *Sepia*, the latter can form a high wall, which has to keep the extremely wide siphuncle open. It is stressed here that the furcal process is not the conus as proposed by Naef (1922, 1923, 1928). The true conus is the labrum. Consequently the derivation of the Sepiida from some spirulid ancestor similar to *Spirulirostrina*

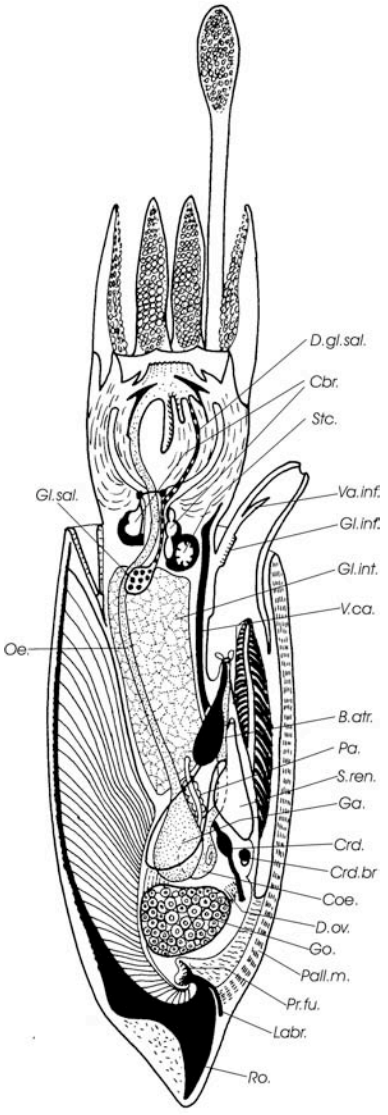

Fig. 11 *Belosepia*. Reconstruction, sagittal section

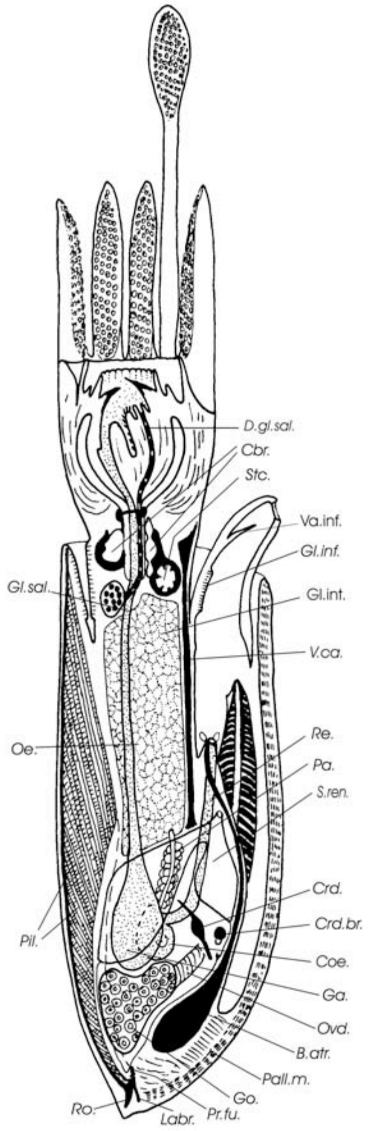

Fig. 12 *Sepia*. Sagittal section

is not correct. The labrum is the ventral (posterior) portion of the concha of *Belosepia* s.l. (Fig. 10, 13 A) and *Sepia* s.l. (Fig. 13 B, 14). It consists of the central shell layer which is a thick organic sheet equivalent to the periostracum, and perhaps also of some organic pellicles representing the internal layer. The epiconcha is secreted on the outside of the periostracum by the secondary epithelium of the shell sac. Unlike in *Belosepia* s.l. where the elements of the shell are rather clear, the apical part of the *Sepia* shell is rather obscured. The furca is an independent structure, but in some species the processus furcae has a rather chaotic growth. Thus only vestiges of septa are present, calcification is irregular, and at some sites only organic material is secreted. Sometimes coarse calcareous layers are produced. Some species do not calcify their labrum and instead produce only crumpled organic membranes. Fig. 14 shows some of these features which may have some importance below.

In the **Sepiolidae** the eccentric growth of the logarithmic spiral is so extreme that the dorsal side of the shell becomes almost straight. Calcification becomes totally reduced and instead of a shell the gladius consists only of organic pellicles. The gladius may degenerate as an organic rod or it is completely lost. The original form of the sepiolid gladius can best be studied in *Rossia* where it superficially resembles that of the loliginids (Fig. 15). It can be described as an extremely elongated cuttlebone of *Sepia*. The initial chamber in *Rossia* can only be reconstructed using the shape of the embryonic shell sac. This lacks all form of an organic pellicle. It is important to know that the extremely slender gladius is equivalent to a *Sepia*-like cuttlebone and not to the type of proostracum seen in

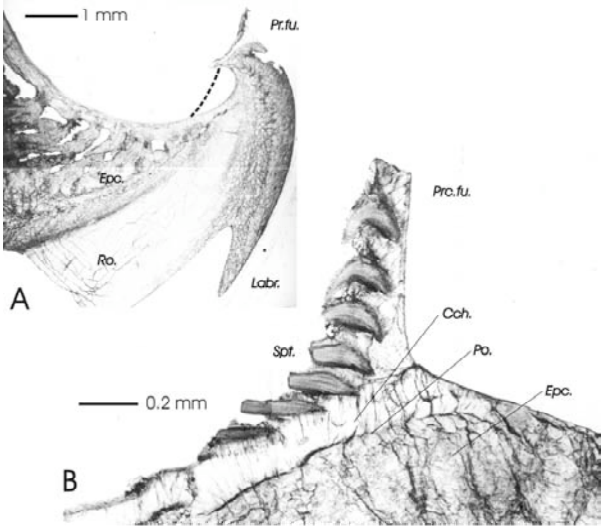

Fig. 13 *Belosepia blainvillei* (Deshayes). Lutetian, Bois Gouet, Loire Atlantique, France. Sagittal (**A**) and parasagittal (**B**) sections of the apical part of the cuttlebone to show posterior parts of septa and dorsal outline of the protoconcha (to the right of dashed line, caecum and prosipho unknown)

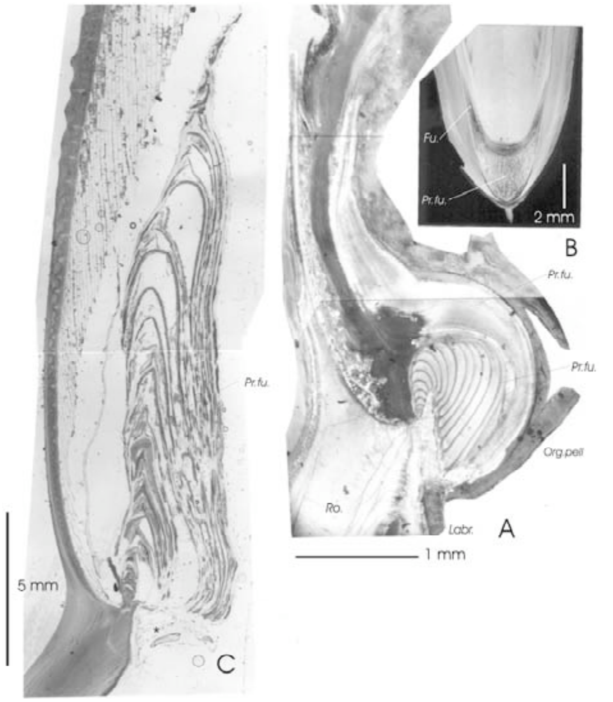

Fig. 14 Apical portions of cuttlebones of two species of *Sepia* with extreme development of the furcal process. **A** *Sepia officinalis* (L.). Large senescent specimen. Sagittal section. **B**, **C** *Sepia pharaonis* (Ehrenberg). Long furcal process, Labium degenerated, consisting of traces of crumbled organic pellicles (asterisk).

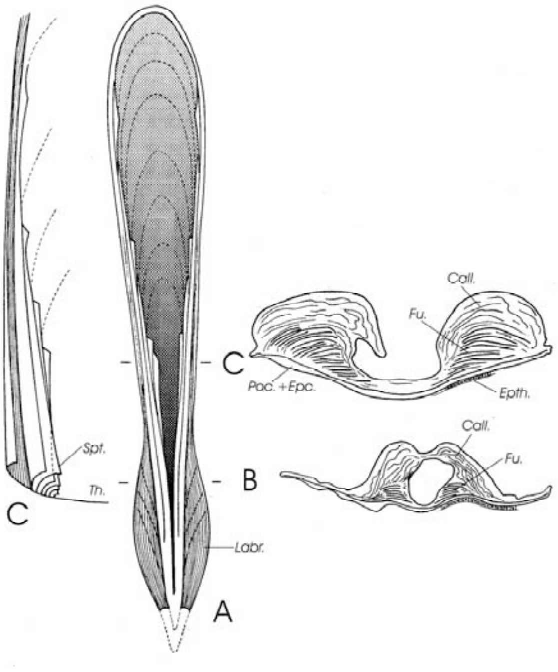

Fig 15 *Rossia*. Gladius. **A** Ventral view Gladius (length ca. 4 cm) is imagined as an uncalcified extremely eccentric shell of *Sepia* with remnant of the Labrum. **B**, **C** Cross sections. **D** Scheme of the anterior portion of the gladius with organic theca and densely packed septa almost parallel to the theca

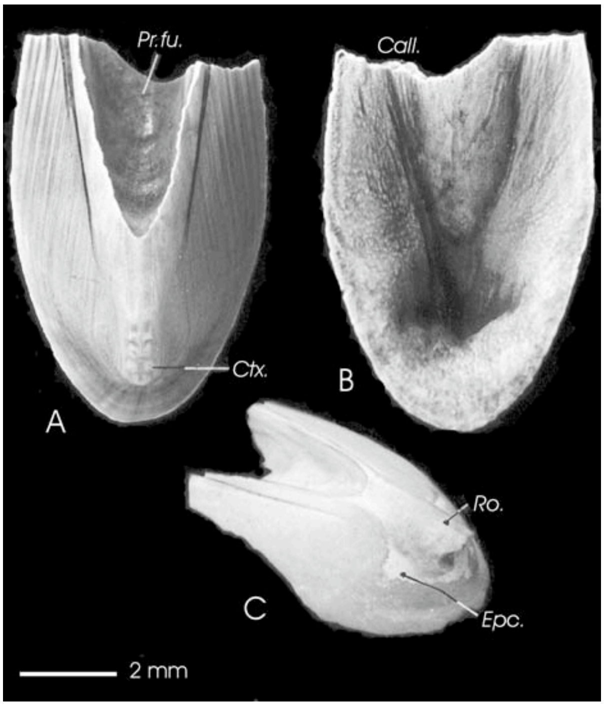

Fig. 16 *Belosepiella parisiensis* Alessandri. Lutetian, Paris Basin (after Haas 1997). Apical parts of shells. **A** Dorsal view showing a cicatrix, the epiconcha is not preserved. One part of the dorsal shell is broken in so that the inner surface of the furcal process is visible. Note the longitudinal slits explained in Fig.17. **B** Same specimen as in A. Ventral view showing callus covering the furcal process and the spoon-like cavity of the labrum. **C** Other specimen in oblique dorsal view. The basis of the rostrum is preserved. Only a small portion of the epiconcha is calcified

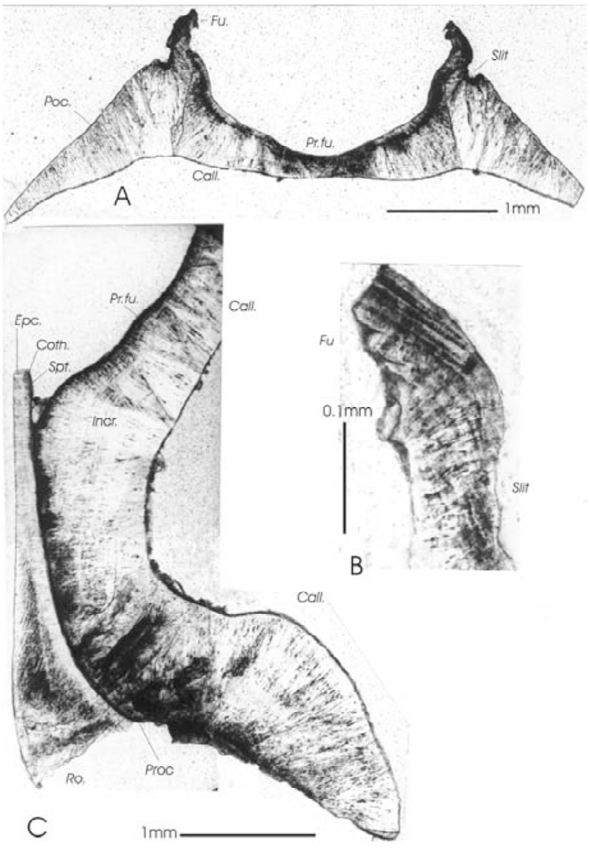

Fig. 17 *Belosepiella parisiensis* Alessandri. Lutetian, Paris Basin. Thin sections through the apical part of the concha.
A Cross section. Dorsal part of shell is broken in. The dorso-lateral outline equals the periostracum with perhaps epiconchal organic pellicles. Cross sections of the longitudinal slits (slit) in Fig. 16 A, C may represent the sites where the uncalcified components of the theca were located. Dorsal hook-like structures represent parts of calcified septarium. Ventral side consists proximally of the processus furcae and the callus. **B** Cross section of dorsal hook-like structure with growth increments indicating lateral parts of the septa. **C** Sagittal section through the specimen figured in Fig. 16 C. (see also Fig. 18) to show the rostrum, the epiconcha and the theca. The protoconcha and adjacent chamber are totally calcified

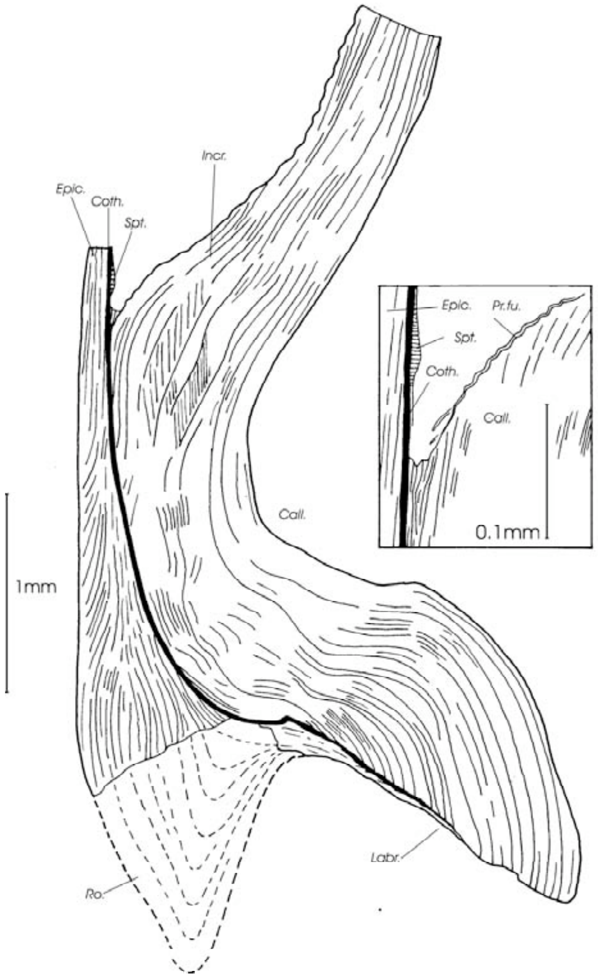

Fig. 18 *Belosepiella parisiensis* Alessandri. Diagram of longitudinal section of Fig. 17 C. See there for explanation. Insert shows a magnification of the upper-left part of the Figure

Oegopsida and Loliginida. This can be demonstrated by the broad nuchal cartilage and in the great transversal distance between the stellar ganglia, which normally are situated close to the lateral borders of the shell (Naef 1922, 1923, 1928). The same is true for the fin pocket in connection with narrowing of the gladius (Boletzky & Boletzky 1973, Boletzky 1982). The fins themselves are reduced *Sepia*-fins. *Rossia* lacks buoyancy control and is a bottom dweller.

Study of the shell of ***Belosepiella*** (Fig. 16) and especially of the growth lines in thin sections (Figs 17, 18), enables the reconstruction of an Eocene ancestor of the Sepiolidae. The preserved parts show that the original concha is calcareous only in certain areas. The narrowing of the cuttlebone is obvious and the covering of the theca by the epiconcha is already strongly reduced. The septa were composed mainly of organic substance and are therefore only visible as delicate traces at the dorsal side of the theca. They are tilted so that the are nearly parallel to the dorsal wall of the conotheca. Though the apex of the cuttlebone is present and even calcified the first septa cannot be differentiated against the calcareous cameral deposits. The calcified secretion in the first chamber, which in *Sepia* produces supporting pillars and walls, fills all free spaces in *Belosepiella*. The theca with the protoconcha, which can be traced by the course of the well preserved periostracum, is very flat. The labrum is narrow and reduced and seems to be filled with some sort of a calcareous callus, which indicates the continuation of growth of a rather obscured processus furcae. A similar situation is described from some apical shell portions of *Sepia* (Fig. 14 A). Reconstructions of the shell and the animal are given in Fig. 19. As in *Rossia*, the cuttlebone of *Belosepiella* is incorporated as a rudiment in a rather wide muscular mantle. The labrum was no longer necessary to protect the visceral sac.

CONCLUSIONS

Detailed study of fossils is important to understand the evolutionary problems of the Decabrachia. A morphological approach reveals important evolutionary steps which form the basis for systematics. Gaps have been filled but there remains much to do, invoking both the imagination and some fantasy shown herein. An alternative approach to the phylogeny of the living Decabrachia has been made by Young and Vecchione (1996) and based on numerical systematics. Both methods reveal that great uncertainty still exists when trying to solve the ramifications surrounding the Oegopsida, Spirulida and Sepiida. Perhaps further DNA-analyses will help to solve their relationship

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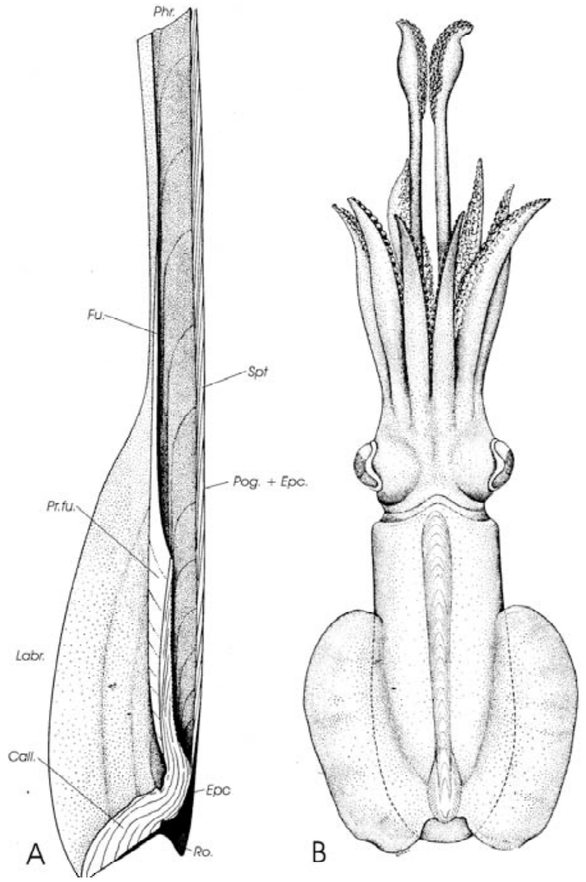

Fig. 19 *Belosepiella*. Reconstructions. **A** Apical part of the concha, half section. **B** Dorsal view of the animal (after Haas 1997). Above the concha the muscular mantle is thought to be translucent. The reconstruction is based on an animal similar to *Rossia*. This is not necessarily true in respect to the head which could have looked like that of *Sepia*. The concha is inserted into the muscular mantle like the gladius of *Rossia*. As in the latter it had only stabilisation functions for the mantle. The fins have been delineated as somewhat intermediate between *Sepia* and *Rossia*. The life style of *Belosepiella* must have been like in *Rossia* as an animal living near the see-bottom

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APPENDIX 1

LIST OF APOMORPHIES LISTED IN TEXT-FIG. 1

Neocoleoidea

A. Suckers.

Octobrachia

B. Various apomorhies of the Octobrachia, i. a. second pair of arms reduced. Fleshy Suckers.

Decabrachia

1. Suckers with horny rings.
2. Tentacles (4th arm-pair).
3. Renal sacs fused.

Oegopsida

4. Retardation of arm-pair 3 and 5 during ontogenesis.
5. Small exterior yolk-sac.
6. Loss of accessory nidamental glands.
7. Loss of calcification of the shell.
8. Dorsal position of the rectum in relation to the bifurcation of the Vena cava.
9. Arteria pallealis posterior runs far backward.
10. Arteria genitalis does not branch off directly from the heart but from the Arteria posterior.

Uniductia

11. Right gonoduct atrophied. Tendency of endogastric curving of the shell.

Spirulida

12. Rudimentation of proostracum.
13. Complete loss of proostracum
14. Endogastric involution of the phragmoconus.
15. Formation of wings on the rostrum of *Beloptera*.
16. Shifting of the palleal mantle exteriorly.
17. Loss of the rostrum.
18. Loss of the radula.
19. Terminal light organ.

Myopsida

20. Protoconcha secondarily bowl-shaped and asymmetrical.
21. Accessory nidamental glands fused.
22. Oblique position of the septa.
23. Myopsid eye.
24. Eggs with large yolk volume.
25. Fin-pockets.

Loliginida

26. Extremely long proostracum.
27. Loss of shell calcification.
28. Giant nerve I fused in the chiasma.
29. Elongated spiral coecum.

Sepiida

30. Widening and smoothing out of the proostracum.
31. Extreme spiral curving of the dorsal shell.
32. Loss of the Commissura interstellaris.
33. Olfactory pits in a groove.
34. Loss of radula platelets.
35. Tentacle pockets can stow tentacles completely.
36. Secondary eye lid.
37. Buccal funnel without suckers.

38. Distance between septa narrow; calcareous intercameral supporting-structures; degeneration of the furcal complex.

Sepiidae

39. Brain more compact than in Sepiolidae (Ganglium brachialis and Ganglium pedalis close to each other).
40. Inc sac lateral from Rectum.

Sepiolidae

41. Extremely flattened shell.
42. Palleal septum.
43. Loss of protective membrane of the arms.
44. Suckers spherical.
45. Reduction or complete loss of the shell.
46. Statocyst simplified.
47. Sinus mesentericus.
48. Pharetra or insemination in the funnel pocket.
49. Other apomorphies of the Sepiolidae.

APPENDIX 2

LIST OF ABBREVIATIONS USED IN TEXT-FIGURES.

A.ce. Kopfarterie, cerebral Artery, Arteria cerebralis.
Al.epc. Flügel der Epiconcha, epiconchal wing, Ala epiconchae.
Al.proo. Flügel des Proostracums, proostracal wing, Ala proostraci.
Al.co. Conusflügel, conus wing, Ala coni.
B.atr. Tintenbeutel, inc sac, Bursa atramentaria.
Br. sessiler Arm, sessile arm, Brachium sessile.
Bra. Kieme, gill, Branchium.
Ca.t. Endkammer, last chamber, Camera terminalis.
Cae. Cäcum, caecum, Caecum.
Call. Kallus, callus. Callus.
Cart.nu. Nackenknorpel, nuchal cartilage, Cartilago nuchealis.
Cart.pinn. Flossenknorpel, cartilage of the fin, Cartilago pinnae.
Cav.pall. Mantelhöhle, mantle cavity, Cavitas pallii.
Cbr. Gehirn, brain, Cerebrum.
Cch. Concha, concha, Concha.
Clm. Cölom, coelom, Coelom.
Co. Conus, conus, Conus.
Coe. Magenbblindsack, spiral coecum, Coecum.
Coll.spt. Siphonaldüte, septal neck, Collis septi.
Conn. Bindegewebe, connective tissue, Connectivum.
Coth. Conothek, conotheca, Conotheca.
Crd. Herz, heart, Cardia.
Crd.branch Kiemenherz, branchial heart, Cardia branchialis.
Ctx. Cicatrix, cicatrix, Cicatrix.
D.atr. Tintenbeutel, inc sac, Ductus atriculamentarius.
Epc. Epiconcha, epiconcha, Epiconcha.
Ept. Epithel, epithelum, Epithelium.
Fu. Gabel, forc, Furca.
Ga. Magen, stomach, Gaster.
Gg.cer. Cerebralgabglion, cerebral ganglion, Ganglium cerebrale.
Gg.palvi. Palleovisceral-Ganglion, palleovisceral ganglion, Ganglium palleo-viscerale.
Gl.inf. Trichterdrüse, infundibular gland, Glandula infundibuli.

Gl.int. Mitteldarmdrüse, midgutgland, Glandula intestinalis.
Gl.ni. Nidamentaldrüse, nidamental gland, Glandula nidamentalis.
Gl.sal. Giftdrüse, salivary gland, Glandula salivaria.
Gla. Gladius, gladius, Gladius.
Go. Gonade, gonad, Gonata.
God. Gonoduct, gonoduct, Gonoductus.
Incr. Wachstumslinie, growth increment, Incrementum.
Inf. Trichter, funnel, Infundibulum.
Labr. Labrum, labrum, Labrum.
M.rtr.cap. Kopfretraktor, retractor muscle of the head, Musculus retractor capitis.
M.rtr.inf. Trichterretraktor, retractor muscle of the infundibulum, Musculus retractor infundibuli.
Mb.si. Siphonalmembran, siphonal membrane, Membrana siphonalis.
N. Needham´sche Tasche, Needham´s pocket, Bursa Needhami.
Oe. Ösophagus, esophagus, Oesophagus.
Org.pell. organische Häutchen, organic pellicles, Pelliculae.
Ov. Ovarium, ovary, Ovarium.
Ovd. Oviduct, oviduct, Oviductus.
Pa. Pankreas, pancreas, Pancreas.
Pall.m. Muskelmantel, musclular mantle, Pallium musculosum.
Phr. Phragmoconus, phragmoconus, Phragmoconus.
Pil, Pfeilerchen, pillar, Pilum.
Pinn. Flosse, fin, Pinna.
Poc. Periostracum, periostracum, Periostracum.
Proc. Protoconcha, protoconch, Protoconcha
Proo. Proostracum, proostracum, Proostracum.
Re. Enddarm, rectum, Rectum.
Rh. Rhacis, rhachis, Rhachis.
Ro. Rostrum, rostrum.
S.ren. Nierensack, renal sac, Saccus renalis.
Si. Sipho, siphuncle, Sipho.
Spt. Septum, septum, septum.
Spt.pall. Mantelseptum, mantle septum, Septum pallii.
Stc. Statocyste, statocyst, Statocystis.
T. Tentakel, tentacle, Tentaculum.
Te. Testes, testes, Testes.
Th. Schalenwand, shell-wall, Theca.
V.ca. Vena cava, vena cava, Vena cava.
Va.inf. Trichterklappe, infundibular valve, Valva infundibuli.