

THE UNIVERSITY OF KANSAS
PALEONTOLOGICAL CONTRIBUTIONS

August 1994

Number 5

PHYLOGENY AND SYSTEMATICS OF THE COLEOIDEA

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Abstract.—The Coleoidea are a monophyletic group of cephalopods characterized by the endocochleate condition of their shell. A phylogeny presented here demonstrates that the Coleoidea comprises three natural groups, ranked as superorders: Belemnnoidea Hyatt, Decabrachia Boettger, and Octobrachia Fiorini. The Belemnnoidea (belemnites and aulacocerids) contains rostrum-bearing coleoids possessing a closing membrane and multilayered conotheca. The Decabrachia (teuthids and sepiids) is characterized by the possession of ten arms in which the fourth pair is modified as tentacles. The Octobrachia (octopods and vampyromorphs) contains cephalopods in which the ten-armed condition has been modified so that the second arm-pair has been lost or modified. A fourth group, the Phragmoteuthidida, is imperfectly known and may represent a stem group to the Decabrachia and Octobrachia. The systematics of the Coleoidea is revised, and an outline classification of the Coleoidea presented. The systematic status of coleoids from the Devonian Hunrückschiefer (Germany) and Permian Phosphoria Formation (Utah, USA) and the stratigraphical range of the Belemnitida are discussed. Detailed reports of the taxonomic status of the following genera are presented: *Acanthoteuthis*, *Belemnites*, *Belemnosepia*, *Belopeltis*, *Conoteuthis*, *Geoteuthis*, *Kerunia*, *Loligosepia*, *Orcagnia*, *Ostracoteuthis*, *Paraplesioteuthis*, *Plagioteuthis*, *Platylithophycus*, *Produvalia*, *Spirulirostrina*, and *Trachyteuthis*. Lectotypes are designated for the following species: *Acanthoteuthis speciosa*, *Archaeosepia naefi*, *Belopeltis sinuatus*, *Conoteuthis dupinianus*, *Ostracoteuthis superba*, and *Trachyteuthis ensiformis*. Finally, three new taxa are erected in the taxonomic appendix: Actinosepiidae, *Bairstowius*, and *Hungarosepia*.

INTRODUCTION

The Coleoidea are a group of cephalopod molluscs that are largely characterized by the possession of an internal (endocochleate) shell. As a group, they have received relatively little attention. Although many papers have appeared that describe belemnites or fossil squids (teuthids) and related forms, there are few comprehensive treatments of the group, at least since the pioneering work of A. Naef (1921, 1922), whose expertise spanned both living and fossil coleoids. Until his death, the foremost coleoid expert, J. A. Jeletzky, had planned to write the Coleoidea volume of the *Treatise on Invertebrate Paleontology*. This volume was to follow the publication of a major paper (Jeletzky,

1966), the first attempt at a modern revision of the Coleoidea. Responsibility for production of the Coleoidea volume has now passed to the authors, with D. T. Donovan as coordinating author. In this paper we set out our interpretation of the phylogeny of the group and outline the proposed classification to be used in the *Treatise*. In the course of our work it has been apparent that a number of taxa are nomenclaturally or otherwise unstable: these taxa are dealt with in the last part of the paper. Finally, a new belemnite genus, planned by Dr. Jeletzky in one of his unpublished manuscripts, is published here in an appendix in order that it might be included within the forthcoming Coleoidea volume. Bibliographic references are not given for taxa above genus rank for consideration of space.

PHYLOGENY OF THE COLEOIDEA

In recent years the phylogeny of the Coleoidea has been given much attention in cladistic treatments (Berthold and Engeser, 1987; Engeser and Bandel, 1988; Engeser, 1990a, 1990b). These papers largely concur with earlier studies (e.g., Jeletzky, 1966; Donovan, 1977) on the mostly uncontentious broad phylogeny of the belemnites and related taxa (e.g., aulacocerids and diplobelids). With one or two exceptions, most authors accept the monophyly of the natural group of rostrum- and chambered-phragmocone-bearing coleoids. Debate has, however, centered on the origin, affinity, and monophyly of the so-called teuthids or fossil squids, with, for example, much discussion on the vampyromorph affinities (e.g., Bandel and Leich, 1986).

The phylogeny presented below takes into consideration these and other works in an effort to present a workable and phylogenetically sound classification for the Coleoidea. Recent cladistic papers (e.g., Berthold and Engeser, 1987; Engeser, 1990b), although adding much to our understanding of the group, suffer in their lack of a workable hierarchical classification. Thus, although the

broad phylogenetic approach can be sound, the resulting classification often has no meaning in current systematics. An attempt to remedy this is given below.

The phylogeny.—The phylogeny presented in summary in Figures 1 and 2 is based on the generally held tenet (e.g., Jeletzky, 1966; Donovan, 1977; Engeser and Bandel, 1988) that the Coleoidea arose from orthoconic ancestors, possibly via the Bactritida as stem group or direct from the Orthocerida.

There are some important differences between our phylogeny and that of Engeser and Bandel (1988, fig. 2). First, by implication, Engeser and Bandel illustrated an origin for the Cirrata and Incirrata (our Cirroctopoda and Octopoda, respectively) that predates that of the Prototeuthida (approximating our Loligosepiida). In our phylogeny (Fig. 1, 2), we consider the Loligosepiida to have been the more ancient lineage, the octopods being derived much later on. Second, these authors regarded the Sepiida plus Teuthida as a sister group of the Spirulida with a more recent common ancestor, whereas we consider the Sepiida plus Spirulida as the sister group of the Teuthida (Fig. 2). Third, we regard the Phragmoteuthida as a stem group of the Octobranchia and Decabrachia,

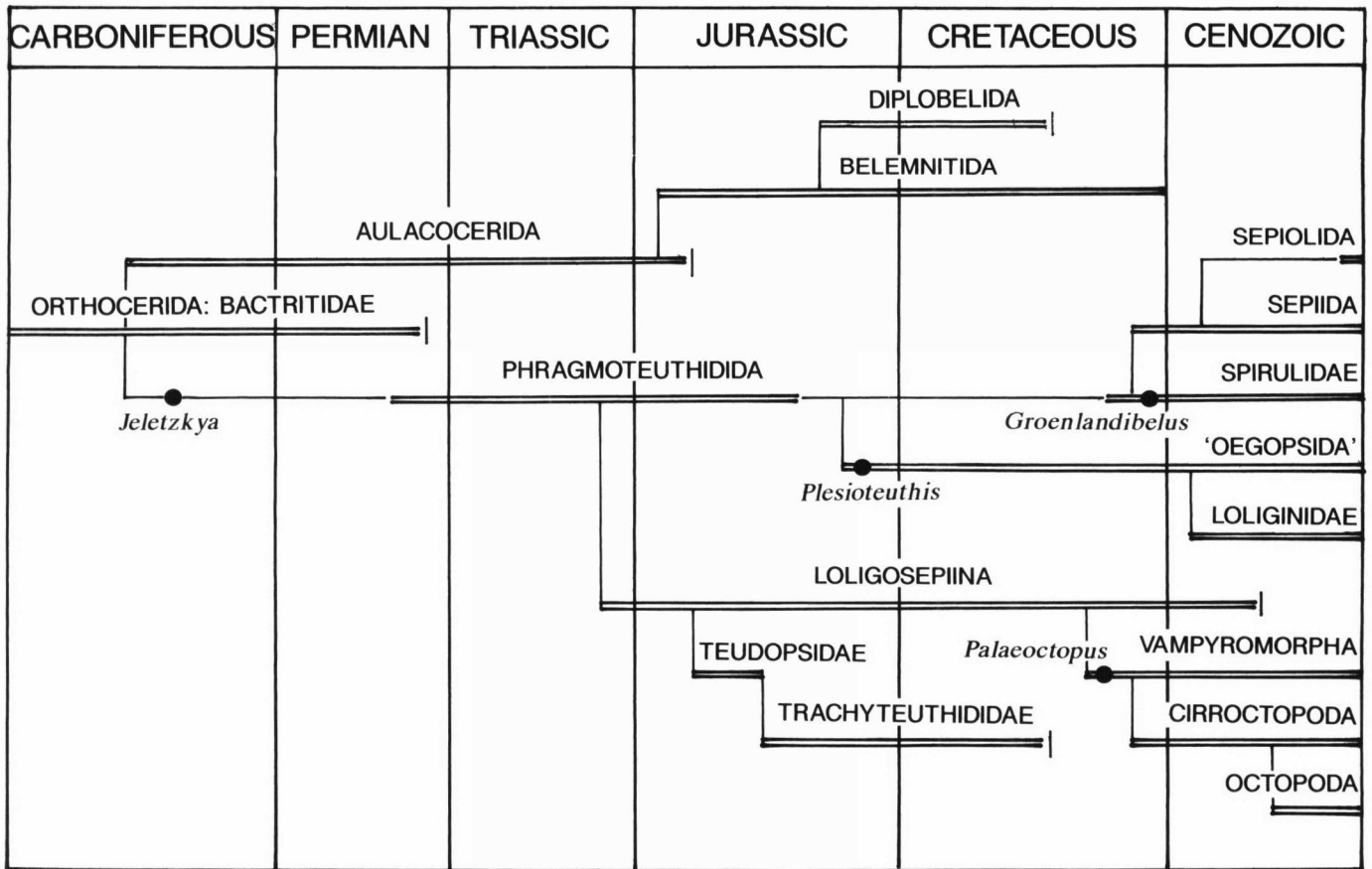


Figure 1. Phylogenetic tree of the Coleoidea. Note that the Coleoidea are derived from orthocone (bactritid) ancestors some time in the late Paleozoic. As discussed in the text, this tree excludes the doubtful records of Paleozoic ancestors of the Decabrachia-Octobranchia line (e.g., Gordon, 1971; Bandel *et al.*, 1983). It also excludes the possibility of Triassic belemnites. Note that ranges in time are conjectural for the Vampyromorpha, Cirroctopoda, and Octopoda, which have limited or no fossil record.

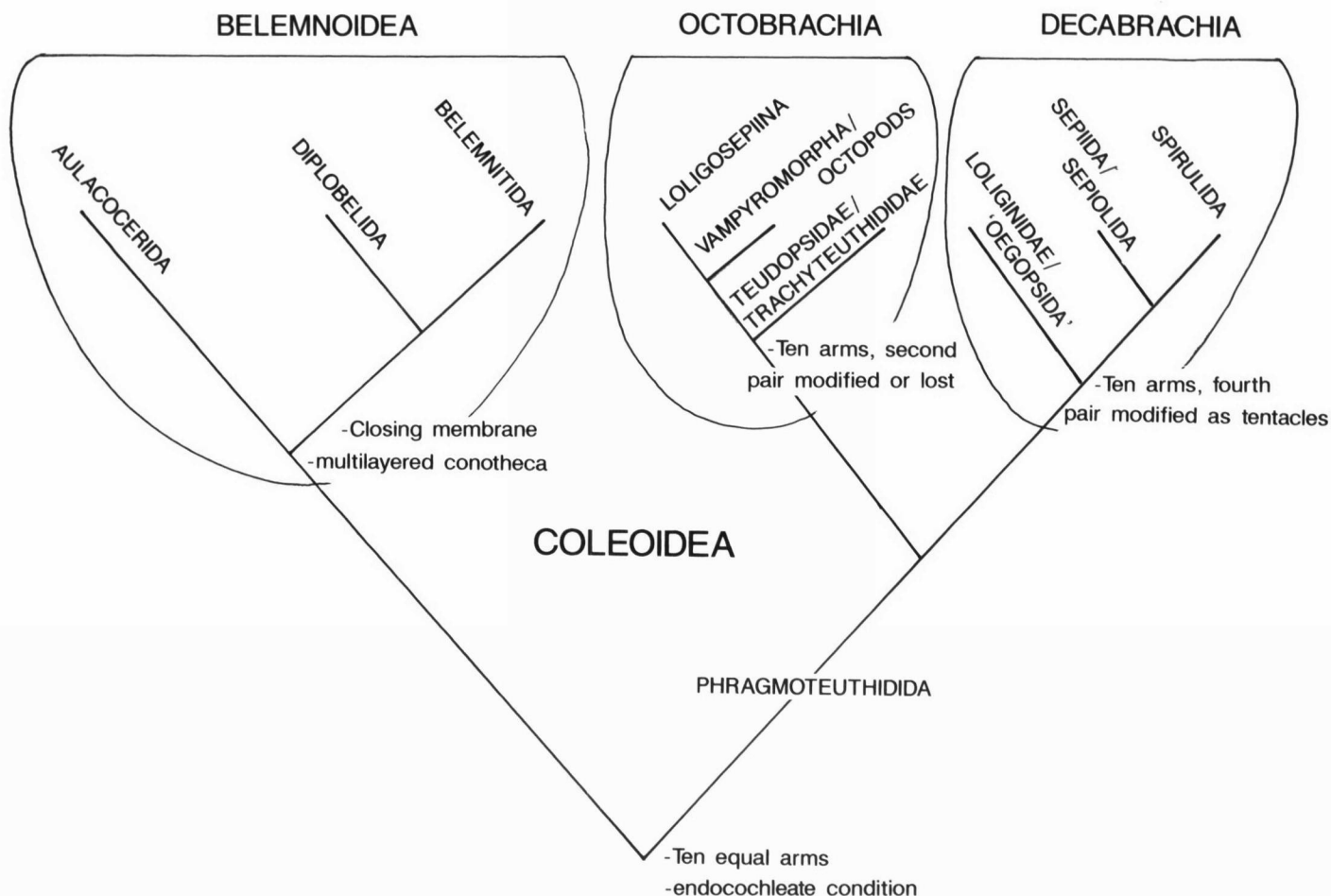


Figure 2. Phylogram of the Coleoidea illustrating the major groups and the key apomorphies as discussed in text. Note that the plesiomorphic state is that of a ten-armed, endocochleate cephalopod with entire body chamber.

rather than a sister group of the Belemnoidea (Fig. 2; cf. Engeser and Bandel, 1988, fig. 4).

Apomorphies of the Coleoidea have been discussed in detail elsewhere (Berthold and Engeser, 1987; Engeser and Bandel, 1988; Engeser, 1990a, 1990b) and are not considered further here. However, we infer that the primitive coleoid had ten similar arms because that is the simplest pattern that could have been modified to produce the arm patterns in existing groups and because there is at least one early coleoid (the Upper Carboniferous *Jeletzkyia*) with ten arms preserved (Fig. 1). Engeser (1990a) suggested that having ten arms is a plesiomorphic character state for the Coleoidea that was derived from echtocochlean ancestors, but no evidence is available to confirm this.

The phylogeny set forth in Figure 2 demonstrates three natural monophyletic groupings within the Coleoidea. The Phragmoteuthidida consists of imperfectly preserved fossils and may not easily be further classified without more work, including, in particular, a detailed examination of phragmocone and protoconch. In recognition of this, the three main groups are given the rank of superorder below (cf. Engeser and Bandel, 1988), while the Phragmoteuthidida is maintained at ordinal level until its supraordinal affinities can be confirmed. The groups are:

- Superorder Belemnoidea Hyatt, 1884
- Superorder Decabrachia Boettger, 1952
- Superorder Octobrachia Fioroni, 1981
- Order Phragmoteuthidida Jeletzky, 1965

Apomorphies (derived characters) for these groups are given below and are discussed in detail by Berthold and Engeser (1987) and Engeser (1990a, 1990b).

Superorder Belemnoidea

Synapomorphies of the Belemnoidea: closing membrane to the protoconch (i.e., no caecum); conotheca consisting of five layers (see Engeser, 1990a, 1990b).

The form of the protoconch, with its closing membrane and lack of a caecum, and the multilayered conotheca are common to all the members of this group. The presence of a rostrum, at least in a primitive form, was considered by Engeser and Bandel (1988, p. 108) to be plesiomorphic, derived from the common ancestor, with homologous rostra in the Decabrachia. Phylogenetic weight has previously been given (e.g., Jeletzky, 1966) to the observed difference in mineralogy between belemnite and aulacocerid rostra (low-magnesium calcite and aragonite, respectively). Recent studies by Bandel *et al.* (1984) and Bandel and Spaeth

(1988), however, have indicated that the belemnite rostrum may in fact develop a mixed aragonitic-calcitic mineralogy through ontogeny and may even develop a wholly aragonitic rostrum, as in *Belemnotheutis*. Use of this character is therefore regarded as unsafe.

Stratigraphically the Aulacocerida are the most primitive, first appearing in the Lower Carboniferous or possibly even Devonian (Doyle, 1990b) (Fig. 1). This group has the plesiomorphic character of an entire body chamber that was derived from the orthoconic ancestor and not seen in the Belemnitida or the Diplobelida. Differences in septal necks—orthochoanitic to hemichoanitic in belemnites (Jeletzky, 1966) but achoanitic to prochoanitic (Jeletzky, 1966) or retrochoanitic (Mutvei, 1971) in aulacocerids—do not necessarily militate against derivation of belemnites from aulacocerids. This is in keeping with earlier ideas in the first half of this century regarding the close relationship of belemnites and aulacocerids (discussed by Jeletzky, 1966, p. 12), with the former being directly derived from the latter. Recent cladistic treatments of belemnite phylogeny (e.g., Engeser and Bandel, 1988) also suggest that derivation from the Aulacocerida, perhaps via the Phragmoteuthidida, may have occurred (see below). The presence of arm hooks in all the groups except the Aulacocerida (although *Jeletzkyia* may belong here, see below) is an apomorphy of the Belemnoidea, although in the phylogeny presented here, it is plesiomorphic.

Superorder Decabrachia

Synapomorphy of the Decabrachia: ten arms, fourth pair modified as tentacles.

Engeser (1990b) has noted the mostly plesiomorphic conditions of the shell of the Decabrachia, as the Spirulida in particular are characterized by a phragmocone with simple, three-layered conotheca partially covered in some fossil taxa by an aragonitic rostrum. This condition is modified in the Sepiida and in the Teuthida.

We differ from Bandel and Leich (1986), Engeser and Bandel (1988), and Engeser (1988) in that we retain the Plesiototeuthidae in the Decabrachia. Evidence for the octobranchian (vampyromorph) affinity of *Plesiototeuthis* is weak, resting on the presence of stellate arm prints in which the central part is blank. This is claimed to show that the arms were held apart by a web similar to that of *Vampyroteuthis* (Bandel and Leich, 1986), but there is no actual imprint of the web. Following the comments of Donovan and Toll (1988, p. 98), we consider that the gladius of *Plesiototeuthis* is homologous with that of present-day squid (Oegopsida), and this evidence, together with the general squidlike aspect of this genus, is at least as compelling as the supposed web.

Superorder Octobrachia

Synapomorphy of the Octobrachia: ten arms, second pair modified or lost.

We accept the octobranchian (vampyromorph) affinities of the Loligosepiidae given the relative similarity in form of the gladius (Donovan, 1977; Donovan and Toll, 1988). Similar gladii are present in taxa of the Teudopsidina (=Mesoteuthina Naef), for example in *Teudopsis*. We retain the ordinal rank of the Loligosepiidae, however, and restrict the Vampyromorpha to the single, living, monogeneric family.

The phylogeny presented necessitates the loss of the phragmocone more than once in the course of evolution (Fig. 2). Certainly, in the Octobrachia there is no trace of phragmocone. Robson (1932, p. 129) was satisfied that the octopodan shell-vestige is homologous with the decapoden shell and has a similar origin in a shell-sac, but if so the shell-vestige is so reduced as to be of no use for comparison with an outgroup. Indeed, Engeser (1990b) has for this reason considered that reduction of the phragmocone is an apomorphy of the Octobrachia, despite a similar reduction in the Teuthida (Decabrachia). The alternative is to assume that specialization of the fourth pair of arms took place more than once, in the teuthids and sepiids; and this is less likely given the general similarity of the tentacles in the two groups.

Order Phragmoteuthidida

The phylogenetic position of the Phragmoteuthidida is under some debate. So far, it is unclear whether the Phragmoteuthidida possessed a typical belemnoid protoconch and phragmocone. It is clear, however, that the group has an apomorphy in the unusual form of its proostracum, with a three-lobed, anterior margin springing from three-quarters of the phragmocone circumference (Jeletzky, 1966; Donovan, 1977). This is unique in the coleoids and supports the generally held hypothesis of progressive loss of shell within the Coleoidea. Authors have indicated the importance of the phragmoteuthids in the phylogenetic development of the Coleoidea by suggesting the three possible phylogenies shown in Figure 3.

The phragmoteuthid phragmocone has been little studied (see below) and no detailed examination has been published. In general terms the phragmocone is conservative, broadly similar to that of the belemnoids (Jeletzky, 1966). A possible, extremely thin, rostrumlike layer has been detected in phragmoteuthids from the Lower Jurassic of Dorset (J. A. Jeletzky, MS notes). Phragmoteuthids are known to have had ten arms equipped with hooks (Donovan, 1977; Riegraf, Werner, and Lörcher, 1984, fig. 43c). These are all plesiomorphic characters of the Coleoidea and do little to elucidate the lineages outlined above. Deriving the phragmoteuthids from the aulacocerids relies on the loss or at least major reduction of the massive aragonitic rostrum, which is later redeveloped, albeit predominately in calcite, if we interpret the belemnitids as having been derived from the lineage aulacocerids-phragmoteuthids-belemnitids (Engeser and Bandel, 1988).

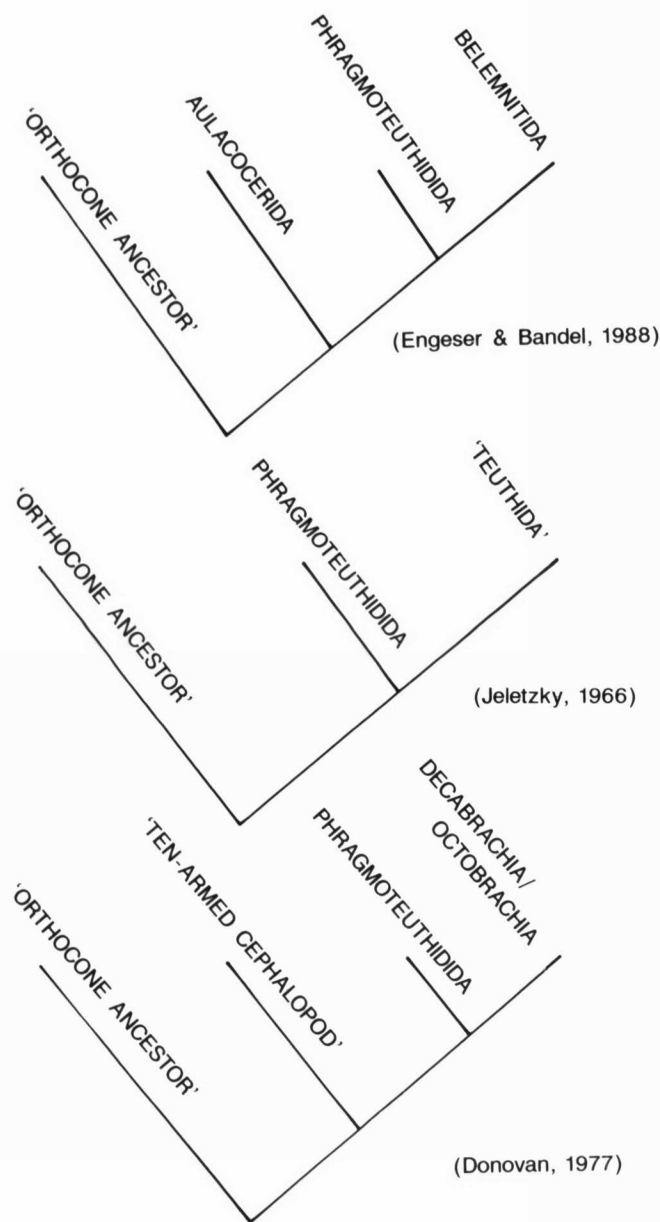


Figure 3. Conjectural phylogenies involving the Phragmoteuthidida.

Erben's (1964) idea of a diphyletic origin of the Belemnoidea, with separate derivation of the belemnites and aulacocerids from bactritid ancestors, is not supported.

Deriving the Decabrachia and Octobrachia from the phragmoteuthids is attractive. The phragmocone is reduced, and the proostracum is similar in form to the gladii of succeeding groups (e.g., *Loligosepia*, Jeletzky, 1966). This interpretation is accepted here as the most parsimonious alternative (Fig. 2), although detailed study of the phragmoteuthid protoconch is needed. Recognition of whether a prosiphon or caecum is present (as in the Decabrachia but not Belemnoidea), for instance, would clarify the phylogeny.

CLASSIFICATION OF THE COLEOIDEA

The classification shown in Table 1 is to be the basis of the Coleoidea volume of the *Treatise*. In our classification we have used typified rather than descriptive taxa (as recommended by Storabogatov, 1991) to a greater extent than previous classifications. Thus, the Prototeuthoidea and Mesoteuthoidea of Naef (1921), retained by Jeletzky (1966) with reservations, are finally discarded. The sole remaining exceptions at the ordinal level are Teuthids (which may appear to be a typified name, but *Teuthis* is a fish), Vampyromorpha, and Cirroctopoda.

OUTSTANDING PROBLEMS

Devonian coleoids

Bandel *et al.* (1983) and Stürmer (1985) have described coleoids from the Lower Devonian Hunsrückschiefer of Germany. These are mostly poorly preserved and described from X-radiographs.

Protoaulacoceras longirostris (Bandel *et al.*, 1983) was described from a number of specimens. A rostrum with alveolus forming the holotype has since been reidentified as a fish spine (Engeser, 1990b; J. Dzik, personal communication, 1991), and evidence of specific coleoid affinities of the rest of the specimens is weak. It is probable that these specimens have nautiloid affinities and therefore that the Protoaulacoceratidae is untenable as a coleoid family.

Bandel *et al.* (1983) described a new superorder, the Palaeoteuthomorpha containing two orders, the Boletzkyida and the Naefiteuthida. Septa and protoconch of the specimens illustrated are clear, and these specimens (assigned to two genera, *Boletzkyia* and *Naefiteuthis*) display a keeled body chamber or proostracum. The interpretation of these specimens is difficult. Bandel *et al.* (1983) considered them to be ancestral to the Loligosepiidae and modern teuthids; Engeser (1990b) placed stem-lineage representatives close to the Octopodiforms (=Octobrachia), while Riegraf (personal communication, 1992) regarded them as aulacocerids. Bandel *et al.* (1983, p. 407, 413) suggested that the phragmocones described are close to those of orthoconic nautiloids and that the body chamber of *Naefiteuthis breviphragmoconus* resembles that of a Triassic *Aulacoceras*. That these fossils are bactritids cannot be ruled out; Termier and Termier (1971) employed a similar line of argument to that of Bandel *et al.* (1983) in describing what they considered to be incipient proostraca in some possible bactritids from Morocco. Clearly, interpretation of these fossils is difficult, and for the purposes of the *Treatise* they will be treated as *incertae sedis*.

Eoteuthis was described by Stürmer (1985) for fossils that superficially resemble modern teuthids, so much so that this author placed his new genus in the family Loliginidae. Engeser (1990b, p. 130) was less convinced and suggested, in fact, that, this fossil was an orthoceratid. On the other hand, Riegraf (personal communication, 1992) treated

Table 1. Classification of the subclass Coleoidea. An approximate stratigraphical range is given for each taxon of ordinal rank. Details of the ranges of family-group taxa were given by Doyle (1993). Neither synonymies of family-group taxa nor full bibliographic references are given for consideration of space.

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- Class CEPHALOPODA Cuvier, 1794
- Subclass COLEOIDEA Bather, 1888
- Superorder BELEMNOIDEA Hyatt, 1884 (?Devonian; Carboniferous–Cretaceous)
- Order AULACOCERATIDA Stolley, 1919 (?Devonian; Carboniferous–Jurassic)
- Family AULACOCERATIDAE Mojsisovics, 1882
- Family PALAEOBELEMNOPSIDAE Chen, 1982
- Family XIPHOTEUTHIDIDAE Naef, 1922
- Family CHITINOTEUTHIDIDAE Müller-Stoll, 1936
- Order BELEMNITIDA Zittel, 1895 (Jurassic–Cretaceous)
- Suborder BELEMNITINA Zittel, 1895
- Family PASSALOTEUTHIDIDAE Naef, 1922
- Family SALPINGOTEUTHIDIDAE Doyle, 1992
- Family HASTITIDAE Naef, 1922
- Family CYLINDROTEUTHIDIDAE Stolley, 1919
- Family OXYTEUTHIDIDAE Stolley, 1919
- Suborder BELEMNOPSEINA Jeletzky, 1965
- Family BELEMNOPSEIDAE Naef, 1922
- Family DICOELITIDAE Saks and Nal'nyaeva, 1967
- Family PSEUDODICOELITIDAE Saks and Nal'nyaeva, 1967
- Family DUVALIIDAE Pavlow, 1914
- Family BELEMNITELLIDAE Pavlow, 1914
- Family DIMITOBELIDAE Whitehouse, 1924
- Suborder BELEMNOTHEUTIDIDINA Stolley, 1919
- Family BELEMNOTHEUTIDIDAE Zittel, 1885
- Order DIPLOBELIDA Jeletzky, 1965 (Jurassic–Cretaceous)
- Family DIPLOBELIDAE Naef, 1926
- Superordinal Status Uncertain
- Order PHRAGMOTEUTHIDIDA Jeletzky, 1965 (Permian–Jurassic)
- Family PHRAGMOTEUTHIDIDAE Mojsisovics, 1882
- Superorder DECABRACHIA Boettger, 1952 (Cretaceous–Holocene)
- Order SPIRULIDA Stolley, 1919 (Cretaceous–Holocene)
- Family GROENLANDIBELIDAE Jeletzky, 1966
- Family VASSEURIDAE Naef, 1921
- Family BELEMNOSEIDAE Wiltshire, 1869
- Family BELOPTERIIDAE Naef, 1922
- Family SPIRULIROSTRIDAE Naef, 1921
- Family SPIRULIROSTRINIDAE Naef, 1921
- Family SPIRULIDAE Orbigny, 1826
- Order SEPIIDA Zittel, 1895 (Cretaceous–Holocene)
- Family BELOSEPIELLIDAE Naef, 1921
- Family BELOSEPIIDAE Dixon, 1850
- Family SEPIIDAE Keferstein, 1866
- Family SEPIADARIIDAE Naef, 1921
- Family ACTINSEPIIDAE fam. nov. (see appendix)
- Order SEPIOLIDA Fioroni, 1981 (Holocene)
- Order TEUTHIDA Naef, 1916 (Jurassic–Holocene)
- [includes living Oegopsida of authors]
- Family PLESIOTEUTHIDIDAE Naef, 1921
- no other families in the fossil record
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- Superorder OCTOBRACHIA Fiorini, 1981 (Triassic–Holocene)
 - Order LOLIGOSEPIIDA Jeletzky, 1965 (Triassic–Neogene)
 - Suborder LOLIGOSEPIINA Jeletzky, 1965
 - Family LOLIGOSEPIIDAE Regteren Altena, 1949
 - Family GEOPELTIDIDAE Regteren Altena, 1949
 - Family LEPTOTHEUTHIDAE Naef, 1921
 - Family MASTIGOPHORIDAE Engeser and Reitner, 1985
 - Family NECROTEUTHIDIDAE Kretzoi, 1942
 - Suborder TEUDOPSIDINA Storabogatov, 1983
 - Family PALAEOLOLIGINIDAE Naef, 1922
 - Family TEUDOPSIDAE Regteren Altena, 1949
 - Family KALAENIDAE Naef, 1921
 - Family TRACHYTEUTHIDIDAE Naef, 1922 (see below)
 - Order VAMPYROMORPHA Robson, 1929 (Holocene)
 - Order OCTOPODA Leach, 1817 (Neogene–Holocene)
 - Family ARGONAUTIDAE Reeve, 1841
 - No other families in the fossil record.
 - Order CIRROCTOPODA Young, 1989 (Jurassic/Cretaceous–Holocene)
 - Family PALAEOCTOPODIDAE Dollo, 1912
 - no other families in the fossil record
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Eoteuthis as an aulacoceratid. *Eoteuthis* has clearly been overinterpreted and will be treated as a doubtful coleoid in the *Treatise*.

The earliest and latest belemnites

Although the belemnites are relatively well characterized, there is considerable latitude in the estimates of the longevity of the group, ranging from Devonian to Paleogene in the widest sense, to Jurassic to Cretaceous in the narrowest sense. Although work is still needed to clarify this, the following discussion is a justification of the line to be followed in the *Treatise*.

Records of Carboniferous belemnites exist in the form of *Eobelemnites caneyensis* Flower and *Jeletzkyia douglassae* Johnson and Richardson. The belemnite taxa described from the Mississippian of North America by Flower and Gordon (1959) are actually all representative of the Aulacocerida with the exception of an additional specimen assigned to *Eobelemnites*, now regarded as a nautiloid phragmocone (Gordon, 1966).

Most authorities agree that the only true specimen of *Eobelemnites* is indeed a belemnite phragmocone, indistinguishable from Jurassic examples (Flower, 1945; Jeletzky, 1966, p. 116), there being no evidence for the re-entrants in the proostracum reconstructed by Flower (1945, fig. 1c). However, as this specimen was not collected by the authors of the species and as the only evidence of its age is

its museum label, its stratigraphical location must surely be treated as dubious and unsafe. *Jeletzkyia* is without doubt a Carboniferous cephalopod, but evidence for its belemnite affinities rest with its ten, hook-bearing arms (Johnson and Richardson, 1968; Gordon, 1971). No phragmocone or rostrum has been observed in detail, and Saunders and Richardson (1979) argued for teuthid origins through the identification of so-called gladii in the same strata (since identified as fish scales by Riccardi and Sabattini, 1985). Arm hooks are known from Permian phragmoteuthids (Engeser and Clarke, 1988), and *Jeletzkyia* is just as likely to be a phragmoteuthid, or even an aulacocerid for that matter, as no aulacocerid arm crowns have yet been recovered. Discounting both these records as equivocal, we are left with two other pre-Jurassic records of belemnites, from the Permian and Triassic of China.

Chen and Sun (1982) described a new family from the Permian of South China, the Palaeobelemnopsidae, which they considered to be ancestral, early belemnites. This family occurs with the aulacocerid *Stenoconites* and has recently been reassigned to Aulacocerida by Doyle (1990b) on the basis of characteristics of the phragmocone. Triassic records include that of Erben (1964, p. 496, footnote), who argued that several breviconic phragmocone species from the alpine Triassic are true belemnites; but this was discounted by Jeletzky (1966), who included them in his new aulacocerid genus, *Mojsisovicsteuthis*. Zhu and Bian

(1984) described a Triassic coleoid family from China, the Sinobelemnitidae. From surface morphology, these appear to be true belemnites and are remarkably closer in form to Middle and Late Jurassic belemnites (Belemnopseidae; e.g., Yang and Wu, 1964) than to the Early Jurassic Belemnitidae. The structure of the rostrum in many ways resembles that of representatives of the Aulacocerida, with little evidence of concentric laminae. Further investigations of the phragmocone and rostra of these coleoids is necessary to determine their true nature. Certainly, these are the only serious contenders in the search for pre-Jurassic belemnites (Doyle, 1993). Thus, until serious further study can be done, the earliest belemnites are considered to be of Early Jurassic age (*Planorbis* Zone) and to comprise simple, conical rostra without grooves and with generalized lateral lines. Phylogenetically this makes the most sense, but further research may yet determine the Chinese Triassic records to be the earliest belemnites.

At the other end of the geological time scale, the last appearance of the belemnites has also taxed the minds of paleontologists. There are two possibilities: first, that the last belemnites appeared in the Maastrichtian and went extinct with the ammonites at the Cretaceous-Tertiary boundary and, second, that the belemnites continued into the Paleogene where they were represented by a solitary genus, *Bayanoteuthis*. The story is complicated by the existence of rostrum-bearing spirulids (e.g., *Vasseuria*; see Curry, 1955) and of pennaculacean coral homeomorphs (Branco, 1885; Riegraf, 1991). *Bayanoteuthis* has not been studied in sufficient detail to allow a definite decision. However, the form of the rostrum is quite unlike its stratigraphically viable belemnite ancestors, and to date no phragmocone has been demonstrated to belong to this taxon. Therefore, for the purposes of the *Treatise*, we propose to treat this genus as a doubtful taxon, thus restricting true belemnites to the Mesozoic.

Permian teuthids

Gordon (1971) described a series of fossils from the Permian Phosphoria Formation of Utah, which he interpreted as primitive squid gladii. These specimens were referred to a new genus and species, *Glochinomorpha stifeli* Gordon. We have examined some of the type specimens from the United States National Museum, USNM 170612, 170613, and 170606, which are extremely small fossils (approximately 5 mm long) superficially resembling calaenid-type teudopsids. Specimens USNM 170612 and 170606 possess a ribbed, conuslike structure associated with an elongate rhachislike structure. Specimen USNM 170613 possesses only a ribbed conus. In each specimen the supposed conus has a series of ribs dispersing from the apex, with finer striae between them. The conus is not quite symmetrical, and its shape and form are more suggestive of a flattened umbrellalike form than a conus. The rhachis associated with specimens USNM 170612 and 170606 is an

elongate structure of irregular form; in USNM 170606 it is clearly offset from the center of the apex of the conus; in USNM 170612 its position is equally uncertain. Both these features are unlike those of any coleoid.

Authors have already questioned the true affinity of these specimens (Engeser and Phillips, 1986; Engeser, 1990b), suggesting that they may be of vegetable origin. It is possible that they represent umbrellalike structures associated with the reproductive organs of plants (e.g., a fern indusium) (M. Collinson, personal communication, 1992). Therefore, for the purposes of the *Treatise*, *Glochinomorpha stifeli* Gordon will be treated as a doubtful coleoid.

NOTES ON SOME GENERA

ACANTHOTEUTHIS Wagner in Münster, 1839

This genus was proposed by Rudolph Wagner in the work by Münster (1839, p. 94) along with an alternative name for the same form, *Acanthopus*. Münster apparently preferred *Acanthoteuthis* and described three species bearing this name in the same paper: *A. speciosa* (p. 94, pl. 9), *A. Férussacii* (p. 95, pl. 10, fig. 1), and *A. Lichtensteinii* (p. 96, pl. 10, fig. 2). The first two of these species had previously been published as *nomina nuda* in the combinations *Onychoteuthis speciosa* and *O. Férussacii* by Münster (1837, p. 252). *Acanthoteuthis speciosa* was listed as type species by Bülow-Trummer (1920, p. 268), constituting a valid subsequent designation. Because of the considerable complications associated with the stability of the genus, an application has been made to the ICZN to conserve the nominal genus *Acanthoteuthis* (Donovan, in press).

Acanthoteuthis was proposed for fossils from the Solnhofener Plattenkalk with arms bearing double rows of hooks. The figured specimen of the type species shows the arm crown only, but Münster (1839) described two other examples that showed parts of the body as well. Engeser and Reitner (1981) reviewed the status of *Acanthoteuthis* but did not designate a lectotype. Therefore, we herein designate the original specimen of Münster's (1839) plate 9 the lectotype of the species *Acanthoteuthis speciosa*.

The nominal genus *Acanthopus*, published intentionally as an alternative name, is an objective synonym of *Acanthoteuthis* and a junior primary homonym of the nominal genus *Acanthopus* Klug, 1808.

BELEMNITES Lamarck, 1799

The problems associated with this nominal genus and the application for its suppression have been discussed elsewhere (Doyle and Riegraf, 1986; Tubbs, 1989, 1992; Doyle, 1991, 1992). However, it is pertinent to record that in June, 1993 the nominal genus *Belemnites* and its type species *B. paxillosa* were suppressed for the purposes of the Principle of Priority, and the family group name Passaloteuthididae was placed upon the Official List of Family-Group Names in Zoology (ICZN, 1993, Opinion 1721).

BELEMNOSEPIA Buckland, 1836

This nominal genus is taxonomically unstable. Although sometimes attributed to Agassiz (1835), the first valid publication of the genus was by Buckland (1836a), who published a description of fossil coleoids with associated ink sacs from the Lower Jurassic of Lyme Regis. In the same year Buckland published a second description with illustrations (Buckland, 1836b). The fossils described and illustrated by Buckland (1836a, 1836b) can now be referred to *Belemnoteuthis montefiori* Buckman, 1880 (T. Engeser, personal communication, 1992), though neither of Buckland's publications referred to a species in conjunction with the new name. In fact Buckland implied that his taxon *Belemnosepia* was apparently to include all ink-sac-bearing belemnites. This is clear from Buckland's statement (1836b, p. 374, footnote): "Each of these specimens contains an ink-bag within the anterior portion of the sheath of a perfect Belemnite; and we are henceforth enabled with certainty to refer all species of Belemnites to a family in the class of Cephalopods, for which I would, in concurrence with M. Agassiz propose the name *Belemno-sepia*."

Although Buckland referred to this as a family name for belemnites, Orbigny (1845 in 1845–1846) subsequently used it as a generic name for nonbelemnite coleoids, and he was thus the first author to refer species to the genus. These species are now attributed to several genera of Loligosepiida and include *Loligo bollensis* Zieten, 1832 (in 1830–1833), the type species of *Loligosepia* Quenstedt, 1839; *Geoteuthis sagittata* Münster, 1843, the type species of *Paraplesioteuthis* Naef, 1921; and *Teudopsis agassizii* Deslongchamps, 1835, the type species of *Jeletzkyteuthis* Doyle, 1990a. Because these species were the first to be referred to *Belemnosepia*, they represent the type series, from which a type species should be chosen. Such an action would effectively invalidate one of the above commonly used generic names. Therefore an application to the International Commission on Zoological Nomenclature for them to use their plenary powers is warranted and has been prepared by Engeser and Donovan (in press) in order to suppress the nominal genus *Belemnosepia*.

BELOPELTIS Voltz, 1840

The genus *Belopeltis* was the subject of a detailed memoir by Voltz (1840a). The memoir was presented by the author to a meeting of the Société géologique de France on December 2, 1839, and an extended summary was published in the report of the meeting (Voltz, 1840a). This paper is here regarded as the primary publication of the genus.

Voltz (1840a, p. 45) gave a diagnosis and included five nominal species, all *nomina nuda* (except where based on previous illustrations) and all described in the later paper (Voltz, 1840b): *Belopeltis simplex*, described and figured by Voltz (1840b, pl. 2, fig. 1); *B. regularis*, described and fig-

ured by Voltz (1840b, p. 24, pl. 2, fig. 2); *B. Bucklandi*, based on Buckland (1836, pl. 30); *B. acuminatus*, based on Buckland (1836, pl. 29, fig. 1), as reported by Voltz (1840b) [Voltz's (1840a) reference to plate 28, figure 1 is an obvious misprint, as this is a recent *Loligo*]; and *B. sinuatus*, based on Zieten (1832 in 1830–1833, pl. 25, fig. 6) and figured by Voltz (1840b, pl. 1, fig. 2) [Voltz's (1840a) reference to Zieten, plate 25, figure 4 was corrected (Voltz, 1840b) to plate 25, figure 6, and this is presumed to be correct given that figure 4 was used as a basis for Zieten's *Loligo aalensis*].

Voltz later (1840b) added *B. marginatus* (p. 25, pl. 1, fig. 1) to the list of nominal species originally included in the genus in his first paper (1840a).

In neither of Voltz's papers (1840a, 1840b) was a type species designated for *Belopeltis*. Naef (1921) accepted the genus *Belopeltis* and cited *Loligo aalensis* Zieten under this name, and later (1922, p. 125) he noted that "Als typische Art muss die folgende gelten: *Belopeltis Aalensis* (Zieten, 1830 [*recte* 1832 in 1830–1833])," which was not an originally included nominal species. Regteren Altena (1949, p. 57) accepted Naef's designation because he considered that the specimen figured by Zieten (1832 in 1830–1833, pl. 25, fig. 6), the type of Voltz's *B. sinuatus*, was an illustration of *Loligo aalensis*. This view was repeated by Engeser (1988), but is incorrect as discussed below under *Loligosepia*. In describing *Belopeltis aalensis*, Naef (1922, p. 126) listed *B. sinuatus* (Voltz, 1840a) and *B. marginatus* (Voltz, 1840b) as junior synonyms. In so doing, according to Article 69(a) of the Code, Naef effectively fixed *B. sinuatus* as the type species of the genus, as *Loligo aalensis* was not an originally included species, and *B. sinuatus* is the senior of the two included synonyms. This is accepted here, and the original of Voltz's own specimen (Voltz, 1840b, pl. 1, fig. 2) is herein designated as lectotype of the type species.

CONOTEUTHIS Orbigny, 1842

This genus was published in three places: in a paper in the *Annales des sciences naturelles* (Orbigny, 1842a), in a faunal list with an explanatory footnote in *Paléontologie française* (Orbigny, 1842b, p. 620), and in a summary of the first paper in the *Bulletin* of the Geological Society of France published in 1842.

The paper in the *Annales* was read in May 1842 and published in June 1842. Pages 431 to 662 of *Paléontologie française* were published in 1842, and the British Museum (Natural History) copy has an annotated receipt date of October 1842 for the latter pages of this part (p. 575 onwards). It is clear that the original valid publication of this genus was that published in the *Annales* (Orbigny, 1942a).

Orbigny (1842a, p. 377) referred to two specimens in his description of *Conoteuthis dupinianus*, the type species by monotypy. Only one was figured (Orbigny, 1842a, pl. 12, fig. 1–5), and this is herein designated as lectotype.

KERUNIA Mayer-Eymar, 1900

This curious genus was validly published as a coleoid by Mayer-Eymar (1900), with *K. cornuta* the type species by monotypy. It was subsequently discussed by two authors, Oppenheim (1902) and Nopcsa (1905). Oppenheim considered it to be a hydrozoan; Nopcsa regarded it as the unlikely combination of a symbiotic *Belosepia*-like cephalopod and a hydrozoan. Hill and Wells (1956) listed it as a possible synonym of the hydrozoan genus *Hydractinia* Beneden, 1844 (developed in symbiotic habit with a hermit crab!), and their interpretation is accepted here.

LOLIGOSEPIA Quenstedt, 1839 and GEOTEUTHIS Münster, 1843

The nominal genus *Loligosepia* was first proposed by Quenstedt (1839), who included two species: *Loligo aalensis* Zieten (1832 in 1830–1833, p. 34, pl. 25, fig. 4) and *Loligo bollensis* Zieten (1832 in 1830–1833, p. 34, pl. 25, fig. 5).

Although Regteren Altena (1949, p. 56, footnote) stated that Zieten described two different species under the name *L. bollensis* (represented by plate 25, figures 5 and 6), only figure 5 is referred to alongside the heading of the section dealing with the species. Doyle (1990a, p. 196) designated this specimen (Zieten, 1832 in 1830–1833, pl. 25, fig. 5), preserved in Tübingen, as lectotype.

Regteren Altena (1949) regarded the two species of Zieten (1832 in 1830–1833) as subjective synonyms and stated (p. 57) that *L. aalensis*, the prior name on the page, must be the type species. This can be taken as subsequent designation of the type species, contrary to Engeser (1988, p. 9) and Doyle (1990a, p. 196), who incorrectly regarded the type species by monotypy to be *L. bollensis* and *L. aalensis*, respectively.

In describing his new genus *Geoteuthis*, Münster (1843, p. 68) discussed eight nominal syntype species, one of which was *Loligo bollensis* Zieten. Bülow-Trummer (1920, p. 252) stated *L. bollensis* was type, which was accepted by Regteren Altena (1949, p. 56), thus making *Geoteuthis* a junior subjective synonym of *Loligosepia*.

ORCAGNIA Oppenheim, 1899

Oppenheim (1899, p. 32) described a new coleoid genus and single species, *Ocagnia trivigiana*, from the Venetian Priabonian strata. He illustrated a fragment of a rostrumlike shell fragment with a strong, perhaps midventral groove and with possible dorsal growth lines resembling conothecal striae. There seems to be little evidence of a phragmocone, and therefore the growth lines are particularly puzzling. It seems probable that *Orcagnia* is not a cephalopod, but without closer examination of the type specimen it is difficult to be sure of the true affinities of this fossil. Therefore, it will be treated as *incertae sedis* in the *Treatise*.

OSTRACOTEUTHIS Zittel, 1884

This genus was first used, without explicit statement that it was new, by Zittel (1884, p. 510) in his famous

Handbuch der Palaeontologie. Figures were given of the new species *Ostracoteuthis superba*, from the Solnhofener Plattenkalk of Eichstädt (p. 511, fig. 703a–c), which is the type species by monotypy. In later editions of his *Handbuch*, Zittel regarded the genus as a synonym of *Acanthoteuthis* Wagner, a decision upheld by Bülow-Trummer (1920, p. 232).

Zittel (1884) did not designate a holotype for the type species. His three figures show a phragmocone with proostracum bent at a right angle (fig. 703a), the impression of part of a phragmocone (fig. 703b), and a well-preserved proostracum (fig. 703c). The original of figure 703a is here selected as lectotype.

PARAPLESIOTEUTHIS Naef, 1921

Naef proposed this genus (1921, p. 534) as *Paraplesioteuthis* nov. His note 2 (p. 539) reads: "Hierher zunächst die wohlbekannte '*Geoteuthis*' *sagittata* Münster, 1843, die als Typus der Familie betrachtet werden darf."

Geoteuthis sagittata Münster is thus type species by monotypy, being the only species mentioned. Later, Naef (1922, p. 112) included two species in the genus, *P. sagittata* (Münster, 1843) and *P. hastata* (Münster, 1843). The first is preceded by the words *Massgebende Art* (standard species), but this does not represent a subsequent designation by Naef as stated by Engeser (1988, p. 54).

PLAGIOTEUTHIS Roemer and Dames, 1890

This genus and its type species by monotypy, *Plagioteuthis moscoviensis*, were erected by Roemer to contain a single, peculiarly distorted specimen from the Russian Jurassic (Roemer and Dames, 1890, fig. 1–5). The sole specimen consists of a belemnitelike rostrum, although Roemer also compared it with the spiruliids *Belosepia* and *Spirulirostra*. It is clear from the illustration of the solitary specimen that it is pathologically deformed. As this is the only specimen, the nominal genus and species must be described as *incertae sedis*.

PLATYLITHOPHYCUS Johnson and Howell, 1948

There is no taxonomic problem with this genus, but it may be useful to set out its complicated history. The specimen upon which it was based was found in the Upper Cretaceous Niobrara Formation of Kansas by George Sternberg, who sold the major portion of it to the University of Nebraska (Miller and Walker, 1968). Other pieces of the same fossil went to the University of Kansas Geological Museum (No. 11402); the Fort Hays Kansas State College Museum (No. 4091–4093); the Colorado School of Mines (Johnson collection, No. JA 5018); Princeton University (No. 59554); and the Carnegie Museum, Pittsburgh (No. 25758). The last named fragment was described by Johnson and Howell (1948) as the holotype of a new fossil calcareous alga, *Platylithophycus cretaceum*. They mentioned the Colorado and Princeton pieces as "fragments of the holotype" but apparently did not know of the University of Kansas or Fort Hays College pieces.

Miller and Walker (1968) cited unpublished work by M. K. Elias that showed that the specimen was, in fact, a fossil coleoid. Miller and Walker (1968) reviewed *Platylithophycus* and illustrated several of the fragments in general views, noting that the specimen was (at least at that date) the earliest known sepiid.

PRODUVALIA Schwegler, 1949

In his paper on belemnites from the Schwabian Jura, Schwegler (1949) employed a system of open nomenclature. He divided the family Duvaliidae into three genera (p. 306), two as previously described nominal taxa (i.e., *Conobelus* and *Duvalia*), and a third, referred to as "Kleine Gruppe von Vorläufern der typischen Duvalien ("Produvalia") aus dem unteren und mittleren Malm."

Although there was no further description, it was not explicitly stated that the genus was new, and no type species was designated, although a single species, *Belemnites argoviensis* Mayer, was included. Despite not originally being given in italics (recommendation E2 of the *International Code of Zoological Nomenclature*), the nominal genus *Produvalia* Schwegler, 1949 is an available name as it satisfies Article 13 of the *Code*. The type species by indication (Art. 68d, monotypy) is clearly *Belemnites argoviensis* Mayer, 1863. *Produvalia* Riegraf, 1981 (type species *Belemnites monsalsvensis* Gilléron, 1873) is therefore a junior synonymous homonym of *Produvalia* Schwegler, 1949.

SPIRULIROSTRINA Canavari, 1892

This genus was validly published in two places: the *Processi verbale* of the Societa toscane delle Scienze naturale (Canavari, 1892a) and the *Bollettino* of the Societa Malacologica Italiana (Canavari, 1892b). The first of these was the report of the meeting held on 17 January, 1892, and was probably published soon afterwards. It said that the description of the genus and species with illustrations "is being published" ("sta pubblicando") in the *Bollettino*. Although the report of the meeting was probably published first, the illustrated account (Canavari, 1892b) is accepted as the definitive publication.

TRACHYTEUTHIS Meyer, 1846

The type species of *Trachyteuthis* is usually said to be *Sepia hastiformis* Rüppell (e.g., Bülow-Trummer, 1920, p. 248; Engeser, 1988, p. 88), but this was not one of the originally included species.

The genus was set up by Meyer in a letter to one of the editors of the *Neues Jahrbuch* (Meyer, 1846, p. 598) in which he gave brief accounts of various fossils that had come to his attention. He mentioned two species of *Trachyteuthis* represented by specimens in the Ansbach collection: *T. oblonga* and *T. ensiformis*, the latter of which, Meyer noted, was figured by Münster in his 1846 paper (pl. 9, fig. 2). Meyer (1846) gave neither description nor bibliographic reference for *T. oblonga*; it is therefore a *nomen nudum*.

We herein designate *Trachyteuthis ensiformis* Meyer as type species of *Trachyteuthis*, since Münster's earlier (1846)

illustration was not accompanied by an explanation nor referred to in the text. The type series of *T. ensiformis* includes the unfigured material in the Ansbach collection, seen by Meyer, as well as the specimen figured by Münster. We herein designate the original of Münster (1846, pl. 9, fig. 2) as lectotype of *T. ensiformis*.

The systematic position of *Trachyteuthis* is a problem. The fossil is particularly common in the Solnhofen Limestone of Bavaria. Donovan (1977, p. 32) claimed that it was the earliest sepiid on the basis of the very close resemblance of the dorsal aspect of the gladius to that of the living *Sepia*, explaining the lack of fossil evidence for a phragmocone by the fact that aragonite is not preserved in the Solnhofen limestone. Other authors have not followed this view (see discussion in Doyle, 1991, p. 171). One specimen in the Teyler Museum, Haarlem, Netherlands (no. 6022) provides additional evidence from its preservation of its soft parts. This specimen shows lobe-shaped, subterminal, posterior fins quite unlike the fins of living *Sepia*, which run the length of the mantle. In view of the continuing debate, we have included the family Trachyteuthidae Naef, 1921, in the suborder Teudopsidina (see above) because of broad similarities between teudopsid and trachyteuthid gladii.

TAXONOMIC APPENDIX

Order SEPIIDA Zittel, 1895

Family ACTINOSEPIIDAE new family

Type genus.—*Actinosepia* Whiteaves, 1897.

Diagnosis.—Sepiida with dorsal shield possessing 3 or more rows of closely spaced tubercles radiating and diverging from the posterior.

Range.—Cretaceous (Campanian to Maastrichtian), Great Plains, Canada.

Order BELEMNITIDA Zittel, 1895

Suborder BELEMNITINA Zittel, 1895

Family HASTITIDAE Naef, 1922

[The following generic description is edited from the late Dr. J. A. Jeletzky's unpublished manuscript notes and is published here for inclusion in the *Treatise*.]

Genus BAIRSTOWIUS Jeletzky, new genus

Figure 4

"*Pseudohastites*" *sensu* Lang, 1928, p. 211, *non* Naef, 1922, p. 234 *gen. nov.*; Doyle and Marriotti, 1991, p. 355.

Type species.—*Belemnites junceus* Phillips, 1867.

Included species.—*Bairstowius cultellus* (Lang, 1928); *B. longissimus* (Miller, 1826); *B. charmouthensis* (Mayer, 1866); *B. arundineus* (Lang, 1928).

Derivation of name.—After Mr. L. Bairstow, formerly curator of the fossil coleoids in the British Museum (Natural History).

Diagnosis.—Hastitidae with an elongated, spicular to feebly hastate, compressed to moderately compressed ros-

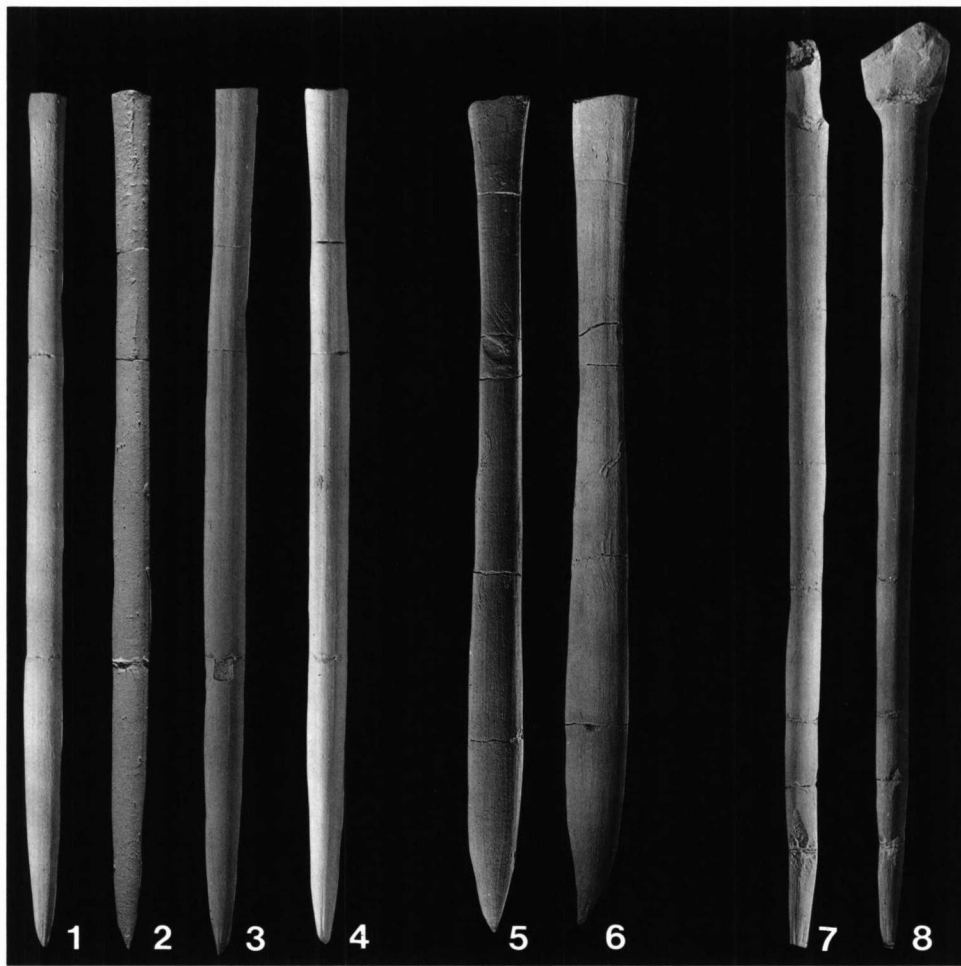


Figure 4. *Bairstowius* Jeletzky new genus. All specimens are from the Lower Pliensbachian Belemnite Marls, Charmouth, Dorset, England. Specimens whitened with ammonium chloride. All specimens housed in the Natural History Museum (NHM), London. —1–4. *B. junceus* (Phillips, 1867), NHM C.42562; 1, dorsal, 2, ventral, 3, left lateral, and 4, right lateral views, $\times 1$. —5–6. *B. charmouthensis* (Mayer, 1863), NHM C.29044; 5, ventral and 6, left lateral views, $\times 1$. —7–8. *B. longissimus* (Miller, 1827), NHM C.29007; 7, ventral and 8, left lateral views, $\times 1$.

trum. Apical section long, tapering slowly to an acute, needlelike apex. Rostrum-bearing, incised, triple longitudinal lateral furrows of *Hastites*-like form; apex commonly striated. Alveolus shallow (one-eighth to one-twentieth of rostrum length), ortholineate. Phragmocone structure as in *Hastites*. Earliest juvenile rostra conorostrid, increasing rapidly in length and obtaining spicular or subhastate form early in ontogeny.

Remarks.—Lang's (1928) interpretation of the genus *Pseudohastites* (Naef, 1922) to include forms typified by the species *Belemnites junceus* is erroneous. *Pseudohastites* is a passaloteuthid (type species, *Belemnites scabrosus* Simpson, 1866) closely related to the genus *Passaloteuthis* (see Doyle, 1990c, p. 23). The hastitid form of *B. junceus* was recognized by Lang (1928) and later workers (e.g., Schwegler, 1962; Jeletzky, 1966; Schumann, 1974), and therefore erection of the new genus is warranted. *Bairstowius* differs from *Hastites* Mayer in its extreme elongation and in its spicular or only feebly subhastate form. *Bairstowius* can be distin-

guished from contemporary passaloteuthids by its *Hastites*-like pattern of lateral furrows, its compressed rostrum, and absence of apical grooves.

Range.—Lower Jurassic (upper Sinemurian, *Raricostatum* Zone to middle Pliensbachian, *Jamesoni* and *Ibex* Zones), Europe and Turkey (Doyle and Mariotti, 1991).

**HUNGAROSEPIA, *nom. nov.* herein, *pro*
ARCHAEOSEPIA Szörényi, 1934**

This genus was published by Szörényi in a paper dated 1933. However, as the part includes papers read in December 1933, it is likely the part was not actually published until 1934. This is taken as the date of publication of the genus.

In erecting her genus, Szörényi included two species, *Sepia hungarica* Lörenthey, 1898, and a new species, *Archaeosepia naefi*. A type species was not fixed in the paper (Szörényi, 1934). According to the *International Code of Zoological Nomenclature*, Article 13b, Szörényi's genus, pub-

lished after 1931, is unavailable, as the original publication did not include fixation of a type species either by original designation (Article 68b) or by indication (Articles 68c–e).

We hereby erect a replacement name for the genus, *Hungarosepia* and designate *Archaeosepia naefi* Szörényi, 1934 as type species. Diagnosis is as given by Szörényi (1934, p. 186) and reproduced here: “Der Schulp is längsoval, nach vorn breiter und etwas zu gespitzt. Die Rückenplatte ist mit starken, breiten konzentrischen Rippen bedeckt. Längs des Schulpes verlaufen faine, nach vorn zu divergierende, seichte Furchen. Rostrum unbekannt.” The lectotype of *H. naefi*, designated herein, is the original of Szörényi (1934, pl. 1, fig. 1), from the Lutetian of Tatabánya, Hungary, repositied in the National Museum, Budapest.

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