Phylogenetic Classification of Coleoid Cephalopods

(Phylogenetische Systematik der coleoiden Cephalopoden)

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With 5 Text Figures

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Abstract: A new classification scheme of the major groups of coleoid cephalopods is presented which is based on phylogenetic systematics. The Coleoidea comprise two evolutionary lines: the extinct monophylum Belemnoidea, and the Vampyromorphoidea and Decapoda ("sucker-bearing" coleoids) with both fossil and living representatives. The Vampyromorphoidea (main synapomorphy: 2^{nd} arm pair reduced) diverged into two lines: the Octopoda and the Vampyromorpha. The alleged ancestral "teuthids" (Prototeuthida Naef 1921 s.l.), known from the Late Triassic to the Late Cretaceous, are in fact vampyromorph coleoids and can be placed in the stem line of the Vampyromorpha. The Decapoda (main synapomorphy: 4^{th} arm pair modified) also show two evolutionary lines, the Spirulida and the "higher decapods" (Teuthida and Sepiida). The radiation of the three main evolutionary lines of coleoid cephalopods probably took place in Late Silurian/Early Devonian times. The fossil record, however, is far from complete.

Zusammenfassung: Eine neue Klassifikation der coleoiden Cephalopoden wird vorgestellt, die auf der Methode der pylogenetischen Systematik basiert. Demnach umfassen die Coleoidea zwei evolutionäre Linien: das ausgestorbene Monophylum Belemnoidea, sowie die Vampyromorphoidea und die Decapoda ("Saugnapf-tragende" Coleoiden), mit sowohl rezenten wie auch fossilen Vertretern. Die Vampyromorphoidea (Haupt-Synapomorphie: 2. Armpaar reduziert) teilt sich in zwei Linien auf, die Octopoden und die Vampyromorpha. Die angeblichen Vorfahren der Teuthiden (Prototeuthida Naef 1921 s.l.), bekannt von der Oberen Trias bis zur Oberen Kreide, sind in Wirklichkeit vampyromorphe Coleoiden und können in die Stammlinie der Vampyromorpha gestellt werden. Die Decapoda (Haupt-Synapomorphie: 4. Armpaar modifiziert) weisen ebenfalls zwei evolutionäre Linien auf, die Spirulida und die "höheren Decapoden" (Teuthiden und Sepien). Die Radiation der drei evolutionären Linien der coleoiden Cephalopoden fand vermutlich bereits im Obersilur/Unterdevon statt. Die Fossilüberlieferung der Coleoiden ist aber noch mit sehr vielen Lücken versehen.

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1. Introduction

Neither the present classification of the major groups of coleoid cephalopods nor the "biological" classification of Voss (1977), or the "palaeontological" classification of Jeletzky (1966) is satisfactory. Both Voss' and Jeletzky's classification schemes are based on phenotypic comparisons. The purpose of this paper is to present a new classification for the major groups of Recent and fossil coleoid cephalopods using phylogenetic systematics, or cladism. This method has been proven to be the most consistent for determining phylogenetic relationships.

2. Previous classification of coleoid cephalopods

Earlier, biologists and palaeontologists used a slightly different classification. The "biological" classification (fossils not included) of Voss (1977) considered four orders:

— Order Sepioidea Naef 1916
— Order Teuthoidea Naef 1916
— Order Octopoda Leach 1818
— Order Vampyromorpha Pickford 1939,

whereas Young (1977) emphasized the following scheme:

— Order 1 Belemnoidea
— Order 2 Vampyromorpha
— Order 3 Decapoda
  Suborder 1 Sepioidea
  Suborder 2 Teuthoidea
— Order 4 Octopoda.

Jeletzky (1966) in his "...phylogeny and classification of fossil Coleoidea", presented six orders:

— Order Aulacocerida Stolley 1919
— Order Phragmoteuthida Jeletzky in Sweet 1964
— Order Belemnitida Zittel 1895
— Order Octopida Leach 1818
— Order Teuthida Naef 1916
  Suborder Myopseina d'Orbigny 1835
  Suborder Oegopseina d'Arbigny 1835
  Suborder Vampyromorphina Robson 1929
  Suborder Prototeuthina Naef 1916
  Suborder Mesoteuthina Naef 1916
  Suborder Loligosepiina Jeletzky 1965
— Order Sepiida Zittel 1895

This scheme has been revised by Engeser & Reitner (1981) and Drushchits et al. (1984). They gave the suborders Belemnoteuthida Stolley 1919 and Diplobelida Jeletzky 1965 order status. In the classification schemes of Jeletzky (1966) and Voss (1977) the Teuthoidea and Sepioidea are ranked too high considering their overall similarity (Young 1977). In all schemes, however, *Spirula* seems to be underrepresented (compare Donovan 1977).

Other more recent ideas concerning the evolution of coleoid cephalopods have just been outlined very roughly (Bonik et al. 1977, Salwini-Plawen 1980, Dzik 1982); therefore, these studies are not discussed here.

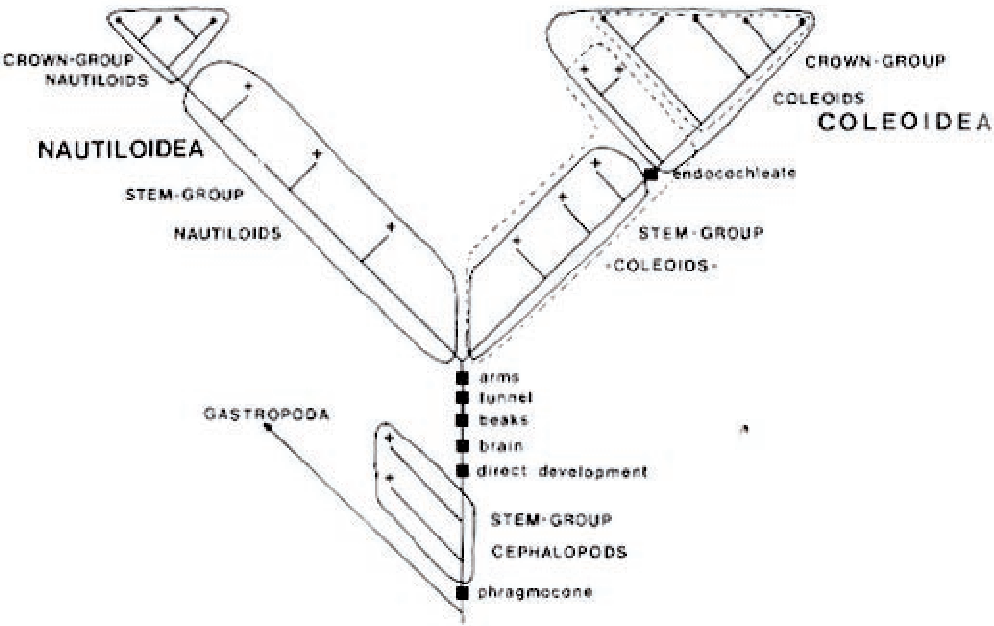
Since it is impossible to construct an essentially new classification system, we tested whether or not the existing systematic units are monophyletic groups. Phylogenetic systematics yields a clade from which the phylogenetic relationship of particular groups can easily be understood. Because the ranks are somewhat arbitrarily determined, only sister-group relationships are indicated here. Extinct monophyla are regarded as + *plesia* (sing. + *plesion*) (see *plesion* concept by Patterson & Rosen 1977). Data were taken from Naef (1921-27, 1922), Jeletzky (1966), Young (1977) and Boletzky (1984), as well as from the authors' own published and unpublished observations.

3. The Cephalopoda as a monophylum

The Cephalopoda are considered a monophylum. They share some unique synapomorphies. Since it is not the aim of this paper to outline the entire system of the cephalopods, only a few autapomorphies of the Cephalopoda are specified here. For intergroup comparisons, all other mollusk groups were used.

Synapomorphies of the cephalopods are:

1. chambered shell (phragmocone) with siphunle, allowing possible buoyancy by gas;
2. transformation of the anterior foot into arms, and shift of the oral opening into the arm crown;
3. transformation of the posterior foot into the funnel apparatus;
4. buccal apparatus with chitinous beaks;
5. concentration of the neural system (development of a brain); and
6. direct development of a meroblastic germ without true larval stages.



Text Fig. 1. Phylogenetic tree of the Cephalopoda with explanation of the terms, crown-group, and stem-group.

Important symplesiomorphies include:
1. marine life;
2. mantle (characters 2 to 5 are synapomorphies of all mollusks);
3. radula;
4. two gills in pallial cavity;
5. eyes; and
6. shell (from the common ancestor of all conchiferan mollusks).

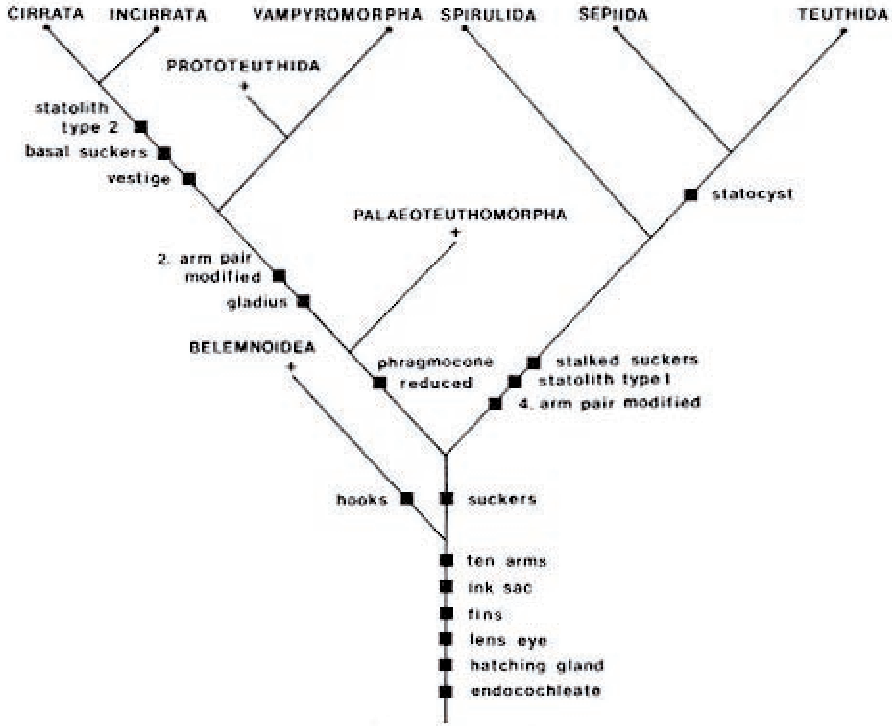
The gross classification of the cephalopods shows two lineages. These are the Nautiloidea lineage and the Coleoidea lineage (Text Fig. 1). Most fossil cephalopods are placed in either the nautiloid line (stem-group nautiloids) or the coleoid line (stem-group coleoids). Other fossils are stem-group cephalopods (Bandel 1982, 1983). Because the stem-group "coleoids" also includes ectocochleate cephalopods, the term Coleoidea is restricted to the crown-group coleoids plus the Belemnoidea (Text Fig. 1).

4. The Coleoidea — a monophylum

Most likely, the Coleoidea are a monophyletic group. They are characterized by at least eight important synapomorphies — certainly more may be defined. Recent *Nautilus* can be used for intergroup comparisons.

Synapomorphies of the Coleoidea groups with living representatives are (Text Fig. 2):
1. inner shell;
2. hatching gland;
3. fins;
4. eye with lens;
5. ink sac;
6. ten arms, not differentiated. Although all living coleoids have differentiated arms (Vampyromorpha: 2nd arm pair; Teuthoidea, Sepioidea, Spirulida: 4th arm pair) or have even lost two arms (Octopoda), the ancestral form of all coleoids possessed ten undifferentiated arms.
7. primitive, pedunculate suckers, two rows of cirri. When extinct belemnoids are considered (see below) this character turns out to be a synapomorphy of the coleoid groups with living representatives (Vampyromorphoidea and Decapoda = "sucker-bearing" coleoids). The common ancestor of all coleoid cephalopods had two rows of cirri and probably adhesive grooves on each of the ten arms.
8. fusion of pedal and visceral ganglion; and
9. venom glands. This character is not unique among mollusks. However, the development of venom glands in the Coleoidea seems to be a convergent formation rather than a plesiomorphy; e.g., *Nautilus* lacks venom glands.

Important symplesiomorphies (from the cephalopod ancestor) include:
1. phragmocone with a small aragonitic rostrum. Although most living coleoids lack a phragmocone or possess a modified phragmocone (*Sepia* shell), the common



Text Fig. 2. Phylogenetic tree of the "sucker-bearing" Coleoidea.

ancestor of all coleoids had a straight or cyrtocone phragmocone with a proostracum or body chamber;

2. straight body form, clearly demarcated head;
3. small eggs (when compared with *Nautilus*);
4. buccal membrane;
5. funnel with valve; and
6. crop.

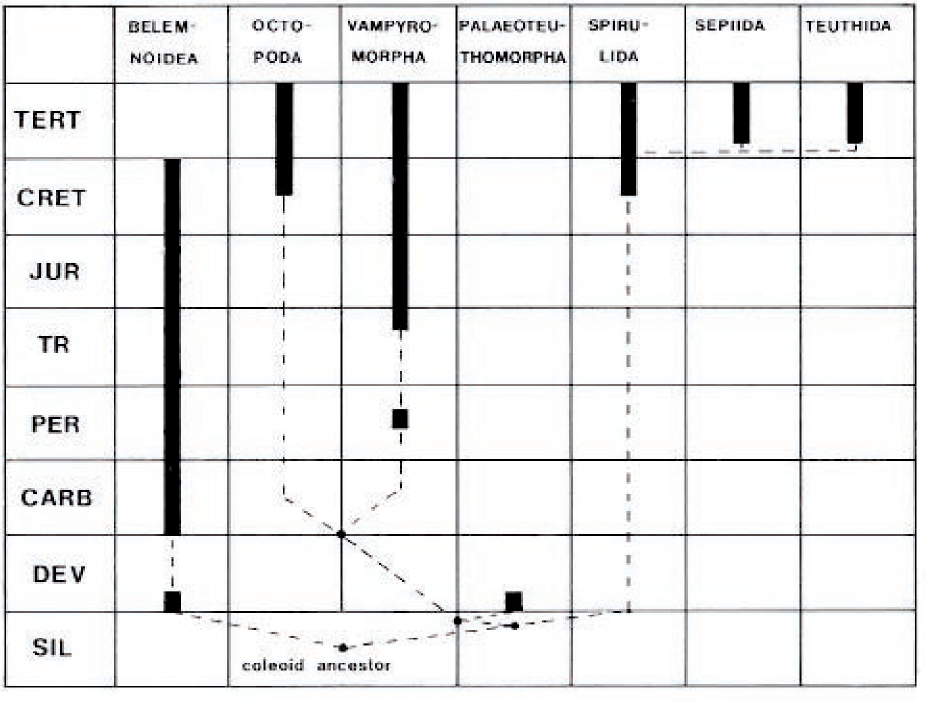
All Recent coleoid cephalopods can be placed in two monophyletic lineages which are characterized mainly by the modification of a particular arm pair: the Vampyromorphoidea (2nd arm pair) and the Decapoda (4th arm pair) (Boletzky 1978-79). The extinct Belemnoidea are stem-group coleoids and the sister-group of all coleoid groups with living representatives (see Text Fig. 3, and following chapter).

5. Vampyromorphoidea — a new monophylum

Autapomorphies are:

1. modification of the second arm pair into filaments (in octopods these are lost);
2. step-wise reduction of the phragmocone into a gladius. In the Octopoda, the gladius is reduced to a vestige.
3. loss of buccal membrane; and
4. arm ganglia connected by a commisure.

The Palaeoteuthomorpha, a group from the Early Devonian with a very small phragmocone and an almost complete body chamber (Bandel et al. 1983), may be placed as a +*plesion* in the stem line of the Vampyromorphoidea. Recent Vampyromorphoidea diverged into two lines, the Vampyromorpha and the Octopoda. Whereas the Octopoda show unique synapomorphies, such as sessile suckers, a particular statolith type, and reduction of the shell to a vestige, the Vampyromorpha remained "primitive". The alleged ancestors of the Recent teuthids known from the Late Triassic (?Permian) to the Late Cretaceous turned out to be vampyromorphs (Bandel & Leich 1985). They may be placed either as a +*plesion* in the stem-group of the Vampyromorphoidea or in the stem line of the Vampyromorpha, with the latter possibility being more likely. *Palaeoctopus* from the Late Cretaceous is probably a crown-group octopod. The so-called "oldest" octopod — *Proteroctopus*



Text Fig. 3. Stratigraphic distribution of the "sucker-bearing" Coleoidea.

from the Middle Jurassic — might be either a stem-group octopod or a fossil vampyromorphid (Engeser, in press). The stratigraphic record of the Vampyromorphoidea show large gaps (Text Fig. 3). Vampyromorphoidea and Decapoda diverged earlier than the Late Triassic (?Permian) (terminus post quem non), most likely in the Late Silurian/Early Devonian when the first radiation of coleoid cephalopods occurred.

6. Decapoda

Autapomorphies of the Decapoda are:
1. modification of the 4th arm pair into tentacles;
2. pedunculate suckers with horny sucker rings;
3. statolith type.

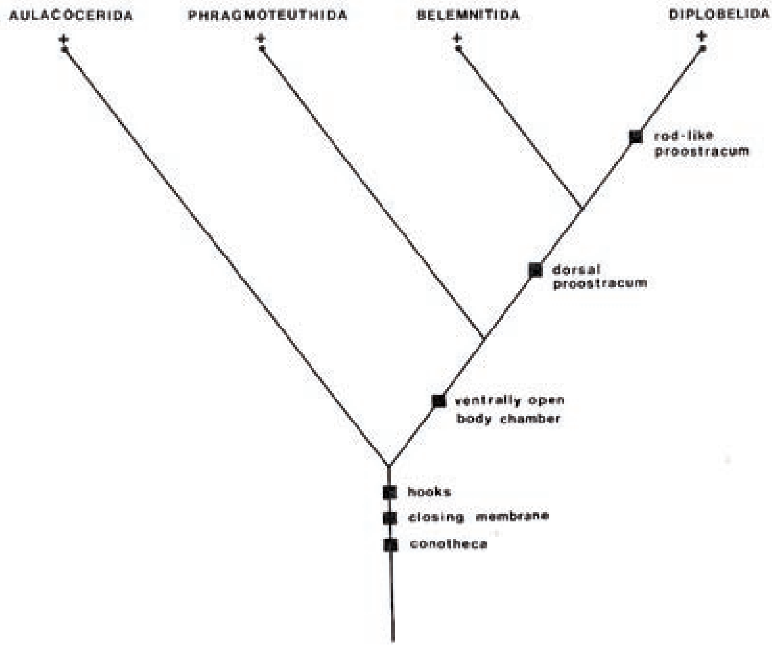
Important coleoid synplesiomorphies include:
1. straight phragmocone with a proostracum and a small aragonitic rostrum; and
2. oegopsid eyes.

The most primitive decapod is *Spirula*. It is the sister-group of all other decapods (the "higher decapods"). The "higher decapods" exhibit strikingly similar statocysts, which can be interpreted convincingly as a synapomorphy (Young 1977). The gladius of Recent teuthids is probably derived from a *Sepia*-like shell by loss of mineralization. Loss of shell mineralization occurred convergently at least four times during the evolution of the Coleoidea.

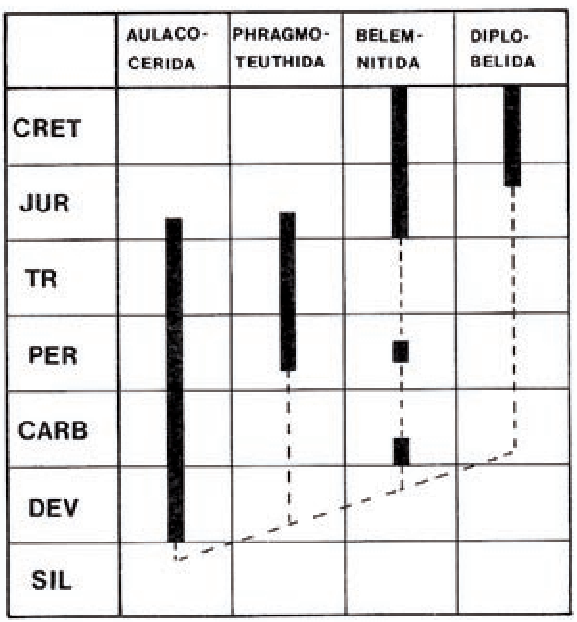
The fossil record of the Decapoda is rather unsatisfactory due to an extremely low fossilization potential. Genuine decapodan fossils are not known from earlier than the Late Cretaceous (fam. Groenlandibelidae), although Decapoda and Vampyromorphoidea have been separated probably since Late Silurian/Early Devonian times. The so-called fossil "teuthids" are vampyromorph coleoids (see Bandel & Leich 1985) and have to be excluded from the Decapoda. True decapodon fossils are commonly found in the Tertiary. The radiation of the "higher decapods" probably took place in the Early Tertiary quite some time after the belemnoid coleoids became extinct. Teuthid statoliths belonging to Recent genera have been described from the Late Eocene of North America (Clarke & Fitch 1979). Some Late Eocene sepiid remains (e.g., *Archaeosepia*) may be regarded as crown group sepiids. However, other so-called fossil "sepiids" are representatives of the stem line of the "higher decapods" while others may be seen as crown-group spirulids (e.g. *Spirulirostra*).

7. Belemnoidea

The extinct Belemnoidea (Early Devonian to the Cretaceous/Tertiary boundary) share three synapomorphies and can be regarded as a monophylum. The Belemnoidea are the sister-group of the "sucker-bearing" coleoids (Vampyromorphoidea and Decapoda). However, in accordance with Patterson & Rosen (1977) they are called a + *plesion*.



Text Fig. 4. Phylogenetic tree ot the Belemnoidea.



Text Fig. 5. Stratigraphic distribution of the Belemnoidea.

Autapomophies are:

1. arm hooks in double rows on all ten subequal arms. The arm hooks of the belemnoid coleoids have nothing in common with the arm hooks of Recent teuthid coleoids (Engeser & Clarke, in press). The arm hooks of the Belemnoidea are derived from cirri, while the arm hooks of Recent teuthids are modified suckers. The chitinous composition of both hook types is different. The authors see the development of arm hooks in belemnoid coleoids as the alternative strategy to the formation of suckers in the "sucker-bearing" coleoids.
2. closing membrane of the phragmocone. The closing membrane (first organic septum) seals the embryonal chamber close to the first mineralized septum. The siphuncle ends on this membrane (compare Jeletzky 1966, Bandel et al. 1984).
3. the conotheca. The belemnoid shell consists of the nacreous septum ("*Spirula* nacre", Bandel 1982, 1985), the inner prismatic conotheca layer, the inner nacreous conotheca layer ("*Nautilus* nacre", Bandel 1982, 1985), the outer prismatic conotheca layer and the outer organic conotheca layer.

In some groups the existence of one or two of these characters still has to be demonstrated, e.g., hooks in Aulacocerida (Bandel 1985). The most likely arrangement of the belemnoid groups can be seen in Text Fig. 4. The stratigraphic distribution is seen in Text Fig. 5.

8. The new classification scheme of the Cephalopoda

In the following scheme only sister-group relationships are indicated.

Cephalopoda Cuvier 1797
- Nautiloidea Agassiz 1847
- Coleoidea Bather 1888
  - (+ *plesion* Ammonoidea)
  - + *plesion* Belemnoidea Gray 1849
  - Vampyromorphoidea new name
    - + *plesion* Palaeoteuthomorpha Bandel, Reitner & Stürmer 1983
    - Octopoda Leach 1818
      - Cirrata Grimpe 1916
      - Incirrata Grimpe 1916
    - Vampyromorpha Robson 1929
      - + *plesion* Prototeuthida Naef 1921 s.l.
        - + *plesion* Prototeuthina Naef 1921
        - + *plesion* Mesoteuthina Naef 1921
  - Decapoda Leach 1818
    - Spirulida Stolley 1919
    - "higher Decapoda"
      - Teuthida Naef 1916
      - Sepiida Zittel 1895

In a classification scheme with ranks, Nautiloidea and Coleoidea may be seen as subclasses, as before, the other groups as follows:

Subclass Coleoidea Bather 1888
- Superorder Belemnoidea Gray 1849
  - Order Aulacocerida Stolley 1919
  - Order Phragmoteuthida Jeletzky in Sweet 1964
  - Order Belemnitida Gray 1849
  - Order Diplobelida Jeletzky 1965

Superorder Vampyromorphoidea new name
- Order Octopoda Leach 1818
  - Suborder Cirrata Grimpe 1916
  - Suborder Incirrata Grimpe 1916
- Order Vampyromorpha Robson 1929
- Order Prototeuthida Naef 1921
  - Suborder Prototeuthina Naef 1921
  - Suborder Mesoteuthina Naef 1921

Superorder Decapoda Leach 1818
- Order Spirulida Stolley 1919
- Order "higher decapods" (new name to be created)
  - Suborder Teuthina Naef 1916
  - Suborder Sepiina Zittel 1895

9. Discussion

The use of the cladistic method for classifying fossil cephalopods does not simplify systematics but makes it more clear. This is because some cephalopod groups have so few apomorphies (e.g., bactritids) that a phylogenetic classification seems almost impossible. Many cephalopod groups are poorly understood, and the classification of major groups is often based on data gained from just a few investigated specimens. A future task is to reinvestigate these groups with modern methods in order to obtain new data and more characters.

On the other hand application of the cladistic method may be suitable particularly for the classification of goniatitids and ammonoids, since these groups show relatively numerous characters. A consistent application of phylogenetic systematics certainly will shift many major fossil cephalopod groups from the nautiloid line to the coleoid line or vice versa, especially when more data of the embryonic development become available. Furthermore, the phylogenetic clades which result from the phylogenetic systematics approach point out gaps in the fossil record and indicate where future research in fossils may be most fruitful.

The method also allows detailed "reconstructions" of common ancestors of particular cephalopod groups, an attempt already undertaken by Naef (1921-27, 1922). He called these fictive animals ("ideale Urformen"): *Prototeuthis*, *Protodibranchus*, *Protodecapus*, *Protoctopus* and *Protosepioides*. However, such reconstructions can become more precise. In any case, phylogenetic systematics will help elucidate the evolution of the cephalopods more precisely than the previous phenotypic classification.

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