



## The Evolutionary History of the Eight-armed Coleoidea

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11 Text-Figures

*Cephalopoda*  
*Coleoidea*  
*Octobrachiomorpha*  
*Evolution*

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### Die Evolutionsgeschichte der achtarmigen Tintenfische

#### Zusammenfassung

Die achtarmigen Tintenfische (Octobrachiomorpha) können von Coleoidea mit 10 Armen hergeleitet werden. Die Geschichte ihrer Evolution kann an Hand von allometrischem Wachstum und Reduktion des Gladius-Mittelfeldes dargestellt werden. Auf die Bedeutung des fossilen *Palaeoctopus* als Stammgruppen-Vertreter der Incirrata wird besonders hingewiesen. Die Evolution der Coleoidea-Kiemer wird rekonstruiert. Ein *Loligo*-artiger Grundtypus kann angenommen werden. Die Kiemer der modernen Octopoden stellen eine Modifizierung dieses Typus dar. Die Kiemer der fossilen „Trachyteuthimorpha“ sind dagegen ursprünglich. Die „Trachyteuthimorpha“ sollten daher als Stammgruppen-Vertreter der Octobrachiomorpha angesehen werden.

#### Abstract

The eight armed coleoids (Octobrachiomorpha) can be derived from Coleoidea with 10 arms. Their evolutionary history can be demonstrated by allometric growth and reduction of the middle field of the gladius. The significance of the fossil *Palaeoctopus* as a stem-group representative of the Incirrata is emphasized. The evolution of the coleoid gills is reconstructed. A loliginid basic type can be recognised. The gills of the modern octopods represent a modification of this type. The gills of the fossil „Trachyteuthimorpha“ still show the basic type of the Coleoidea. They may be considered stem-lineage representatives of the Octobrachiomorpha.

### 1. Introduction

The three known suborders of the order Octobrachiomorpha, the Vampyromorpha, Cirrata and Incirrata, form a monophylum within the Coleoidea (BERTHOLD & ENGESER, 1987; ENGESER, 1990; HAAS, 1989a, 1989b) (Text-Fig. 1): Octobrachiomorpha and Decabrachiomorpha together constitute the Neocoleoidea characterised by possession of suckers whereas their adelphotaxon Palaeocoleoidea (containing the belemnites), have arm hooks in addition to other apomorphies (closing

membrane of the protoconcha). The most relevant synapomorphies of the Octobrachiomorpha are the gradual reduction and subsequent loss of the second arm-pair and the reduction of the phragmoconus. All living and fossil Octobrachiomorpha, except some highly questionable Devonian forms, have lost the phragmoconus completely and do not show any trace of a guard. Only a conchyolinic gladius or rods remain. Thus, already in the early evolution of the Octobrachiomorpha, the buoyancy system with a

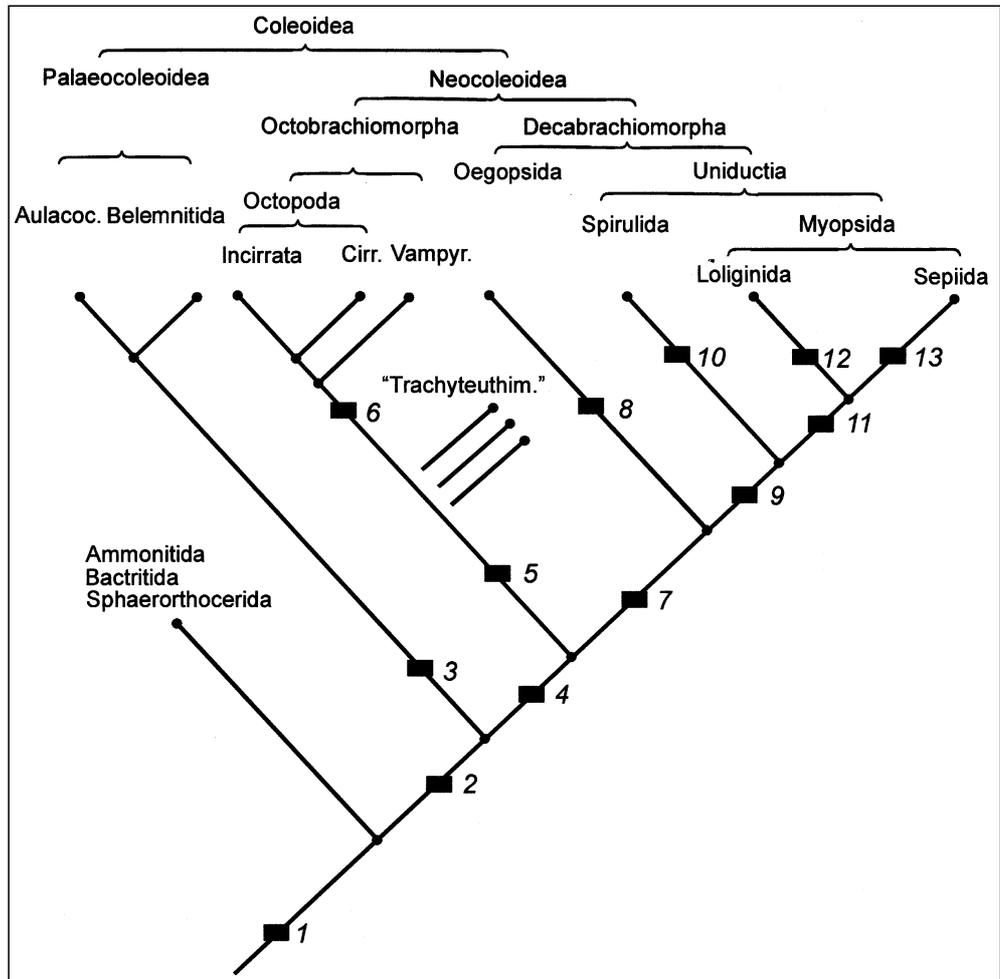
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Text-Fig. 1.

Cladogram of the Coleoidea with the relevant synapomorphies.

1 = Spherical; initial chamber, (presumably two gills). 2 = Internal shell; fins; ink sac; muscular mantle. 3 = Closing membrane of the protoconcha; arm-hooks. 4 = Suckers. 5 = Loss of the phragmoconus; remaining gladius, not or only weakly calcified. 6 = Multiplicate gill laminae. 7 = Suckers with horny rings; nephridial sacs fused; tentacles. 8 = Complete loss of calcareous shell; gladius. 9 = Right gonoduct aborted. 10 = Coiling of the shell increasing; descensus viscerum. 11 = Myopsid eye; eggs with large amount of yolk. 12 = Gladius extremely elongated. 13 = Broadening of the cuttle bone; vaulting of the dorsal shell.

Aulacoc. = Aulacoceratida; "Trachyteuthim." = "Trachyteuthimorpha"; Vampyr. = Vampyromorpha; Cirr. = Cirrata.



gas filled phragmoconus was totally abandoned. To maintain their depth position the animals were dependant on jet propulsion with the funnel, movements of the fins and the arm crown in combination with a well developed web, or on floating. Except in some stem-group representatives, calcification of the gladius was abandoned. An important synapomorphy of the living Octobrachiomorpha is the outer lymph-sac of the statocyst. The urogenital system is primitive in that the renal sacs are still separated, whereas in Neocoleoidea they are fused.

It is the intention of this contribution to review the fossil representatives and to demonstrate the evolutionary history of the Octobrachiomorpha. Thus only the most relevant characters are dealt with in this publication. In a recent paper, YOUNG, VECCHIONE & DONOVAN (1998) used another approach but reached a similar conclusion as the present author regarding the evolution of the Octobrachiomorpha. A cladistic approach on the systematics of the living Octobrachiomorpha based on morphologic characters has recently been made by YOUNG & VECCHIONE (1996) and VOIGHT (1997).

In depicting the pathways in the evolutionary history of the known fossil and living eight-armed Coleoidea by using HENNIG'S method inevitably conflicts with taxonomic nomenclature arise, especially in the higher systematic categories when their systematic content has to be changed. As far as possible, the present author has preferred traditional names which were adapted then to his phylogenetic concept.

## 2. Morphologic Trends

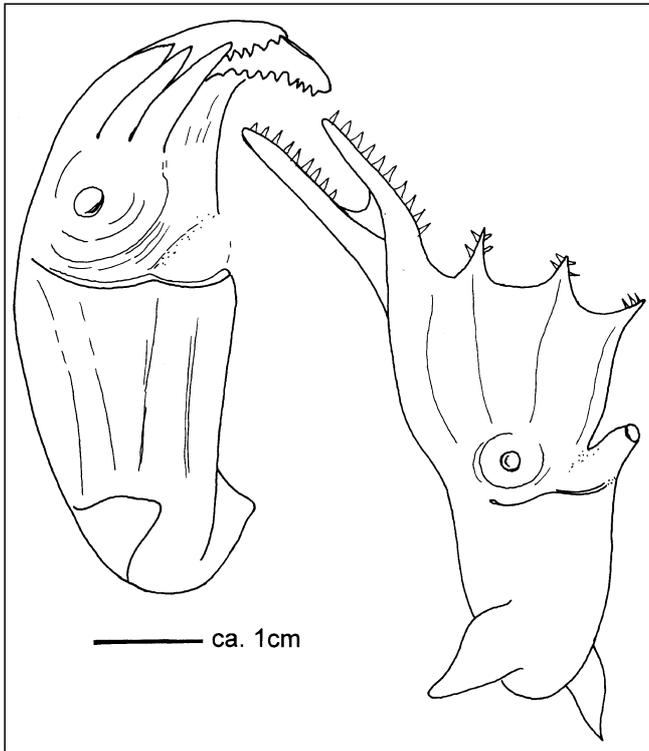
### Presumed earliest Octobrachiomorpha

Although the Octobrachiomorpha lack a phragmoconus, it can be assumed that the earliest representatives

had a calcareous shell with a spherical protoconch, a phragmoconus with few crowded septae, and a long body chamber which, in analogy with the Palaeocoleoidea, just began to open the ventral wall to provide space for the muscular mantle. The genera *Boletzky* and *Naefiteuthis* from the Devonian Hunsrück Slate described as early octobrachiomorphs by BANDEL, REITNER & STÜRMER (1983), when reconstructed in the above sense are rather doubtful Octobrachiomorpha and may well be Sphaerorthocerida. Should their octobrachiomorph nature be proved, then their systematic position would be within the stem-group of the Octobrachiomorpha.

### Vampyromorpha

This Order contains only the living deep sea form *Vampyroteuthis infernalis*. This species, like that of most fossil "Trachyteuthimorpha" (PICKFORD, 1939), has a conchyloneous gladius with a long middle field and wings. *Vampyroteuthis* has ten arms, the second pair of which is reduced to tiny filaments (YOUNG, 1977). The remaining eight arms are similar to those of primitive Octobrachiomorpha (Cirrata) in bearing a median row of fleshy, unstalked globular suckers without horny rings and with cirri. The cirri are presumably homologous with the arm-hooks of the Belemnites (HAAS, 1989b). Thus *Vampyroteuthis* shows the evolutionary pathway towards the true eight-armed coleoids. The presence of an outer lymph-sac of the statocyst indicates the typical octobrachiomorph synapomorphy. Other octobrachiomorph characters are the web and the crop. Fins are present and these are a symplesiomorphy of the Coleoidea. As a result of living in the deep sea, together with other features, the length and number



Text-Fig. 2.

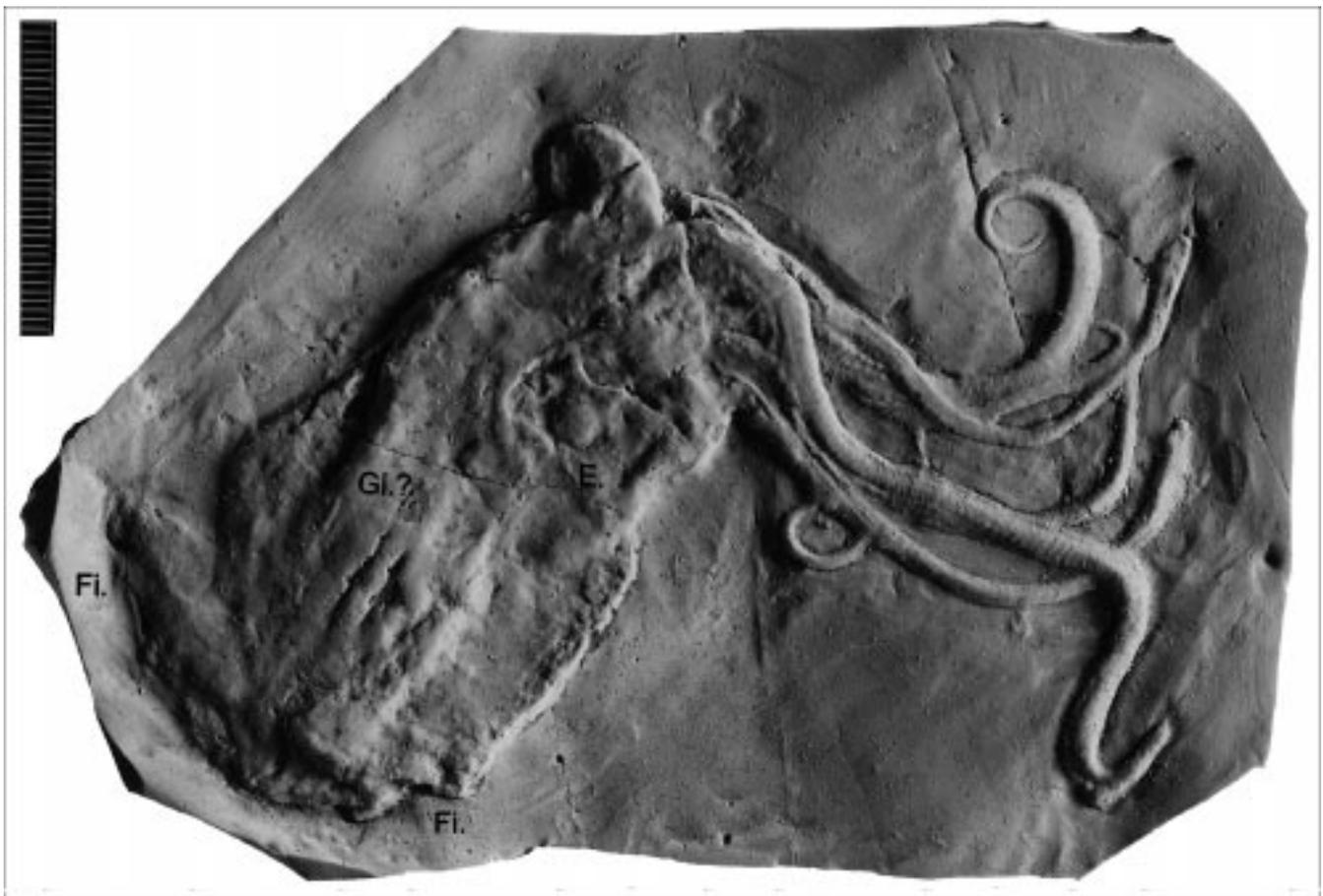
A new "Trachyteuthimorpha" from the Callovian of La Voulte-sur-Rhône (FISCHER & HAAS, in prep.) and reconstruction to show elongated arm-pair I.

The animal may have stirred up the sea bottom or it may have used some flapping mechanism with its web.

### "Trachyteuthimorpha"

From the Triassic to Cretaceous there are many fossil forms which have gladii similar to *Vampyroteuthis*. Some common genera are: *Plesioteuthis*, *Loligosepia*, *Lioteuthis*, *Trachyteuthis*, *Geoteuthis*, *Parabeloteuthis*, *Belopeltis*, *Jeletzkyteuthis*, *Kelaeno*, *Palaeololigo*, *Leptotheuthis* etc. The morphologies of the gladii in these is quite remarkable and points to a great variety of life styles. Because of the similarity of the gladii with those of Oegopsida and Loliginida, NAEF (1922, 1923, 1928) and JELETZKY (1966), assigned these forms to the "Teuthida" and thus the Decabrachiomorpha. It could be demonstrated that *Plesioteuthis* and *Trachyteuthis* (BANDEL & LEICH, 1986) and some undescribed taxa from the Callovian of La Voulte-sur-Rhône (FISCHER & HAAS, in prep.) have eight arms. This confirms the earlier supposition of PICKFORD (1939). Based on their gross morphology, it seems to be reasonable to suggest that all the fossil "teuthoids" belong within the Octobrachiomorpha. As will be discussed later, they form together the paraphylum "Trachyteuthimorpha". Recently VECCHIONE, YOUNG, DONOVAN & RODHOUSE (1999) regarded the Middle Jurassic genus *Mastigophora* as an animal with a typical teuthid aspect, and assigned it to the Decabrachiomorpha. *Mastigophora* pos-

of blades in the multi-plicate gills are strongly reduced and the ink sac is completely reduced. Both characters can be evaluated as autapomorphies of the Vampyromorpha.



Text-Fig. 3.

*Proteroctopus ribeti* FISCHER & RIOU from the Callovian of La Voulte-sur-Rhône. Silicon cast of the holotype in the Musée nat. Hist. natur. Paris.

sesses no more than eight pairs of arms. Some of them show vestiges of suckers, apparently of the sessile octobrachiomorph type. Some of the arms carry relatively long filaments which are cirri rather than supports of the protective seam as in Decabrachiomorpha (for details of these structures, HAAS [1989b]). The present author does not agree that transverse swelling on the ventral side of the head represents true tentacles homologous with those of the Decabrachiomorpha (In Decabrachiomorpha it is the arm-pair IV which is transformed into the tentacles). It may be that *Mastigophora brevipinnis* had an elongated arm-pair like those trachyteuthimorph taxa from La Voulte-sur-Rhône (Text-Fig. 2) or that the swelling is merely an artefact or remains of cartilage. The filaments representing the reduced second pair of the arms in *Vampyroteuthis*, are not preserved. In preparations of *Vampyroteuthis* they are often withdrawn indicating that there is little hope of them being visible on fossils. The tiny filament-like feature, winding along the body of *Rhomboteuthis lehmanni* (FISCHER & RIOU, 1982, Pl. 3, Fig. 1; Text-Fig. 3) is the arm of an ophiuroid. The gills known from *Plesioteuthis* and discussed below, are of the loliginid type, which is the plesiomorph expression of at least the Neocoleoidea.

It may be concluded from the weakly calcified gladius of *Mastigophora* (ENGESER, pers. comm.) that this was also the case in many other trachyteuthimorphs. Calcification may be a reminiscence from common ancestors or it may be an autapomorph acquisition of certain taxa due to their life styles and body sizes. According to our poor present knowledge of the biomineralisation in "Trachyteuthimorpha" presence or absence of lime in their shells is not a useful character for phylogenetic reconstruction and is not important within the range of transition from "Trachyteuthimorpha" to Vampyromorpha.

The concept of the paraphylum "Trachyteuthimorpha" presented in this paper is not fully concordant with the one proposed by DOYLE, DONOVAN & NIXON (1994). Since these authors present their system as the basis for the Coleoidea-part of the Treatise on Invertebrate Palaeontology some annotations should be made: Although within the "Trachyteuthimorpha", groups of family rank can be identified by autapomorphies, these taxa lack appropriate synapomorphies and thus their phylogenetic interrelationship cannot be traced. Further, it is not correct to regard the Loligosepiina JELETZKY as the adelphotaxon of the Vampyromorpha/octopods (see DOYLE, DONOVAN & NIXON [1994], diagrams: Text-Figs. 1, 2). The Loligosepiina JELETZKY together with the Teudopsidina STORABOGASOV (which include the Trachyteuthididae NAEF) and the Plesioteuthididae NAEF are stem lineage representatives of the Octobrachiomorpha and together, constitute the paraphylum "Trachyteuthimorpha".

*Plesioteuthis* and its allies are without doubt octobrachiomorphs because of their eight arms (BANDEL & LEICH, 1986), the possession of cirri and a median row of suckers on each arm. Consequently *Plesioteuthis* cannot be the antecedent of loliginids and oegopsids as DOYLE, DONOVAN & NIXON (1994) propose. Moreover, regarding the phylogenetic distance between Oegopsida and Loliginida within the Decabrachiomorpha (Text-Fig. 1), this can hardly be the case (for further discussion see: BERTHOLD & ENGESER [1987]; ENGESER [1990]; HAAS [1989a, 1997]). Moreover, an attempt to delineate the origin of higher systematic categories throughout the coleoids by comparing the shape and the growth lines must fail because these characters are almost completely identical in systematic-

cally far distant belemnoids, trachyteuthimorphs, loliginids and oegopsids.

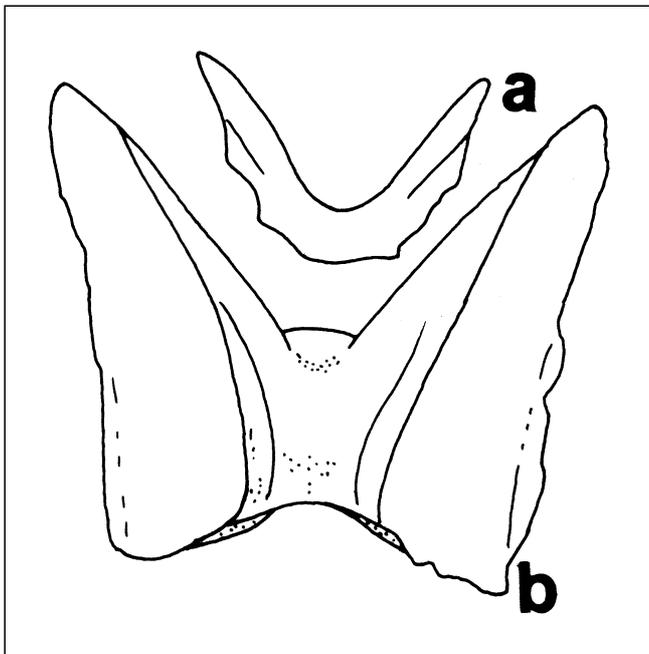
Another question raised by DOYLE, DONOVAN & NIXON (1994) is the position of the Phragmoteuthida JELETZKY, interpreted by them as stem-lineage representatives of the Neocoleoidea. The authors have pointed out that the protoconch is unknown and consequently one cannot say whether there was a closing membrane, as in belemnites, or a caecum as in all other cephalopods. Thus no unambiguous decision can be made as to whether the phragmoteuthids are Palaeocoleoidea (see ENGESER & BANDEL, 1988; HAAS, 1989b). The similarity of the growth lines in *Phragmoteuthis* with those of certain Neocoleoidea ("Trachyteuthimorpha", Loliginida and Oegopsida) encouraged DOYLE, DONOVAN & NIXON (1994) to follow JELETZKY (1966) in recognising phylogenetic relations between these groups. If this idea were true, the Devonian *Boletzky* and *Naefiteuthis*, because of their closed endchamber, would not fit in the Octobrachiomorpha lineage at all. By morphological comparison *Phragmoteuthis*, together with other forms like *Belemnoteuthis*, *Acanthoteuthis* and *Permoteuthis* are all close to the belemnites. This can be supposed from the evolutionary stage of its arm-hooks (HAAS, 1989b).

The Carboniferous *Jeletzkyia douglassae* JOHNSON & RICHARDSON was recognised by DOYLE, DONOVAN & NIXON (1994) as an early stem line representative of their Phragmoteuthida and thus assigned to the Neocoleoidea. From the original description of JOHNSON & RICHARDSON (1968) the specimen is preserved in a phosphatic nodule and shows an arm-crown with ten arms of equal length. Each arm bears hooks of the aulacoceratid type on its edges. There are no traces of suckers on the arms which, if they were present, must have been preserved in the fine grained sediment. Consequently one can conclude that *Jeletzkyia* did not bear suckers. With the exception of the preserved last septum, the nodule does not include the phragmoconus and the rostrum. *Jeletzkyia douglassae* is more likely to be a palaeocoleoid and since it has arm-hooks of the aulacoceratid type it seems most advisable to assign it to the Aulacoceratida.

*Proteroctopus ribeti* FISCHER & RIOU 1982 from the Callovian of La Voulte-sur-Rhône (Text-Fig. 3) has been considered an incirrate because it lacks cirri along the long arms. However, this may be an artefact as the suckers are supposed to be present and it is likely that the cirri have been withdrawn. The mantle sac is relatively short and bears terminal fins. The gladius is not known although a fold on the dorsal covering tissue may be an indication of it. If this were the case, the middle field was enclosed by a relatively narrow angle and consequently it was not reduced medially as shown later in *Palaeoctopus*. Thus, in spite of its shortened mantle sac which might suggest relationship with the Incirrata, there is some greater probability that *Proteroctopus* was a trachyteuthimorph (ENGESER, 1988).

### Cirrata

The living families of this order are inhabitants of the deep sea. So far, no representatives are known as fossils. With their primitive characters such as arms with a median row of suckers and cirri and possession of fins, the Cirrata are close to the Vampyromorpha. The loss of the ink sac in Cirrata and in *Vampyroteuthis*, is a convergence due to life in the deep sea. The most striking feature is the reduction of the median field of the gladius so that only some clasp-like conchylineous structure remained which is not separated sagittally and which mainly consists of the wings. It



Text-Fig. 4.  
Cirrata, clasp-like gladii.  
a) *Chunoteuthis ebersbachi* (after MANGOLD, 1989).  
b) *Cirrothauma murrayi* (after ALDRED, NIXON & YOUNG, 1987).

serves the support for the fins and the depressor muscles (Text-Fig. 4). The gill is of the multi-plicate incirrate type.

#### Incirrata

The arms in members of this order carry the sessile fleshy type of suckers with a projecting acetabulum on a broad columnar stem. In some taxa there are two rows of suckers on each arm, but these are different from the double row of suckers in the Decabrachiomorpha (HAAS, 1989b). All living Incirrata have lost the cirri. In the adult animals the fins have been completely reduced and rudimentary fins are known only in the prehatching stage (NAEF, 1928). In most taxa the ink sac is retained. A pair of conchyolineous rods, the stylets, (Text-Fig. 5), serving the support of the retractor muscles are all that remains of the gladius (APPELLÖF, 1898). In *Argonauta* they are absent. The complete reduction of the gladius seems to be the consequence of floating in open sea. The incirrate taxa Bolitaenidae, Ocythoidea and Octopodidae are treated in the cladograms of YOUNG & VECCHIONE (1996) and VOIGHT (1997) as a Paraphylum lacking appropriate apomorph characters for further systematisation. In spite there are no conspicuous morphological apomorphies in the Octopodidae (VOIGHT, 1997) v. BOLETZKY (1992) pointed out that their benthic life style must be derived from the pelagic ancestors of all Octopoda. Text-Fig. 11 shows a simplification of this situation. The complete loss of the gladius in *Argonata*, which represents the end of the morphologic line of gladius reduction, does not constitute a major phylogenetic event because the Argonautinae are merely an offspring from the Ocythoidea clade with an unknown adelphotaxon.

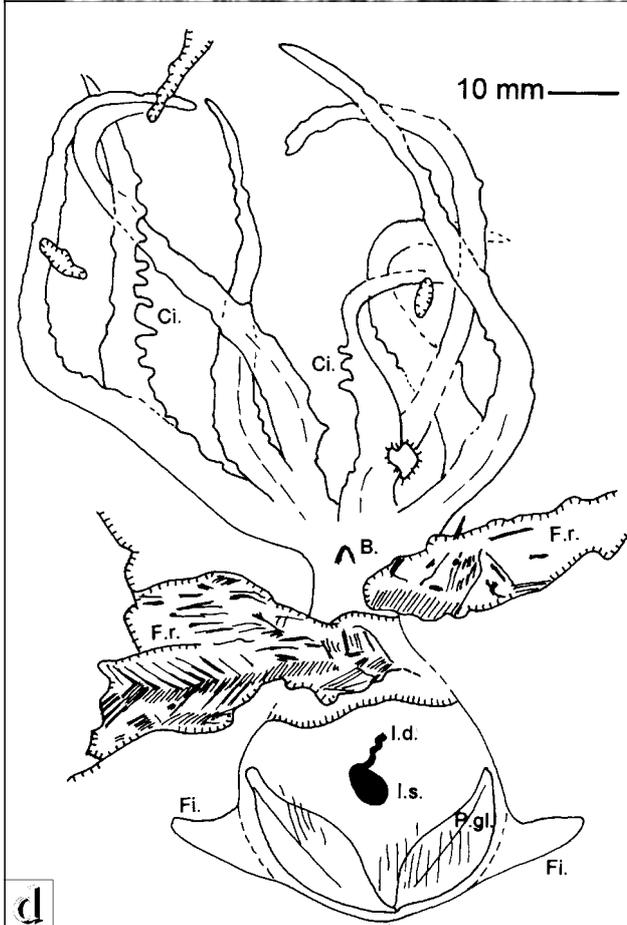
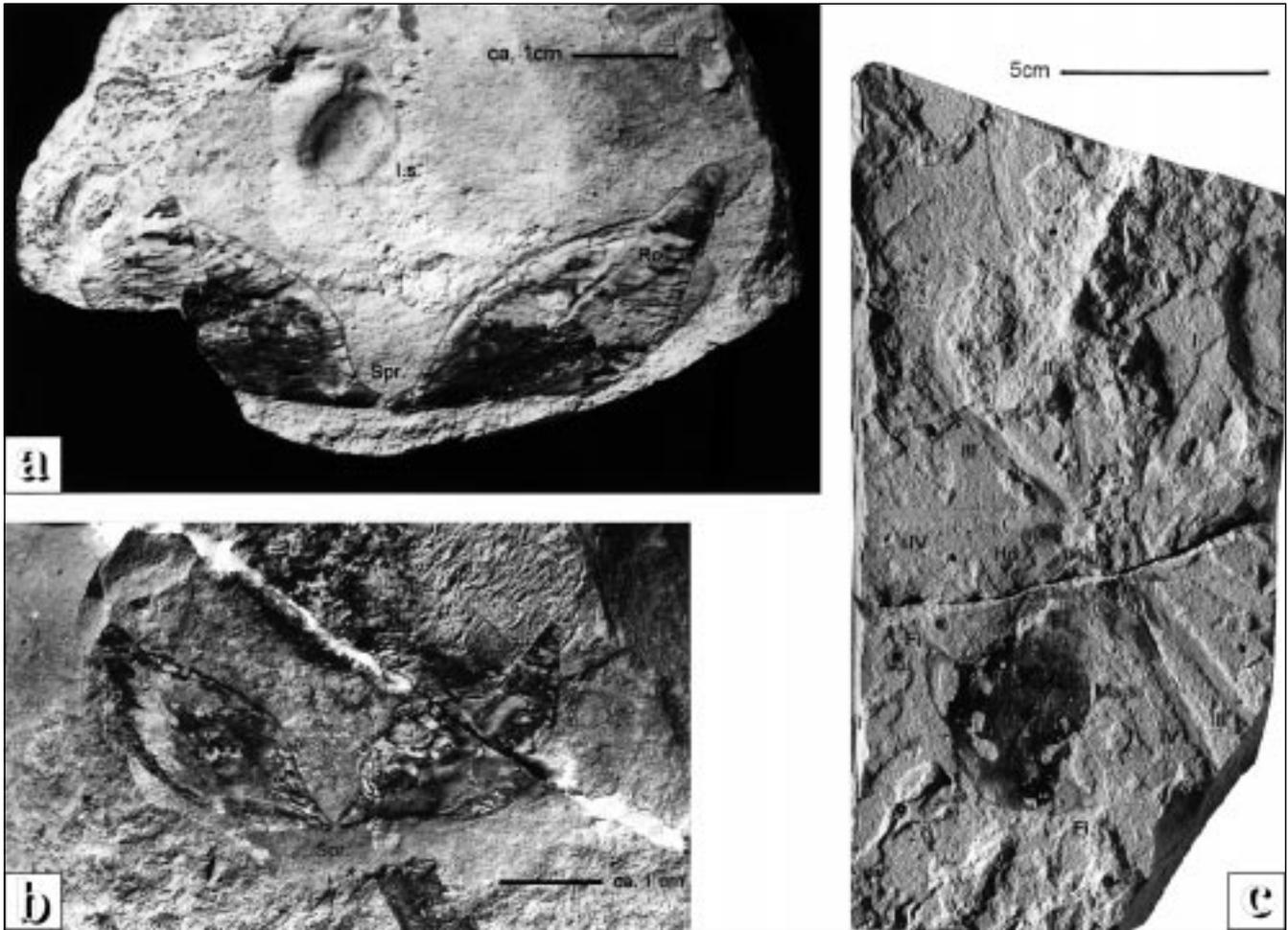
#### Fossil Incirrata

*Palaeoctopus newboldi* (WOODWARD) from the Upper Cretaceous of the Lebanon (Text-Fig. 6) has a rather small head with long arms and a spherical mantle sac. In this respect the latter resembles the mantle sac of extant octopods



Text-Fig. 5.  
Cross section through the stylet of *Eledone moschata* with inserting muscles.  
Ep = epithelium secreting the stylet; M.ma. = muscular mantle; M.r. = retractor muscle; St = stylet consisting of concentric conchyolin sheets.

which becomes inflated when the living animal is placed in formalin without prior anaesthetisation. Perhaps the Lebanese specimens died as a result of a toxic event in the sea water. On the type specimen, housed in The Natural History Museum, London, the long arms show a median row of suckers and cirri, whereas in the other known specimens cirri and suckers are stripped off together with the epidermis in a similar manner to that observed in decaying recent cephalopods. At the posterior end of the body there are triangular fins on each side. Their position is closely related to the corresponding halves of the gladius which consists of two sigmoidal-lanceolate conchyolin plates separated from each other in the midline. Such a blade is made of a diagonal rod which seems to be equivalent to the lateral keel strengthening the gladii of some "Trachyteuthimorpha". The rods of the two separated parts of the gladius include a very wide angle. Anterior from that rod there is a narrow leaf like area broadest towards the exterior. This may be a rudiment of the median field. Behind the rod is a semilunular area which can be identified as the wing of the trachyteuthimorph and vampyromorph gladius. The separation of the two gladii plates is the reason why many isolated plates of the gladius are found. They have been identified as diagenetically deformed gladii of normal "Trachyteuthimorpha" [*Beloteuthis libanotica* NAEF 1922, redescribed by ENGESER & REITNER, 1986 as type



Text-Fig. 6.  
*Palaeoctopus newboldi* (WOODWARD).  
 a,b) Separated Gladius. Musée Hist. natur. Paris.  
 c) Complete specimen. Pal. Inst. Bonn.  
 d) Diagram of the specimen in the British Museum of Natural Hist. to show cirri on two arms.  
 B. = beak; Ci. = cirri; Fi. = fin; F.r. = fish remains; Hd. = head; I.d. = ink duct; I.s. = ink sac; Ma.s. = mantle sac; P.gl. = separated part of the gladius; Ro. = rod; Spr. = site of separation between the two parts of the gladius; I-IV = arms.

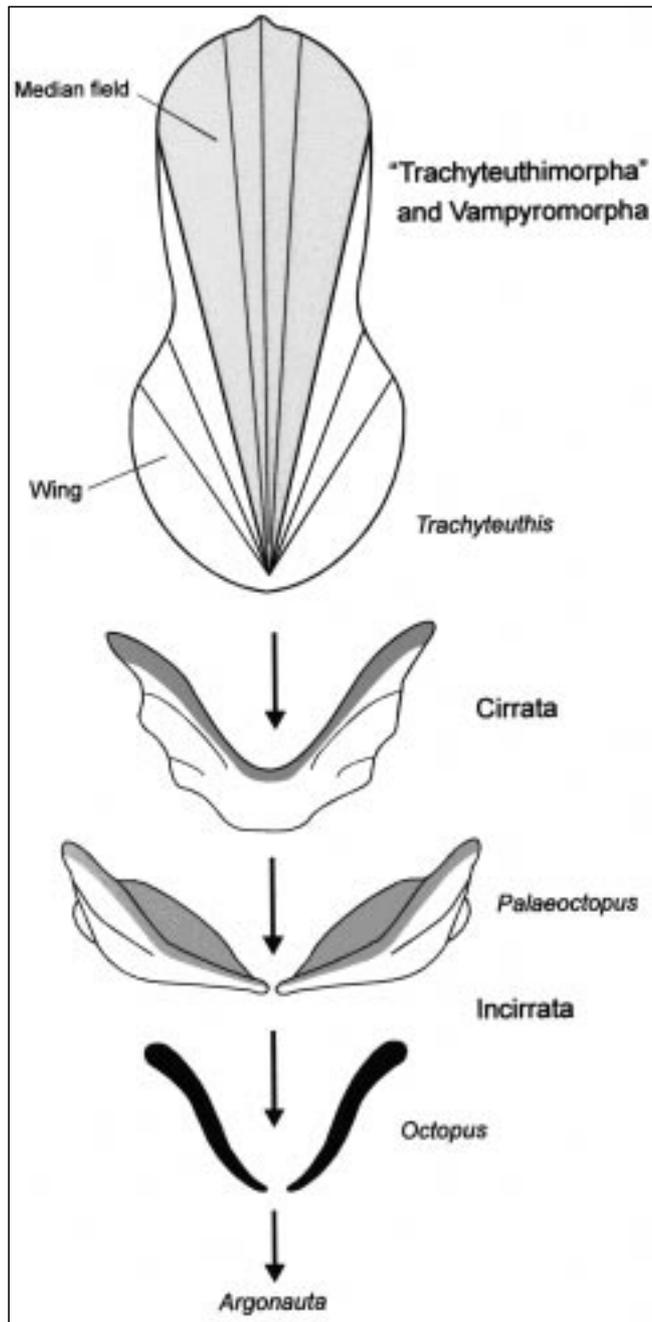
species of *Parateudopsis* ENGESER & REITNER 1986 = *Palaeoctopus newboldi* (WOODWARD 1896)].

The bipartite gladius of *Palaeoctopus* shows that the separation of the shell sac in *Palaeoctopus*, typical for the Incirrata (v. BOLETZKY, 1992), must have already been realised. The new acquisitions such as possession of Kölliker's organs of the hatchlings, stalked egg cases and egg care, all linked to incubation (v. BOLETZKY, 1992), were not yet developed. *Palaeoctopus* retained its fins throughout life and therefore Kölliker's organs, as a prerequisite of incubation, do not make sense with a finned hatchling. According to v. BOLETZKY (1992) the main purpose of the Kölliker's organs is to keep the hatchling in suspension when their bristles are spread out. Consequently an additional drive by fin movement would be conflicting. With its fins and arm-cirri *Palaeoctopus* had the appearance and, most probably, the pelagic life style of a cirrate. Nevertheless the systematic position of this animal within the stem-group of the Incirrata, contrary to VOIGHT (1997), is no longer questionable. In this context the arguments of v. BOLETZKY (1992) that the Incirrata must be derived from a cirrate-like pelagic ancestor can be supported. The stylets of the Octopoidae can easily be demonstrated as homologous with the two parts of the *Palaeoctopus* gladius and that they are not autapomorph structures of the incirrates as VOIGHT (1997) has

proposed. In functional respect the sagittal interruption of the gladius in *Palaeoctopus* has improved the capability of the muscular mantle for more vigorous inflation and deflation during swimming and breathing. These strong movements cannot be performed with the stiff undivided clasp of the antecedents and thus the situation found in the fossil already alludes to the life style of the living incirrates. In their phylogenetic tree of the Coleoidea DOYLE, DONOVAN & NIXON (1994, Text-Fig. 1) place *Palaeoctopus* close to the origin of the octobrachiomorphs. Following the arguments discussed above this idea cannot be accepted.

### 3. Conclusion on the Morphology

In the evolutionary history of the Octobrachiomorpha it can be demonstrated that there is considerable enlarge-



Text-Fig. 7.  
Diagram showing the reduction of the gladius in the Octobrachiomorpha.

ment of the angle including the median field of the gladius and a consequent reduction of the latter (Text-Fig. 7). Thus in the "Trachyteuthimorpha" and the Vampyromorpha the median field is long and complete, becoming clasp-like by broadening and reduction in the Cirrata and with medially interrupted sides in *Palaeoctopus* into stylets in the Incirrata and finally a complete loss of the gladius in *Argonauta*.

Other reductions in the course of evolution are the loss of the fins and of the cirri in the Incirrata (Text-Fig. 11). The loss of the ink sac in *Vampyroteuthis* and the Cirrata is convergent due to life in the deep sea.

### 4. Comments on the Gills of the Coleoidea

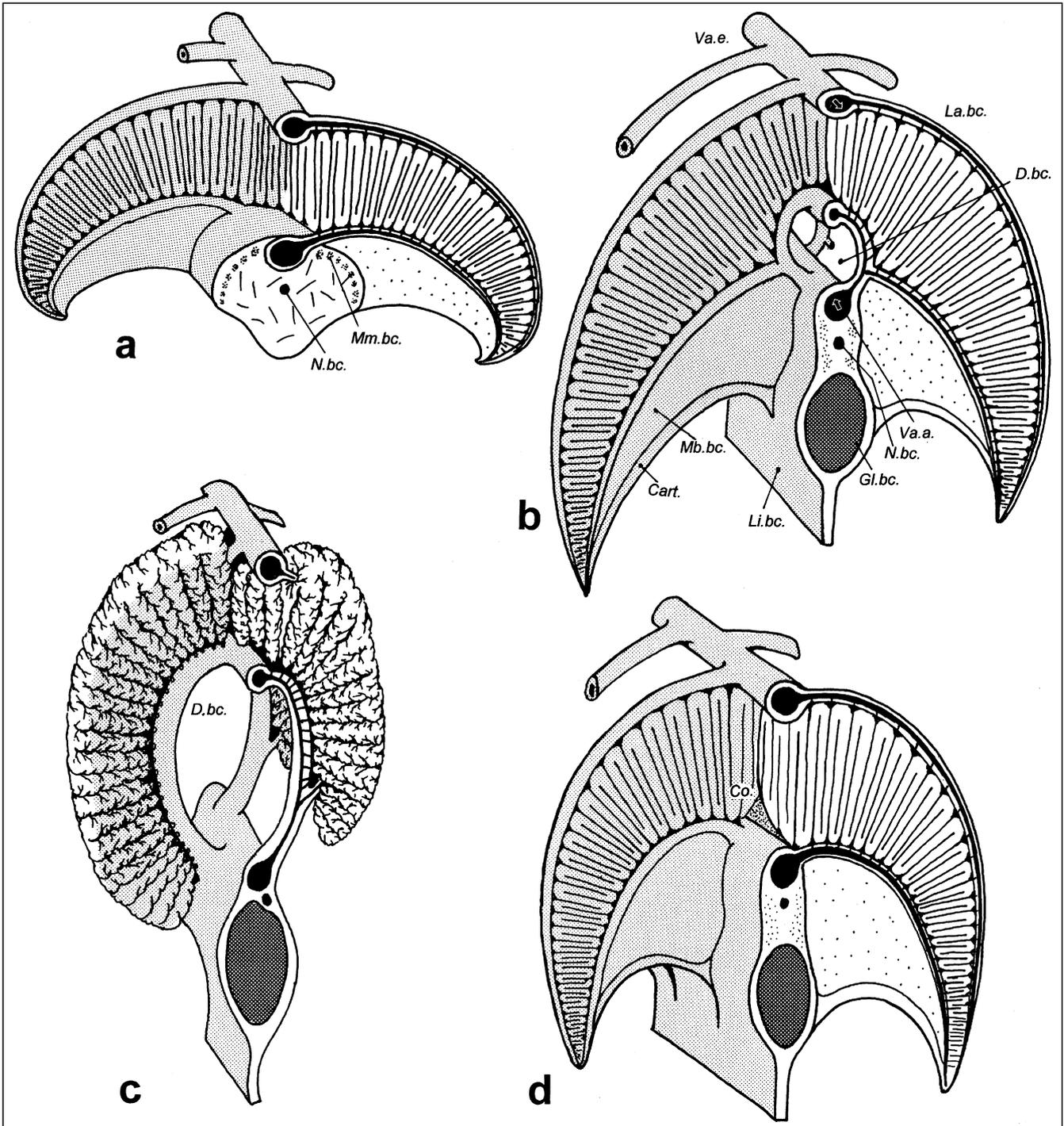
In some cases, the presence of gills preserved in fossil Coleoidea allows some speculations on the evolution of their gills in general and their bearing on the evolution of the octobrachiomorph gill. The coleoid gill can be derived from a type retained in the living *Nautilus* (Text-Fig. 8a). In *Nautilus* the fleshy gill axis, which is not connected to the roof of the mantle cavity, contains distally the longitudinal muscles, the Vas afferens (gill artery) and more proximally the Nervus branchialis. The Glandula branchialis of the Coleoidea is not present. The Laminae branchiales resemble scythe-blades in shape. They insert transversally and distally to the gill axis with right and left side alternating. The Lamina branchialis contains the double folded respiratory distal part and the membrane connecting it to the branchial axis. The Vas efferens (gill vein) occurs along the ridge of the gill with branches following the outer margins of the gill blades. These in turn give off smaller vessels to the respiratory filaments. The side-branches of the Vas afferens run along the proximal edges of the respiratory filaments.

In Oegopsida and Loliginida (Text-Fig. 8b) the inner edges of the Laminae branchiales between the Vas afferens and Vas efferens form exteriorly convex arc-pillars, mainly consisting of connective tissue, each containing a branch of the afferent vessel. The alternating arc-pillars unite at their distal ends to form a longitudinal and undulating string often containing a longitudinal vessel receiving the vessels from the pillars. Together the pillars and the longitudinal string cavity of the Ductus branchialis aids rapid circulation of the ventilating water. From the vessel of the arc-pillars another springs off running along the proximal edge of the respiratory part of the Lamina branchialis.

In general, sepiids (Text-Fig. 8d) and *Spirula* show the same plan of construction as in Oegopsida and Loliginida but there is no Ductus branchialis because its strengthening pillars are degenerated. Similar conditions can be seen in *Idiosepius*.

In Octobrachiomorpha (Text-Fig. 8c), in particular, the presence of a Ductus branchialis indicates a gill similar to that in the squids. As described below, only the Laminae branchiales are modified.

According to the results from phylogenetic systematics of the Cephalopoda (BERTHOLD & ENGESER, 1987; ENGESER, 1990; HAAS, 1989a, 1997) one can conclude that the Octobrachiomorpha and the Decabrachiomorpha constitute the monophylum Neocoleoidea, because of the possession of suckers. Thus the Ductus branchialis, present in both taxa, represents the plesiomorph character within the Decabrachiomorpha. In the latter the lack of the Ductus branchialis is then a secondary stage. In considering Spirulida and the Sepiida, the lack of the Ductus branchialis is the result of convergent evolution.



Text-Fig. 8.

Diagrams of cephalopod gills.

a = *Nautilus*; b = *Loligo* (also in Oegopsida); c = *Eledone*; d = *Sepia* (also in *Spirula*).

Cart. = cartilage of the gill lamina; Co. = connective tissue; D.bc. = gill duct; Gl.bc. = branchial gland; La.bc. = branchial lamina; Li.bc. = branchial ligament; Mb.bc. = branchial membrane; Mm.bc. = branchial muscles; N.bc. = branchial nerve; Va.a. = afferent vessel; Va.e. = efferent vessel.

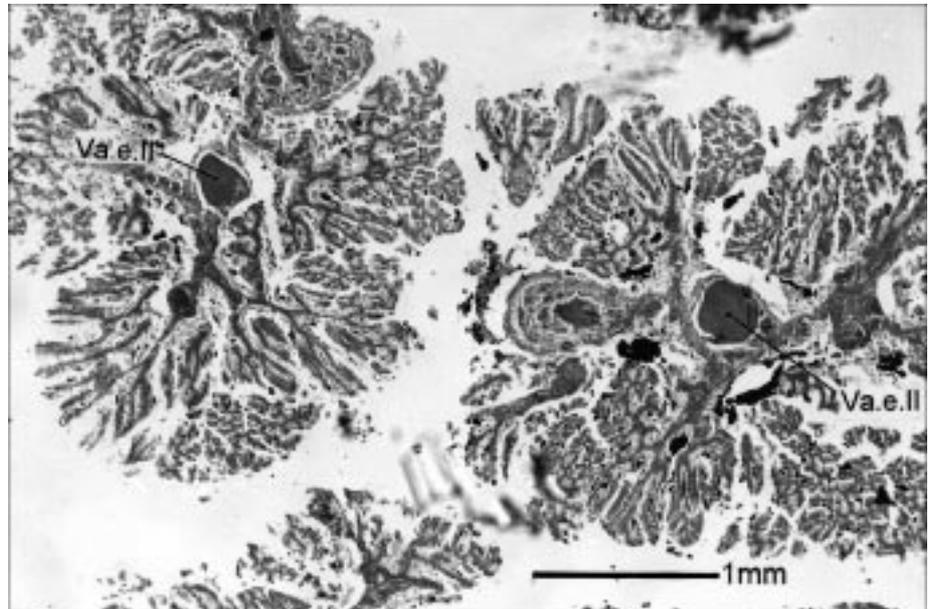
Following the physiological arguments of WELLS & WELLS (1982, 1991) the evolution towards forms without a gill duct may indicate that the rapid swimming Oegopsida and Loliginida travel mainly by jet propulsion. Here, the oxygen extraction rate is low, but the oxygen intake is increased as a result of a high metabolic rate and a high rate of ventilation. The sepiids on the other hand only rarely use jet propulsion and they travel rather slowly in using normal ventilation or movement of their fin-seams. With their large gills they can extract a large quantity of oxygen from sea water (35 %). Likewise *Spirula* is not a propulsion-swim-

mer. It has a similar low metabolic rate to that of *Sepia* so that it can dispense with a Ductus branchialis.

The gills of the recent Octobrachiomorpha have retained the Ductus branchialis though their metabolic rate and oxygen extraction is comparable to that of sepiids (WELLS & WELLS, 1982, 1991). The reduction in the number of gill blades must be compensated by increase of their surface and thus they are complexly folded (up to 8 times) and resemble a brain. This pattern of construction is found in the Vampyromorpha, the Cirrata and the Incirrata, suggesting that the brain-like gills represent the synapo-

Text-Fig. 9.

Horizontal cross section through two multi-plicate gill blades of *Eledone moschata* to show the inner position of efferent vessel of second order (Va.e.II).



morphic character of that group. The arcs of the Ductus branchialis are rather conspicuous. As in Oegopsida and Loliginida, the Octobranchiomorpha gills each contain a branch of the Vas afferens but the lateral branch, present in the oegopsids and loliginids, is degenerated, due to the strong plication of the Laminae branchiales. In living Incirrata the branches of the Vas efferens cannot be seen from

the outside of the gill because it is embedded within the interior of the gill lamina (Text-Fig. 9). *Plesioteuthis* from the Upper Jurassic of Germany (Text-Fig. 10) is, without doubt, a representative of the Octobranchiomorpha (BANDEL & LEICH, 1986) and the shape of its gladius places it close to the Vampyromorpha. Some of the specimens show relics of gills (BANDEL & LEICH, 1986; KLINGHARDT, 1932, 1943; MEHL, 1990). Only the Vas efferens and its branches are preserved. The gills proper are elongated and have a greater number of gill blades (23–26 pairs) than in living Octobranchiomorpha (12 pairs). As the branches of the efferent vessel can be observed at the external edge of the Lamina branchialis the whole gill shows the normal cephalopod shape. It is assumed that they possessed a Ductus branchialis because this is present in all living Octobranchiomorpha. If as indicated, the brain-like type laminae were the synapomorphy of the three living taxa, then the more primitive gills of *Plesioteuthis* and allied forms mean that these need to be assigned to a paraphylum "Trachyteuthimorpha" and are thus stem-line representatives of the Octobranchiomorpha (Text-Fig. 11).

The ideas outlined above on the gills of the "Trachyteuthimorpha", are supported by the configuration studying the x-ray photographs of the gills of *Phragmoteuthis* (MEHL, 1990; REITNER & MEHL, 1989), a palaeocoleoid closely related to the belemnites, from the Lower Jurassic of Holzmaden. The rather long gills show the stout Vas efferens of the first order with alternating straight branches of the second order. Although the Ductus branchialis cannot be seen, these palaeocoleoid gills could be of the loliginid type. In terms of cladistics the shape of the gill and development of the efferent vessels in the Palaeocoleoidea in "Trachyteuthimorpha" resembles that of the loliginid type which must be a plesiomorph character of the Coleoidea assuming that the gill of living Octobranchiomorpha contains the plesiomorph character of a Ductus branchialis.

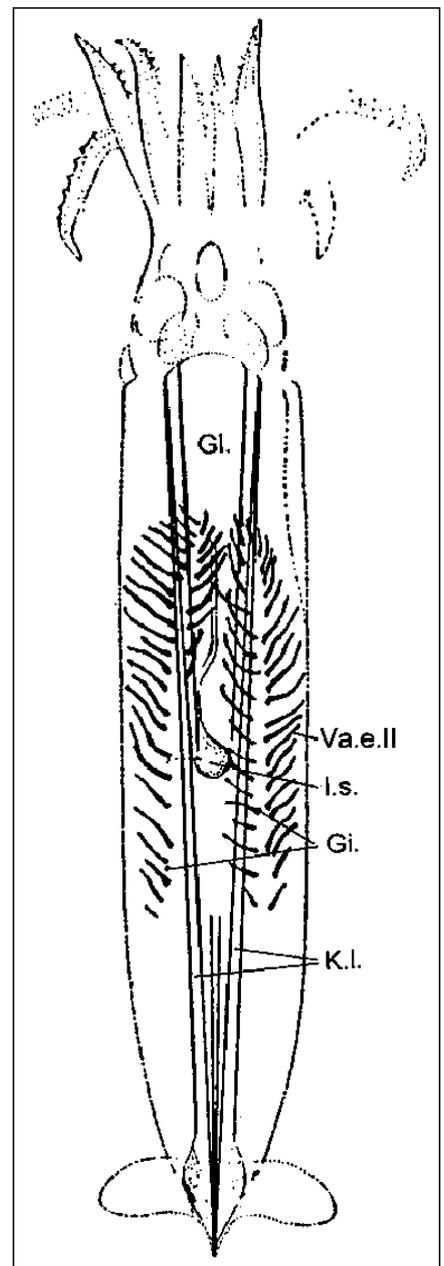
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Text-Fig. 10.

Reconstruction of *Plesioteuthis prisca* RÜPPEL with inscription of gills impressions on the muscular mantle (after MEHL, 1990).

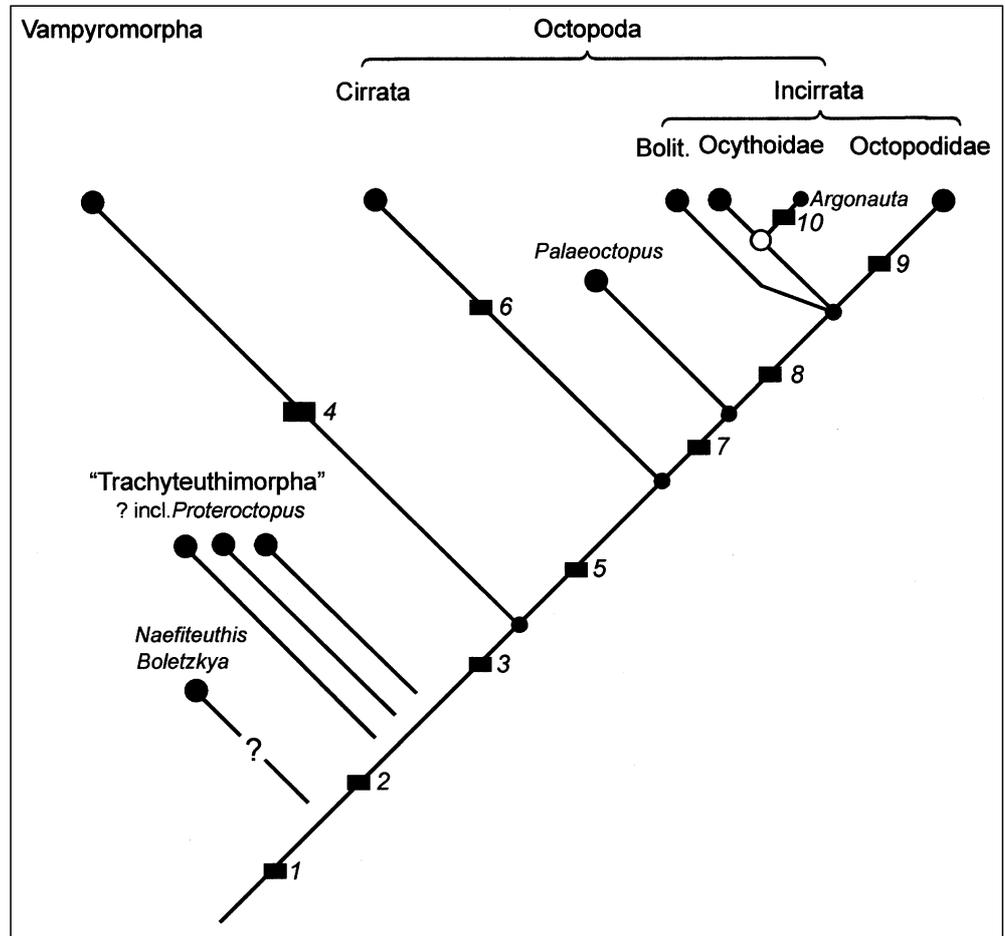
Gl. = gladius; Gi = gill impression; I.s. = ink sac; K.I. = lateral keel of the gladius; Va.e.II = efferent vessel of the second order.



Text-Fig. 11.

Cladogram of living and fossil Octobranchiomorpha showing the position of the "Trachyteuthimorpha" and *Palaeoctopus*.

1 = Strongly reduced phragmococcus, beginning of reduction of second arm-pair. 2 = Second arm-pair markedly reduced; gladius. 3 = Multi-plicate laminae branchiales. 4 = Loss of ink sac; life in deep sea. 5 = Reduction of the middle field of gladius; complete reduction of second arm-pair. 6 = Loss of ink sac; life in deep sea. 7 = Separation of the gladius-sides along midline. 8 = Loss of fins (rudiments in embryonic Incirrata present); loss of cirri; wings of gladius transformed into conchyolinic stylets; crista divided into nine sections; Kölliker's organs; stalked egg cases; incubation. 9 = Enlargement of the middle lobe of brain as a consequence of benthic life style. 10 = Complete loss of gladius; calcareous egg-case secreted by the dorsal arms of the female. Bolit. = Bolitaenida.



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