THE JURASSIC BELEMNITE SUBORDER BELEMNOTHEUTINA

by PETER DOYLE *and* EMMA V. SHAKIDES

ABSTRACT. The Belemnotheutina is a monophyletic group of mostly late Jurassic belemnites that possess largely plesiomorphic characters of ten subequal arms with hooks, a simple, conical, rostrum, a narrow breviconic phragmocone and a spatulate pro-ostracum. Although some of the best-preserved belemnites with soft parts have been described from this group, until recently, its status has been in question. A new genus from the Upper Jurassic of Antarctica, *Antarctiteuthis* is described which, like *Acanthoteuthis* (= *Belemnotheutis* of authors), possesses unique rostral surface morphology of raised ridges with accompanying grooves unknown in other true belemnites. This is an important apomorphy for the group, which is considered to be a monophyletic suborder of the Belemnitida.

KEY WORDS: Jurassic, belemnites, Belemnoidea, Belemnotheutina, *Belemnotheutis*, *Antarctiteuthis* gen. nov., Antarctica.

THE Belemnoidea is a monophyletic group distinguished by its possession of ten subequal arms with hooks, a multilayered conotheca (the outer wall of the phragmocone) and an organic first septum closing the protoconch (Jeletzky 1966; Engeser 1990). These characters are relatively uncontroversial, and ranked as a superorder, the Belemnoidea may be subdivided into the orders Aulacocerida, Belemnitida and Diplobelida, based largely on body chamber form (Doyle *et al.* 1994). The Aulacocerida retains a plesiomorphic, enclosed body chamber, while in the Belemnitida and the Diplobelida, the so-called 'true' belemnites, a ventrally open body chamber is apomorphic, with spatulate and rod-like pro-ostraca respectively. The Aulacocerida is also characterized by an aragonitic rostrum, while 'true' belemnites have mostly low magnesian calcite rostra.

Although the Belemnoidea is thought to represent a natural, monophyletic group, there are outstanding problems, not least of which is the taxonomic position of the Jurassic genus *Belemnotheutis* (= *Belemnoteuthis* of authors; see Donovan and Crane 1992 for discussion of the correct spelling of this nominal taxon) and its related taxa. *Belemnotheutis* has a spatulate pro-ostracum, but possesses an aragonitic, much reduced, and sheath-like rostrum that is unusual for the Belemnoidea as a whole (Bandel and Kulicki 1988; Donovan and Crane 1992). The purpose of this paper is to present a taxonomic revision of the Belemnotheutidae, to describe a new genus, known so far only from Antarctica and Argentina, and to discuss the implications for coleoid phylogeny.

BELEMNOTHEUTID CHARACTERS AND THEIR TAXONOMIC SIGNIFICANCE

Belemnites have notoriously few characteristics upon which to carry out a systematic revision. Many of the most important characters appear to be plesiomorphic, shared by the Belemnoidea, and although they are useful in determining its monophyly, they are less useful in the subdivision of the group as a whole. The most often preserved feature is the rostrum (guard of some authors); phragmocones and especially pro-ostraca are less commonly preserved. Five character groups are considered below: (1) rostrum form; (2) phragmocone; (3) protoconch form; (4) pro-ostracum form; and (5) arm hook morphology.

Rostrum

The majority of belemnite taxa are distinguished by their general rostral morphologies. The possession of a mostly calcitic rostrum is usually considered to be an apomorphic character state, possessed by the

Belemnitida and the Diplobelida, the plesiomorphic state being an aragonitic rostrum as developed in the Aulacocerida (Jeletzky 1966). In belemnites the initial, cone-shaped primordial rostrum consists of aragonitic and organic components, and is attached to the protoconch (Bandel *et al.* 1984), again demonstrating that the plesiomorphic state is that of an aragonitic rostrum. However, the ontogeny of the belemnite rostrum proper is primarily that of the addition of concentric layers of low magnesian calcite to a conical rostrum (Saelen 1989). In some cases there is an additional unit of rostral growth, the epirostrum, which is also aragonitic, and which probably represents the development of dimorphic characters in sexual maturity (Doyle 1985; Bandel and Spaeth 1988). Rostra may be developed in a variety of shapes, varying from conical/cylindrical to hastate and blade-like, but ontogenetically it is clear that the dominant early rostrum shape is conical, and this is characteristic of the earliest members of the Belemnitida, and is also typical in the Diplobelida.

Belemnitid rostrum. Subdivision of the Belemnitida into suborders has traditionally been accomplished through the recognition of surface features of the rostrum, including grooves, lateral furrows and slits (Jeletzky 1965, 1966; Gustomesov 1978). Most belemnites have some form of incised linear features in the form of grooves or furrows, although the plesiomorphic condition is the possession of a smooth, conical rostrum, as demonstrated by the early Jurassic taxa *Schwegleria* and *Nannobelus*. This has proven to be a satisfactory arrangement for most subsequent authors, who have recognized the validity of the subdivision in two main suborders on the basis of apomorphies determined by groove type (e.g. Jeletzky 1966). These suborders are: the Belemnopseina, characterized by grooves which die out adapically from the alveolus, and mostly paired lateral lines; and the Belemnitina, characterized by grooves which die out adorally from the apex of the rostrum, and multiple lateral lines. However, this classification has long been inadequate for the recognition of other groups, particularly those where the rostrum is poorly developed, as in the belemnotheutids.

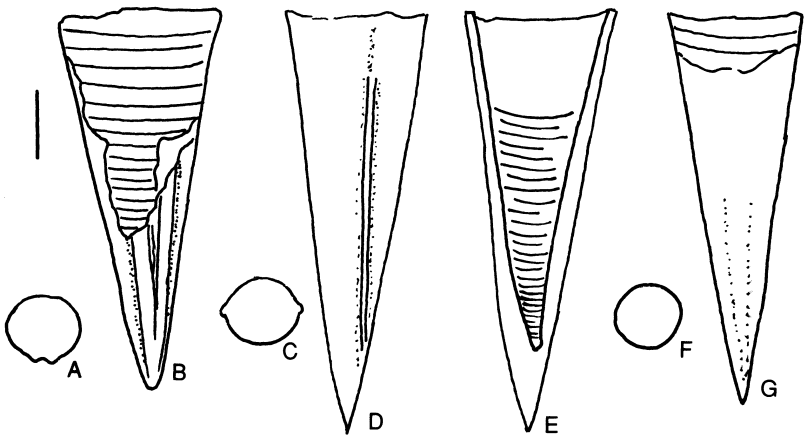
Belemnotheutid rostrum. The belemnotheutid rostrum is characteristically aragonitic, and comprises simply a thin covering of the phragmocone, although possessing the concentric growth typical of the standard belemnitid rostrum. Aragonitic rostra are characteristic of the Aulacocerida, and therefore could represent the plesiomorphic character state, a possibility recently advanced by Engeser (1998). The ontogenetic development from primordial rostra appears to follow the 'normal' belemnite pattern, in *Belemnotheutis* at least (Bandel and Kulicki 1988). As a consequence, the belemnotheutid rostrum is characteristically conical in form.

The possession of a simple, relatively thin and conical rostrum is a plesiomorphic character state for the Belemnitida, typical of the earliest known belemnites in the Hettangian, excluding as equivocal the Triassic belemnites from China (Doyle *et al.* 1994). However, the surface ornament of the belemnotheutids is quite unlike any other type found in belemnites, and has some faint similarity to the ridge and furrow ornament of aulacocerid genera such as *Aulacoceras* and *Dictyoconites*, although this ornament is strongly and pervasively developed in these genera (Bandel 1985). Other ridge-and-groove structures comparable to those of the aulacocerids are found in the aragonitic epirostra of otherwise calcitic orthorostra (Bandel and Spaeth 1988). These may be an unknown function of the development of aragonitic growth in belemnite rostra (K. Bandel, pers comm. 2002).

At least two belemnotheutid genera, *Belemnotheutis* and *Antarctiteuthis* gen. nov., have raised ridges accompanying grooves on the surface of the rostrum (Text-figs 1–2). These are simple and generally paired. This feature can either be considered plesiomorphic (related to the aulacocerid condition) or apomorphic (characteristic of the belemnotheutids alone, cf. Engeser 1990).

Phragmocone

The belemnite phragmocone is usually considered to be conservative. However, few studies have examined the phragmocone in detail, with the last comprehensive study from a number of groups that of Jeletzky (1966). Jeletzky recognized the following characters that have been accepted as plesiomorphic (Engeser 1990):



TEXT-FIG. 1. Drawing to illustrate ridge and groove patterns on the rostra of typical Belemnoteuthina. Scale bar represents 5 mm. A, cross-sectional outline of *Acanthoteuthis antiqua*, based on NHM OR 30460. B, dorsal view of typical *Acanthoteuthis antiqua*, NHM OR 30460, showing prominent ridges. C, cross-sectional outline of *Antarctiteuthis donovani*, based on holotype, BAS D.9103.13. D, profile view of *Antarctiteuthis donovani*, holotype, BAS D.9103.13, showing prominent ridge. E, transverse section of *Antarctiteuthis donovani*, holotype, BAS D.9103.13, showing phragmocone in deep alveolus, and typical protoconch. F, cross-sectional view of *Chondroteuthis wunnenbergi*, based on NHM C.59293. G, outline of *Chondroteuthis wunnenbergi* NHM C.59293, showing weak surface marks.

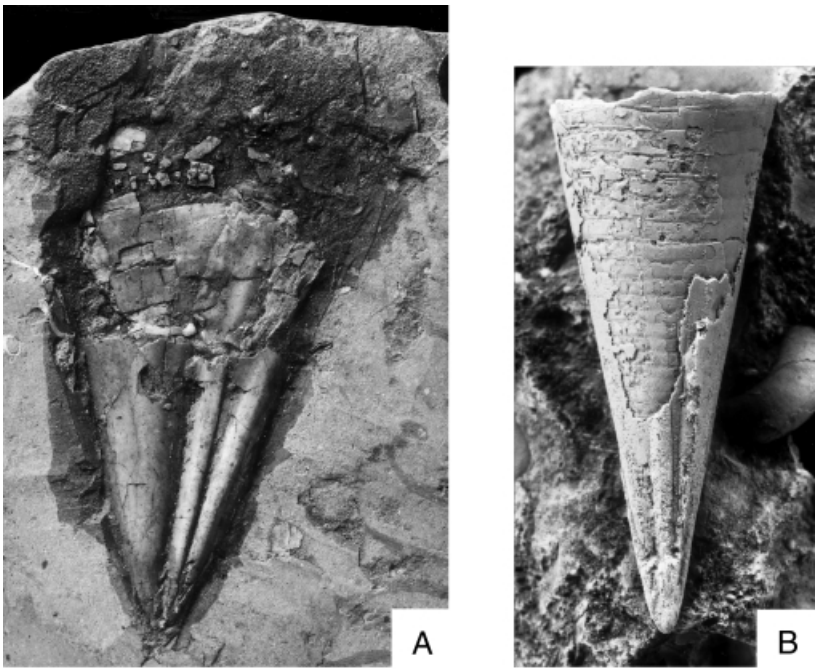
1. Multilayered conotheca. The number of layers has been debated by several authors, but it is clear that there are at least three, and that this appears to be a plesiomorphic character state in the belemnites as a whole. The identification of five conothecal layers by Engeser (1990) was inclusive of aragonitic and organic layers of the primordial rostrum, an interpretation which has since been refuted by this author (Engeser 1998).
2. Orthochoanitic to hemichoanitic septal necks. Where investigated, the majority of belemnites appear to possess orthochoanitic to hemichoanitic septal necks (Jeletzky 1966).
3. Cameral height. True belemnites have relatively low, densely packed camerae, which contrast with the much larger aulacocerid camerae (Jeletzky 1966).
4. Narrow alveolar angle. This is usually within the range of 12–32 degrees and is useful in distinguishing 'true' belemnites from the Aulacocerida, which have apical angles much less than this.

Diplobelinid phragmocones. Diplobelinid phragmocones are broadly consistent with the typical belemnitid form, but differ in the development of a dorsal saddle in the suture line, which is at variance with the simple form of the belemnitid suture (Jeletzky 1966, 1981). This character is unique in the belemnoids and is considered an apomorphy of the Diplobelida.

Belemnotheutid phragmocones. Those belemnotheutid phragmocones which have been studied in sufficient detail are typical of the belemnite type and are therefore plesiomorphic in condition (Makowski 1952; Jeletzky 1966; Bandel and Kulicki 1988; Donovan and Crane 1992). However, apical angles vary from 12–22 degrees and are, therefore, rather more acute than that of the average belemnite phragmocone.

Protoconch

Following the studies of Makowski (1952), the typical form of the belemnotheutid protoconch has been considered as cup-like instead of the more usual sphere, a significant feature as this is unique (Jeletzky 1966; Engeser and Reitner 1981; Reitner and Engeser 1982*a*). However, following the in-depth study of



TEXT-FIG. 2. Typical *Acanthoteuthis antiqua* rostra. A, crushed example from the Oxford Clay (Callovian) of Christian Malford, Wiltshire, NHM OR 88604a; dorsal view showing prominent ridges; ×2. B, uncrushed example from the Kellaway Rock (Callovian) of Wiltshire, NHM OR 37440; dorsal view showing ridges, ×2·5.

well-preserved material by Bandel and Kulicki (1988), it is clear that the cup-like protoconch of *Belemnotheutis polonica* is a preservational artifact and that, in fact, the protoconch is typically spherical with an organic closing membrane, an apomorphy of the Belemnoidea as a whole (including the Aulacocerida), and a plesiomorphic condition for the belemnotheutids.

Pro-ostracum

Pro-ostraca are rarely preserved in belemnoids, but their form may be determined through extrapolation from the growth lines preserved on phragmocone conothecae. In almost all cases, belemnite pro-ostraca are spatulate in shape with or without a median keel (Jeletzky 1966; Engeser 1990). The diplobelids have a rod-like pro-ostracum, which is an apomorphic condition, and is unlike that of the rest of the belemnites.

Belemnotheutid pro-ostraca. Pro-ostraca have been identified in the genera *Chondroteuthis*, *Acanthoteuthis* (= *Belemnotheutis*), and the related genus *Sueviteuthis*. In all of these taxa, the pro-ostracum is spatulate in form, and typical of the belemnite plesiomorphic condition. *Chondroteuthis* has an elongate pro-ostracum, a feature which has been ascribed varying levels of importance by authors (e.g. Jeletzky 1966; Engeser 1990; Doyle 1992; Text-fig. 3). *Sueviteuthis* was originally described with ventral components to the otherwise 'normal' spatulate pro-ostracum (Reitner and Engeser 1982*b*) but these were re-interpreted as dorsal strengthening features, rather than structural elements of the pro-ostracum proper (Riegraf 1983). All other taxa have more or less typical spatulate pro-ostraca, an apomorphy of the Belemnitida as a whole (Jeletzky 1966; Engeser 1990; cf. Engeser 1998).

Arm hooks

Arm hooks have become increasingly important in taxonomic studies, as more coleoids have been found intact with arm crowns. Engeser (1998) has considered the presence of arm hooks to be a plesiomorphic

condition in the Belemnoidea. In his survey of arm hooks from the south German Jurassic, Engeser (1987) distinguished typical 'belemnite' hooks from typical 'phragmoteuthid/belemnotheutid' arm hooks. The first were found to have an extra spur to the hook, while the second were found only with a relatively smooth, simple form. This was supported to a certain extent by Engeser and Clarke (1988). However, the relatively few specimens of belemnites preserved intact with their soft parts/arm crowns, and the low diversity of rostral taxa discovered severely limits the viability of using hook form in taxonomic studies, and therefore the possibility of a greater range of variation in morphology of true belemnite hooks has to be maintained (cf. Riegraf 1996).

Belemnotheutid arm hooks. Engeser (1998) has considered spur-bearing hooks to be an apomorphic character state for the Belemnitida. A large number of belemnotheutid specimens have been found preserved intact, particularly in the Oxford Clay of central England (e.g. Allison 1988; Donovan and Crane 1992; Text-fig. 4). Hooks commonly associated with these specimens are of Engeser's (1987) 'phragmoteuthid/belemnotheutid' type, smooth and sinuous, and lack spurs. Isolated hooks from the Oxford Clay show similar morphologies (Martill 1986*a*, *b*; Text-figs 3, 5). However, hooks resembling these have been found associated with typical Aulacocerida (e.g. Fischer 1947), which may suggest that this type represents the plesiomorphic state for the Belemnoidea, rather than an apomorphy for the Belemnotheutina. No hooks have been identified for the Diplobelida.

BELEMNOTHEUTID SYSTEMATICS

A systematic revision of the belemnotheutid belemnites is given below using the characters discussed, and is outlined in Table 1. Note that, in accordance with Jeletzky (1966, p. 141), all family names bearing the stem part 'teuthid' (but excluding 'theutid') are given as -teuthididae. All specimens are housed in The Natural History Museum, London (NHM) or the collections of the British Antarctic Survey, Cambridge (BAS).

Subclass COLEOIDEA Bather, 1888
Order BELEMNITIDA Zittel, 1895
Suborder BELEMNOTHEUTINA Stolley, 1919

(*nom. corr.* herein, *pro* Belemnoteuthida; = Belemnoteuthida Engeser and Reitner, 1981; Belemnitomorpha Engeser, 1990, *pars*)

Diagnosis. Belemnitida with aragonitic sheath-like rostra exhibiting elongate dorsal, ventral or lateral furrows with corresponding ridges. Pro-ostracum spatulate and typically with a median ridge. Arm hooks slender and smooth, lacking median spur.

Range. Jurassic (Toarcian–Tithonian) of Europe, Antarctica and Argentina. Roger (1944) has recorded a doubtful representative from the Upper Cretaceous of Syria.

Included families. Belemnotheutidae. Junior subjective synonym: Chondroteuthididae Jeletzky, 1965. The related family Sueviteuthidae Reitner and Engeser, 1981 may also be considered a member of this suborder, but requires fuller study.

Discussion. As noted by Donovan and Crane (1992) the correct original spelling of the nominal genus *Belemnoteuthis* Pearce, 1842 is *Belemnotheutis* Pearce, 1842. Family and higher taxa based on this genus are, therefore, also based on this spelling, a practice at variance with some works, but one which has gained acceptance by most noted authorities (e.g. Riegraf 1995).

Several authors have previously distinguished the belemnotheutids at ordinal level, most notably Engeser and Reitner (1981), Reitner and Engeser (1982*a*), and Riegraf (1995). Engeser and Reitner (1981) and Reitner and Engeser (1982*a*) defined the order on the basis of protoconch form, which they interpreted as cup-shaped, presumably following earlier work by Makowski (1952) and Jeletzky (1966). However, as

TABLE 1. Summary of the main characteristics of major belemnoid groups

Order/Suborder	Rostrum	Phragmocone	Protoconch	Pro-ostracum	Hooks
Belemnitida	Calcitic, massive, conical in primitive state, then variable, incised groove ornament	Conservative, simple suture, low camerae, narrow apical angle	Spherical	Spatulate	Spurs
Diplobelida	Calcitic; sheath-like or massive, conical, little or no ornament	Conservative, dorsal saddle, low camerae, narrow apical angle	Spherical	Rod-like	Unknown
Belemnotheutina	Aragonitic, sheath-like, conical, incised grooves/raised ridge ornament	Conservative, simple suture, low camerae, narrow apical angle	Spherical	Spatulate	Smooth curve, no spurs
Aulacocerida	Aragonitic, massive, incised grooves and/or incised grooves/raised ridge ornament	Conservative, simple suture, high camerae, very narrow apical angle	Spherical	Entire body chamber	Smooth curve, no spurs[1]

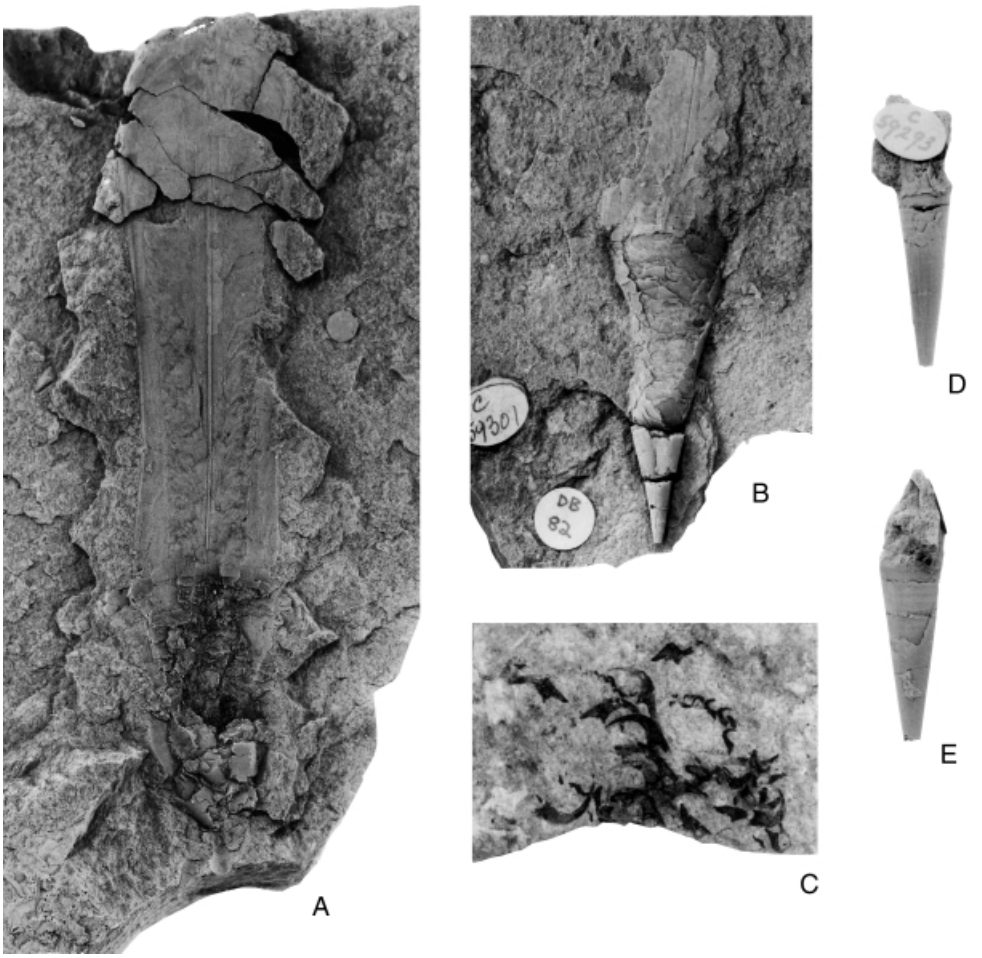
[1] Based on associated hooks (Fischer 1947).

noted by Bandel and Kulicki (1988) the cup-shaped protoconch seen in some representatives of the genus *Belemnotheutis* is actually a preservational artifact, as most have spherical protoconchs. On this basis, Bandel and Kulicki (1988) rejected the ordinal rank of this group, preferring to recognize its overall similarity with the belemnites, particularly in its possession of a belemnitid phragmocone, protoconch and pro-ostracum, a concept which is broadly in agreement with the earlier judgment of Jeletzky (1966).

Engeser (1990) erected the 'adelphotaxon' Belemnitomorpha Engeser, 1990 to contain taxa assignable to the Belemnotheutina together with the Diplobelida, on the basis of an apparently reduced pro-ostracum. This taxon is unnecessary given the availability of other names, and the inclusion of the Diplobelida in this group is not supported. Later work by Engeser (1998) has supported the notion of an ordinal grouping for the belemnotheutids.

Following an earlier assignment to the Phragmoteuthididae (Riegraf 1987), Riegraf (1995) has recently used ordinal rank for this group, but has expanded its concept to include what are probably aulacocerid genera, in *Jeletzkya*, *Breviconoteuthis* and *Permoteuthis*. Riegraf (1995) also followed Engeser and Reitner (1983) in including *Chitinobelus* Fischer, 1981, which possesses a calcareous sheath-like rostrum with an elongate, possibly organic, epirostrum. Epirostra are most common in the Belemnitina, particularly in the Megateuthidinae, Passaloteuthidinae and Salpingoteuthididae, although some examples are known from the Belemnopseina (e.g. *Neohibolites*). The presence of an epirostrum does not, therefore, preclude an assignment to the Belemnotheutina (cf. Engeser 1990), but it is more likely that *Chitinobelus* is a member of the Salpingoteuthididae on the basis of its shell structure and similarity to other members of this family (Fischer 1981; Doyle 1992).

The belemnotheutids are here separated at subordinal rank for the following reasons. Firstly, the belemnitid nature of the group is demonstrated by its belemnitid rostrum, phragmocone, cameral deposits, protoconch and importantly, its spatulate pro-ostracum. There seems little evidence to separate this group at ordinal level. However, the belemnotheutids do not comfortably reside in either of the two belemnitid suborders, the Belemnitina, characterized by conical or cylindoconical calcitic rostra with apical grooves; or the Belemnopseina, characterized by hastate or subhastate calcitic rostra with alveolar grooves (Jeletzky 1966). In particular, the association of elongate grooves and often paired, raised ridges is peculiar to the group although until now, it has only been recognized in the genus *Belemnotheutis*. The discovery of the same character in *Antarctiteuthis* underlines its taxonomic significance (Text-fig. 1). These characters



TEXT-FIG. 3. *Chondroteuthis wunnenbergi* Böde, from the Alderton Fish Bed (Toarcian) of Gloucestershire. A, typical elongate, spatulate pro-ostracum, NHM C.52576; this specimen has previously been interpreted as a pro-ostracum belonging to the genus *Acrocoelites* (see Doyle 1992); ×1. B, rostrum, phragmocone and base of pro-ostracum, NHM C.59301; ×1. C, typical hook form, NHM C.59305; ×2. D, outline and E, profile of NHM C.59293, showing smooth rostrum; ×1.

share some similarity with the ridge and groove ornament of the earlier aulacocerids, but in such taxa as *Aulacoceras* and *Dictyconites* the pattern of grooving is pervasive through the internal structure of the rostrum, with strong and deeply incised 'folding' of the laminae, rather than being surface features common to the belemnitids, including the belemnotheutids.

The possession of an aragonitic rostrum may not be taxonomically significant given the discovery of the bimineralogical composition of certain belemnitid rostra (Bandel and Spaeth 1988; Donovan and Crane 1992), and given the fact that it has only been proven in *Belemnotheutis* itself (Bandel and Kulicki 1988). Finally, differences in arm hook morphology between belemnotheutids and belemnitids, although interesting, remain a matter for debate given the relative paucity of belemnites found complete with shell and arm crowns.

Family BELEMNOTHEUTIDAE Zittel, 1884

(*nom. corr. pro* Belemnoteuthididae; = Chondroteuthididae Jeletzky, 1965)

Type genus. *Belemnotheutis* Pearce, 1842, junior subjective synonym of *Acanthoteuthis* Wagner, *in* Münster 1839.

Diagnosis. Belemnitida with conical aragonitic rostrum forming a thin sheath covering the phragmocone; rostrum typically investing posterior part of phragmocone only, rapidly decreasing in thickness adorally; often characterized by longitudinal furrows flanked by ridges.

Remarks. Jeletzky (1966) distinguished two families: the Belemnoteuthididae Zittel, 1884 and the Chondroteuthididae Jeletzky, 1965. Although Engeser and Reitner (1981) supported the distinction of the two families, Doyle (1992) suggested that the Chondroteuthididae was actually a subfamily of the Belemnoteuthididae. In this paper, the single family Belemnotheutidae Zittel, 1884 is deemed sufficient to represent the range of variation in the group, the recognition of a separate Chondroteuthididae Jeletzky, 1965 being superfluous. Engeser (1990, 1995, 1998) considered that *Chondroteuthis* is actually representative of the Diplobelidae (Suborder Diplobelina) on the basis of the reduced width of the pro-ostracum (Text-fig. 3). This is not upheld here as the diplobelinid pro-ostracum is typically an elongate spike. In addition *Chondroteuthis* does not possess typical phragmocone characteristics of this group, such as sinuous suture lines (Jeletzky 1966, 1981). The nature of the surface ornament of ridges and associated grooves is unknown in any other belemnitid group. These are, however, absent in the oldest genus, *Chondroteuthis*, which is morphologically similar to early Jurassic belemnitid genera such as *Nannobelus* and *Coeloteuthis*. In *Nannobelus* the rostrum is acutely conical, but has a more robust and thickly constructed rostrum. *Coeloteuthis* has a thinly developed rostrum, but is characteristically blunt with a greater apical angle. Neither genus possesses the distinctive surface ornament of ridges and grooves displayed by *Acanthoteuthis* and *Antarctiteuthis* (Text-fig. 1).

Included taxa. Chondroteuthis Böde, 1933, Toarcian of Europe; *Acanthoteuthis* Wagner, *in* Münster 1839 (= *Belemnotheutis* Pearce, 1842), Callovian–Tithonian of Europe; *Antarctiteuthis* gen. nov, Tithonian of Antarctica and Argentina. Possible related taxon: *Sueviteuthis* Reitner and Engeser, 1982 (Toarcian of Germany).

Genus CHONDROTEUTHIS Böde, 1933

Text-figures 1, 3

Type species. C. wunnenbergi Böde, 1933, by original designation.

Diagnosis. Belemnotheutidae with smooth rostrum sometimes bearing elongate striations. Pro-ostracum elongate. Arm hooks strongly curved and hook-like with wide base.

Recent comparable diagnoses. Jeletzky (1966, p. 146), Doyle (1992, p. 74).

Included species. This genus is monospecific.

Range. Lower Jurassic (Toarcian) of Germany and England (Böde 1933; Jeletzky 1966; Riegraf 1982, 1985; Doyle 1992).

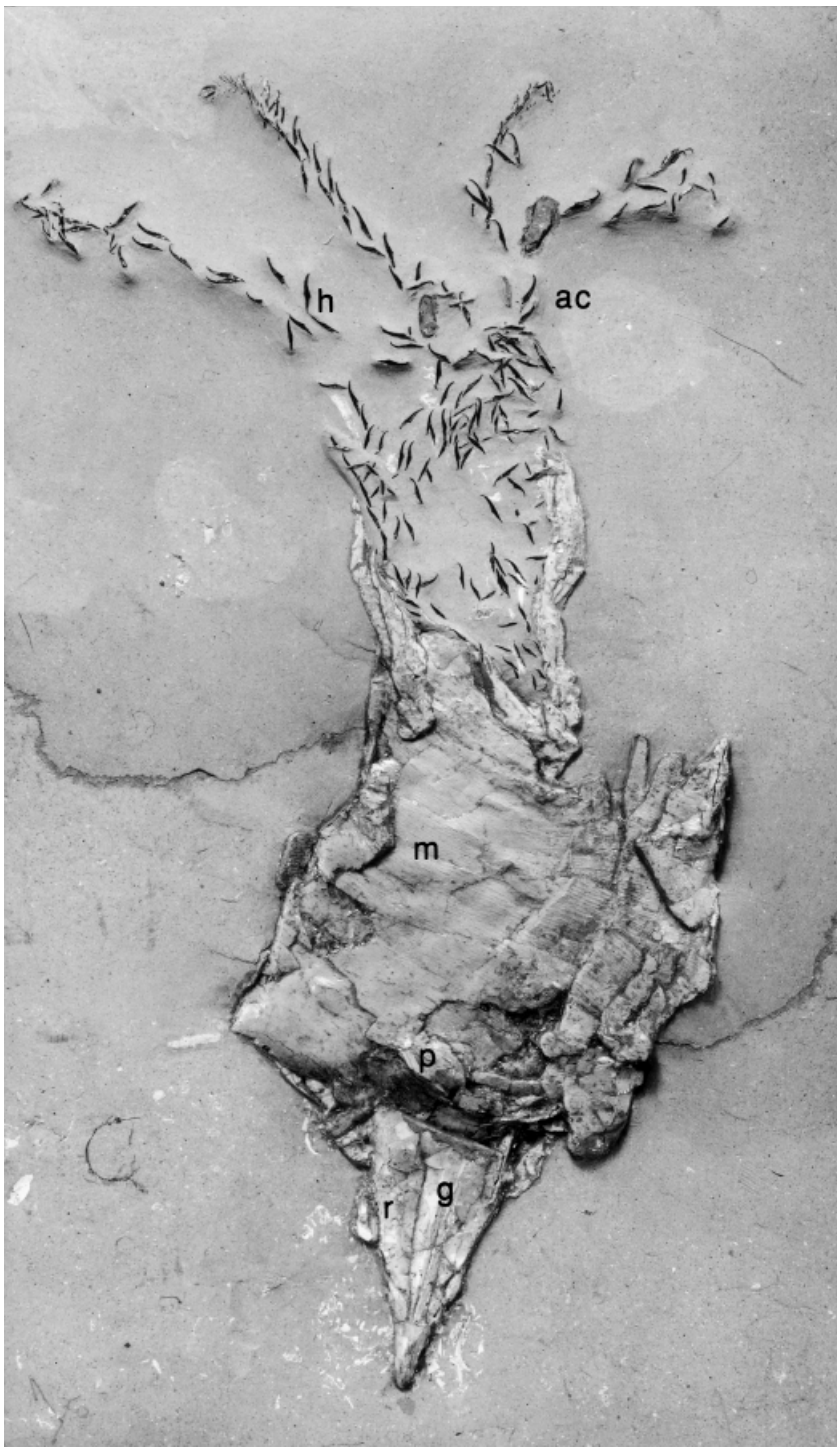
Genus ACANTHOTEUTHIS Wagner, *in* Münster 1839

(= *Belemnotheutis* Pearce, 1842, *Ostracoteuthis* Zittel, 1884, both junior subjective synonyms)

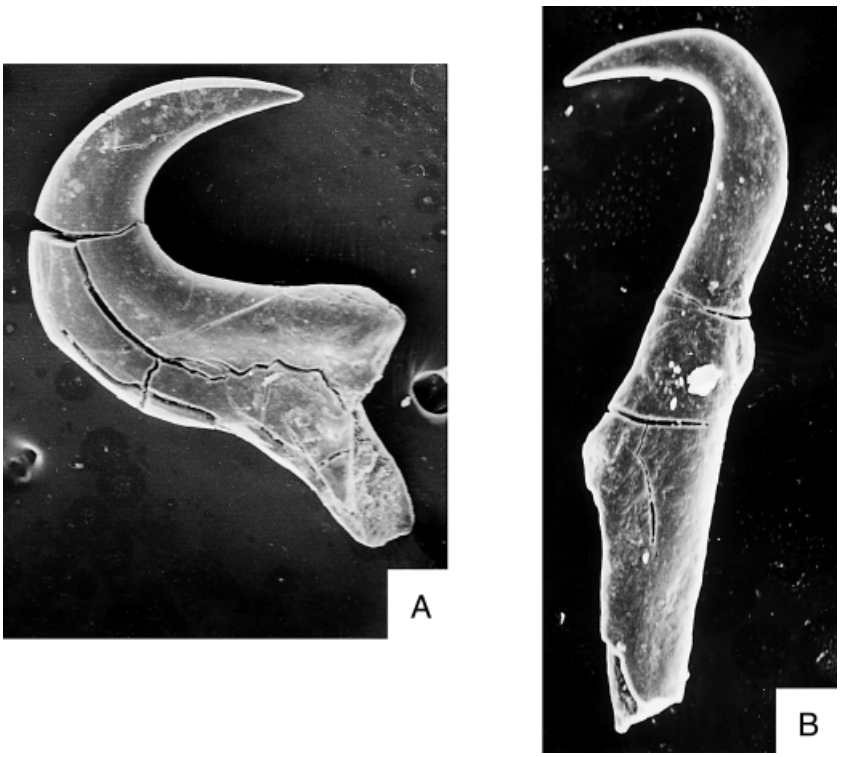
Text-figures 1–2, 4

Type species. *Acanthoteuthis speciosa* Münster, 1839, by subsequent designation (Bülow-Trummer 1920, p. 268). Type species of synonyms: *Belemnotheutis antiquus* Pearce, 1847, by monotypy; *Ostracoteuthis superba* Zittel, 1881, by monotypy.

Diagnosis. Belemnotheutidae with rostrum bearing paired mediodorsal ridges which diverge adorally, separated by a mediodorsal longitudinal furrow which widens adorally. Arm hooks slender and weakly incurved with narrow base.



TEXT-FIG. 4. Complete *Acanthoteuthis antiqua* (Pearce) from the Oxford Clay (Callovian) of Christian Malford, Wiltshire, showing soft part preservation, NHM OR 30460; × 1. Abbreviations: ac, arm crown; g, groove and ridges; h, hooks; m, mantle muscle; p, phragmocone; r, rostrum.



TEXT-FIG. 5. Loose arm hooks from the Oxford Clay (Callovian) of Dogsthorpe Pit (Bed 18b), near Peterborough; examples from the Martill Collection, Portsmouth University. A, possible *Cylindroteuthis* hook. B, possible *Acanthoteuthis* hook. Both *c.* ×80.

Recent comparable diagnoses. Jeletzky (1966, p. 146), and the detailed descriptions by Engeser and Reitner (1981) and Donovan and Crane (1992).

Included species. *A. speciosa* Münster, 1839 (=*A. ferussacii* Münster, 1839, *A. lictensteinii* Münster, 1839; *Ostracoteuthis superba* Zittel, 1884), Lower Tithonian of Germany (Crick 1897; Engeser and Reitner 1981); *A. antiqua* (Pearce, 1847), Lower Callovian–Upper Kimmeridgian of England (Riegraf 1987; Page and Doyle 1991; Donovan and Crane 1992); *A. polonica* (Makowski, 1952), Callovian of Poland (Makowski 1952; Bandel and Kulicki 1988); *A. mayri* (Engeser and Reitner, 1981), Lower Tithonian of Germany (Engeser and Reitner 1981, 1992); *A. leichi* Reitner, 1986, Lower Tithonian of Germany (Reitner 1986). '*Belemnoteuthis syriaca*' Roger, 1944, from the Upper Cretaceous of Syria, is a doubtful member of this genus. However, as described, it possesses a poorly preserved phragmocone, and needs further study in order to confirm its generic assignment (Roger 1944; Engeser 1990). Jeletzky (1966, p. 138) has suggested that this species is actually representative of the diplobelid belemnite genus *Conoteuthis*, although advanced no evidence to support this statement. '*Belemnoteuthis*' *pacifica* Anderson, 1938, has recently been assigned to *Conoteuthis* d'Orbigny, 1842 by Riegraf (1995). However, there is little evidence to support generic assignment to either *Acanthoteuthis* or *Conoteuthis*, as the specimen described by Anderson is simply a large and indeterminate belemnite phragmocone (Engeser 1990).

Remarks. Donovan (1994) has recently set out the case for the formal retention and conservation of the nominal genus *Acanthoteuthis* Wagner, *in* Münster 1839, and his conclusions are supported here.

The generic distinction of *Acanthoteuthis* and *Belemnotheutis* has been historically based upon the apparent absence of a rostrum in *Acanthoteuthis* (e.g. Naef 1922). Engeser and Reitner (1981) and Reitner (1986) both recognized the presence of rostra in specimens of *Acanthoteuthis* described by them, but upheld the generic distinction of *Acanthoteuthis* from *Belemnotheutis* largely on pro-ostracum shape and

arm-hook form. Donovan and Crane (1992) noted that typical specimens of *A. speciosa* possess a narrower phragmocone with fewer septa, and a slightly longer pro-ostracum than *Belemnotheutis antiqua*, although they considered that the arm hooks were broadly comparable. They noted that it was probable that these characters were probably of subgeneric ranking. As Engeser (1990) noted, the majority of the characters of *Acanthoteuthis*, as treated separately from *Belemnotheutis*, are plesiomorphic, the only apomorphy mustered being a difference in the median line of the pro-ostracum, which is of dubious distinction. Clearly there is little to separate the two nominal genera of *Acanthoteuthis* and *Belemnotheutis*, and the senior synonym is used here. This was recently supported by Riegaf (1995) who placed *Acanthoteuthis* in synonymy with *Belemnotheutis*, although retaining the use of the junior nominal synonym for the taxon.

Genus ANTARCTITEUTHIS gen. nov.

Derivation of name. From the discovery of this genus in the Upper Jurassic–Lower Cretaceous rocks of Antarctica.

Type species. A. donovani sp. nov., Tithonian–Berriasian of Antarctica and ?Argentina; Text-figures 1, 6.

Diagnosis. Belemnotheutidae with strong, single ventrolateral ridges and corresponding ventrolateral grooves on each flank. Arm hooks unknown.

Remarks. *Antarctiteuthis* gen. nov. is significantly different from the other genera of the Belemnotheutidae. Although specimens are not sufficiently well preserved to be able to distinguish the detailed characteristics of phragmocone, it can be assumed with some degree of certainty that this corresponds to that of the other known belemnotheutids, as phragmocones are conservative in all other known belemnites. There is no vestige of a pro-ostracum, but this is a usual preservation state in most other belemnite taxa, and so it is not possible to comment on distinctions from the older taxon *Chondroteuthis*. In addition, the specimens described herein have rostra and phragmocones that have been replaced by chlorite (Text-fig. 6), and it is not possible to determine whether the original shell chemistry was aragonite, characteristic of *Acanthoteuthis* itself (Bandel and Kulicki 1988). The decision to erect a new genus has, therefore, been based upon surface characteristics of the rostrum, as is common for most belemnite genera (Jeletzky 1966). The three known genera *Chondroteuthis*, *Acanthoteuthis* and *Antarctiteuthis* are, therefore, distinguishable on the basis of whether they have smooth or weakly-striated rostra (*Chondroteuthis*); double dorsal ridges and associated grooves (*Acanthoteuthis*) or dorsolateral ridges and associated grooves on each flank (*Antarctiteuthis*).

The early Jurassic belemnite genus *Nannobelus* is similar to *Antarctiteuthis*, given its relatively robust, acutely conical rostrum but is distinct in lacking grooves and importantly, associated ridges. This is mostly also true of the less acutely conical early Jurassic belemnite genus *Coeloteuthis.*

Antarctiteuthis donovani sp. nov.

Text-figures 1, 6

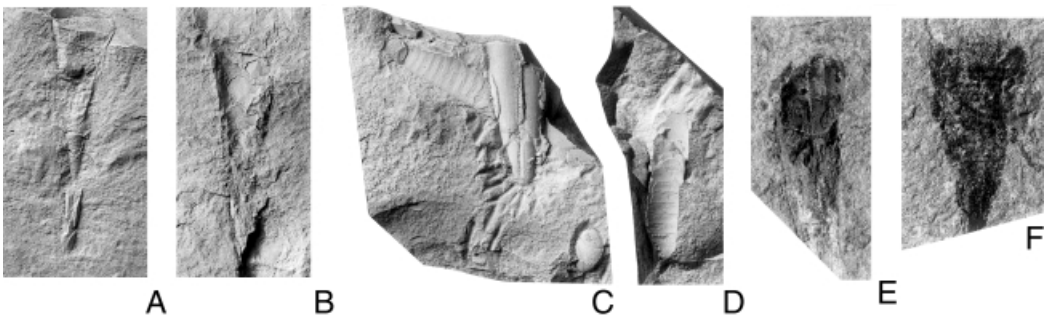
Derivation of name. Named in honour of Professor D. T. Donovan.

Holotype. BAS D.9103.13, Tithonian, Longing Member, Nordenskjöld Formation, Longing Gap, Graham Land, Antarctica.

Paratypes. BAS P.248.17a,b, ?Berriasian, President Beaches Formation, Byers Group, Byers Peninsula, Livingston Island, Antarctica.

Other material. BAS P.2151.13, P.2152.12, Tithonian–Berriasian, Devils Point Formation, Byers Group, Devils Point, Byers Peninsula, Livingston Island, Antarctica. BAS D.9012.86, 96, 103, 114, 116, 117, 119, Tithonian, Longing Member, Nordenskjöld Formation, Longing Gap, Graham Land, Antarctica.

Geological setting. Specimens of the new genus *Antarctiteuthis* described in this paper were collected in 1987–88 from the Upper Jurassic rocks of the Antarctic Peninsula region. Upper Jurassic rocks are exposed on both sides of the peninsula, and are known to contain belemnites (e.g. Howlett 1988). The present material was collected from Longing Gap, on the eastern coast of Graham Land, the northern part of the Antarctic Peninsula (Text-fig. 7).



TEXT-FIG. 6. *Antarctiteuthis donovani* gen. and sp. nov. from the Njordenskjöld and Presidents Beaches formations, Antarctica. A, holotype, rostrum showing phragmocone in place, and B, the counterslab, BAS P.9103.13; see Text-figure 1. C, paratype, showing prominent lateral ridge, BAS P.248.17a. D, paratype, showing phragmocone, BAS P.248.17b. E, example replaced by chlorite, showing position of prominent lateral ridge, BAS D.9012.97. F, example replaced by chlorite, showing phragmocone, BAS D.9012.96. All ×1.

The majority of specimens were collected from the Nordenskjöld Formation (= Ameghino Formation of authors) at its type locality at Longing Gap. The Nordenskjöld Formation consists of *c.* 450 m of alternating black shales and tuffs which were deposited in a barred anoxic basin within an active tectonic zone (Whitham and Doyle 1989; Doyle and Whitham 1991; Whitham 1993). Equivalent facies are found along both margins of the Antarctic Peninsula, which formed an active magmatic arc for much of the Mesozoic. The stratigraphy, sedimentology, fauna and palaeoenvironments of the Nordenskjöld Formation have most recently been described by Farquharson (1983), Whitham and Doyle (1989), Doyle (1991), Doyle and Whitham (1992) and Whitham (1993). Specimens were also collected from the rocks of broadly equivalent age and in some cases facies to the Nordenskjöld Formation, which is exposed on the Byers Peninsula, Livingston Island, north-west of the Antarctic Peninsula. The stratigraphy and sedimentology of the Byers Group has been most recently described by Crame *et al.* (1993), and Pirrie and Crame (1995).

Diagnosis. As for genus.

Description. Small, acutely conical Belemnotheutidae, with an apical angle of typically 10–12 degrees. Rostrum forms a relatively thin investment of the phragmocone, which typically penetrates two-thirds of the rostrum. Phragmocone endogastrically incurved, with typical belemnitid apical angles of around 20 degrees. Profile and outline of rostrum similar, broadly symmetrical. Transverse section of the rostrum subcircular, only weakly compressed. Rostrum bearing single, narrow and sharply defined ridges which are central or broadly dorso-lateral to each flank. These are accompanied by less well-defined groove-like depressions which border the ridges; the rostrum is otherwise smooth. Ontogenetic development seemingly conorostrid, with conical early juvenile rostrum.

Remarks. So far, only one species of this taxon has been discovered, and the distinctiveness of the rostrum ornament makes it difficult to confuse with other taxa of the Belemnotheutididae, or members of the Belemnitina or Belemnopseina.

RELATED TAXON

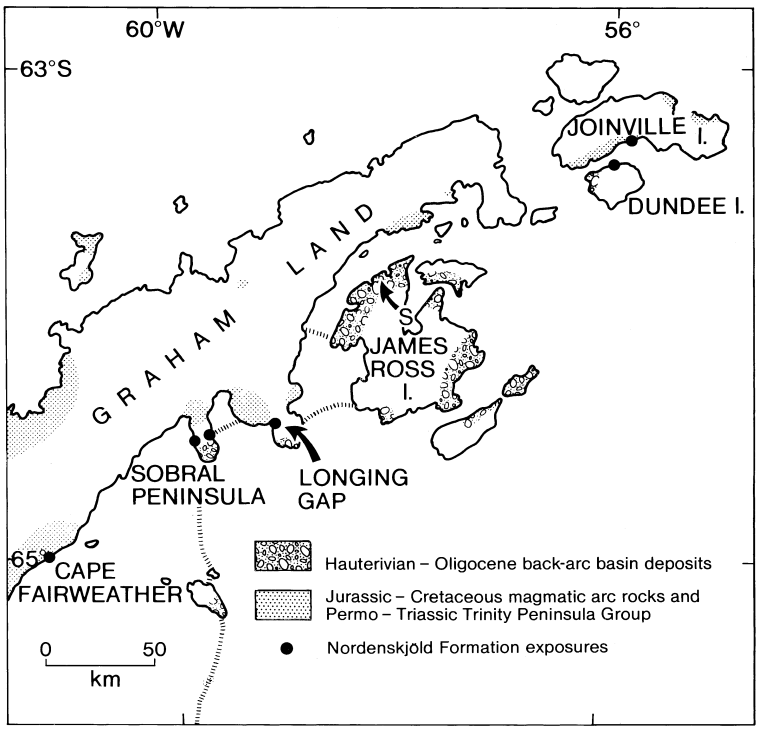
?Genus SUEVITEUTHIS Reitner and Engeser, 1982

Type species. *Sueviteuthis zellensis* Reitner and Engeser, 1982, by original designation.

Included species. *S. zellensis* Reitner and Engeser, 1982; *S. schlierbachensis* Reitner and Engeser, 1982.

Original diagnosis. Reitner and Engeser (1982*b*).

Remarks. The erection of this genus by Reitner and Engeser (1982*b*), and a monogeneric family to house it, was primarily on the basis of its apparent possession of a pair of what appeared to be stiffening rods which extended adorally from the ventral margin of the phragmocone. This led presumably to the assignment by



TEXT-FIG. 7. Sketch geological map of the Antarctic Peninsula (Graham Land), showing the location of Longing Gap, type locality for *Antarctiteuthis donovani* gen. and sp. nov.

Engeser and Clarke (1988) of *Sueviteuthis* as a phragmoteuthid genus, although this was later not supported by Engeser (1990). The rod-like structures were subsequently reinterpreted by Riegraf (1983) as dorsal stiffening rods for the pro-ostracum, and this view has not since been challenged. Riegraf (1983, 1995) has challenged the generic viability of this taxon, and has placed it in synonymy with both *Chondroteuthis* (Riegraf 1983) and *Belemnotheutis* (Riegraf 1995). However, Engeser (1990) maintained the group on the basis of its arm hooks, which are characteristically slender and unlike those of either *Chondroteuthis* or *Belemnotheutis*. As such, the basis of this genus is still open to debate. It is included as a 'related' taxon, subject to much further study.

IMPLICATIONS FOR COLEOID PHYLOGENY

The phylogeny of the Coleoidea has been one of the most strongly debated issues in recent cephalopod studies, despite the apparent stability of the established monophyly for the Belemnoidea (e.g. Berthold and Engeser 1987; Engeser 1990, 1998; Doyle *et al.* 1994; Pignatti and Mariotti 1995). One of the most difficult questions posed by these studies is the relationship of the Belemnoidea with the Phragmoteuthida, a group of coleoids characterized by a ventrally open body chamber which is transitional in form between the enclosed body chamber of the Aulacocerida, and the dorsal pro-ostracum of the Belemnitida. The Phragmoteuthida have no known rostral development, and therefore the resolution to the question is difficult, and revolves around two main factors: (1) the gradual ventral opening of the body chamber: Aulacocerida (enclosed), Phragmoteuthida (partially open), Belemnitida (open); and (2) the development of a massive rostrum, present in the Aulacocerida and Belemnitida, absent in the otherwise apparently 'transitional' Phragmoteuthida. In essence, a derivation of the Belemnitida from the Aulacocerida via the Phragmoteuthida would require a loss of the massive aulacocerid rostrum to develop the Phragmoteuthida, gaining a massive rostrum again for the Belemnitida.

These questions were discussed by Doyle *et al*. (1994), who indicated that the true relationship of the Phragmoteuthida was in need of clarification, particularly pressing being a detailed study of skeletal morphology. In their paper, they considered that it was more parsimonious for the massive rostrum to be developed only once, particularly so that belemnoid (i.e. Aulacocerida and Belemnitida) rostra are homologous, and not simply analogous as with the spirulid rostrum (Doguzhaeva 1996). Unfortunately, one of their figures (Doyle *et al.* 1994, p. 2, fig. 1) unintentionally illustrated a polyphyletic origin for the Coleoidea, which has been rightly criticized (Pignatti and Mariotti 1995; T. Engeser, pers comm. 1996). In fact, both the remainder of the Belemnoidea (Belemnitida and Diplobelida) and the Phragmoteuthida may be derived from a common ancestor, the Aulacocerida, a situation which has also been recently suggested by Engeser (1998), although in a different context. This still leaves in the balance the status of the Phragmoteuthida as a member of the superorder Belemnoidea, as originally suggested by Doyle *et al.* (1994). Haas (1989), Pignatti and Marriotti (1995) and Engeser (1998) clearly favoured the inclusion of the Phragmoteuthida in the Belemnoidea, but as detailed studies of phragmoteuthid shells, and particularly protoconchs, are lacking, there is little evidence of the presence of a closing membrane. Arm hooks are, however, known from this group, as indeed they are from the Aulacocerida (Engeser and Clarke 1988).

The Belemnotheutina have in many ways some relevance to the development of the Belemnitida from the Aulacocerida. Belemnotheutids possess aragonitic rostra characterized by their sheath-like form with raised ridges accompanying furrows, both typical characters of the Aulacocerida. Belemnotheutids also possess a conical form that is plesiomorphic for the Belemnitida as a whole, characteristic as it is of the earliest Jurassic belemnite genera *Schwegleria, Nannobelus* and *Coeloteuthis.* Both these lines of evidence are strongly supportive of a direct derivation of the Belemnitida from the Aulacocerida, and indicative of the importance of the Belemnotheutina, an otherwise typical belemnitid group, as intermediate, without the need for a phragmoteuthid stage.

Acknowledgements. PD is grateful to Alistair Crame, and to Andy Whitham, Dave O'Dowd and Donny Stewart for help in the field. We are grateful to Steve Baker and Dave Martill for photographs, and to Klaus Bandel for his careful review of the paper.

REFERENCES

ALLISON, P. A. 1988. Phosphatized soft-bodied squids from the Jurassic Oxford Clay. *Lethaia*, **21**, 403–410.

ANDERSON, F. M. 1938. Lower Cretaceous deposits in California and Oregon. *Geological Society of America, Special Paper*, **16**, 328 pp.

BANDEL, K. 1985. Composition and ontogeny of *Dictyoconites* (Aulacocerida, Cephalopoda). *Paläontologisches Zeitschrift*, **59**, 223–224.

—— and KULICKI, C. 1988. *Belemnoteuthis polonica*: a belemnite with an aragonitic rostrum. 303–316. *In* WIEDMANN, J. and KULLMAN, J. (eds). *Cephalopods – present and past.* Schweizerbart'sche, Stuttgart, 765 pp.

—— and SPAETH, C. 1988. Structural differences in the ontogeny of some belemnite rostra. 247–271. *In* WIEDMANN, J. and KULLMAN, J. (eds). *Cephalopods – present and past.* Schweizerbart'sche, Stuttgart, 765 pp.

—— ENGESER, T. and REITNER, J. 1984. Die Embryonalentwicklung von *Hibolithes* (Belemnitida, Cephalopoda). *Neues Jahrbuch für Geologie und Palaöntologie, Abhandlungen*, **167**, 275–303.

BATHER, F. A. 1888. Professors Blake and Shelgrove in Cephalopoda. *Annals and Magazine of Natural History*, **1888**, 41–47.

BERTHOLD, T. and ENGESER, T. 1987. Phylogenetic analysis and systematization of the Cephalopoda (Mollusca). *Verhandlungen des Naturwissenschaftlichen Vereins in Hamburg*, **29**, 187–220.

BÖDE, A. 1933. *Chondroteuthis Wunnenbergi* n. gen. n. sp., eine neue Belemnoideenform, in günstiger Erhaltung. *Jahresberich Niedersachen Geologischen Verein*, **25**, 32–64.

BÜLOW-TRUMMER, E. von 1920. *Fossilium Catalogus 1. Animalia Pars 11. Cephalopoda Dibranchiata*. Junk, Berlin, 313 pp.

CRAME, J. A., PIRRIE, D., CRAMPTON, J. S. and DUANE, A. M. 1993. Stratigraphy and regional significance of the Upper Jurassic–Lower Cretaceous Byers Group, Livingston Island, Antarctica. *Journal of the Geological Society, London*, **150**, 1075–1087.

CRICK, G. C. 1897. On an example of *Acanthoteuthis speciosa*, Münster, from the Lithographic Stone, Solenhofen, Bavaria. *Geological Magazine, Series 4*, **3**, 439–443.

DOGUZHAEVA, L. A. 1986. Two early Cretaceous spirulid coleoids of the north-western Caucasus: their shell ultrastructure and evolutionary implications. *Palaeontology*, **39**, 681–709.

DONOVAN, D. T. 1994. *Acanthoteuthis* Wagner in Münster, 1839 and *Kelaeno* Münster, 1842 (Mollusca, Cephalopoda): proposed conservation of usage. *Bulletin of Zoological Nomenclature*, **51**, 219–223.

—— and CRANE, M. D. 1992. The type material of the Jurassic cephalopod *Belemnotheutis*. *Palaeontology*, **35**, 273–296.

DOYLE, P. 1985. Sexual dimorphism in the belemnite *Youngibelus* from the Lower Jurassic of Yorkshire. *Palaeontology*, **30**, 147–177.

—— 1991. Teuthid cephalopods from the Upper Jurassic of Antarctica. *Palaeontology*, **34**, 169–178.

—— 1992. The British Toarcian (Lower Jurassic) belemnites. Part 2. *Monograph of the Palaeontographical Society*, **587**, 50–79.

—— and WHITHAM, A. G. 1991. Palaeoenvironments of the Nordenskjöld Formation: an Antarctic Late Jurassic–Early Cretaceous black shale–tuff sequence. 397–414. *In* TYSON, R. V. and PEARSON, T. H. (eds). *Modern and ancient continental shelf anoxia*. Geological Society, London, Special Publication, **58**, 470 pp.

—— DONOVAN, D. T. and NIXON, M. 1994. Phylogeny and systematics of the Coleoidea. *University of Kansas Paleontological Contributions*, *New Series*, **5**, 1–15.

ENGESER, T. 1987. Belemnoid arm hooks ('onychites') from the Swabian Jurassic – a review. *Neues Jahrbuch für Geologie und Palaöntologie, Abhandlungen*, **176**, 5–14.

—— 1990. Phylogeny of the fossil coleoid Cephalopoda (Mollusca). *Berliner Geowissenschaftlich Abhandlungen*, **124**, 123–191.

—— 1995. Eine neue Art der Gattung *Pavloviteuthis* Shimansky 1957 (Belemnoidea, Diplobelidae) aus dem Oberkimmeridgium von Süddeutschland. *Stuttgarter Beitrage für Naturkunde, Serie B*, **225**, 1–11.

—— 1998. The fossil Coleoidea page. (Last updated October 1998). URL: http://userpage.fu-berlin.de/~palaeont/fossilcoleoidea/welcome.html

—— and CLARKE, M. R. 1988. Cephalopod hooks, both Recent and fossil. 133–151. *In* CLARKE, M. R. and TRUEMAN, E. R. (eds). *The Mollusca, 12. Paleontology and neontology of cephalopods*. Academic Press, San Diego, 325 pp.

—— and REITNER, J. 1981. Beiträge zur Systematik von phragmokontragended Coleoiden aus dem Untertithonium (Malm zeta, 'Solnhofener Plattenkalk') von Solnhofen und Eichstätt (Bayern). *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, **1981**, 527–545.

—— 1983. *Chitinobelus acifer* Fischer, 1981, ein Belemnoteuthide (Coleoidea) mit epirostrum. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **165**, 496–501.

—— 1992. Ein neues Examplar von *Belemnoteuthis mayri* Engeser & Reitner, 1981 (Coleoidea, Cephalopoda) aus dem Solnhofener Plattenkalk (Untertithonium) von Wintershof, Bayern. *Archaeopteryx*, **10**, 13–17.

FARQUHARSON, G. W. 1983. The Nordenskjöld Formation of the northern Antarctic Peninsula: an Upper Jurassic radiolarian mudstone and tuff sequence. *British Antarctic Survey, Bulletin*, **60**, 1–22.

FISCHER, A. G. 1947. A belemnoid from the Late Permian of Greenland. *Meddelelser om Grønland*, **133**, 1–24.

FISCHER, K. C. 1981. *Chitinobelus acifer* n. g. n. sp., ein ungewöhnlicher Belemnit aus dem Lias epsilon von Holzmaden. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, **1981**, 141–148.

GUSTOMESOV, V. A. 1978. The pre-Jurassic ancestry of the Belemnitida and the evolutionary changes in the Belemnoidea at the boundary between the Triassic and the Jurassic. *Paleontological Journal*, **3**, 283–292.

HAAS, W. 1989. Suckers and arm hooks in Coleoidea (Cephalopoda, Mollusca) and their bearing for phylogenetic systematics. *Abhandlungen fur Naturwissenschaften Vereins, Hamburg*, **28**, 165–185.

HOWLETT, P. J. 1988. Late Jurassic–Early Cretaceous cephalopods of eastern Alexander Island, Antarctica. *Special Papers in Palaeontology*, **41**, 1–72.

JELETZKY, J. A. 1965. Taxonomy and phylogeny of fossil Coleoidea (= Dibranchiata). *Geological Survey of Canada, Paper*, **65–2**, 72–76.

—— 1966. Comparative morphology, phylogeny and classification of fossil Coleoidea. *University of Kansas Paleontological Contributions*, *Mollusca*, *Article* **7**, 1–162.

—— 1981. Lower Cretaceous diplobelinid belemnites from the Anglo-Paris Basin. *Palaeontology*, **24**, 115–145.

MAKOWSKI, H. 1952. La faune Callovienne de Luków en Pologne. *Palaeontologia Polonica*, **4**, 1–64.

MARTILL, D. 1986*a*. Fossil belemnite hooks. *Geology Today*, **1986**, 61.

—— 1986*b*. The diet of *Metriorhynchus*, a Mesozoic marine crocodile. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, **1986**, 621–625.

MÜNSTER, G. 1839. *Acanthoteuthis*, ein neues Geschlect der Cephalopoden, zu der Familie der Loligineen oder Teuthidae (Owen) gehörend. *Beitage für Petrefactenkunde*, **1**, 91–97.

NAEF, A. 1922. *Die fossilien tintenfische*. Carl Gustav, Jena, 322 pp.

ORBIGNY, A. d' 1842. Mémoire sur deux genres nouveaux de cephalopodes fossiles (les *Conoteuthis* et *Spirulirostra)* offran des passages, d'un cote entre la spirule et la seiche, de l'autre des bélemnites et les *Ommastrephes*. *Bulletin de la Société Géologique de France*, **13**, 386–398.

PAGE, K. N. and DOYLE, P. 1991. Other cephalopods. 144–162. *In* MARTILL, D. M. and HUDSON, J. D. (eds). *Fossils of the Oxford Clay*. Palaeontological Association, London, Field Guides to Fossils **4**, 286 pp.

PEARCE, J. C. 1842. On the mouths of ammonites, and on fossil contained in laminated beds of the Oxford Clay, discovered in cutting the Great Western Railway, near Christian Malford in Wiltshire. *Proceedings of the Geological Society of London*, **3**, 592–594.

—— 1847. On the fossil Cephalopoda from the Oxford Clay constituting the genus *Belemnoteuthis*, Pearce. *London Geological Journal*, **2**, 75–78.

PIGNATTI, J. S. and MARIOTTI, N. 1995. Systematics and phylogeny of the Coleoidea (Cephalopoda): a comment upon recent works and their bearing on the classification of the Aulacocerida. *Palaeopelagos*, **5**, 33–44.

PIRRIE, D. and CRAME, J. A. 1995. Late Jurassic palaeogeography and anaerobic-dysaerobic sedimentation in the northern Antarctic Peninsula region. *Journal of the Geological Society, London*, **152**, 469–480.

REITNER, J. 1986. *Acanthoteuthis leichi* n.sp. (Cephalopoda) aus dem Untertithonium von Solnhofen (Bayern). *Archaeopteryx*, **1986**, 19–25.

—— and ENGESER, T. 1982*a*. Phylogenetic trends in phragmocone-bearing coleoids (Belemnomorpha). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **164**, 156–162.

—— —— 1982*b*. Zwei neue Coleoidea-Arten aus dem Posidonienschiefer (untertoarcium) aus der gegend von Holzmaden (Baden-Württemberg). *Stuttgarter Beiträge zur Naturkunde, Serie B (Geologie und Paläontologie)*, **84**, 1–19.

RIEGRAF, W. 1982. New Coleoidea from the Lower Jurassic of southwest Germany. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, **1982**, 91–97.

—— 1983. Über '*Sueviteuthis*' *zellensis* Reitner & Engeser, 1982 (Coleoidea) aus dem Untertaorcium von Südwestdeutschland. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **165**, 502–507.

—— 1987. On Lower and Upper Jurassic dibranchiate cephalopods from Germany and England. *Paläontologisches Zeitschrift*, **61**, 261–272.

—— 1995. *Fossilium Catalogus 1: Animalia. Pars 133. Cephalopoda dibranchiata fossiles (Coleoidea).* Kugler, Amsterdam, 411 pp.

—— 1996. Belemnited-Fanghäkchen (Cephalopoda, Coleoidea) aus der Psilonotenbank (Unterer Jura, tiefstes Hettangium) von Südwestdeutschland. *Stuttgarter Beiträge zur Naturkunde, Serie B (Geologie und Paläontologie)*, **239**, 1–38.

ROGER, J. 1944. *Acanthoteuthis (Belemnoteuthis) syrica* n. sp. céphalopode dibranche du Crétacé supérieur de Syrie. *Bulletin de la Société Géologique de France*, **14**, 83–98.

SAELEN, G. 1989. Diagenesis and construction of the belemnite rostrum. *Palaeontology*, **32**, 765–798.

STOLLEY, E. 1919. Die Systematik der Belemniten. *Jahresberichte des Niedersächsischen Geologischen Vereins, Hannover*, **11**, 1–59.

WHITHAM, A. G. 1993. Facies and depositional processes in an Upper Jurassic to Lower Cretaceous pelagic sedimentary sequence, Antarctica. *Sedimentology*, **40**, 331–349.

—— and DOYLE, P. 1989. Stratigraphy of the Upper Jurassic–Lower Cretaceous Nordenskjöld Formation of eastern Graham Land, Antarctica. *Journal of South American Earth Sciences*, **2**, 371–384.

ZITTEL 1881–84. *Handbuch der Paläontologie.* 1. Abteilung, Paläozoologie, 2, Mollusca und Arthropoda. R. Oldenbourg, Munich and Leipzig, 893 pp.

—— 1895. *Grundzüge der Paläontologie (Paläozoologie).* R. Oldenbourg, Munich and Leipzig, 806 pp.

PETER DOYLE

Department of Earth Sciences
University College London
Gower Street
London WC1E 6BT
e-mail peter.doyle@ucl.ac.uk

EMMA V. SHAKIDES

Department of Earth and Environmental Sciences
University of Greenwich at Medway
Pembroke, Chatham Maritime
Kent ME4 4AW, UK

Typescript received 12 September 2002
Revised typescript received 13 March 2003