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THE EVOLUTION OF COLEOID CEPHALOPODS AND THEIR PRESENT BIODIVERSITY AND ECOLOGY

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The present status of phylogeny and classification in coleoid cephalopods and the effect of evolution on the present ecology and biodiversity in the group are examined. The basis of knowledge of cephalopod phylogeny was formulated by Naef in the early 1920s, and his ideas and the progress made in the intervening 75 years are investigated. In the process, the roles that transitions between pelagic and benthic habitats played in the evolution of cephalopods are noted, and the possibility is advanced that the most recent "oceanic anoxic event" may have established a time marker for the divergence of some oegopsid families. The major advances since Naef's work are: 1. The unusual nature of *Vampyroteuthis* has been recognized; 2. The sister-group relationship between the Neocoleoidea and the Belemnoidea has been established, but requires further confirmation; 3. Monophyly has been confirmed for the Decapodiformes (new name), Octopodiformes and Octopoda by molecular and morphological methodologies; 4. The dates of origin of the Belemnoidea, Neocoleoidea, Sepioidea and fossil teuthoids have been extended to considerably earlier times. The major unsolved phylogenetic problems in need of immediate attention are the position of the Myopsida, relationships within the Sepioidea, the identification of the basal nodes within the Oegopsida, and the relationships of most "fossil teuthoids."

This paper, like the symposium for which it was the keynote address, focuses on cephalopod biodiversity, ecology and evolution. These topics blend into one another, and it is often impossible to make sharp distinctions among them. If cephalopod biodiversity and ecology are to be fully understood, they must be viewed in the light of evolution. Evolution moulds the genetic programming of organisms and, in doing so, also moulds their potential for adaptation. For example, the constraints of evolutionary history prevent squid from swimming with the undulatory body motion of fish. Such adaptions determine how an animal interacts with its environment; this is the essence of ecology. Biodiversity, as the end product of evolution, demands a historical perspective.

Evolution is therefore used as the organizing principle for this paper. In a series of monographs on comparative anatomy, systematics, embryology and palaeontology, Naef (1921–1923, 1922) established the foundation for understanding cephalopod evolution. The current goal is to examine how information gathered in the past 75 years impacts on Naef's conclusions about coleoid evolution and to determine promising directions for further advances.

ORIGIN OF COLEOIDEA

The early, rapid diversification of cephalopods, following their origin in the Upper Cambrian (505 million years ago, mya), presumably resulted from their invasion of the pelagic realm where little competition existed. This new independence from the ocean floor was made possible by their chambered, buoyant shell. The Palaeozoic orthoconic cephalopods (straight shells with phragmocone and body chamber) are generally regarded as ectocochleate (shell external) and are thought to have swum by jet propulsion. As such cephalopods lacked the short, deep living chamber presumably needed for *Nautilus*-type funnel-propulsion, the jet was probably produced by head retraction without contraction by the funnel (A. Bidder, U.K., pers. comm. to DTD). Because the volume of water expelled from the mantle cavity would have been small compared to the size of the animal, the animal's speed would have been slow.

The Bactritida – Silurian (c. 428 mya), perhaps Ordovician (c. 470 mya), to late Triassic (c. 216 mya) – have long been seen as the ancestral stock of the Ammonoidea and Coleoidea (Gordon 1966). Bactritids have rather simple orthoconic shells distinguished from their contemporaries by a spherical protoconch and a ventral siphuncle. The Lower Devonian Lamell-orthoceratidae were also orthocones but belonged to the Orthocerida. They possessed calcareous deposits in the apical chambers that, while not an unusual feature, offset the former apical position of their buoyancy chambers and enabled the animal to orientate horizontally. While the lamellorthoceratids are usually regarded as ectocochleate, Bandel and Stanley (1989) offer an alternative reconstruction for one of them: they suggest

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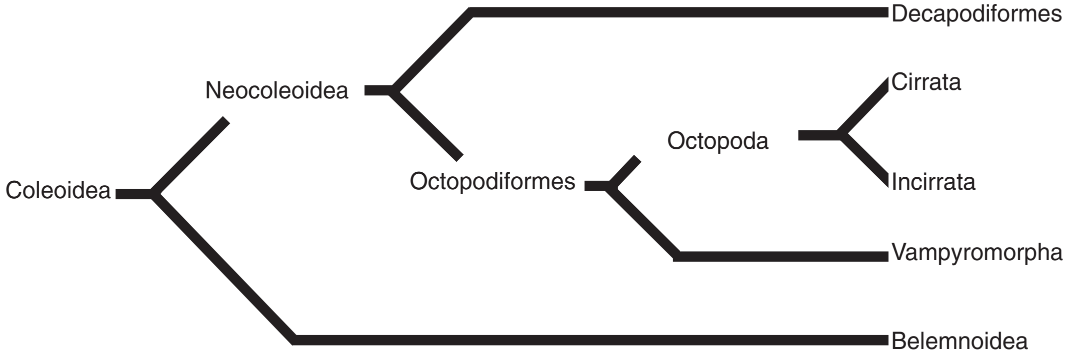

Fig. 1: The basic phylogeny and classification of the Coleoidea

that mantle tissue covered the shell and bore posterior subterminal fins. However, little or no fossil morphological evidence exists for this interpretation.

Other Lower Devonian cephalopods, originally described by Bandel *et al*. (1983), have been reinterpreted from additional material by Bandel and Boletzky (1988). Those authors see *Naefiteuthis* as an animal with a strong dorsal projection of the shell forming the aperture. They call this projection a proostracum and believe a muscular mantle replaced the shell wall laterally and ventrally from it. Their reconstruction is not unlike that suggested for the lamellorthoceratids, the main difference being that the dorsal projection above the aperture of *Naefiteuthis* is longer.

These Lower Devonian animals are plausible, although unproven, early coleoids and could represent a stage in evolution where the shell was only partially internal. They existed at a time when the decline of cephalopod diversity in the later Lower Palaeozoic was correlated with the rise of jawed fish. Fossil records of fish are difficult to interpret before the Devonian, but good fossil records exist from the Devonian onwards. Predatory fish, including the Chondrichthyes and Osteichthyes, probably existed in the Upper Silurian and were well established from the Lower Devonian onwards. In contrast, the diversity of cephalopod genera fell steeply from the Upper Silurian (Kummel 1964, Crick 1990). If the earliest coleoids are Devonian, then the rise of the ammonoids and coleoids at approximately the same time seems more than coincidence. Certainly, the narrow radula, a synapomorphy for coleoids and ammonoids, had evolved by the later Lower Devonian, although Mehl (1984) claimed it was already present in Silurian orthocones. It could be supposed that cephalopod evolution responded to the diversification of fish in the Lower Devonian by giving rise to ammonoids and coleoids.

The interpretation of the current authors of general phylogenetic relationships within the Coleoidea is presented in Figure 1. The term Neocoleoidea identifies the sister group to the Belemnoidea (see Haas 1997); it includes all extant coleoids. This term replaces "Dibranchiata," which also has been used as a synonym of Coleoidea and, further, denotes a structure that may not be unique to the group. The term "Decapodiformes" is used in place of Decapoda to avoid possible confusion of the latter with the crustacean taxon of the same name. However, because of the long history of referring to these cephalopods by the common name "decapods", the latter is maintained as the common name for the Decapodiformes. In addition, the name "Octopodiformes" is used to designate the vampyromorph-octopoda clade because this is considered to be the most appropriate of a variety of names that have been proposed (e.g. Octobrachia, Fioroni 1981; Octo-podiformes, Berthold and Engeser 1987; Vampyromorphoidea, Engeser and Bandel 1988; Vampyropoda, Boletzky 1992).

As indicated by the apparent synapomorphies (shared "advanced" characteristics) of an internal shell, a muscular mantle, 10 arms and an ink sac, coleoids represent a natural group (i.e. they are monophyletic). *Hematites* and *Paleoconus*, belemnoids from the Lower Carboniferous, c. 326 mya (Flower and Gordon 1959) have an internal shell and, therefore, were the first definite coleoids to appear in the fossil record, (Fig. 2). Both have a calcareous "guard" enveloping the apical part of the phragmocone, indicating that the ballast had shifted from a position within an external shell to one on an internal shell. From the outside, a mantle enveloped the shell and presumably secreted the "external" guard. A mantle with muscle of modern type (i.e. parallel arrays of inner and outer longitudinal muscles along with circular and radial muscles) first appeared in the fossil record in the belemnoid *Phragmoteuthis,* Lower Jurassic, c. 185 mya (DTD

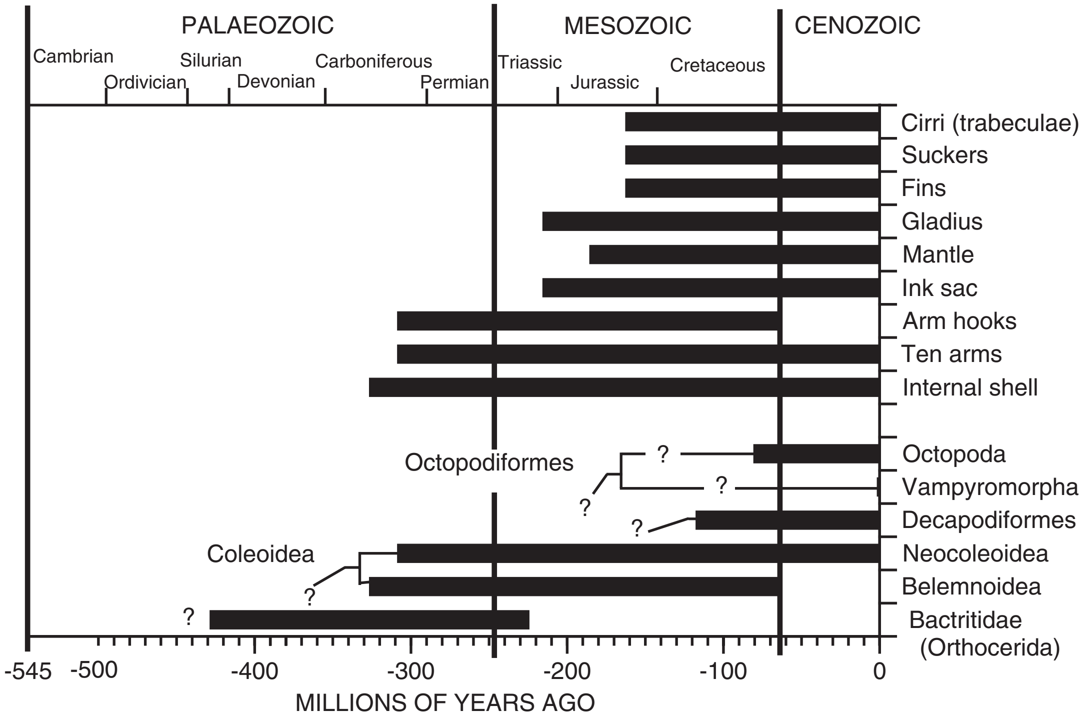

Fig. 2: Palaeochronology of the coleoid fossil record. The upper portion shows structures and the lower portion shows taxa. Solid bars indicate the time range over which a character or a taxon is known

pers. obs.). Ten similar arms first appeared in the fossil record in *Jeletzkya*, an apparent belemnoid from the Upper Carboniferous, c. 308 mya (Johnson and Richardson 1968). *Jeletzkya* also had paired hooks on the arms. Unfortunately, the anatomy of *Jeletzkya*, apart from the arm crown, is virtually unknown; therefore, the status of the shell as internal remains unproven. An ink sac first appeared in the fossil record in *"Loligosepia,"* a neocoleoid from the late Triassic, c. 215 mya (Reitner 1978).

One might expect the presence of fins to be another synapomorphy for the Coleoidea. Surprisingly, there are no clear records of fins in the Belemnoidea, although they are frequently included in reconstructions (e.g. Abel 1916, Naef 1922). True fins are first known in *Mastigophora* ("fossil teuthoid") from the Middle Jurassic, c. 162 mya (Donovan 1983). Another fin showing detailed structure is known from *Trachyteuthis* ("fossil teuthoid") from the Upper Jurassic, c. 145–150 mya (Donovan 1995).

Because the extinct Belemnoidea possessed hooks on the arms, Naef (1921–1923) thought they belonged to the Decapodiformes. He assumed that the hooks were derived from the horny sucker rings found only in decapods. Decapod suckers and belemnoid hooks, however, differ in important ways: sucker rings, unlike belemnoid hooks, are not known to fossilize (Engeser and Clarke 1988); belemnoid hooks, unlike decapod hooks, do not appear to be ontogenetically derived from sucker rings (Engeser and Clarke 1988), although this would probably be difficult to detect; and belemnoid hooks, unlike suckers that alternate and form oblique pairs in extant decapods, are arranged on the arms as opposite one another, forming transverse pairs (Haas 1989). This arrangement of "transverse pairs" also occurs with cirri in octopodiforms. Therefore, belemnoid hooks could be homologous with cirri (Engeser and Bandel 1988) or their early precursors (Haas 1989). In support of this, cirri (= trabeculae) are well preserved in some neocoleoid fossils (see below), but they are unknown in belemnoid fossils.

The problem is further complicated by the finding of apparent suckers and hooks on the same specimen of the belemnoid *Belemnoteuthis antiquus* (Donovan and Crane 1992). These "suckers," however, are more likely the muscular bases from which the hooks arose.

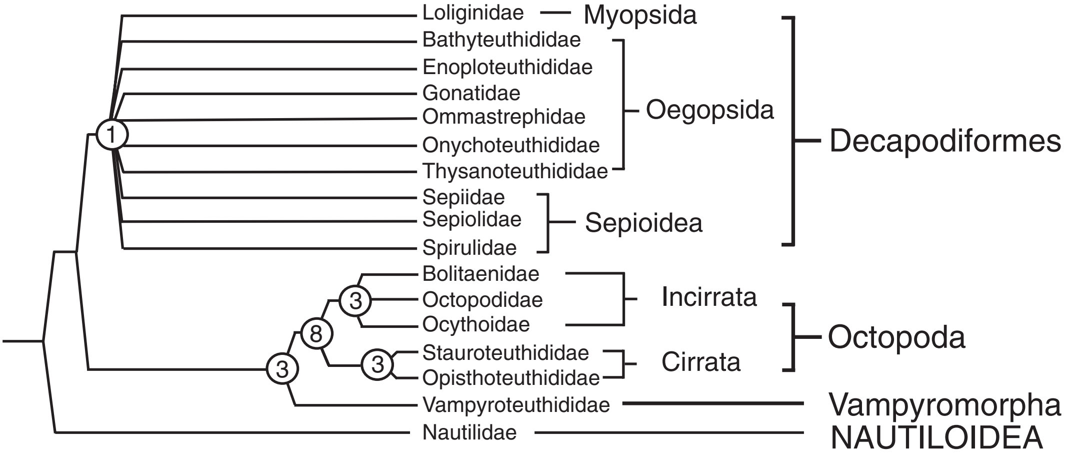

Fig. 3: Left, cladistic analysis of the Coleoidea shows the number of unambiguous characters that support the various taxa (after Young and Vecchione 1996). Note that only representative families were used in their study. Right, classification followed in the present paper

This interpretation strengthens the similarity between fossil hooks and the hooks found today in some squid. The oldest definite suckers are from the "fossil teuthoids" (see below) *Mastigophora,* Jurassic, c. 162 mya (Vecchione *et al.* 1998) and *Plesioteuthis*, about the same age (Bandel and Leich 1986); the first records of trabeculae (= cirri) are from this same specimen of *Plesioteuthis*. If belemnoid hooks and the suckers of neocoleoids are not homologous, then suckers become a character that unites all neocoleoids (Engeser and Bandel 1988). The data of Doguzhaeva *et al.* (1996) on a presumed neocoleoid from the Upper Carboniferous (c. 305 mya) indicate the early divergence of the two lineages. The appearance of cirri, suckers, fins and mantles only in the early Jurassic may be an artifact, because these anatomical features are most commonly preserved in the rare deposits known as "Lagerstätten", which are virtually unknown in the Permian and Triassic.

The separation of the two major coleoid lineages is supported by the structure of their respective shells. The Sepiidae and the Spirulidae are the only Recent neocoleoids that possess a phragmocone. The wall structure of the phragmocone in these families is very different from that of the Belemnoidea. The belemnoids have the same three basic layers in the shell as the ectocochleates (i.e. inner prismatic, nacreous, outer prismatic), whereas sepiids and *Spirula* (as well as the many fossil relatives of *Sepia* and *Spirula* – see below) lack the nacreous layer (Doguzhaeva 1996). The oldest sepioid fossils known are *Adygeya* and *Naefia*, Cretaceous, c. 117 mya (Doguzhaeva 1996). The oldest neocoleoid known is "*Bactrites*" *postremus*, which apparently represents a new group from the Upper Carboniferous and also has a shell wall without a nacreous layer (Doguzhaeva *et al.* 1996). A fossil of a soft-bodied cephalopod from the Carboniferous, c. 308 mya (Allison 1987), appears to have 10 similar arms and structures that may be fins, but the shell/gladius is unknown. This fossil could prove to be an early octopodiform, but more information is needed.

The division of the Neocoleoidea into the Octopodiformes and the Decapodiformes is supported by data on extant forms. In many neocoleoids the only remnant of the shell is the gladius. A stiff gladius, when present, helps maintain a constant mantle length during jet swimming and forms an important attachment site (actually the shell sac) for head and funnel retractor muscles. The first gladius to appear in the fossil record is from "*Loligosepia*" from the Upper Triassic, c. 215 mya (Reitner 1978). In some cases gladii were calcified (e.g. *Trachyteuthis* – Donovan 1977) and the animals are considered benthic, whereas in others, gladii were chitinous and the animals are considered pelagic (e.g. *Loligosepia*, Donovan and Toll 1988). The large variety of cephalopods known from fossil gladii were placed by Naef (1922) in the Teuthoidea. These are referred to as "fossil teuthoids" in this paper. In 1922 the shell of *Vampyroteuthis*, which later proved to be a gladius, was not fully described. Because similar gladii have been independently derived (see below) in the Octopodiformes and the Decapodiformes, the relationships of most of these fossils to the Vampyromorpha or the

Decapodiformes are uncertain. The one feature that can place these fossils into the proper group is the presence or absence of tentacles. Soft parts are rarely preserved and, if they are, the absence of tentacles may simply be a preservation artifact; as a result, their presence can only be assumed. The current authors know of only one case where strong evidence exists for the presence of tentacles: species of *Mastigophora* appear to have tentacles (Vecchione *et al.* 1998). Members of this family, therefore, can be placed in the Decapodiformes. Relationships of all other families based on gladii must remain uncertain at present.

While knowledge of the phylogenetic relationships of various "fossil teuthoids" will greatly advance understanding of coleoid evolution, most were deposited in shallow-water, shelf sediments. If oceanic coleoids played critical roles in evolution, their roles will probably not be demonstrated by the fossil record. Comparative anatomy, embryology and molecular genetics of extant forms must therefore provide the basis for understanding the evolution of modern coleoids.

OCTOPODIFORMES

A variety of different classifications has been used within the Coleoidea (e.g. Berthold and Engeser 1987, Clarke and Trueman 1988, Engeser 1990, Khromov 1990, Doyle *et al.* 1994, J. Z. Young 1995, Haas 1997). For this paper, an older classification is used (Fig. 3) that differs only slightly from that used by Naef and appears in a variety of recent works (e. g. Roper *et al.* 1984, Mangold 1989). In this classification, the Decapodiformes consists of the Sepioidea, the Myopsida and the Oegopsida (the latter two taxa are often combined into the Teuthoidea); the Octopoda consists of the Cirrata and Incirrata. Once a stable phylogeny based on cladistic analyses using morphological, molecular and fossil data is achieved, a new classification may be needed.

The basic arrangement of modern coleoids into two major groups, the Decapodiformes and the Octopodiformes, and the position of the Vampyromorpha and Octopoda as sister groups are supported by morphological (Young and Vecchione 1996) and molecular (Carlini and Graves in press) cladistic analyses, and are given equivocal support by another molecular study (Bonnaud *et al.* 1997). In addition, morphological and molecular cladistic analyses support the monophyly of the Octopoda (Young and Vecchione 1996, Carlini and Graves in press). Figure 3 shows the degree of morphological support for the major groups based on the families examined by Young and Vecchione (1996).

The Octopoda had eight unambiguous character changes that supported its monophyly. The Decapodiformes had just a single apomorphy: modification of the fourth pair of arms into tentacles. The many characters that support the Octopoda probably resulted from major morphological changes that occurred as evolving octopods moved from a pelagic to a benthic existence (see below). Prior to Young and Vecchione (1996) and the molecular studies, a sister-group relationship between the Vampyromorpha and the Octopoda had been controversial. *Vampyroteuthis* was originally placed as a family in the finned octopods (Cirrata), then was later elevated to its own order, although the phylogenetic position of the order was uncertain (Pickford 1939). Two features of *Vampyroteuthis* were pivotal in the elevation: a broad gladius that reached the full mantle length and retractile filaments that seemed to be the modified second pair of arms, thereby giving the animal 10 pairs of arms. The description of a vampire "embryo" (Young and Vecchione in prep.) supports the interpretation of vampire relationships. While the small vampire was a hatchling captured between depths of 1 050 and 1 300 m, morphologically it was still an embryo, as indicated by the incomplete development of the eyes and eyelids and the large internal yolk supply. Characters of particular interest were that the mantle was not fused to the head in the nuchal region, and that the filaments were relatively large. The octopod-like fusion of the head and mantle found in older *Vampyroteuthis*, therefore, is derived independently from the octopods, as indicated by Pickford (1949) and Young and Vecchione (in prep.), and the size and the position of the filaments supports their interpretation as the second pair of arms.

Evolution of the octopodiform lineage may have resulted from early pelagic members adopting an orientation with laterally directed arms, which pre-adapted them to settle oral-end down on the ocean floor. In such a scenario *Vampyroteuthis* approaches an intermediate form. Alternatively, a benthic horizontal animal could gradually shorten its body axis and the buccal crown could rotate ventrally. In that scenario, an intermediate form may be more like that of the sepiolids (Fig. 4).

The close relative, *Vampyroteuthis*, provides clues to which process occurred. Judging from arm morphology, the relaxed vampire probably has its arms spread laterally, as do most octopods. When disturbed, it can curl its web aborally (i.e. posteriorly), making it difficult for a small predator to grasp a portion of the animal, again as in most octopods. This is especially effective because the buccal crown, which could easily be bitten by a predator, is absent in *Vampyroteuthis* and octopods. These interesting similarities do not make a convincing argument. Neither does the superficial morphological similarity between *Vampyroteuthis* and the cirrates,

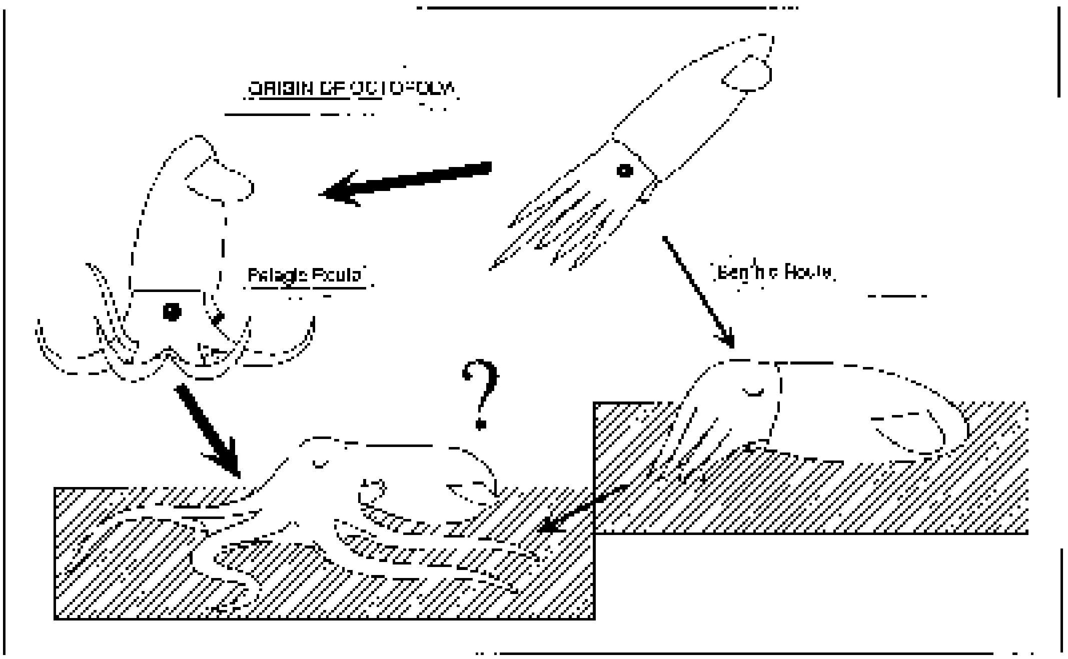

Fig. 4: Hypothetical scheme showing two alternative routes in the evolution of a benthic octopod from a pelagic ancestor. Heavy arrows indicate route favoured by the authors

often considered the most primitive octopods. The cirrates, of course, are the sister group to the incirrates; technically, both groups have a simultaneous origin. Whereas the cirrates have retained a number of primitive features (e.g. fins, cirri), they have lost others (e.g. ink sac, radula in most cases); therefore, they may be highly modified from the common ancestor.

The most telling clue for identifying the process leading to the origin of the Octopoda comes from the structure of the *Vampyroteuthis* brain. One of its peculiar features is the incipient development of an inferior frontal lobe system. This bathypelagic animal apparently has evolved a relatively advanced system for processing complex chemotactile information from the arms, one that surpasses that of shallow-living and benthic decapods. *Vampyroteuthis* apparently uses its arms in an unusual manner. Perhaps *Vampyroteuthis*, like its immediate ancestor (a "preoctopod"), associates with pelagic cnidarians or tunicates and uses its arms and suckers to adhere to and/or explore the surfaces of these gelatinous animals. In such a situation, an oral-end approach would be advantageous; as there would be no consistent orientation relative to gravity, only the oral end would be in contact with the jellyfish/tunicate. Some pelagic incirrate octopods today (e.g. *Argonauta*, *Ocythoe*) sometimes are associated with gelatinous animals, evidently preadapted to do so by benthic ancestry. Perhaps the "pre-octopod" also was preadapted, to a lesser extent, to move onto the ocean floor by the development of exploratory behaviour of large objects (presumably gelatinous animals) with the arms and suckers. Maybe such an association between *Vampyroteuthis* and gelatinous animals will be found; indeed, cnidarians are known to be in the diet of *Vampyroteuthis* (Nixon and Dilly 1977). If correct, this scenario implies that a major evolutionary innovation occurred in the species-poor pelagic environment that made possible a unique type of invasion of the benthos.

This unusual oral-end-down mode of associating with the ocean floor presumably is the stimulus for the pronounced morphological changes associated with the octopod lineage and the evolution of a crawling habit with the use of the arms. Perhaps the habitat of the early octopods was similar to the quasi-benthic one of some cirrates (e.g. "*Grimpoteuthis*") today (see Vecchione and Young 1997, and Fig. 5). The flexibility required by this benthic/quasi-benthic early octopod is incompatible with a rigid gladius; the gladius was reduced to fin supports, as seen today in cirrates. The modified Arms II were lost. The suckers became pro-

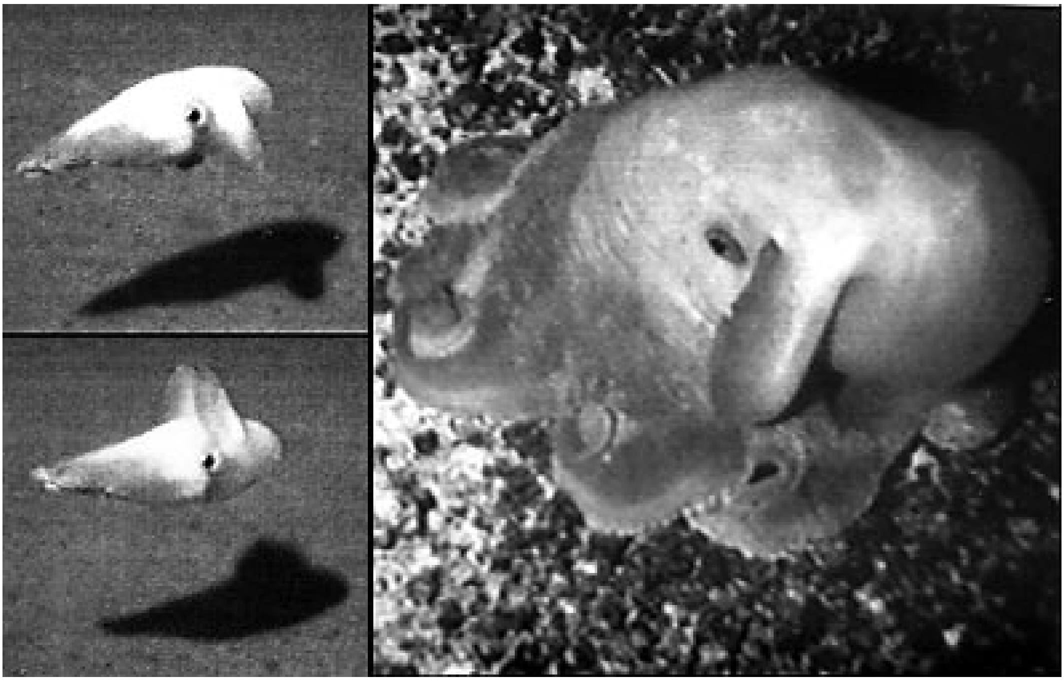

Fig. 5: A cirrate octopod (*Grimpoteuthis* ?) shown swimming (left) using the large fins and sitting (right) on the substratum

gressively more important in detecting and capturing prey and in dealing with the complex substratum, as indicated by the development of the inferior-frontal system of the brain. These ancestral octopods did not evolve corneas to protect their delicate eye lenses but apparently did develop complex inner eyelids similar to those found today in *Opisthoteuthis* (if it is assumed that these represent an early stage in cornea development rather than cornea reduction). The divergence of the early octopods into the two present octopod lineages may reflect the adoption of different habitats: a benthic, cryptic, probably shallow-water habitat by the incirrates and a quasi-benthic, open, deep-water habitat by the cirrates.

CIRRATA

The cirrates are typified by the extreme compaction of their viscera and the reduction of their mantle cavities. Jet propulsion utilizing the mantle seems to have been virtually lost in this group; locomotion relies on swimming with fins (Fig. 5) and medusoid contractions of the arms and web (Vecchione and Young 1997, Villanueva *et al.* 1997). Medusoid swimming also is used by some incirrates as an accessory mode to mantle-based jet propulsion and crawling. The foreshortening of the body is more extensive in cirrates than in incirrates, and it culminates in the nearly flat opisthoteuthids. Some cirrates (e.g. *Stauroteuthis, Cirroteuthis*) are now entirely pelagic, although often living near the bottom, but retain adaptations presumably to their earlier quasibenthic habitat (compaction of the viscera, loss of jet propulsion, presence of a fully formed, inferior frontal lobe system, single oviduct, fusion of the head and mantle, and reduction of the shell).

INCIRRATA

Present incirrates have lost their fins, and only three families (Octopodidae, Alloposidae, Tremoctopodidae) retain remnants of the gladius (stylets), which at one time supported fins. A break in the mantle musculature still marks the former fin-support location in most

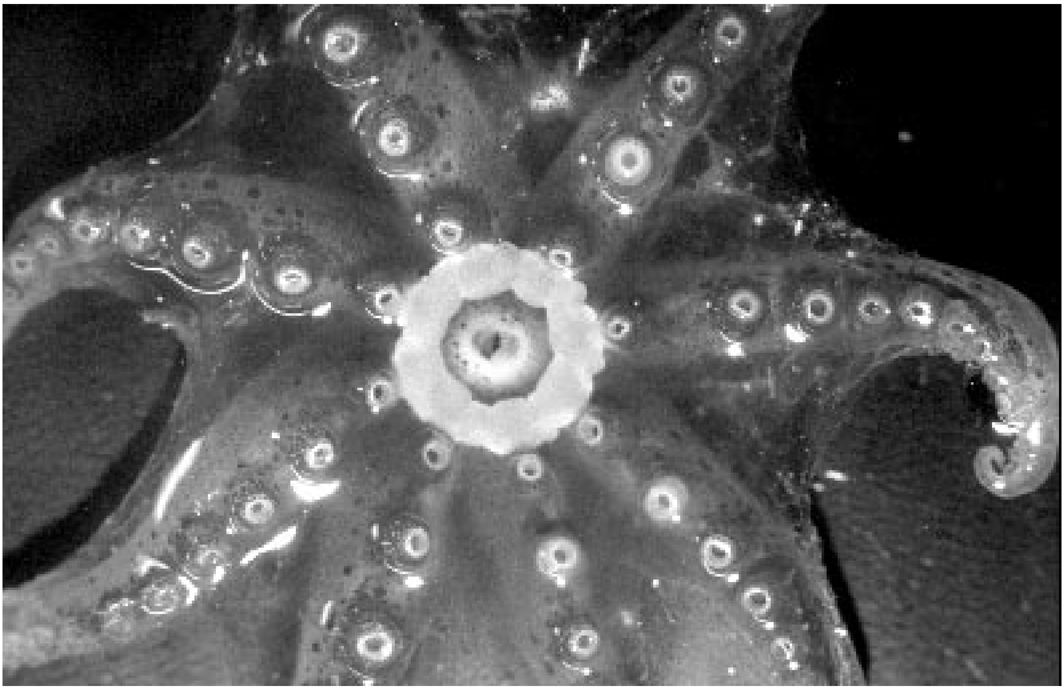

Fig. 6: Oral view of a bolitaenid octopod (*Japetella*) showing the large, lobate, ring-shaped photophore that surrounds the mouth. In life, this organ is bright yellow

families. Although *Palaeoctopus newboldi* from the Late Cretaceous (80 mya) of Lebanon has fins, it has the shape of an incirrate. Because fins probably were present in early incirrates as well as cirrates, the present authors agree with Engeser's (1988) placement of this octopod in the Incirrata. If this placement is correct, the divergence of the two octopod clades occurred prior to the Late Cretaceous. The earliest supposed fossil record of an octopus is *Proteroctopus ribeti* (Fischer and Riou 1982a) from the Middle Jurassic (160 mya) of France. Engeser (1988) questioned the octopod affinity of that fossil, and its cephalopod affinity must also be questioned given the non-cephalopod appearance of the arms (i.e. the presence of regular chevron-shaped marks; the smooth, regular curve to the arms; the uniform thickness throughout most of the arm length rather than gradually decreasing thickness; and the convergence of the arms at a nearly pointed, common apex). The oldest certain fossil incirrates are *Argonauta* shells found in the Oligocene of Japan, c. 25 mya (Noda *et al.* 1986).

The loss of fins and the further reduction of the gladius are easy to understand in the early incirrates. Probably such animals swam infrequently, moved between confined spaces on hard substratum (e.g. reefs) and resided in small holes or buried in the sand. Naef (1921–1923) suggested that the development of corneas to protect the delicate eye lenses was an adaptation for burying in the sand or other sediment.

The reproductive system in the incirrates, as in the cirrates, underwent considerable change. The third arms were modified for the transfer of spermatophores. Judging from the absence of nidamental or accessory nidamental glands in *Vampyroteuthis* and extant octopods, one must presume that these organs were absent in the pelagic ancestors to octopods. Such early octopods would be ill-prepared for benthic spawning without the protective egg coatings provided by such organs. A new behaviour evolved: brooding (care of the embryos until hatching). Females developed eggs with chorions drawn out at one end to provide a stalk for attachment to the substratum. While little is known about the spawning habits of *Vampyroteuthis,* there is no evidence to suggest that either this animal or the cirrates brood their young, and brooding is rare in the decapods (see, however, Okutani *et al.* 1995, Seibel *et al.* 1997a).

Incirrates have also reinvaded the pelagic realm.

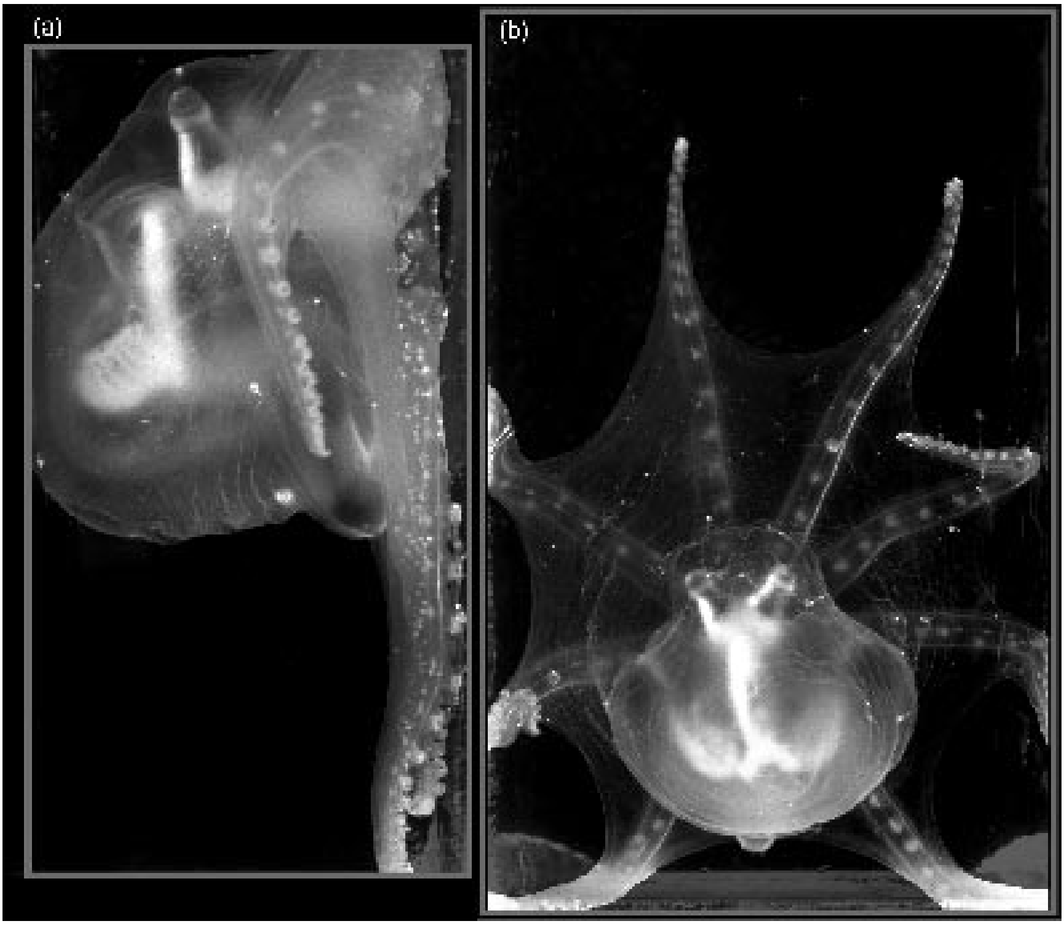

Fig. 7: Amphitretidae (*Amphitretus pelagicus*) viewed in a small ship-board aquarium – (a) Side view as octopod crawls up side of tank – note vertical orientation of the digestive-gland complex as indicated by the strong vertical reflection; (b) Dorsal view as octopod crawls up back of tank – note the diverging optical axes of the eyes

Indeed, seven of the eight incirrate families are pelagic (only the Octopodidae is benthic). However, because pelagic species carry the morphological modifications of their former habitat (i.e. the presence of corneas, absence of shell, fins and cirri, fully formed inferior frontal lobe system, probably stalked chorions and brooding), the benthic lifestyle was clearly the ancestral mode. Little is known about how, or how often, reinvasion of the pelagic realm occurred. Many benthic incirrates today, however, are known to produce pelagic paralarvae that often reach a large size in the plankton. Seemingly, a small change would allow a pelagic paralarva to become permanently pelagic, although the habit of brooding would be an obstacle for transition to pelagic life. The mode of reproduction is unknown in the Amphitretidae, but probably all pelagic incirrate octopods retained the brooding habit in some form (*Ocythoe* and possibly *Vitreledonella* brood their young in the oviducts, the bolitaenids *Tremoctopus* and *Haliphron* within the arm crown, and *Argonauta* first within the oviducts, then in the external “shell”).

The present pelagic families of the Incirrata evolved from a benthic ancestor, but there is only poor understanding of their evolutionary relationships. One of the most distinctive of the pelagic families is the Bolitaenidae (3 genera) that occupy meso- and bathypelagic water. Molecular data from the COI (cytochrome c

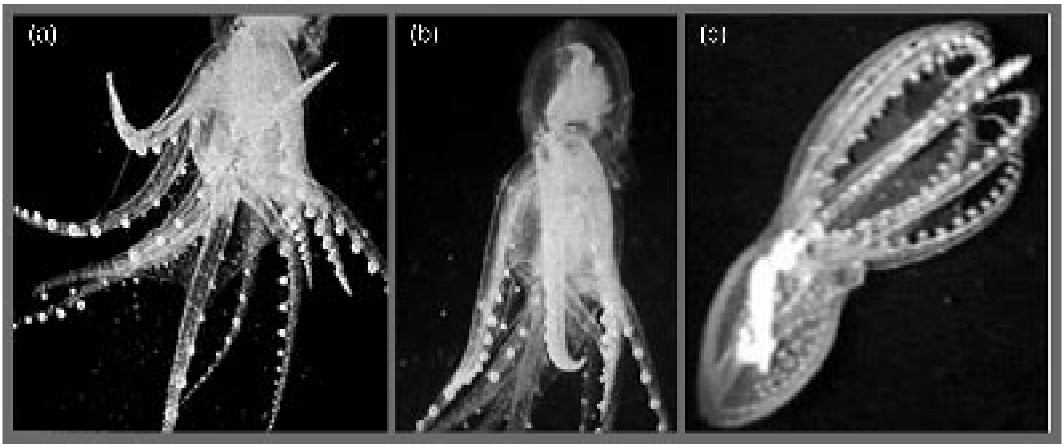

Fig. 8: Vitreledonellidae (*Vitreledonella richardi*) videotaped from submersibles – (a) and (b) Two pictures taken in sequence as the submersible approached the octopods off Hawaii – note that each picture shows two octopods, one engulfed within the web of the other (courtesy C. Young (Harbor Branch Oceanographic Institute, U.S.A., and the University of Hawaii HURL program); (c) Single individual photographed in the Atlantic while moving downwards - note the vertically orientated digestive-gland complex (spindle-shaped, bright reflection; courtesy R. Larsen, Fish and Wildlife Service, U.S.A., and R. Harbison, Woods Hole Oceanographic Institution, U.S.A.)

oxidase I) gene consistently placed bolitaenids with the finned octopods, but without meaningful bootstrap support (Carlini and Graves in press). Perhaps this placement is indicative of an early derivation of bolitaenids from the incirrate lineage rather than from the Cirrata. Members of this family are the only incirrates known to be bioluminescent. Females develop a circular luminescent organ around the mouth at maturity (Fig. 6); presumably the luminescence from this organ is used to attract a male in dark bathypelagic depths (Robison and Young 1981, Herring *et al.* 1987).

The families Vitreledonellidae and Amphitretidae may be closely related (Voight 1997). One of the primary characters supporting this relationship is the supposed position of the stomach and caecum "anterior" to the digestive gland. Normally, in octopods, the stomach and caecum lie posterior to the digestive gland. In living representatives of these two pelagic families, however, the position of those organs maintains a normal positional relationship to one another, with the stomach and caecum tightly adherent to the long and tapering digestive gland. The whole complex, however, has become more slender and elongate and rotated to a transverse position relative to the body axis (e.g. Figs 7, 8, Young *et al.* 1996). When the octopods are orientated horizontally, the digestive gland complex will be orientated vertically and this will, presumably, aid in concealing these opaque structures in these mostly transparent octopods. The slender, vertically orientated complex will cast a reduced shadow at depths where some downwelling daylight exists, and the reflective tissue that covers these structures will reduce their visibility from other angles. During preservation, however, the complex falls forward to place the stomach and caecum in an anterior position, thereby reversing the normal, octopod orientation. As the vertical arrangement is highly adaptive for life in the upper mesopelagic zone, which these octopods, at least occasionally, occupy, the similarity may be convergent.

Each family is represented by a single species and little is known about the biology or ecology of either. *Vitreledonella* has been observed twice from submersibles. A single individual was seen in Bahamian waters obliquely orientated at a depth of 880 m with the digestive gland complex vertically orientated. Two individuals of *Vitreledonella*, one engulfed within the web of the other and presumably mating, were observed at a depth of 909 m off Hawaii (Fig. 8). *Amphitretus* has never been observed from submersibles, but it has been observed in shipboard aquaria. This octopod has two peculiar morphological features that are not well understood: the base of the funnel is fused to the mantle, and the eyes are tubular. Both features are unique in the Octopoda. The eyes are directed dorsolaterally with their optical axes diverging 70°, which contrasts with the tubular eyes found in fish and squid, that have parallel orientation.

Fig. 9: Enlargement of the eye from the photograph in Figure 7, with the outline of a circular lens (white circle) and the corresponding position of a retina (white semicircle) for an eye that obeys Mathiesson's ratio. Note that the semicircle appears well distal to the probable position of the retina

In addition, judging from photographs of a living *Amphitretus*, the eyes seem too elongate to match Mathiesson's Ratio (i.e. lens centre to retina distance is 2.55 × the lens radius), which is demanded of fish and squid, with spherical lenses (Land 1981, Fig. 9). Normally, fish and squid with tubular upward-looking eyes are found living in the upper mesopelagic realm during the day, where faint downwelling light can silhouette animals lacking photophores for concealment. Tubular eyes usually correspond to the core of a large eye; that is, they are large eyes trimmed to a compact shape that has the added advantage of being more easily camouflaged than a hemispherical eye. How the peculiar eyes of *Amphitretus* fit into this scenario is not clear at present.

Four of the remaining incirrate families form a clade, the Argonautoidea, based on the presence of a hectocotylus that is detachable and that develops in a sac. Naef (1921–1923) suggested relationships among these families based on the structure of the hectocotylus. One of the many challenges in moving from the benthic to the pelagic environment is the need to modify the method of mating. In benthic octopodids, mating often takes place with the participants physically separated except for the male hectocotylus, which extends into the mantle cavity of the female; such an arrangement would be difficult to accomplish in the pelagic realm. The mating problem has been solved in the pelagic argonautoids by the presence of a detachable hectocotylized arm that is left with the female at mating.

Apparently, the first family to diverge within the Argonautoidea was the Alloposidae (Naef 1921–1923), known today from a single species that reaches 2 m in length (Nesis 1987). This octopod, whose ecology is poorly understood, usually is found in association with island or continental slopes but, apparently, is pelagic and on occasion found far from land. A brooding female drifting near the ocean floor has been observed from a submersible (R. E. Young 1995), and sometimes this octopod is caught in large numbers by bottom trawls (MV, pers. obs., Burgess 1972). Males reach a large size but not nearly as large as females. The remaining three families of argonautoids (of which *Tremoctopus* apparently diverged first) are noted for the presence of dwarf males. *Ocythoe tuberculata,* the only species in the Ocythoidae, has a bitemperate distribution (Roper and Sweeney 1975) and is caught in surface waters, at least at night (Seki 1997). *Tremoctopus*, the only genus (two species) in the Tremoctopodidae, attains a length of about 2 m (Nesis 1987) and sometimes is seen at the surface during the day in subtropical waters (N. A. Voss, University of Miami, pers. comm., REY, pers. obs.). The more common species, *T. violaceus*, has an extensive web between the slender dorsal arms; portions of this dorsal complex apparently can be autotomized to confuse predators (Portmann 1952).

The most speciose family in the Argonautoidea is the Argonautidae, with at least four recognized species (Nesis 1987). The female "paper nautilus" secretes a calcareous "shell" with the dorsal arms. This structure, which bears no relationship to the true cephalopod shell, acts as a brood chamber and probably a buoyancy device (Young 1960). It also apparently provides some protection from small predators, because argonauts retrieved from the stomachs of lancetfish have all the arms fully retracted inside the "shell" and only the arm bases and beaks are exposed to the predators

(REY, pers. obs.). This defensive behaviour is commonly seen in shallow-water octopodids under attack in rock holes. The earliest known argonaut "shells" from the fossil record (i.e. 25 mya) are more heavily calcified than in *Argonauta,* which suggests an evolutionary trend in this group towards reduction of calcification, apparently exchanging protective features for lightness.

Today *Argonauta* is the sole survivor of several Tertiary genera. Naef (1921–1923) provided a possible explanation for the evolution of this unusual "shell" and its close resemblance to some Cretaceous ammonoids. He suggested that ancestral argonauts occupied empty ammonoid shells during the late Cretaceous. After the ammonoids had become extinct at the end of the Cretaceous (c. 65 mya), the octopods evolved glandular structures on the arms to extend (repair) the occupied shells of the ammonoids. Eventually, the ammonoid shells were completely replaced by secreted "shells" and the secreted "shells" retained the shape of the original moulds. Unfortunately, this innovative suggestion is not supported by the fossil record. A gap of roughly 40 million years exists between ammonoid extinction and the first records of fossil argonauts. However, perhaps Naef's suggestion is essentially correct except that the mould was not an ammonoid shell but that of some other animal, and the resemblance to the ammonoid shell is coincidental. The origin of the argonaut "shell" presents another dilemma. If *Argonauta* is the most recently derived member of the Argonautoidea, as Naef believed, and if a host shell served as a mould, then the host shell must have been floating, because *Argonauta* would already be pelagic. One alternative is that the evolutionary sequence for the Argonautoidea could be reversed, with *Argonauta* the most "primitive" member and the one involved in the benthic to pelagic transition with the "shell" plesiomorphic to this clade. The evolution of the argonaut "shell" remains a challenging problem.

The Octopodidae, the only benthic family among the Incirrata, contains more than 90% of incirrate species. Success of the octopodids can be attributed partially to their remarkable abilities for concealment, which Hanlon and Messenger (1996) call "neurally controlled polymorphism." This term emphasizes that concealment not only involves colour change, although this alone far surpasses the capabilities of all non-cephalopod animals, but it also includes rapid changes in skin texture and body form. In addition to concealment, success of octopodids is aided by their ability to crawl and move through small openings, owing, in part, to the near absence of an internal skeleton and the unusual capabilities of their very long, highly mobile, sucker-laden arms. Many years ago, the late J. Z. Young pointed out the difficult computational problem for a central nervous system that must control structures with a large variety of potential movements. The vertebrate central nervous system can calculate the position of a foot by knowing the movement at a few joints. The octopod arm has an almost infinite number of joints. To solve this problem, octopods transfer control from the brain to ganglia located within the arms. Indeed, the nervous system of the arms contains more than twice as many neurons as the brain (Young 1963). An arm that has been cut from an octopus moves in a very coordinated fashion, its suckers alternately attaching and releasing. Some octopodids can autotomize one or more arms, which continue to move independently, as a defence against predators (Norman 1992). In argonautoids, the detached hectocotylized arm moves freely within the mantle cavity of the female. The unusual arms, combined with their armament of highly versatile suckers (Packard 1988), provided the octopods with new capabilities, such as the ability to locate and capture unseen prey. These abilities helped the octopodids become the most speciose family of the Neocoleoidea.

Many octopodids are found today in deep-sea and polar regions. Voss (1988) listed 11 genera with 48 species in these habitats, and more species have been described since (e.g. Voss and Pearcy 1990). With few exceptions, character states important in the systematics of deep-sea and polar benthic octopods involve degeneration or loss of structures (Voight 1993). While typical of deep-sea faunas (Marshall 1979), such losses highlight a major problem in deciphering evolutionary relationships. If character states are to be informative in cladistic analysis, homology must be distinguished from homoplasy. In octopodids, for example, the presence of an ink sac and a radula is the ancestral state, and their absence in some deep-sea and polar species is common. Multiple invasions of these habitats could easily generate multiple losses of such structures. In fact, the shared loss or reduction of these structures in cirrates and deep benthic incirrates is certainly a result of convergence. Typically, one looks for evidence of convergence by carefully examining the structure and development of the characters in question; however, the morphology of lost characters cannot be compared. Young and Vecchione (1996) found it prudent to avoid such characters in cladistic analyses. Unfortunately, the number of informative morphological synapomorphies remaining for deep-sea and polar octopodids is far too few to make sense of relationships. Many more deep-sea and polar species await discovery and these will compound the problem of unraveling evolutionary relationships. These remote habitats offer a major challenge to cephalopod phylogeneticists. Clearly, both molecular studies and delineation of new morphological or developmental characters will be necessary

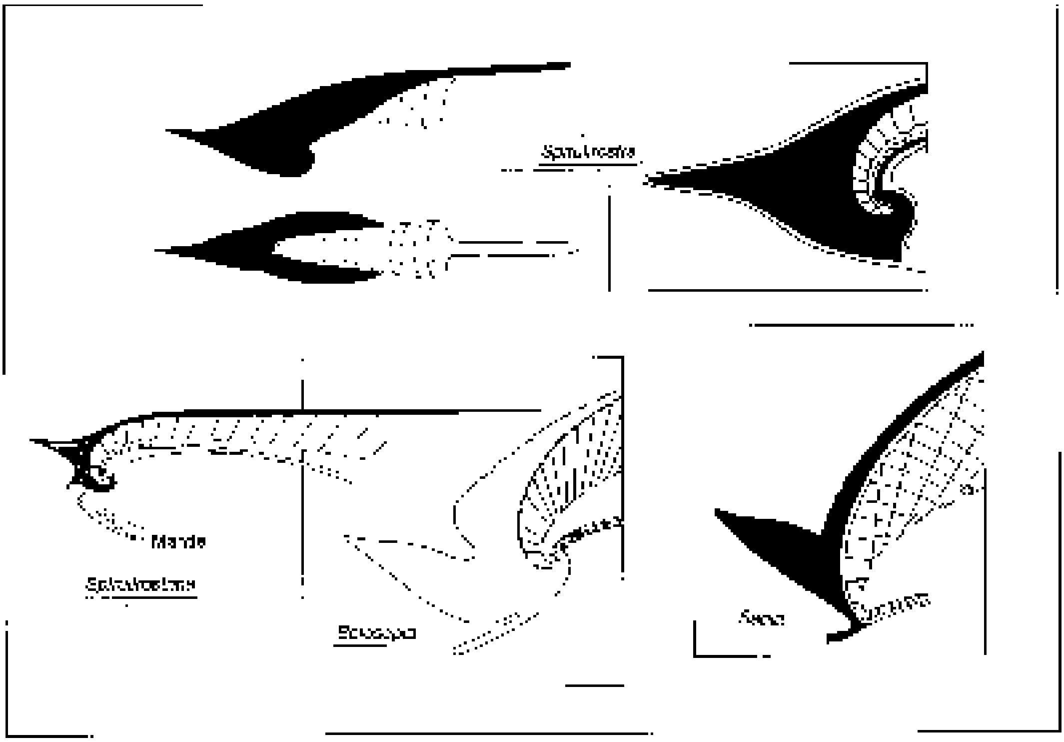

Fig. 10: Sepioid shells. The upper figures show two whole views and one partial longitudinal section of the fossil *Spirulirostra* shell. The lower figures show longitudinal sections of the shells or portions thereof of fossil *Spirulirostrina* (*sensu* Naef) and *Belosepia* and modern *Sepia* (modified from Naef 1922

before it will be possible to understand the evolution of incirrates in deep and polar seas.

DECAPODIFORMES: SPIRULIDAE

Considerable fossil evidence exists in the Decapodiformes and facilitates interpretation of their evolution. Such evidence exists for the spirulids. *Spirula spirula*, the only living member of the Spirulidae, is a mesopelagic, vertically migrating animal and one of the most peculiar of all Recent cephalopods. It has a number of primitive features, the most dramatic being the retention of a phragmocone. The shell shape exhibits an unusual ventral coiling, which has had a strong effect on the structure and organization of the viscera. A number of fossils have similarities to *Spirula* and these seem to form a natural group (Doyle *et al.* 1994). Among them are fossils in which the phragmocone is strongly curved ventrally; the best known are members of the Spirulirostridae (Fig. 10).

This curvature provides evidence concerning the evolution of the *Spirula* shell. As early as 1845, d'Orbigny (in de Ferussac and d'Orbigny 1835–1848) noted the similarity between *Spirula* and the fossil *Spirulirostra*. The Spirulirostridae are known from the Early Oligocene (c. 32 mya) to the Miocene (c. 14 mya), and other similar families are also known, including the Belemnoseidae from the Eocene (c. 46 mya) to the Lower Oligocene and the Belopteridae from the Palaeocene (c. 60 mya) to the Lower Oligocene (Engeser 1990). *Spirula* is known from the Pliocene (c. 3.5 mya, Engeser 1990). Older sepioid fossils with orthoconic phragmocones are known (Groenlandibelidae, Jeletzky 1966, Doguzhaeva 1996) from the Middle (119 mya) to Late Cretaceous (70 mya). *Spirulirostra* had a calcareous guardlike sheath (terminology of Jeletzky 1966, equals "outer plate" of Doguzhaeva, 1996, and other authors) of complex and asymmetrical shape that covered much of the phragmocone. This sheath is unique to the Sepioidea (Jeletzky 1966,

Fig. 11: Photograph of (a) a preserved ommastrephid (*Sthenoteuthis oualaniensis*) with the eyelid open; (b) a living ommastrephid (*Ommastrephes bartramii*) with a closed eyelid as a response to a touch to the eyelid

Doguzhaeva 1996) and the complex, asymmetrical elaboration of the sheath is unique to Cenozoic Sepioidea. The sheath is positioned to function as a counterweight that allows the animal to orientate in a horizontal attitude, an advantage for a bottom-associated or benthic animal that swims just above the bottom (Naef 1921–1923). The sheath's lateral projections also provide attachment sites for the mantle musculature (Naef 1921–1923). The shell of *Spirula* has a rudimentary sheath and it only partially covers the shell. In addition, the ventral curvature of the shell has been accentuated. Presumably, the adoption of a neritic, benthic lifestyle by *Spirulirostra*-like spirulids led to ventral coiling and elaboration of a large, asymmetrical sheath, whereas the secondary adoption of a mesopelagic habitat in *Spirula* led to reduction of the sheath and an increase rather than an abandonment of ventral coiling. This evolutionary history of *Spirula,* however, is not accepted by all palaeontologists (e.g. Jeletezky 1966).

The geographical distribution of *Spirula* shows a clear association with landmasses, and the youngest stages are captured in the deepest tows. These features caused Bruun (1943) to suggest that *Spirula* deposits its eggs on the ocean floor. Clarke's (1969) data on the vertical distribution of *Spirula,* which was especially abundant near the Canary Islands, is compatible with Bruun's suggestion. Often, the presence of a cornea indicates a benthic history in a pelagic group. *Spirula* shows no trace of a cornea. The circular eye opening, however, is very different from those of most other cephalopods. The typical "oegopsid eye" has an anterior optic sinus that allows the eye to close completely, via rather complex muscular action, to a sideways T-shaped slit (Fig. 11). A circular eyelid with a simple sphincter would cause the eyelid to pucker as the eye opening became smaller, so preventing a good seal. Perhaps in the case of *Spirula,* a cornea was completely lost and the corneal pore became the present eye opening, because the eye opening-closing problem seems reversed in this animal. When fully open, the lid seems more like a stretched pore. Indeed, the illustration of a 5.6 mm *Spirula* shows an eye opening that is little more than a pore without any noticeable pucker (Kerr 1931).

SEPIIDAE

The sepiids (Miocene to Recent) are a group with high species diversity and with individuals whose intelligence and capabilities for neurally controlled polymorphism are surpassed only by the octopodids. The most distinctive feature of this group, and presumably one that contributed strongly to their success, is the retention of a specialized phragmocone (= cuttlebone). The phragmocone moved into a dorsal position on the body where the centres of buoyancy and gravity appear to align vertically. This allows the neutrally buoyant cuttlefish to be stable in a horizontal orientation (Denton and Gilpin-Brown 1961, Fig. 12). Thus, the sepiids achieved what *Spirulirostra* achieved, but in a more elegant manner.

In addition to the cuttlebone, there are other features possibly important to sepiid success and diversity. First, the tentacles are completely retractile into large pockets beneath the eyes. The divergence in function between the tentacles and the arms seems to have increased; when the tentacles are not needed they are put away, where they will not interfere with other activities. Tentacle-pockets are present in all sepioids as well as in the myopsids and their close relatives, but the complete retraction of the tentacles may be restricted to sepiids. A second important feature is that sepiids spawn large, benthic eggs. This reproductive

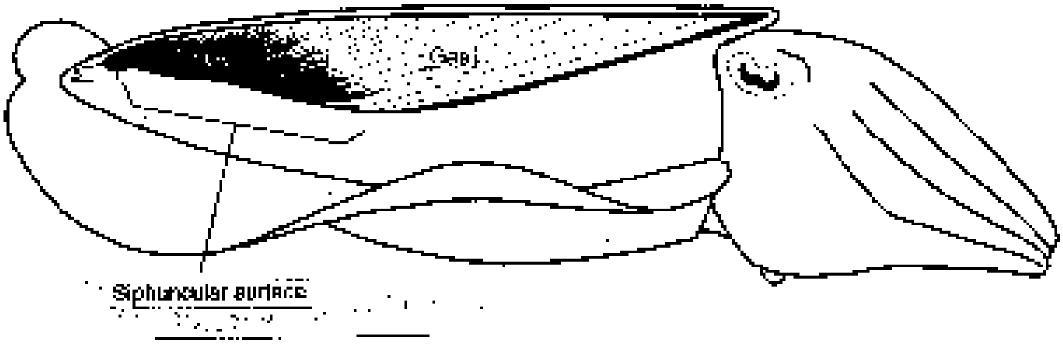

Fig. 12: *Sepia,* showing the position of the cuttlebone (modified from Denton and Gilpin-Brown 1961) – note the highly modified forward position of the phragmocone to allow neutral buoyancy in a horizontal orientation

strategy is common in octopods, although some octopods produce small eggs that release young into the plankton. Perhaps the cuttlebone constrains sepiid development and prohibits a strategy of small eggs and planktonic young. The sepiids are the secondmost speciose family among living coleoids, and the spawning of large eggs is probably a major reason for this high diversity. The absence of a planktonic stage presumably restricts dispersal and gene flow. Such a correlation between number of species and egg size has been suggested for octopodids (Voight 1998).

Early cuttlebones, slightly less specialized than those of sepiids, belong to the family Belosaepiidae (Eocene – Oligocene). The oldest cuttlebone belongs to *Ceratisepia* from the early Palaeocene (Meyer 1993), but its familial affinities are uncertain. The cuttlebones of belosaepiids show many similarities to the shells of the spirulirostrids such as *Spirulirostra* and *Spirulirostrina sensu* Naef (1922) – Fig. 10. (Jeletzky 1969 suggests that the latter genus belongs within *Spirulirostra.*) Both types of shells have the distinct ventral curvature of the apical end and the asymmetrical elaboration of the sheath that includes such similarities as a rostrum and a ventral process. Naef (1921–1923) noted many additional similarities, especially with *Spirulirostrina*. A mismatch in stratigraphy makes *Spirulirostrina* or *Spirulirostra* unlikely ancestors of belosaepiids. The similarities, however, suggest that they all share a common ancestor.

The distinctive sheath of Cenozoic sepioids has evolved in opposite ways in the extant genera. As already indicated, the sheath, apparently, was greatly reduced in *Spirula*, whereas in *Sepia* it was modified to form much of the large, broad dorsal shield, secondary proostracum, lateral edges, reduced rostrum and recurved ventral process (Naef 1921–1923). Both *Spirula* and *Sepia* are relatively recent cephalopod innovations. Because the Spirulidae and Sepiidae are often thought of as an ancient group owing to their possession of a phragmocone, their recent derivation may seem unlikely to some biologists. The retention of a primitive character, however, provides no evidence of the time of the group's derivation.

Considerable morphological evidence, much of it known to Naef, supports the close relationship between *Spirula* and *Sepia* (e.g. structure of the tentacular clubs, absence of a nuchal commissure, absence of a branchial canal, presence of accessory nidamental glands, ventral buccal location of spermatheca, non-terminal position of the mantle-locking cartilages, absence of a beak angle point, presence of a tentacle pocket, fins not united posteriorly). Unfortunately, only a few of these characters can be polarized. Molecular analysis of phylogenetic relationships based on the mitochondrial 16S gene questioned the position of the Spirulidae in the Sepioidea (Bonnaud *et al.* 1994). A second molecular study, based on the cytochrome c oxidase III gene (COIII), concluded that the Spirulidae should be excluded from the Sepioidea (Bonnaud *et al.* 1996), and in a later study with more taxa added, the position of *Spirula* within the Decapodiformes was ambiguous (Bonnaud *et al.* 1997). COI data, however, nestled the Spirulidae far within the Oegopsida, although bootstrap support was lacking (Carlini and Graves in press). Those authors felt confident, however, that their data indicated a closer relationship of *Spirula* to the Teuthoidea than to the Sepioidea (Carlini and Graves in press).

Naef (1921–1923) suggested that the Sepiolidae are derived from one of the *Spirulirostra*-like families and pointed to the loss of a connection between the shell sac and the genital ligament as evidence of their relationship to *Spirula.* Most members of the Sepiolidae are benthic and, like many sepiids, bury themselves in sand or mud. One subfamily, the Heteroteuthinae, has become secondarily pelagic, although it may still

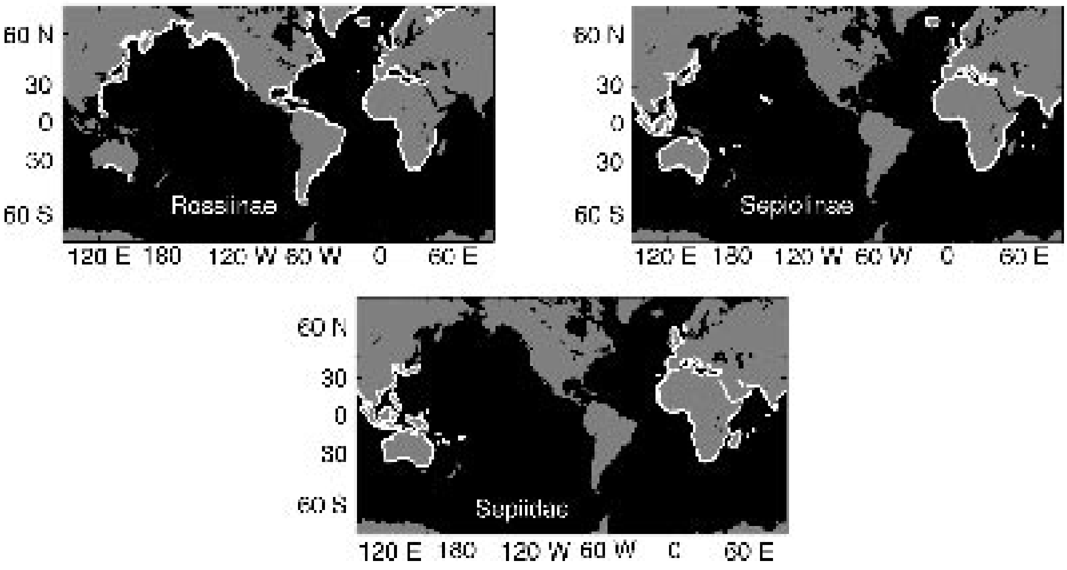

Fig. 13: Distribution maps of two benthic subfamilies of the Sepiolidae (Rossiinae and Sepiolinae) and the benthic family Sepiidae. The white coastline indicates presence. Note the absence of warm-water groups (Sepiolinae, Sepiidae) from the Americas, but the presence there of the cold-tolerant Rossiinae based on data in Nesis 1987 and Nesis pers. comm.)

deposit its eggs on the ocean floor (Boletzky 1978). Its members possess a large bacterial light organ and produce some of the most spectacular luminescent displays of any cephalopod. Strong morphological similarities have resulted in the placement of the sepiolids in the Sepioidea; however, this relationship has been frequently challenged (e.g. Fioroni 1981, Clarke, 1988). Molecular results from the 16S gene (Bonnaud *et al.* 1994) and the COIII gene (Bonnaud *et al.* 1997) as well as eye-lens electrophoretic and immunological analyses (Boucher-Rodoni and Bonnaud 1996) suggest that the Sepiolidae should be separated from the Sepioidea. The COI gene study also excluded the Sepiolidae from the Sepioidea, but placed it adjacent to the Sepiidae, the Idiosepiidae and the Sepiadariidae. The study, however, found little bootstrap support for this arrangement (Carlini and Graves in press). Morphological data show many similarities between sepiolids and sepiids, but again the characters have yet to be polarized and cladistic analyses are lacking.

These molecular data on the Sepioidea question the conclusions drawn from Naef's work. Molecular studies, however, are in their infancy, and there are many difficulties associated with analysing the data. Up to now they have not offered unambiguous evidence as to the branching order within the Decapodiformes. Actually, in the most extensive study (Carlini and Graves in press), the data are quite close in support of Naef's phylogeny, except for the position of *Spirula.*

The peculiar biogeography of the sepioids may also reveal something about their evolution The Sepiolidae contains three subfamilies: Rossiinae, Sepiolinae and Heteroteuthinae. The last subfamily has pelagic and benthopelagic members and is not confined geographically in the same manner as the other subfamilies. The members of the Rossiinae are mostly cold-water cephalopods, with some species living at temperatures <2°C (Shevtsov and Radchenko 1997) and at depths of nearly 2 000 m (Villanueva 1992). The other benthic subfamily of the Sepiolidae, the Sepiolinae, live mostly in warm, relatively shallow water, although one species, *Sepietta oweniana,* may be found in waters as cold as 7°C (Mangold-Wirz 1963) and at depths of nearly 1 000 m (Villanueva 1992). The biogeography of the subfamilies reflects these temperature/depth differences.

The Rossinae occur along the fringes of most of the world's oceans, whereas the Sepiolinae, which also lives throughout much of the world's ocean margins, is absent from the waters of the Americas, as is the Sepiidae (Fig. 13).

The tropical/temperate Sepiidae, known from the surface to depths of about 600 m (Lu and Roper 1991) and temperatures above 8°C (Augustyn *et al.* 1995), echo the unusual biogeographic pattern of the Sepiolinae. The absence of the Sepiolinae and Sepiidae from the Americas may be related to lack of proper habitat but, considering the large geographic area, this is unlikely. The most likely explanation involves the temperature/depth/distance barriers of the ocean basins, which would affect the Sepiolinae and Sepiidae but not the Rossiinae. The timing of the formation of these barriers, therefore, may provide clues to the timing of the families' origin.

A number of sepioid fossils are known from the Americas. These include Miocene representatives of the Spirulidae (Jeletzky 1969) and Eocene representatives of the Belemnoseidae (Jeletzky 1969) and the Belosaepiidae (Allen 1968). In addition, late Cretaceous fossils (lacking phragmocones) of Actinosepia are relatively common in North America and are thought by some to be related to the Sepiidae (Waage 1965). The shallow-water tropical bridge between Africa and South America was severed in the late Cretaceous, leaving the northern rim of the Atlantic Basin as the only migration route for demersal animals between the New and Old Worlds.

Khromov (1998) notes clear biogeographic patterns among subgenera of sepiids and discusses the origin of these patterns from a historical standpoint. He suggests that, during the early Cenozoic (Palaeocene and Eocene), a series of radiations began in the warm waters of the Tethys Sea and resulted in the broad colonization of the Belosaepiidae. Apparently, movement across the Atlantic could arise by migration around the top of the basin, where temperatures were tolerable. After this family became extinct in the Oligocene, the Sepiidae emerged in the Old World, the only location of fossils currently known. The latter's latitudinal distribution was restricted by the colder conditions during this period, preventing the connection utilized by the Belosaepiidae. Therefore, the fossil record, palaeoceanography and present biogeography support a very recent origin of the Sepiidae *sensu stricto*.

While no clear fossil record of the Sepiolidae exists, the biogeography, along with morphological evidence of a relationship with the Spirulidae and Sepiidae, suggests that the Sepiolinae may also have a Late Cenozoic origin. The current authors suggest, as Naef (1921–1923) and others did, that the Spirulidae and the Sepiidae evolved, probably along with the Sepiolidae and Sepiadariidae (not discussed here), in the Early Cenozoic by invading the benthic environment and that some species (*Spirula* and the Heteroteuthinae) became secondarily pelagic (see also Engeser 1997). This hypothesis, however, awaits confirmation from morphological and molecular cladistic techniques and from a better understanding of the fossil record.

One group, placed by Naef (1921–1923) in the Sepioidea, is especially problematic: the Idiosepiidae. These are the smallest known decapods; the males of some species become mature at 8 mm mantle length *ML* (Nesis 1987). They are benthic and possess a special adhesive organ on the dorsal mantle that allows them to adhere to grass blades. Among their many unusual anatomical features is the absence of tentacles at hatching (Natsukari 1970) and the absence of accessory nidamental glands (Lewis and Choat 1993). Their small size has caused secondary simplification and makes determination of relationships by morphological methods difficult. Molecular studies on the COI gene consistently placed this family with the Sepiadariidae and either with or adjacent to the Sepiidae, although bootstrap support was lacking (Carlini and Graves in press). The COIII gene study, however, placed the idiosepiids with the oegopsids (Bonnaud *et al.* 1997); perhaps the COIII cladogram might have resolved the idiosepiid relationships differently had sepiadariid taxa been included in the study.

"FOSSIL TEUTHOIDS"

Although "fossil teuthoids" are generally rare, a substantial number have accumulated in museums. Unfortunately, as mentioned above, with the exception of mastigophorids, difficulties exist in their interpretation, and arguments can be made for placing them as decapods or octopodiforms (e.g. Bandel and Leich 1986, Doyle *et al.* 1994). Indeed, if myopsids belong on the sepioid line, then gladii probably have evolved at least four times in extant lineages (Vampyromorpha, Oegopsida, Myopsida and Sepiolidae), and the problem becomes even more complex. As most calcareous coleoid shells probably have a gladius buried within the structure (see Young and Vecchione 1996), evolution of a gladius is probably not a difficult step.

Evidence for the placement of most of the "fossil teuthoids" in the Octopodiformes rests primarily on the similarity of the gladius of *Vampyroteuthis* to that of some "fossil teuthoids," such as *Loligosepia*, which has a broad median field and a large conus (Donovan 1977, Donovan and Toll 1988, Doyle *et al.* 1994). Vecchione *et al.* (1998), however, suggest that the former feature at least is plesiomorphic and therefore of no value in determining relationships. The gladius of the Upper Jurassic *Plesioteuthis* is so similar to that of oegopsid squids of the family Ommastrephidae

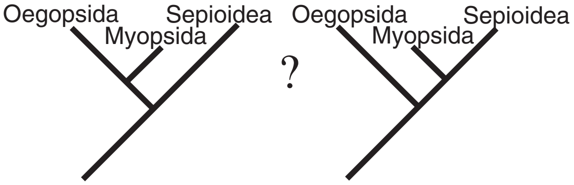

Fig. 14: The two primary alternative phylogenies for the Decapodiformes

(Donovan and Toll 1988) that it either represents relationship or remarkable convergence. Because the ommastrephid gladius, however, is unlike that of other oegopsids and appears highly specialized rather than primitive, it should be considered that:

(i) *Plesioteuthis* is an ancestral ommastrephid and, *in lieu* of evidence that ommastrephids are stem oegopsids, that one or more earlier oegopsid lineages must have existed, or
(ii) the similarity is convergent.

Also, contrary to Naef's opinion, definite tentacles are not known in any fossil plesioteuthid, although possible tentacles are present in specimens from Ardèche, France (Fischer and Riou 1982b). Unfortunately, there is no definitive evidence, at present, to associate most of the "fossil teuthoids" with any group of extant cephalopods. Without clear resolution of the affinities of these fossils, evidence for the time of origin of various clades remains unknown.

MYOPSIDA

The phylogenetic position of the Myopsida (Loliginidae) has been controversial since the last century. The basic question is: are myopsids derived from the oegopsid line, as Naef (1921–1923) thought, or from the sepioid line, as suggested by many other workers before and after Naef?

While the two arrangements of the Myopsida in Figure 14 may not seem greatly different, resolution is critical to understanding which character states are plesiomorphic and which are apomorphic in the Decapodiformes. The myopsid position may actually be more complicated than this figure shows: Haas (1997) and Engeser (1997) put the group on the sepioid line. Haas (1997), however, places them after separation of the spirulids, whereas Engeser (1997) places them after the spirulids and sepiids.

The loliginids, the only members of the Myopsida (Brakoniecki 1996), are benthic spawners; they possess a cornea and have their olfactory organs in pockets. These features suggest that they were derived from demersal ancestors. If Naef is correct regarding the evolution of the cornea, then it can be assumed that the loliginid's ancestors could bury themselves in the sediment.

Prior to Naef's rearrangements of cephalopod systematics, loliginids had been placed with the sepioids for several reasons, including the presence of a cornea and the production of benthic eggs. Naef, however, bothered by the very different shells of the two groups, could not envision a common origin for these structures short of a distant ancestor among the belemnoids. Today, relationships are determined by the relative position of divergences regardless of the length of the subsequent branches. The difference between the shells of the two groups, therefore, does not rule out a common origin. Still, the myopsids remain a difficult group to place. In many ways they are intermediate between sepioids and oegopsids; certainly in general appearance they resemble oegopsids. Figure 15 summarizes the present dilemma.

While a long list of characters is presented, only four can be polarized as probable synapomorphies and three of these are known to exhibit homoplasy in other groups. The remaining characters, which have little potential for determining polarity, are of no use in resolving this node. Fortunately, there are two families, Bathyteuthididae and Chtenopterygidae, which appear related to the Loliginidae. These families should help resolve the phylogenetic position of the Myopsida because they also share many sepioid and teuthoid characters, although the combinations differ from those of the loliginids. Nevertheless, it is not possible yet to perform a cladistic analysis based on morphology. None of the molecular studies has yet resolved the position of the Myopsida. In molecular cladograms, myopsids usually fall out as a sister group to the Oegopsida, although without bootstrap support.

Today the loliginids are the dominant squid of the neritic region, a habitat they share with the sepioids. While most sepioids are demersal, loliginids are completely pelagic. However, some loliginids are known to sit, propped up on their arms, tentacles and posterior tip of their mantle, on the ocean floor for short periods (as do some ommastrephid oegopsids). Unlike the sepioids, loliginids usually occur in shoals and often schools, which sometimes number thousands of animals. Therefore, they present a major target for commercial fisheries (Hanlon and Messenger 1996).

As the fossil record (i.e. "fossil teuthoids") cannot be interpreted with confidence at present, little is known about the evolutionary history of the loliginids.

Myopsida and Sepioidae

- **Cornea**
- **Suckers with circularis muscle**
- **Beak without angle point**
- **Vena cava ventral to intestine**
- Genital artery position
- Buccal crown with suckers
- External yolk sac
- *Accessory nidamental glands*
- *Giant-fibre lobe in stellate ganglion*
- *Seminal vesicle position*
- *Tentacle pockets*
- *Benthic eggs*

Myopsida and Oegopsida

- Gladius similar
- Branchial canal
- *Tentacular clubs similar*
- *"Appearance" similar*
- *Innerstellate connective*

- **apomorphic?**
- plesiomorphic?
- *not polarized*

Fig. 15: Character states of myopsids that show similarities to sepioids or oegopsids. Note that only a few characters have states that are apparently apomorphic and, therefore, are of use in deciding relationships of the Myopsida

Even among extant species, there is considerable uncertainty concerning generic affinities (Vecchione *et al*. 1998). According to Natsukari's (1984) interpretation, however, many genera separate geographically. If correct, this suggests that the phylogenetic topology may eventually match the biogeographic pattern, as is seen in the sepiids. The origin of the Loliginidae has been placed in the Cenozoic by Doyle *et al.* (1994) and Engeser (1997), among others. The loliginids, therefore, may also be a recent cephalopod innovation (a crown group), yet derived from a stem lineage that separated from other decapods deep in the Mesozoic.

Present understanding of coleoid phylogeny is summarized in Figure 16. Considerable cephalopod diversification apparently arose in the Cenozoic. This approximately coincides with the extinction of the abundant belemnoids at the Mesozoic/Cenozoic boundary. Although belemnoids may have occupied a similar habitat to that of the loliginids today, the effect that their extinction had on the evolution of the loliginids and, perhaps, the Recent sepioids is uncertain. Clearly, understanding the affinities of the "fossil teuthoids" will help establish the time frame for divergences. The presence of "fossil teuthoids" in the Upper Triassic probably means that the Decapodiformes and Octopodiformes had split by that time, because the stem lineage of both groups had a phragmocone. In the Jurassic, a variety of different forms within the "fossil teuthoids" appeared. These may well prove to represent both lineages. Indeed, major cephalopod divergences, into Octopodiformes, Oegopsida, Myopsida and Sepioidea, may have occurred during this period or earlier. One of the most obvious features of Figure 16, however, is the large number of question marks, which emphasizes current gaps in knowledge. A summary, even if speculative, of the probable time frame over which divergences occurred is necessary, because researchers using molecular methods need a time frame to guide the selection of appropriate genes to study.

Surprisingly, the phylogeny presented in Figure 16 is not much different from that proposed by Naef (1921–1923). This does not necessarily mean that Naef was correct, but rather that there has been little advance beyond the foundation he established. The few major advances are:

(i) the status of *Vampyroteuthis* has been recognized and confirmed;
(ii) the separate position of the belemnoids as the sister group to the neocoleoids has been recognized, but still requires more confirmation;
(iii) the monophyly of the Decapodiformes, Octopodiformes and Octopoda has been confirmed;
(iv) the ages of the belemnoids, neocoleoids, decapods and "fossil teuthoids" have been extended to considerably earlier times.

There is good reason to expect, however, that progress will be rapid in the near future. Already molecular methods have contributed substantially to knowledge of cephalopod phylogeny, and their future potential is great. These methods, however, are not a panacea. Currently they are laden with many problems. When combined with morphological research and cladistic methodologies, however, molecular methods promise an early solution to the major problems of the position of the Myopsida, the relationships among the Sepioidea, and the major clades of the Oegopsida. Determining the major clades of the Oegopsida

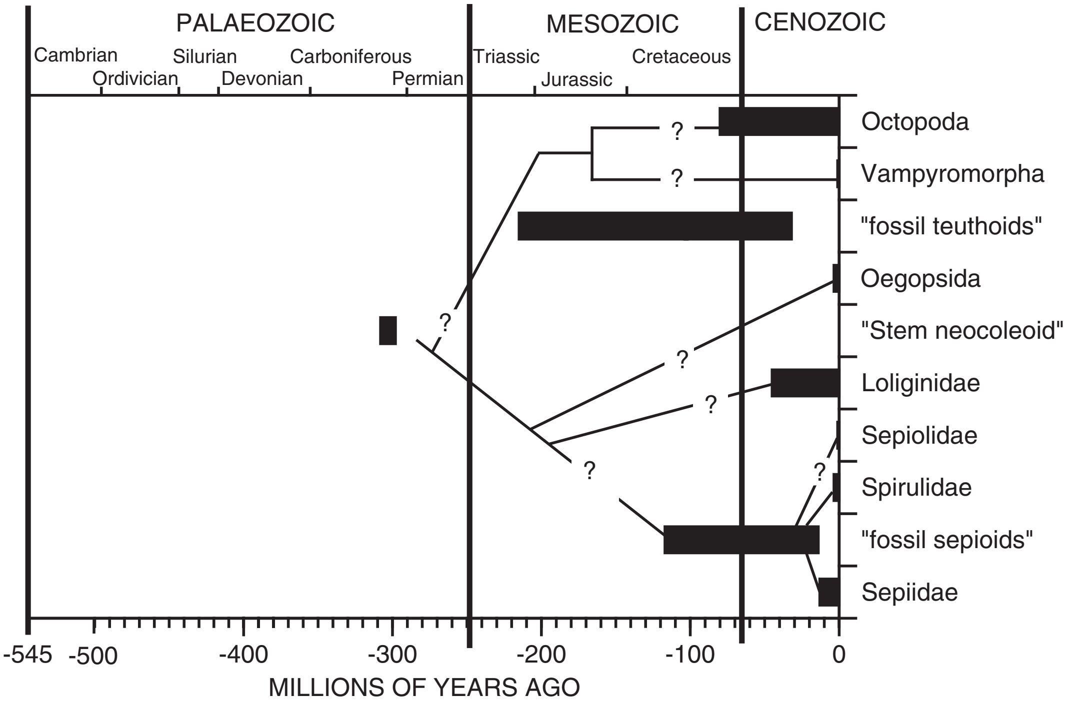

Fig. 16: Illustration of present understanding of coleoid phylogeny, with emphasis on the Decapodiformes. Solid bars indicate known time of occurrence

should aid in sorting out relationships among the "fossil teuthoids." Once a basic, evolutionary framework is established for oegopsids, numerous, more-focused studies will be possible.

OEGOPSIDA

This summary of coleoid phylogeny was presented without discussing the Oegopsida, because of current ignorance concerning the ancestry of that group. The Oegopsida, essentially, is a phylogenetic void. Defining the basal nodes in oegopsid genealogy is one of the major challenges in cephalopod phylogeny. Before this can be accomplished, however, the relationships of the loliginids and related families must be established firmly, or errors in polarization could defeat the attempt. The Oegopsida is a special challenge because it possesses a wide range of morphological types. With 25 families, the group contains more families than all other extant coleoid groups combined (18 families, Fig. 17). Oegopsids are the overwhelmingly dominant cephalopods of the oceanic pelagic realm and account for 85% of the species and 70% of the families. The dominance of family-level diversity in the pelagic realm applies also to the Octopodiformes, where the ratio of pelagic to benthic families is 9:2. Perhaps in the case of octopods, the benthic-to-pelagic transition, which may have happened several times, produced profound morphological change and contributed strongly to pelagic diversity. There is no evidence, at present, to suggest any exchange between the pelagic and benthic realms in oegopsid history. Although a number of explanations could explain the high oegopsid diversity (such as more potential life styles, longer time in the pelagic habitat, or much larger habitat), there is a lack of convincing evidence for any explanation.

Many pelagic families of coleoids exhibit little generic or specific diversity. Of the 43 families of extant coleoids, only eight (Sepiidae, Sepiolidae, Loliginidae, Enoploteuthididae, Ommastrephidae, Cranchiidae, Octopodidae, Opisthoteuthididae) have more than 20 species. Of the 43 families, 22 have a single genus; 21 of those are pelagic families (the

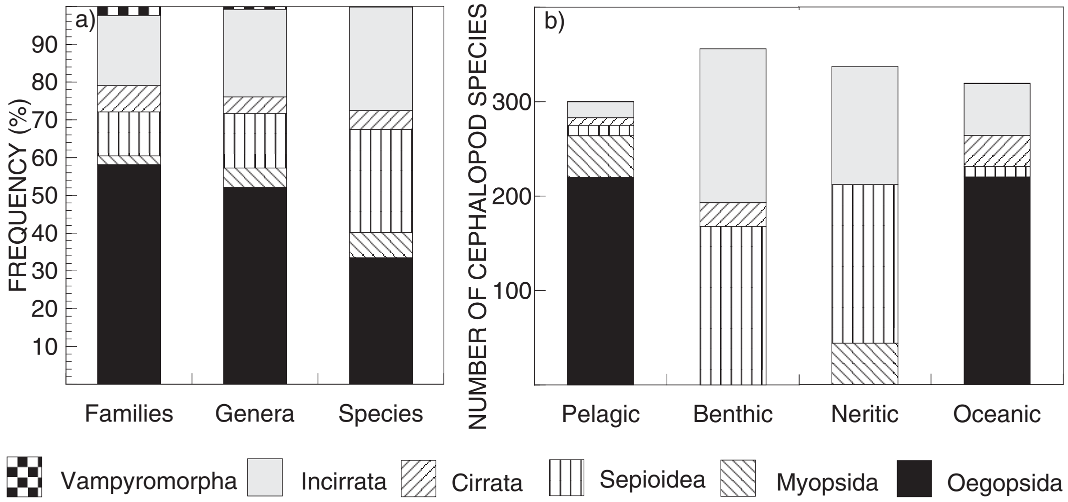

Fig. 17: Histograms showing the relative contribution of major taxa to (a) the number of families, genera and species comprising the Neocoleoidea, (b) the number of pelagic or benthic species in the Neocoleoidea and (c) the number of neritic or oceanic species in the Neocoleoidea (based on data from Sweeney and Roper 1998)

exception is the Idiosepiidae) and 13 of the pelagic, monogeneric families are oegopsids. Of the 21 pelagic families that are monogeneric, 17 have three or fewer species and 12 have a single species. In the oceanic pelagic environment, only eight of 35 families contain more than 10 species. The high family-level diversity in this realm, therefore, does not reflect species-level diversity trends.

The high species diversity, noted above among benthic incirrates, is also found among decapods. A rough estimate, based on the cephalopod species list of Sweeney and Roper (1998), yields 365 benthic species and 300 pelagic species of extant coleoids. Although only 14% of the families are benthic or predominantly benthic, they contain 55% of all species. The lower pelagic species diversity within the far larger pelagic environment presumably reflects

(i) an environment with low habitat diversity resulting from the virtual lack of permanent physical boundaries, and
(ii) great potential for stabilizing gene flow owing to the constant motion of water.

The difference between pelagic and benthic diversity, however, can be misleading. Off Hawaii, for example, about 20 benthic species and 64 pelagic species are present. Most localities probably have similar ratios. Species turnover with geographic change is much greater in the benthic realm and, therefore, total benthic diversity is higher than total pelagic diversity. Although knowledge of oegopsid habitat requirements is limited, the eight most abundant oegopsid families (Enoploteuthididae, Cranchiidae, Ommastrephidae, Onychoteuthididae, Gonatidae, Mastigoteuthididae, Chiroteuthididae, Histioteuthididae) all have some species that are bottom-associated. This association presumably limits geographical distribution and, thereby, contributes to species diversity. Indeed, this habitat along continental or island slopes may be a source region for pelagic speciation (Reid *et al.* 1991).

If neritic and oceanic species are compared (there is broad overlap in species distributions between these categories, so comparisons are approximate), the ratio is nearly unity (i.e. 335:330). If species diversity among major taxa is compared, the number of oegopsid species (c. 220) is approximately the same as that of sepioids plus the Myopsida (c. 223), which is not very different from the total Octopodiformes (c. 215).

The high familial diversity of oegopsids is reflected in their variety of ecological roles. Oegopsids range from powerfully swimming ommastrephids capable of gliding over the ocean surface to a variety of deep-sea forms relying more on fin propulsion than jet propulsion. Many have become neutrally buoyant through the use of light fluids, rather than gas spaces in phragmocones, and those squid often are weak swimmers.

While discussion of phylogenetic relationships within the Oegopsida is premature, some evolutionary

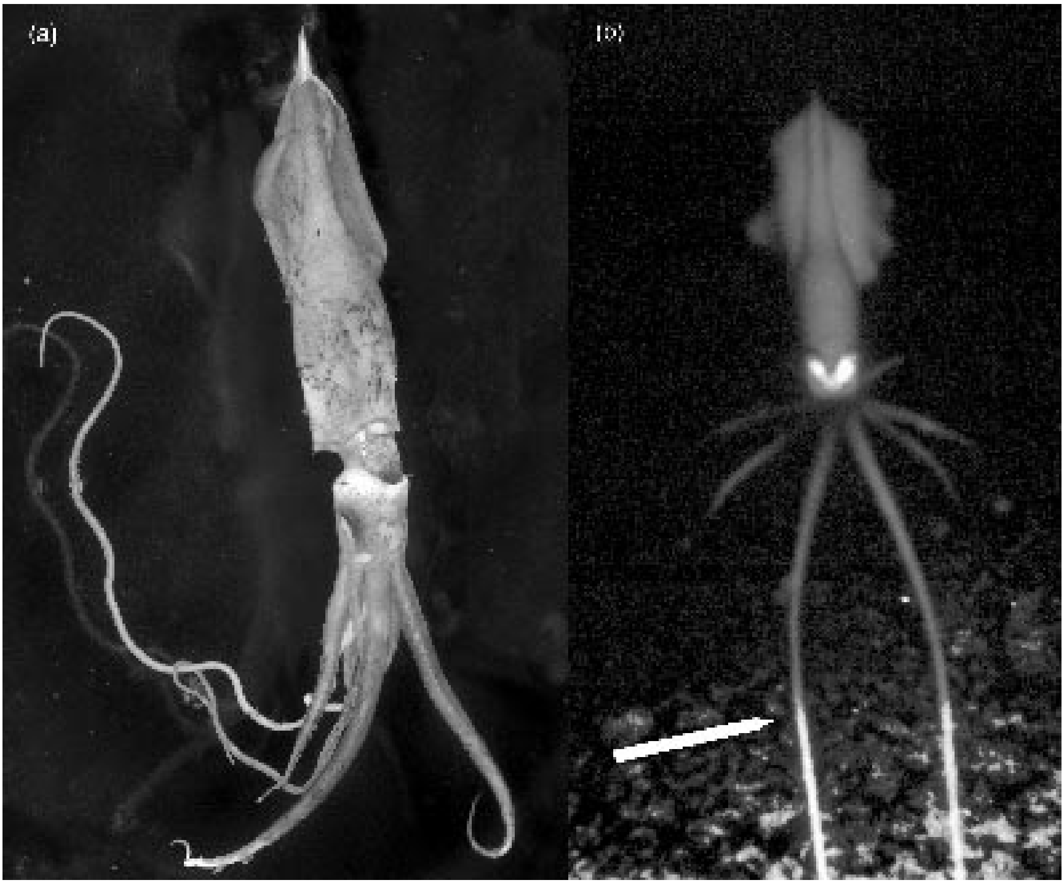

Fig. 18: (a) Photograph of *Mastigoteuthis inermis* taken lying in a pan aboard ship shortly after capture – note the long ventral arms and the whip-like tentacles spread to the left. (b) Photograph of *Mastigoteuthis* sp. taken from a submersible off Hawaii (courtesy of the Hawaii Undersea Research Laboratory) – note the splayed six smaller arms and the seeming continuity of the ventral arms and the tentacles (the arrow points to a change in reflectivity which probably coincides with the emergence of the tentacles from the sheath of the ventral arms)

trends are apparent. Two merit discussion here: feeding and bioluminescence.

Feeding

As expected, much evolutionary experimentation involves feeding mechanisms. The variety of feeding methods seemingly increases in deep-water squid, where darkness changes the morphological demands for catching prey and avoiding predators. For example, a quick move by the prey may place it out of sensor range of the predator, making a predator's strong swimming abilities of little use (Seibel *et al.* 1997b).

In one apparent oegopsid clade, the "chiroteuthid families," feeding specialization seems to have centred on radical modifications of the tentacles. Surprisingly, this avenue apparently opened via the loss of the true club and its replacement by various elaborations of suckers on the stalks (Young 1991). This process can be observed in the ontogeny of *Chiroteuthis* spp., where the larval club is lost (resorbed?) and the adult club develops along the tentacular stalk (Naef 1921–1923). Perhaps the most unusual specialization within this group of families is in mastigoteuthids, which possess long, whip-like tentacles bearing suckers

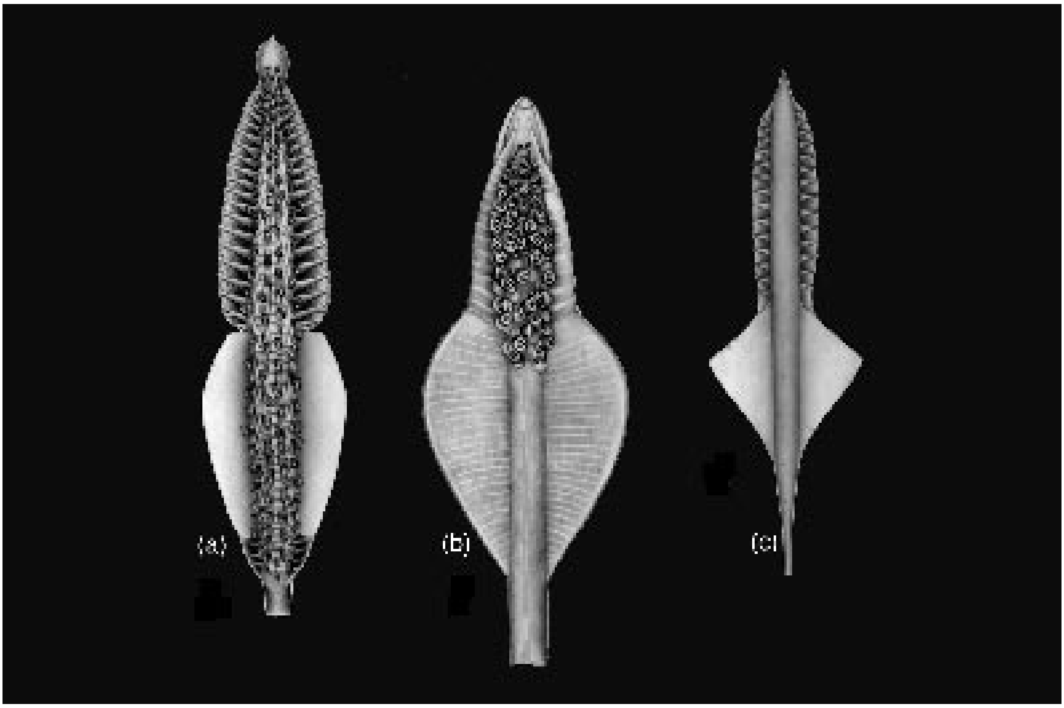

Fig. 19: Drawings of the oral view of chiroteuthid tentacular clubs from species of (a) *Chiroteuthis,* (b) *Asperoteuthis* and (c) *Grimalditeuthis* (from Roper and Young in prep.)

sometimes numbering in the thousands and so small (c.100 µm) as to be virtually unresolvable by the unaided human eye. Submersible observations of *Mastigoteuthis magna* in the North-West Atlantic indicate that they capture prey by drifting with dangling tentacles just above the ocean floor (Roper and Vecchione 1997). The tentacles emerge from a sheath formed by the enrolled lateral membranes (= tentacular sheath) of the very long fourth arms. The tentacle length may be 3–4 times the length of the mantle and the tentacles are held apart by the fourth arms, apparently to prevent tangling. The very small size of the suckers allows capture of small bottom-associated zooplankton and yet, because of the cumulative power of the numerous suckers, could be equally effective in the similarly passive capture of much larger prey. A single photograph of a *Mastigoteuthis* in the same attitude from a depth of 885 m off Hawaii suggests that this behaviour may be common within the family (Fig. 18).

Most members of the Chiroteuthididae have unusually long tentacles and, in some species, long tentacles with long clubs. The tentacles of *Chiroteuthis* spp. are often many times the length of the mantle and are very slender, with bushy clubs possessing suckers attached by long stalks. The tentacles bear peculiar photophores along their length with an especially large, lidded photophore at the tip of the club. Perhaps the terminal photophore acts as a lure, which can be slowly drawn toward the arms by contraction of the tentacles (see Voss 1956). The fourth arms are especially long; shipboard and submersible observations show the tentacles withdrawing into the sheath-like lateral membranes of the fourth arms, as in *Mastigoteuthis*. The closely related *Asperoteuthis* has similar tentacles but, strangely, the proximal half of the club is bare of suckers. This peculiar feature is extended in *Grimalditeuthis*, which has clubs devoid of suckers and lacks photophores on its clubs or its very slender tentacular stalks (Fig. 19). Are the tentacles of *Grimalditeuthis* only sensory or do they still function as a lure in some manner that does not require bioluminescence?

Another member of the clade, *Joubiniteuthis portieri*, the sole member of the family Joubiniteuthididae, has adopted a different approach to feeding. The tentacles of this squid are short and slender, with small clubs, and seem secondary in importance to the peculiar

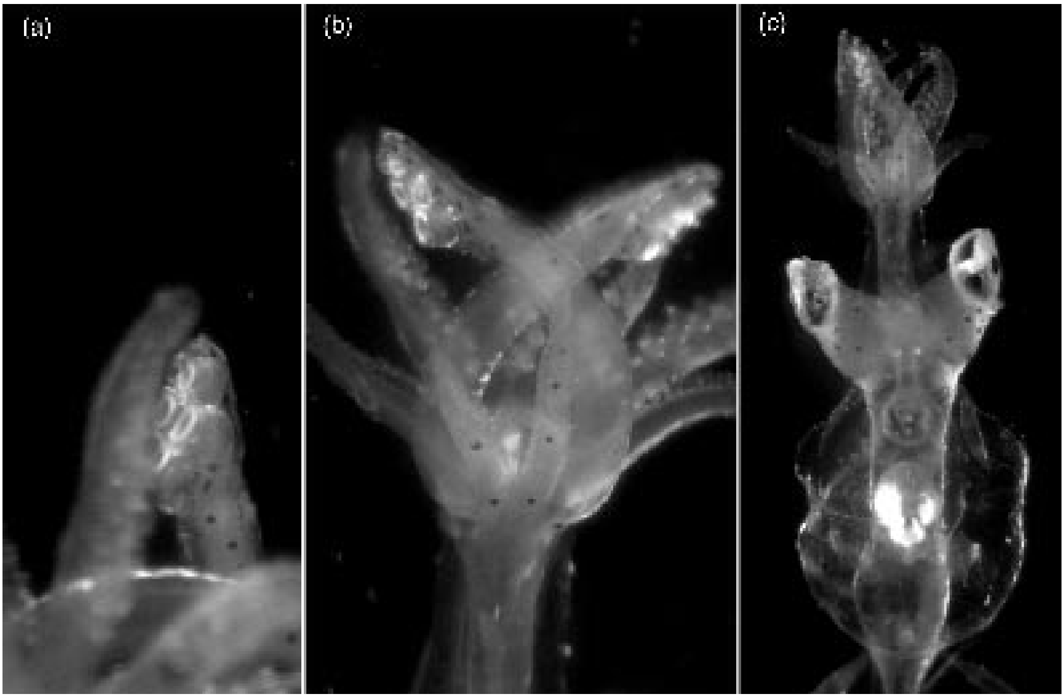

Fig. 20: Photomicrographs of a 10 mm *ML* paralarva of *Lepidoteuthis grimaldii* – (a) and (b) high magnification of the tentacular clubs, (c) lesser magnification that shows the terminal position of the fins

arms. The six dorsal arms are extremely elongate and each carries six rows of small suckers. Although they have never been observed from submersibles, the arms may fan out to form an effective trap for a passing animal. In all four of these families, the slender tentacles surely are incapable of the rapid extension seen in ommastrephids and loliginids.

A rather different trend has occurred in two families, Octopoteuthididae and Lepidoteuthididae. The results of molecular (Carlini and Graves in press) and morphological studies (Clarke 1988, Young 1991) suggest that these families are closely related to one another and to the chiroteuthid families. None of the studies, however, are sufficiently robust to give confidence in their results. Although adults in the two families look very different, they share an unusual feature: the absence of tentacles. The paralarvae in both families do have tentacles with peculiar and very similar clubs, and this is one feature that suggests their relationship to each other (Fig. 20). The loss of tentacles occurs in only one other squid genus, *Gonatopsis* spp., family Gonatidae. Perhaps the extreme specialization of the tentacles, in some ways similar to that seen in *Grimalditeuthis*, led to the abandonment of this major offensive weapon as evolutionary pressures changed.

Of course, many squid have "normal" arms and tentacles. Differences in their feeding mechanisms may be more subtle or more behaviourally mediated than seen in the chiroteuthid families. These squid often exhibit differences in sucker size and dentition. Many species have exaggerated dentition in which the horny sucker ring is modified into a hook. In the families Enoploteuthididae, Pyroteuthididae and Ancistrocheiridae, the possession of hooks probably represents the adaptation of a common ancestor, but in the families Gonatidae, Octopoteuthididae, Cranchiidae, Neoteuthididae and Onychoteuthididae, hooks have apparently arisen independently (Young and Harman 1998). Species with hooks tend to have some normal suckers as well. Indeed, most gonatids have arms with two rows of hooks bordered on each side by a row of suckers. The most speciose family in the Oegopsida (the Enoploteuthididae) have predominantly hooks on the arms and tentacles. The relative feeding advantages of hooks v. suckers, however, are unknown. Are hooks designed for sinking into soft-bodied prey, such as other squid, or do they act as grappling hooks for hard-bodied, spiny prey, with which suckers would have difficulty making a seal? Of course, there are many different types and arrangements of hooks. For example, onychoteuthids have hooks on the tentacular clubs, but only suckers on the arms, whereas this situation is reversed in *Pterygioteuthis*. Simple answers are not expected, but solution of this problem should provide insight on how the hook-bearing belemnoids fed.

Bioluminescence

Perhaps the most spectacular adaptations among oceanic squid involve the widespread evolution of photophores. Most bioluminescent squid occupy the mesopelagic habitat during the day, and many of their photophores and associated bioluminescent behaviour appear to be adaptations to this habitat. The structures of the photophores differ greatly among families, which indicates that the families diverged in evolution prior to evolving photophores and, therefore, prior to their invasion of the mesopelagic zone. At least two exceptions to the independent derivation of photophores exist: the families Lycoteuthididae and Pyroteuthididae. They share a remarkable similarity in the placement and structure of their photophores (Herring *et al.* 1985). Good evidence places these families at the terminal branches on a clade including the Enoploteuthididae and the Ancistrocheiridae (Young and Harman 1998). The four families possess a number of apparent apomorphies, the most unusual being the site of attachment of spermatangia in the nuchal region (Young and Harman 1998). Although the Lycoteuthididae and Pyroteuthididae appear very different in many aspects of their morphology (presence v. absence of hooks, fin shape, tentacle modifications, etc.), they are closely related. It is here suggested that, unlike other families of luminescent squid, they diverged when living within the mesopelagic habitat.

Mesozoic seas were very different from the well-mixed modern oceans. Anoxic waters were not uncommon. Black shales are common deposits formed under anoxic conditions and, as such, may indicate anoxic conditions in overlying water, especially when a macrobenthos is absent (Arthur and Sageman 1994). At the Cenomanian-Turonian boundary (c. 93 mya) during the latter part of the Cretaceous, the last clearly defined near-global formation of “black shales” occurred. During this “Oceanic Anoxic Event” (duration < 1 million years), mesopelagic depths may have been anoxic (Schlanger *et al.* 1987) and, thus, uninhabitable by squids. If this scenario is correct, the end of that anoxic event would mark the time that modern invasion of the mesopelagic zone began. Many extant oegopsid families then would have already diverged prior to this event and would have a Mesozoic or an earlier origin, whereas at least two families would have diverged subsequent to it and, like their sepioid relatives, would have a Cenozoic or near-Cenozoic origin.

CONCLUSIONS

Periods of great diversification and retrenchment have marked the evolution of cephalopods during their long history. Vertebrates have been a key element in this evolution. Today, fish, the marine vertebrates closest to cephalopods in average size, have come to dominate the nekton in diversity, numbers and biomass. One major reason for the dominance of fish is their ability to feed on small particles via filter-feeding or “particle picking,” made possible by the odd evolutionary innovation of a perforated pharynx. Packard (1972) stated that, functionally, cephalopods are fish. While this is true in the most general sense, there are striking differences between the groups. In some ways, cephalopods have not matched the sophisticated physiology and swimming biomechanics of fish. In other ways, fish have not matched the elaborate mechanisms of cephalopods for capturing and handling prey. Cephalopods use their arms, tentacles, suckers, hooks, beaks and radulae to grab, manipulate and chop up large prey, often including the particle-picking fish. Nor have fish matched the rapid, complex concealment devices of cephalopods. Although the evolution of cephalopods and vertebrates has entwined during their long histories, cephalopods as a group are not in a struggle with vertebrates. Rather, each cephalopod species is in a struggle with all other marine species, including other cephalopods. Today cephalopods are not as dominant as they have been at times in the past. Their present success, however, is apparent in their high diversity and abundance and in the major roles they play in the ecology of the sea.

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