Features of Development and Functional Morphology required in the Reconstruction of Early Coleoid Cephalopods

(Grundzüge der Entwicklung und Funktionsmorphologie in ihrer Bedeutung für die Rekonstruktion früher Coleoiden)

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With 11 Text Figures

Bandel, K. & Boletzky, S. v. (1988): Features of Development and Functional Morphology required in the Reconstruction of Early Coleoid Cephalopods. [Grundzüge der Entwicklung und Funktionsmorphologie in ihrer Bedeutung für die Rekonstruktion früher Coleoiden.]. *In:* Wiedmann, J. & Kullmann, J. (Eds.), Cephalopods - Present and Past, pp. 229-246. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart.

Abstract: The authors review data allowing the reconstruction of fossil coleoids, starting with the earliest known representatives from black shales of the Lower Devonian that have been studied using radiographic methods. Fossil evidence of ontogenetic changes in the shells is presented, and correlations between shell shape and the extent of the mantle musculature are discussed. Particular attention is paid to shell architecture and its possible relation to the location of muscular fins. Finally, the mantle complex is scrutinized from the viewpoint of its adaptation to particular conditions required at hatching.

In contrast to the mantle complex, little can be derived from fossils in terms of arm and tentacle development. The final section merely emphasizes the basic positional relationships between the components of the arm crown, and the necessity to take them into consideration in the phylogenetic systematics of coleoids, especially with regard to vampyromorphic and octopodan relationships.

Kurzfassung: Eine Zusammenstellung der Daten wird vorgelegt, die eine Rekonstruktion der fossilen Coleoiden ermöglichen, ausgehend von den frühesten bekannten Vertretern aus Schwarzschiefern des Unteren Devon, die mit röntgenographischen Methoden untersucht wurden. Ontogenetische Veränderungen können an den fossilen Gehäusen belegt werden und eine Korrelation zwischen Gehäuseform und der Ausdehnung der Mantelmuskulatur wird diskutiert. Besondere Aufmerksamkeit gilt der Gehäuse-Architektur und ihrer möglichen Beziehung zum Flossen-Ansatz. Schließlich wird geprüft, welche Anpassungen der Mantelkomplex an die speziellen Erfordernisse des Schlüpfens besessen haben muß.

Im Gegensatz zum Mantelkomplex kann das fossile Material wenig zur Frage der Arm- und Tentakel-Entwicklung beitragen. So kann im abschließenden Kapitel lediglich auf die Notwendigkeit aufmerksam gemacht werden, die Lagebeziehungen zwischen den Komponenten der Armkrone als Grundlage einer phylogenetischen Systematik der Coleoiden zu berücksichtigen. Dabei ist besonders an die Beziehungen von Vampyromorphen und Octopoden gedacht.

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1. Introduction

The origin of the coleoid cephalopods is obscure. Several recent authors have presented hypotheses attempting to explain the basic change from an animal with an external shell (ectocochlean) to the apparently more advanced construction in which the shell is entirely enclosed in a well defined part of the mantle (endocochlean). Thus Jeletzky (1966) took up the earlier suggestions of Schindewolf (1933) and Erben (1964), who imagined a progressive covering of a basically ectocochlean shell by skin folds of the mantle edge. This should have happened along a bactritid line (in the Carboniferous), essentially by increasing the acceleration of adult mantle flap differentiation, leading finally to their appearance in the embryonic phase. It is interesting that Naef (1922, 1928) never presented such an intermediate state in any of his reconstructions of post-embryonic stages. He thought that the essential process of shell covering must have been completed in the egg (Naef 1928, fig. 30). Careful analysis of the development of Recent cephalopods, combined with the detailed knowledge he had of fossil material, allowed Naef (1923, fig. 23) to propose a very coherent model of the evolution of coleoid (endocochlean) organization from a hypothetical "Protodibranchus" with ten subequal arms. However, no fossils were available that could have provided any sort of positive evidence. Recent findings from Lower Devonian fossils recovered in the Hunsrück Shale in the southeastern Rheinisches Schiefergebirge (near Gmünden, F.R.G.) can now be interpreted in detail, thanks to radiography (Bandel et al. 1983). Two fairly distinct types of shell were encountered that clearly differ from any fossil so far described from the Devonian. They show striking similarities not only with the shell of more recent forms with a rostrum (which are known from the Carboniferous to the end of the Cretaceous) but also with the shell of others without a rostrum (which are known from the Upper Carboniferous to the Recent). The latter type corresponds to what Naef (1923) derived from his hypothetical "Protodibranchus". The question of what type of fossil cephalopod shell can be considered internal has always focussed attention on the presence or absence of a rostrum, because this shell component can only be explained by secretion on the outside of the primitive shell. Does the absence of a rostrum-like structure mean that no tissue covered the shell?

2. Fossil evidence of ontogenetic changes in shells from the Hunsrück Shale

In order to approach the question asked at the end of our introduction, we must first summarize the results of Bandel, Reitner & Stürmer (1983).

2.1 Protoaulacoceras

This form must have hatched with a shell 3 mm in total length, with only the initial chamber closed, which has an elongate ovoid shape and measures 0.3-0.4 mm in diameter and 0.8-1.3 mm in length. The living chamber is almost cylindrical, with an apical angle of only 2-3°. Post-embryonic growth closely resembles conditions

known in ordinary Orthoceratids in that the phragmocone becomes longer in relation to the living chamber. Only after completion of about 40 chambers does formation of a purely organic guard become distinct.

2.2 Boletzkya

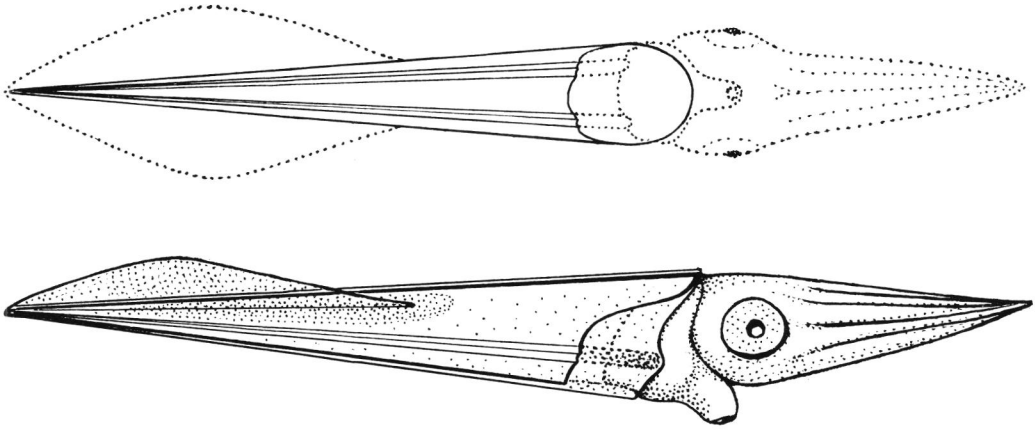
The young animal must have hatched with a shell ca 3 mm in total length, with a globular initial chamber measuring 0.5-0.9 mm in diameter, and possibly one more chamber closed off. The living chamber is clearly conical, with an apical angle of 6 °. During post-embryonic development, the general form of the shell is maintained until it reaches a length of 8-10 mm. At that time, the phragmocone with its 6-10 chambers occupies about one half of the shell length; the aperture of the living chamber is circular. Then a rapid change takes place in that the living chamber becomes oval in cross section (higher than wide), additional septa are more narrowly spaced, and the dorsal part of the living chamber grows slightly faster than the ventral part, while one dorsal and a pair of lateral keels are formed. During further growth, the living chamber progressively increases in length relative to the phragmocone. The maximum length of the shell observed is 16.5 cm, with an apertural width of 17 mm. The phragmocone then measures only about one tenth of the total length of the shell.

2.3 Naefiteuthis

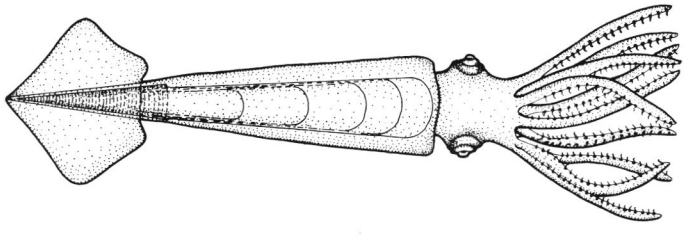
The hatchling has a shell very similar to newly-hatched *Boletzkya* but it is more conical in shape (apical angle 10-15 °). With a total shell length of ca 3 mm, the living chamber occupies nearly 2 mm; the phragmocone consists of one globular initial chamber and at least one more chamber. At a shell length of 4 mm, formation of a dorsal keel started; soon, lateral keels also appeared. The maximum number of chambers observed is 6 to 7. In contrast to *Boletzkya*, the dorsal shield of the living chamber becomes greatly enlarged and forms an actual proostracum, as demonstrated by very recent findings. In other words, the ventral wall of the living chamber lags behind the dorsal wall from later juvenile stages onwards.

The adult shell can now be reconstructed from 22 specimens kindly provided for study by Prof. W. Stürmer (Erlangen). These fossils measure between 2 and 13 cm in length and have the original shell or parts of it flattened into one plane of preservation that appears on both slabs of the slate when opened along the embedding plane. During diagenesis, the specimens were compressed and contorted, and they changed totally in their composition. Our reconstruction takes advantage of previous work on other coleoids (Bandel et al. 1983), orthoconic Lamellorthoceratids (Bandel & Stanley, in press), and ammonites (pers. observations of K. B.). Furthermore, better known coleoids from the Upper Jurassic (Solnhofen lithographic limestone) were viewed for comparison. They revealed a similar, though less destructive, diagenetic past.

The shells of *Naefiteuthis*, with or without adherent soft parts, generally settled on the bottom sediment after death in an oblique orientation, dorsal side down and anterior end first. This is very similar to the situation observed in *Plesioteuthis* (Bandel & Leich 1986), a slender squid from the Solnhofen Limestone. In *Naefi-*

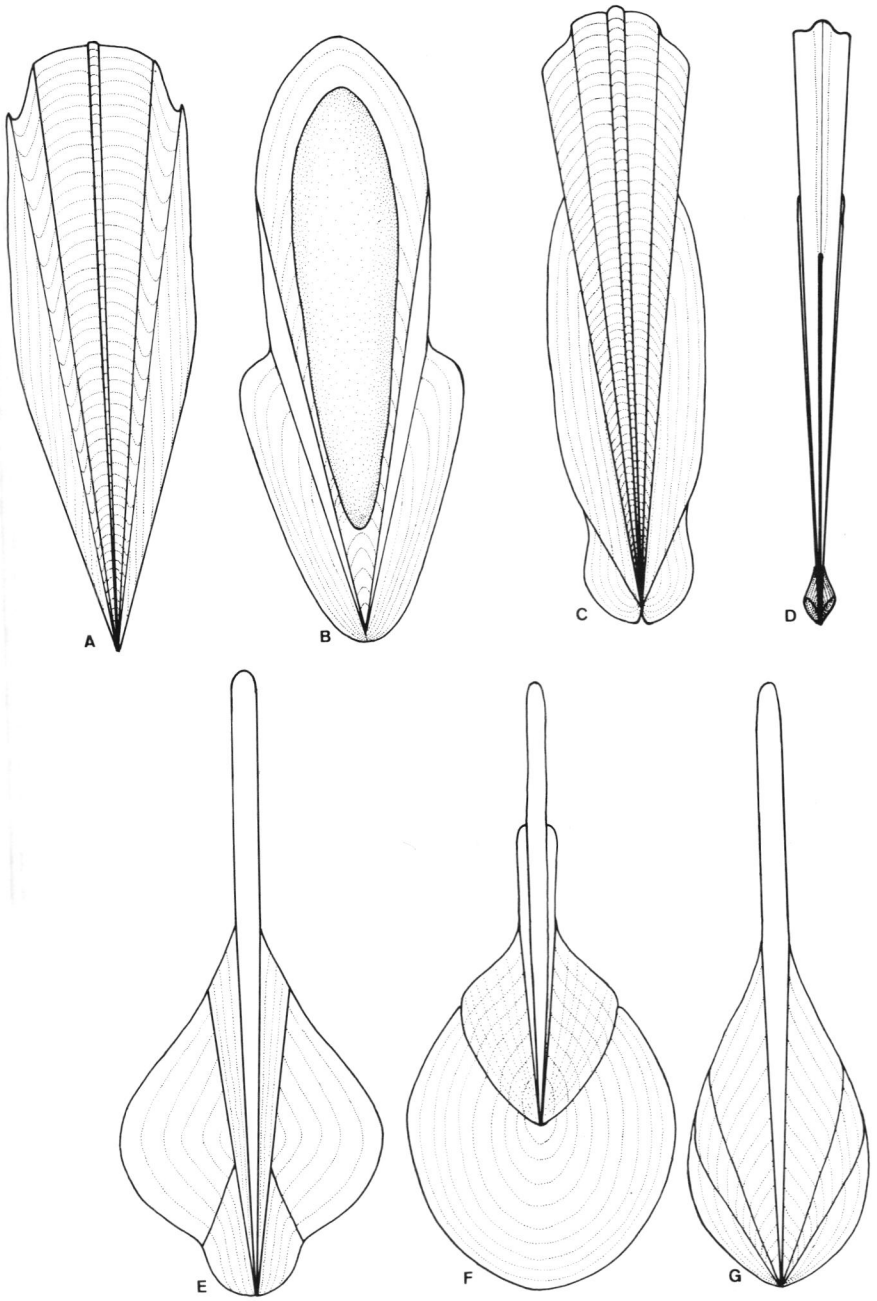


Text Fig. 1. Reconstruction of the shell of *Naefiteuthis,* with a conceivable soft body surrounding it, in ventral view (stippled outline) and in lateral view. The length and form of the fins in this reconstruction is based on the absence of strong anchoring structures on the shell, the ventro-lateral keels lying apparently below the plane of a functionally convincing fin position (see text).



Text Fig. 2. Reconstruction of *Acanthoteuthis* from Solnhofen, in dorsal view.

teuthis this landing position does not necessarily indicate that the shell was more buoyant in the short chambered phragmocone, although this may indeed have been the case (*Plesioteuthis* shells had no phragmocone and yet landed in the same manner). The dead animal was rapidly covered with fine mud rich in lime, which soon filled most of the inner portions of the shell, the aragonitic components of which were progressively dissolved. Again, conditions can be compared to those observed in the sediments of Solnhofen where aragonitic shells were totally demineralized while calcite remained intact, and where even soft parts were fossilized. In the mud of the Hunsrück environment, total demineralization was preceded by formation of pyrite which filled the deep, partly tubular furrows of the lateral keels of the shell of *Naefiteuthis.* Pyrite also filled chambered portions in other chambered cephalopods found in this sediment as well as the spaces between calcitic lamellae in the chambers of the orthoceratid *Arthrophyllum* (Bandel & Stanley, in



Text Fig. 3. Gladii of "vampyromorphic" squids from the Jurassic. A: *Loligosepia aalensis* from Holzmaden (F.R.G.), B: *Trachyteuthis hastiformis* (65 cm) with calcareous cover on the dorsal shield, from Solnhofen, C: *Leptoteuthis gigas* (65 cm) from Solnhofen, D: *Plesioteuthis* sp. (22 cm) from Solnhofen, E: *Celaenoteuthis* sp. (7.6 cm) from Solnhofen, F: *Celaenoteuthis scutellaris* (6 cm) from Solnhofen, G: *Palaeololigo oblonga* (13.4 cm), from Solnhofen. Note that there are various forms of central and lateral fields and more or less distinct "conus fields". A clear homology between separating folds and thickened ridges or keels is not recognizable.

press). The sediment subsequently became compacted and shrank, due partly to the dissolution of calcareous particles, to about one tenth of its original volume. During this process, the demineralized shell was flattened, and its structure and composition changed. The largely organic lateral keels thus became the most solid shell parts, while the calcified actual shell wall (probably mostly nacre) was transformed into an elastic sheet of organic shell remnants, which was stretched and twisted laterally due to the flow of the compacting sediment. In this process, one or both of the lateral keels were torn apart at their anterior end. Pyritic filling of the keels seen in X-ray photographs of such fossils thus show a characteristic Y shape. The proostracum (outer lip) was embedded a few mm deeper than the remaining part of the shell and is therefore generally found in a deeper slab of the slate. Growth lines are preserved only in the thick lateral keels (similar lines appearing on the shell between the keels are artefacts due to the slate structure).

Adult animals had a shell up to 20 cm in length, according to our reconstruction (Text Fig. 1). It was slender in shape and had an apical angle of about 11°. The outer lip formed a proostracum of about 3 cm in width and of at least 4 cm in length in adults. In one of the fossils, a proostracum is preserved with fragments of the mantle attached to the shell both from above and below. Reconstruction is particularly facilitated by knowledge gained from well-preserved coleoids of the Solnhofen limestone, such as *Acanthoteuthis* (Text Fig. 2).

In this form, one finds a step-like discontinuity in the preservation of the proostracum at the connection with the tubular shell, showing up as two "unconnected" fossils lying in different embedding planes. The fossilized tissue can also be seen above and below the demineralized proostracum. Viewing belemnites from the Posidonia shales, one again finds much better preservation of mainly organic shell components. The margins of the outer lip are preserved and show dense growth lines, whereas the normally aragonitic proostracum has partly or totally disappeared.

In *Naefiteuthis,* the shape of the keels changes with growth. While in small individuals the median keel is dominant, it disappears with increasing size of the shell, and the lateral keels become dominant. A very similar process appears in *Plesioteuthis* of the Upper Jurassic (Text Fig. 3). Conceivable functions of these lateral keels could be either the anchoring of the fins (cf. section 4) or the insertion of a specialized structure of the muscular mantle. However, a function related to fin positioning would require a lateral or dorso-lateral position of the keels. The reconstruction presented in Text Fig. 1 is based on the assumption that the lateral keels are *ventro*-lateral, so that they may have provided a template and insertion site of, e.g., cartilaginous bands similar to the ventral funnel-locking device (which is now independent of the shell margin) in Recent decapods. This hypothesis is discussed in the following section.

3. Correlations between shell shape and the extent of mantle musculature

Adult *Naefiteuthis* clearly present a situation close to some Recent coleoids, especially when one considers the proostracum. The surface not occupied laterally and ventrally by a shell wall can only represent the existence, in the living animal, of a muscular sheet forming the contractile mantle typical of coleoids. The entire complex of shell and mantle musculature must have been surrounded by a continuous integument. Remnants of the latter have in fact been found in one specimen.

The functional counterpart of the muscular mantle in coleoids is the funnel apparatus (represented by the hyponome of *Nautilus*). The funnel comprises two parts of different morphogenetic origin : the funnel tube is formed from a pair of folds representing part of the molluscan foot, whereas the funnel pouch (or "collar") develops from a distinct rudiment (a nuchal fold of the visceral complex) which is secondarily joined in the statocyst area by the funnel tube folds. The final step of funnel development in coleoid embryos is the differentiation of funnel retractors from the collar rudiment, and the fusion of the edges of the paired funnel tube folds (Naef 1928).

Originally, this muscular funnel apparatus was the only locomotory organ (as can still be seen in *Nautilus*). Water entering the mantle cavity through the peripheral slits between the collar and the mantle edge (mainly laterally) is ejected through the funnel tube by muscular retraction of the entire funnel complex. This ejection is made possible by the automatic closure of the inlets when the collar is driven against the inner mantle surface by water pressure. The funnel returns to its original position partly by passive shape recovery when the muscles relax and partly by the contraction of anteriorly situated funnel adductors inserted at the lower side of the head. In a slow sequence, this water exchange is the typical respiratory movement, which is repeated regularly. More vigorous water ejection always has a locomotory effect. The efficiency of the funnel apparatus for active locomotion depends on the stability of the funnel, especially of the tube which directs the water jet. For rapid swimming, a cylindrical tube (with the edge of the primitive hyponome permanently fused) is necessary.

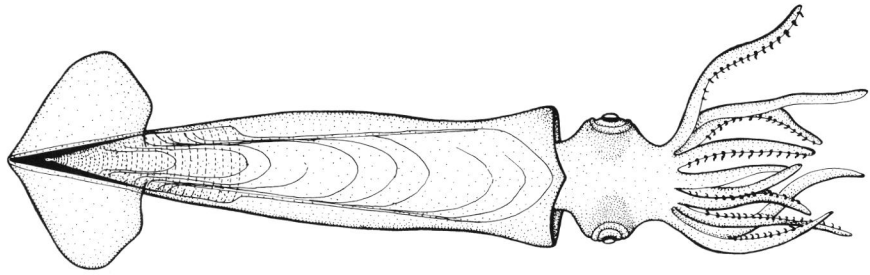
In Recent coleoids, and especially in the Decapoda, close contact of the funnel pouch with the inner mantle surface is achieved at two ventro-lateral points. This mode of local adhesion, which in some species becomes a permanent attachment, prevents the funnel pouch from being driven beyond the mantle edge under high water pressure (which would reduce the locomotory effect).

Given this correlation between funnel and mantle structures, it is conceivable that muscular concentration at the mantle edge was originally related to the tightening function. Once established, this muscular band progressively expanded ventrolaterally at the expense of the shell wall, and finally took on an additional function as a contractile element of its own; at the end of this adaptive process, "decoupling" of stiffening devices (related to the funnel) from the shell margin may have occurred (cf. section 2). The first stage of this process may be seen in the shell of *Boletzkya*. In a more advanced stage, the situation would correspond to the shell form of *Naefiteuthis* (Text Fig. 1). Indeed the hypothetical "Protodibranchus" of

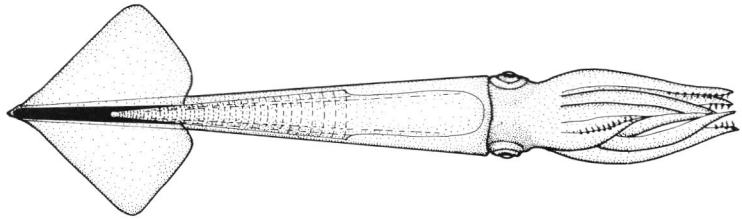
Naef (1923) represents a mixture of both *Boletzkya* (relatively large phragmocone) and *Naefiteuthis* (well developed muscular mantle).

4. Shell architecture and the location of muscular fins

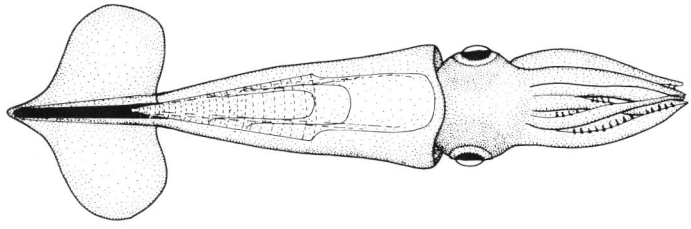
So far, we have considered the mantle-funnel "pump". A typical feature of all coleoids is the presence of muscular fins situated on both sides of the posterior mantle surface (in incirrate octopods, they are only recognizable as early rudiments and disappear entirely after organogenesis). What are possible traces of fins on fossil cephalopod shells?



Text Fig. 4. Reconstruction of *Brachybelus* from Dogger Alpha 3 of Niedermerseberg (Franconia, F.R.G.), from a shell 18 cm in length.



Text Fig. 5. Reconstruction of *Belemnites paxillosus,* a typical belemnite from the Lias δ of Unterstürmig with a shell ca. 50 cm in length (total length of the animal ca. 70 cm).

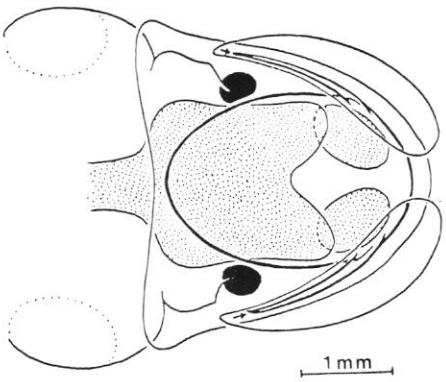


Text Fig. 6. *Cylindroteuthis puzosi* reconstructed from the illustration of Mantell (1850). The shell from the Oxford Clay (Upper Jurassic) measured ca. 22 cm in length.

There are clear indications in the development of Recent coleoids that the primitive position of the fins is terminal or sub-terminal (Naef 1928). We will return to this essentially embryological aspect in the following section.

Secondarily, fins may become greatly elongated. An extreme form exists in the living *Sepia*, where they form an "undulatory margin" of the mantle (Text Fig. 7) or in fossil *Trachyteuthis* (Naef 1922, Bandel & Leich 1986). Fins are always anchored, either directly on the shell sac, or (*via* articulating pouches derived from it) to the mantle surface (Naef 1923, Boletzky 1982a). The base of the fin musculature is stiffened by a cartilaginous plate. We suppose that guards and guard-like structures, no matter whether they are purely organic or mineralized, reflect a particularly intimate junction between cartilaginous fin bases and the shell sac surface. Conversely, the absence of guard-like structures suggests not the absence of fins, but rather a less massive development of the fin cartilage attached to the shell sac or a detachment of the fin cartilage from the actual shell sac by formation of articulating pouches.

The application of these ideas to what we know of *Protoaulacoceras* suggests that fins of this form were attached to a relatively long flattened ridge lying on either side of the phragmocone. In the typical belemnites, the fin insertion was behind the phragmocone, and it probably formed a closed cartilaginous tube around the guard, with ridges resting in the longitudinal guard depressions, possibly reducing shear stress. If this picture is realistic, the presence of a rather large phragmocone can be interpreted as a buoyancy element *maintained* to counteract the considerable weight of the guard, rather than as a passive counterweight *developed* in response to the tilting effect of a terminal phragmocone. The wide variety of guard shapes manifest in belemnite evolution may then be explained by differences in life style and swimming performance (Text Figs. 4, 5, 6). We consider that a massive terminal guard reflects the presence in the living animal of powerful terminal fins similar to recent

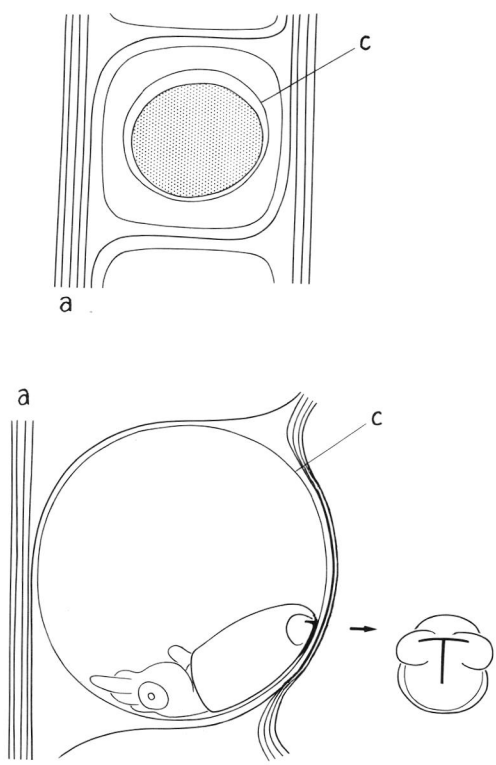


Text Fig. 7. The mantle complex of an embryo of *Sepia officinalis* at stage XVII of Naef (1928), reconstructed from cross sections, showing the inner yolk sac (stippled), the collar between the rear part of the head and the stellate ganglia (black), the shell sac (oval outline) with the articulating pouches (small arrows), and the long fins.

Ommastrephids. It thus appears that the presence of such guards in different groups, like some aulacoceratids, belemnites, and some phragmoteuthids, can be explained by evolutionary convergence.

5. The mantle complex and its role in hatching

So far, we have not approached the question of the *origin* of fins and of the associated mantle cover of the shell. An essential feature of the embryonic mantle that has already been described by Naef (1928) is the position of Hoyle's organ. It appears as an integumental differentiation of the mantle surface in a position corresponding exactly to the "scar" of the shell sac closure. Naef (1928) did not yet know its function as a hatching gland, which was demonstrated by Wintrebert



Text Fig. 8. A schematic representation of one egg (stippled) of a loliginid squid, embedded in oviducal jelly surrounding the chorion (c). Only a small part of the spirally coiled oviducal jelly is represented, with the central axis (a) of the common capsule. At the end of embryonic development (lower part of figure), the chorion is greatly enlarged; the hatchling can move freely in the perivitellin fluid, but normally remains quiescent, lying on its back, with the hatching gland close to the chorion. At the lower right arrow a caudal view of the anchor-shaped hatching gland and the fins.

(1928). However, he clearly recognized the positional relationship between this organ and the fin rudiments. The combined evidence of a hatching gland derived from the edge of the mantle fold covering the shell, and of fins closely associated with this gland, now allows us to consider both in a common context of correlated morphogenetic processes.

From observations on living coleoid hatchlings we know that enzymes released by the hatching gland *locally* dissolve the innermost envelope (chorion) and the surrounding nidamental covers (where they exist). This perforation of the envelopes can conly be achieved if the hatching gland is brought into, and held in, close contact with the envelope. In decapods, the gland is an anchor-shaped complex of three glandular bands, one dorsal branch joining at the rear mantle end two lateral branches, the distal ends of which lie on the fin bases. These form a *lateral support stabilizing the position of the mantle end* at the onset of hatching (Text Fig. 8). At that time, the animal still lies on its dorsal side. As soon as the chorion is perforated by the action of the hatching gland enzyme, release of the inner pressure in the chorionic space enhances the penetration of the mantle end into the outer gelatinous envelopes.

In order to cross the gelatinous envelopes, which in some forms are very thick, the animal must have special *locomotory* equipment. Indeed, as long as it is hindered by this gelatinous material, mantle pumping has no locomotory effect. In squid hatchlings, locomotion is achieved entirely by the ciliature of the integument, especially by bands of short, very densely set cilia of the mantle integument (Boletzky 1982b). In the incirrate octopods, the integument is devoid of cilia, and an entirely different set of integumental structures serves during hatching. It has no active locomotory function, but a passive guiding function by providing a shingle-like "one way gliding" surface (Boletzky 1966).

5.1 Shell form and hatching-gland organization : how to make a hole

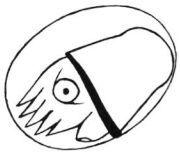
From the evidence on hatching mechanisms in living coleoids, it is tempting to postulate an "endocochlean" hatchling for all fossil cephalopods. A strong point in favour of this idea is the presence of tissue *surrounding* the embryonic shell of *Nautilus* (Arnold, this vol.), but we do not yet know how long it lasts. Let us consider two types of hatchling, one "ectocochlean", the other "endocochlean", both representing special cases derived from a situation similar to the *Nautilus* embryos so far observed. Early stages of shell formation are summarized here in order to show where the hatching gland arises.

As in all conchiferan molluscs, an ectodermic area differentiates into a distinct epithelium : a central field secreting a laminar primary shell (generally organic), which remains attached around its periphery to the shell-secreting cells. These cells will form the actual periostracum groove as soon as the peripheral attachment is interrupted.

The central epithelium (i.e., the part surrounded by the periostracum groove) will develop into the typical shell-producing area; it is only here that the characteristic mineral structures with their organic matrix are produced (prismatic structure or nacre; a slightly modified nacreous structure in cephalopods (Bandel & Boletzky 1979).

Beyond the periphery of the central epithelium and periostracum groove, the ectoderm differentiates into the cover of a muscular ring-shaped mantle. This muscular ring in a "normal" gastropod or bivalve becomes a free mantle edge that provides the mould for the material secreted by the periostracum groove. In many cases, like the freshwater bivalves *Pisidium* and *Sphaerium* or the gastropods *Viviparus* and *Cepaea,* in which the embryo contains a large amount of yolk, the mantle edge attaches itself to the outside of the embryonic shell. In some cases, like the "amphibian" gastropod *Succinea putris,* the muscular mantle fold even closes completely over the shell and is only secondarily retracted before hatching. A similar process might take place in *Nautilus* at late embryonic stages. If we follow our hypothesis of two hatchling types and assume as a common ancestral feature of cephalopods a concentration of special cells in the form of a hatching gland lying at the *edge of the mantle,* then we have to consider what shell form would be compatible with either "endocochlean" (fused edge) or "ectocochlean" conditions at hatching.

The "ectocochlean" hatchling with a glandular mantle edge only slightly protruding beyond the rim of the shell would achieve the broadest possible contact between the hatching gland and the chorion if it had a very *short,* nearly globular or an *exogastrically coiled shell.* A prerequisite of this optimal contact is that either the chorion surrounds the animal rather tightly (Text Fig. 9a); or that the height of the living chamber of a coiled shell is sufficiently low to make the ventral shell wall (with the mantle edge) rather broad and only slightly curved in order to permit



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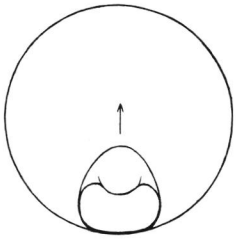


b

Text Fig. 9. a) A schematic representation of an ectocochlean hatchling with a glandular mantle edge (black) lying normally in close contact with the chorion. b) A schematic representation of the broad contact between the ventral mantle edge and the chorion in an exogastrically coiled ectocochleate shell. The arrow symbolizes the likely buoyancy that would remove the hatchling from the "bottom" in a strongly expanded chorion (cf. Text Fig. 8).

maximal contact between the ventral mantle edge and the inner surface of a spherical chorion having a large diameter (Text Fig. 9b). In such a wide chorion (similar to squid eggs at late embryonic stages) the "ectocochlean" hatchling would, of course, have to be negatively buoyant in order to have "bottom" contact. A hatchling with neutral or even slightly positive buoyancy in sea water would inevitably float in the perivitellin fluid, which has a salt concentration slightly higher than sea water. Tight enclosure by the chorion, possibly enhanced by a tough outer egg coat as in *Nautilus*, would thus appear a "safer" method as far as hatching is concerned (see reconstruction of the egg of an ammonite in Bandel 1986).

An "ectocochlean" hatchling with a *straight shell* would also be facing the problem of how to achieve close contact between the mantle edge and the chorion, especially if it hatched with a shell of some length. Unless the chorion were elongate (similar to Recent *Octopus* eggs) thus enclosing the hatchling rather tightly, it would have been difficult for the hatchling to bring the mantle edge into close contact with the chorion.

Taking all these aspects into consideration, we may postulate the following "dichotomy" :

1. "Ectocochlean" hatching conditions are conceivable in subglobular hatchlings, either with a *rudimentary* "orthoconic" shell, or with an exogastrically coiled shell (the latter allowing an evolutionary increase in hatchling size).

2. "Endocochlean" hatching conditions appear necessary in elongate hatchlings with either a straight shell or a shell beginning to coil endogastrically (as in *Spirula*).

In viewing the correlations between the form of the hatchling shell, the organization of the hatching gland, and the form and size of the chorion surrounding the hatchling, we have not yet covered all aspects of the "bottleneck" of hatching conditions. We now have to return to the problem of *locomotion* in hatching, already mentioned in the introductory part of this section.

5.2 Egg cases and hatching equipment : how to move through a hole

The function of the hatching gland is to perforate the chorion and surrounding envelopes (where these exist). This function does not involve the hatching *movements* by which the animal may have to free itself. Even in the absence of gelatinous envelopes surrounding the chorion, as in the incrirrate octopods, the hatchling has to free itself by active movements, the effect of which depends on the skin structure (Kölliker's organs). This structure is co-adapted, or — to use a more appropriate term — synorganized with the hatching gland (a simple transverse strip of glandular cells in incirrate hatchlings) and with the structure of the chorion (Boletzky 1966). Among living decapods, we find another example of active hatching movements in the sepiolids. In *Rossia,* the outer layer of the nidamental envelope hardens and thus forms a rigid shell, which has to be broken by the hatchling. The leading structure in this breakage is the so-called "terminal spine" (a tough uvula of connective and muscular tissue) underlying the rear end of the hatching gland. The hatchling props its arms against the wall of the rather narrow egg case opposite to the hatch opening and pushes its pointed mantle tip through the first opening of the shell, which then breaks under pressure from the mantle (Boletzky 1982b).

In contrast to the active hatching movements of octopods and sepiolids, the locomotion of squid hatchlings traversing the gelatinous nidamental envelopes is passive in that no muscular contractions are involved. Indeed, "jetting" movements of the mantle-funnel complex have no locomotory effect as long as the animal is surrounded by gelatinous material. Locomotion is achieved entirely by the ciliature of the integument (Boletzky 1982b).

Even if we were willing to assume that a hatchling with a long straight shell could open the egg case by means of a hatching gland situated at the anterior rim of the shell, we would have considerable difficulty in finding a conceivable mechanism allowing the animal to move through the hatch opening, head-foot first, pulling the naked shell forwards. Only well-developed muscular arms equipped with adhesive organs (suckers *s.l.*) allowing firm contact with a substrate would seem able to achieve such a task.

6. The arm crown and its modifications during the evolution of coleoids

At the end of the preceding section, the question is raised as to whether ectocochlean hatchlings could use their arms to work themselves through the hatch opening, in a way reminiscent of the crawling mode in many octopus hatchlings (Boletzky 1978-79). Unfortunately we have no fossil record of early arm development and we therefore depend entirely on the evidence of fossil adults, on adult morphology and on the development of arms in living cephalopods.

In considering arm development in coleoids, the embryonic development of the so-called tentacles of *Nautilus* will probably not provide more than a confirmation of the general lay-out and positional relationships known in the living coleoids : the arms, called tentacles in *Nautilus,* are derived from a common rudiment, part of which forms the funnel tube, called the hyponome in *Nautilus.* How the arm crown rudiment is subdivided in development is the next question to be approached. The observations of Arnold (this volume) on *Nautilus* embryos now provide a basis for embryological comparisons. Here we consider only the arm development in living coleoids. Four generalizations can be made from the available data:

1. The early rudiment of the arm crown is a bilaterally symmetrical, clasp-like tissue concentration lying at the periphery of the cap forming the embryo proper, i.e., next to the outer yolk sac (see Boletzky, this vol.);

2. Within the "arm crown" rudiment, individual "arm" rudiments appear very early in the form of bud-like tissue elevations;

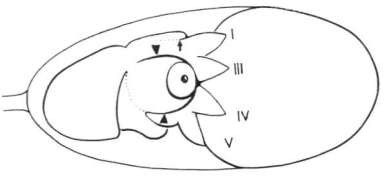
3. The number of arm buds varies among the greater groups of cephalopods: within the Decapoda (Sepioidea and Teuthoidea) there are five pairs of buds in cuttlefish, sepiolid, and loliginid squids, whereas there are only three pairs in ommastrephid squids (in which the missing pairs appear later); in the Octopoda, there are always four pairs of arm rudiments at early developmental stages;

4. Finally, the positional relationships among arm buds, and between them and the secondary head cover (primary lid), are stable throughout the known coleoids.

The last point was shown to be crucial for the establishment by Naef (1928) of homologies. In fact when arm pairs are numbered from 1 to 5, starting with the "dorsal" pair (in the physiological orientation of the animal; cf. Boletzky, this vol.), it appears that in the Decapoda the specialized tentacles are always formed from the rudiments of the fourth pair of arms. The primary lid is formed on either side of the head by two folds, one starting at the base of arm no. 3 (dorsal component of primary lid), the other starting at the base of arm no. 4 (tentacle). In the ommastrephid squids, where only three pairs of buds are visible at early stages, subsequent development shows that these are the rudiments of arm nos. 1, 2 and 4 (tentacles).

In the octopods, embryos always have four pairs of arm rudiments. The question then is to which decapodan rudiments they correspond. Naef (1928) has shown that primary lid development clearly indicates the homology of the third octopodan arm with the tentacle of decapods (no. 4). In other words, the true octopodan arm crown can not be explained by phylogenetic elimination of the decapodan tentacles (that *ontogenetic* loss of tentacles exists *within* the decapods will be discussed below). Naef suggests arm no. 1, but more recent embryological findings make it very likely that arm no. 1 in octopods is homologous to arm no. 1 in decapods (Boletzky 1978-79). It then remains to decide whether no. 2 or no. 3 are missing in the octopods. If no. 3 were not differentiated, the dorsal component of the primary lid would be formed from the base of arm no. 2 (similar to the temporary situation described by Naef (1928) for ommastrephid embryos). However, it is more likely that arm no. 2 has been eliminated (Text Fig. 10); this pair is highly modified and reduced in size in *Vampyroteuthis* (cf. Robson 1931, Pickford 1949, Young 1977). The eight "normal" arms of *Vampyroteuthis* are very similar to those of cirrate octopods.

In the interpretation of "eight-armed" fossil cephalopods (cf. Bandel & Leich 1986), one has to keep in mind that from an evolutionary "grade" characterized by ten subequal arms and thus corresponding to the hypothetical Protodibranchus of Naef (1922), two completely different processes might be responsible for an eight-armed adult condition. Within a truly decapodan lineage, the tentacles (arm pair no. 4) may atrophy and/or autotomize during juvenile development as in the living *Octopoteuthis, Grimalditeuthis, Lepidoteuthis,* and *Gonatopsis*. In contrast to this ontogenetic loss of the specialized tentacles, the truly octopodan condition is

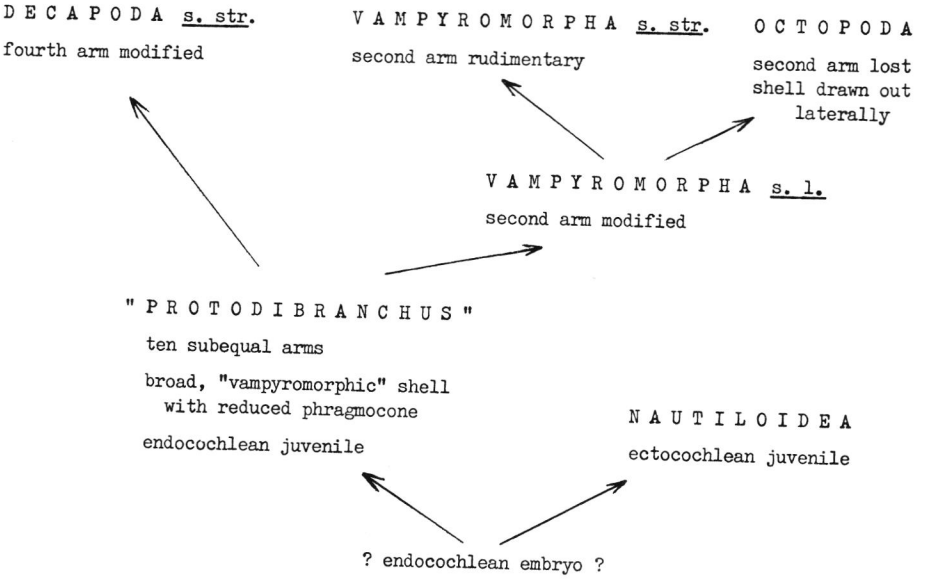


Text Fig. 10. A late organogenetic stage of an embryo of *Octopus vulgaris* in its narrow chorion, with the still large yolk sac at right. The arrow heads indicate the upper and lower components of the primary lid, the small arrow points to the buccal mass being overgrown by the base of arm no. 1. The numbering of the arms takes account of the lack of arm no. 2 (see text).

achieved by phylogenetic elimination of one pair of arm rudiments, probably of no. 2, in other words *via* a vampyromorphic arm crown (whether or not the retractile filaments (arm pair no. 2) of living *Vampyroteuthis* would be recognizable in a fossil is difficult to assess).

7. Discussion and conclusion

Pickford (1949), in describing the gladius of *Vampyroteuthis infernalis,* has drawn attention to the close resemblance of this delicate shell with the gladius of the Prototeuthoidea and Mesoteuthoidea as defined by Naef (1922, 1923). However, these squids of the Upper Jurassic and Cretaceous periods were supposed to have had the typical decapodan arm crown with arm no. 4 differentiated as a tentacle. The only way out of the dilemma of whether features of the shell or the arm crown should be given priority in phylogenetic considerations would seem to start at the Protodibranchus grade, which is characterized by a broad, gladius-like shell with a reduced phragmocone and 5 pairs of subequal arms. Any fossil with ten subequal arms, no matter how much the phragmocone is reduced, represents this grade and must be assigned to a lineage derived directly from an ancestor with ten subequal arms. From this "symplesiomorphic" condition of the arm crown, and largely independently of the tempo of shell modification, the only two known "apomorphic" conditions of the arm crown as a whole can be derived : modification of



Text Fig. 11. Constructional features of the shell derived from an endocochlean embryo, and positional relationships of coleoid arms derived from an ancestor having ten subequal arms.

the fourth pair of arms in the Decapoda *s. str.*, and modification of the second pair of arms in the Vampyromorpha *s.l.* (Text Fig. 11). In the latter, one line of descent leads to the living Vampyromorpha *s. str.*, whereas the other represents the Octopoda characterized by the lack of arm pair no. 2 and a thoroughly transformed shell reduced antero-posteriorly. In the Cirrata, it still forms a saddle-like support for the fins. In the Incirrata it is further reduced along with the rudimentation of the fins; in this group, the cirri on the arms are entirely eliminated.

From a physiological and developmental viewpoint, the modifications of the shell reflect more or less drastic changes in the secretory program of the closed shell sac with its distinct zones, each of which is competent for the production of specific shell material placed in a well-defined position relative to other components. In the history of the coleoids, these modifications have led to the complete elimination of the "phragmocone program" in the majority of the decapods and vampyromorphs, while it has been retained (and modified in two different directions) in the spirulirostrid lineage leading to the pelagic spirulids and the nekto-benthic sepiids, respectively, both showing *endogastric* curvature of the shell.

In contrast, the arm crown provides no evidence of variability going so far as to overthrow the positional plan of the four or five arm pairs. Variation *within* this polarized series of rudiments is concerned only with the specific "equipment" of each arm, differentiated according to specific morphogenetic programs accomodating: suckers (and sucker-derived hooks) on the adoral surface; cirri or palp-like extensions embedded in marginal skin membranes on either side of the suckers; and integumental extensions forming a web on the aboral surface of the arms.

Wherever the fossil record offers insight into these differentiations, the morphological features of the arm crown must be scrutinized before conclusions can be drawn from shell structures (cf. Engeser & Bandel, this vol.).

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