

TEUTHID CEPHALOPODS FROM THE UPPER JURASSIC OF ANTARCTICA

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ABSTRACT. Two teuthid cephalopods, *Trachyteuthis* cf. *hastiformis* (Rüppell) and muensterellid gen. et sp. nov., are described from the Nordenskjöld Formation (Upper Jurassic) of the northeastern Antarctic Peninsula. These specimens, the only recorded teuthids from Gondwana, are closely related to European species and suggest a more widespread distribution in the Late Jurassic than was previously known.

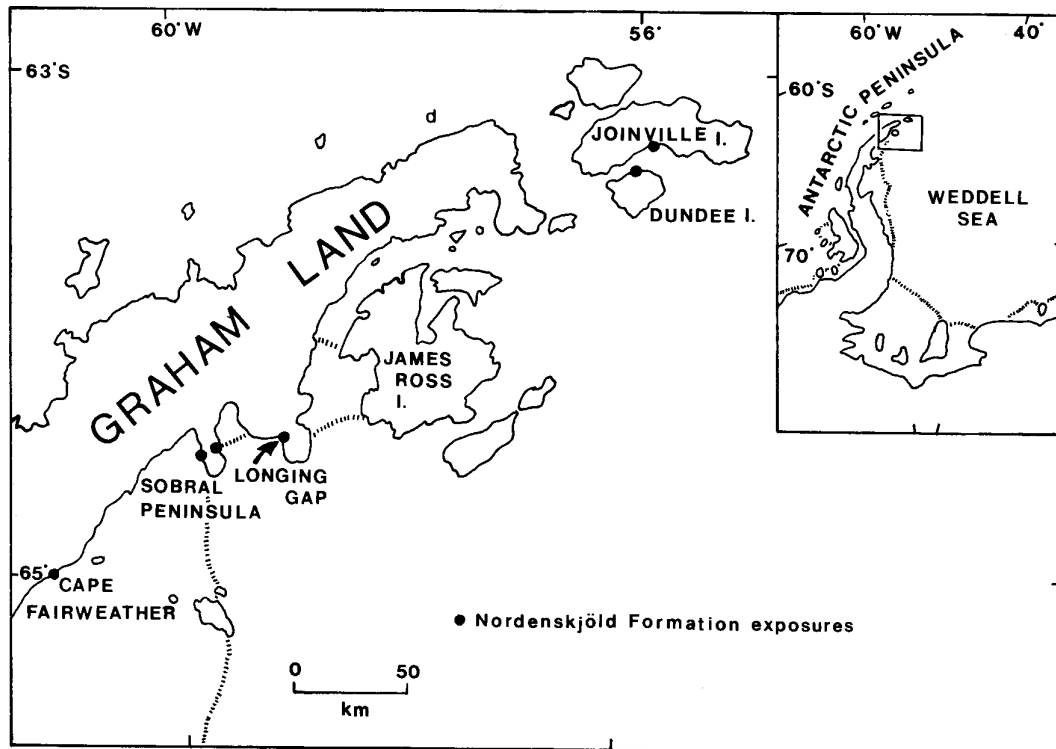
DURING the Antarctic summer of 1987–1988 two fossil teuthid specimens were collected by the author from the Nordenskjöld Formation, a late Jurassic–early Cretaceous black shale sequence exposed in the northeastern Antarctic Peninsula (Text-fig. 1). These specimens represent the only known teuthids from any of the Gondwana continents, and as such are of importance to our understanding of teuthid distribution.

Teuthids (= Vampyromorpha of Bandel and Leich 1986 and Engeser 1988*b*) are rare fossils given the relative abundance of other fossil cephalopods (ammonites and belemnites). A survey of the teuthid fossil record shows that these cephalopods are most commonly preserved in fine-grained sediments deposited under anoxic or otherwise restricted conditions, and the present specimens are no exception. Lower Jurassic specimens are commonest, especially from the widespread Toarcian black shales of Europe (Posidonienschiefer, Jet Rock, e.g. see Riegraf *et al.* 1984; Engeser 1988*b*; and Doyle 1990 for summaries), and North America (Fernie Formation, e.g. Hall 1985; Hall and Neuman 1989). Exceptionally well preserved specimens are also known from the Middle Jurassic (Callovian) Oxford Clay of England (e.g. Donovan 1983), and similar-aged anoxic sediments in the Ardèche, France (Fischer and Riou 1982). Upper Jurassic teuthids are well represented in the Solenhofen Limestone of southern West Germany (Crick 1896; Bandel and Leich 1986; Engeser 1986) and in the Kimmeridge Clay of England (Owen 1855; Hewitt and Wignall 1988). Cretaceous restricted facies have also yielded teuthids: from the Lower Aptian 'Tock' of northern West Germany (Engeser and Reitner 1985), the Santonian Fish Bed of the Lebanon (Woodward 1883; Roger 1946; Engeser and Reitner 1986), and the Upper Cretaceous Niobrara Formation (Kansas) and Pierre Shale (Manitoba) of North America (e.g. Miller and Walker 1968; Nicholls and Isaak 1987).

The relative paucity of teuthid specimens has led to an anomalous distribution pattern. Thus, apart from the specimens found in anoxic sediments in the United States, Cuba (Schevill 1950), the Lebanon, and the Cape Verde Islands, West Africa (Reitner and Engeser 1982), the majority of specimens are from Europe (see Engeser 1988*b*). Prior to the present study, teuthids were unknown from Gondwana, as the only record from Queensland, Australia (Moore 1870) has been found to be an indeterminate bivalve fragment (Engeser and Phillips 1986). The purpose of this paper is to document the new record and discuss its implications for palaeobiogeography.

GEOLOGICAL SETTING

From late Jurassic to early Tertiary times the northern Antarctic Peninsula was an active volcanic arc formed by the southeastward subduction of the proto-Pacific plate. During subduction, a 5–6 km thick sedimentary sequence was deposited in a retro-arc basin (the Larsen Basin) to the east of the arc. The Nordenskjöld Formation is a distinctive sequence of air-fall ashes and black



TEXT-FIG. 1. Locality map for the northeastern Antarctic Peninsula, showing the distribution of known Nordenskjöld Formation exposures. The specimens described below were collected from the type locality at Longing Gap.

mudstones of late Jurassic to early Cretaceous age which is thought to form the base of the Larsen Basin succession (Macdonald *et al.* 1988). The Nordenskjöld Formation is exposed at five localities along the northeastern coast of the Antarctic Peninsula (Farquharson 1983; Text-fig. 1), and its stratigraphy has recently been revised by Whitham and Doyle (1989).

Two members are recognized within the Nordenskjöld Formation at Longing Gap, the type locality for the formation (Text-fig. 1). The Longing Member ranges in age from Kimmeridgian to Tithonian and is dominated by parallel-laminated black mudstones with subordinate, thin ash layers. The Ameghino Member ranges in age from Tithonian to Berriasian and is characterized by structureless mudstones and thicker ash layers (Whitham and Doyle 1989). A detailed sedimentological study of the Nordenskjöld Formation is currently being carried out by Dr A. G. Whitham (British Antarctic Survey).

Both teuthid specimens were obtained from near the top of the Longing Member at Longing Gap. They were associated with a fauna consisting of the ammonites *Virgatosphinctes* spp. and *Lithacoceras* sp., and the bivalves *Retroceramus* spp. and *Arctotis* sp., of Tithonian age (Whitham and Doyle 1989). Sedimentological (parallel lamination, etc.) and palaeoecological (low faunal diversity, a lack of true benthos and trace fauna) indices show that the Longing Member was deposited under low oxygen, anaerobic to episodically dysaerobic conditions (Doyle and Whitham in press). Although the Longing Member fauna had a primarily pelagic or pseudoplanktonic mode of life, the teuthids were collected from an interval with some benthic colonization, though lacking

bioturbation, suggesting dysaerobic rather than the anaerobic zone conditions characteristic of the lower part of the member (Doyle and Whitham in press).

SYSTEMATIC PALAEOONTOLOGY

The terminology used below is discussed in detail in Jeletzky (1966), and the classification largely follows that of Engeser (1988*b*) (see discussion below). Both specimens are housed in the collections of the British Antarctic Survey (BAS) in Cambridge. Comparative material was examined in the British Museum (Natural History) (BMNH), London. Annotation of synonymy lists follows the convention of Matthews (1973).

Subclass COLEOIDEA Bather, 1888
Order TEUTHIDA Naef, 1916

Remarks. Jeletzky (1966) employed the order Teuthida Naef, 1916 for all known fossil squid. However, Bandel and Leich (1986) studied in detail specimens of the Solenhofen teuthids *Leptoteuthis*, *Plesioteuthis* and *Trachyteuthis*, and concluded that they possessed only eight arms, linked by basal webs, and were therefore most closely related to the Recent cephalopod *Vampyroteuthis*. This led to the adoption of the order Vampyromorpha Robson, 1929 for all fossil 'teuthids' by Berthold and Engeser (1987), Engeser and Bandel (1988) and Engeser (1988*b*), and the contention that the fossil 'teuthids' were not directly ancestral to the Recent Teuthida. The more conservative usage of the order Teuthida Naef, 1916 is maintained below, however, as the specimens discussed below shed no further light on this discussion.

Suborder MESOTEUTHINA Naef, 1921
Family TRACHYTEUTHIDIDAE Naef, 1921
Genus TRACHYTEUTHIS Meyer, 1846

(= *Coccoteuthis* Owen, 1855, *Voltzia* Schevill, 1950; junior subjective synonyms)

Type genus. *Septa hastiformis* Rüppell, 1829, by subsequent designation (Bülow-Trummer 1920, p. 248).

Diagnosis. See Naef (1922, p. 137).

Remarks. The form of *Trachyteuthis*, and its relative similarity to the present-day cuttlebone of *Sepia officinalis*, has led some authors to consider that this genus is actually representative of the Sepiida rather than the Teuthida. Schevill (1950) described a new genus from the Oxfordian of Cuba, *Voltzia*, which he considered distinct from *Trachyteuthis*, as it apparently possessed 'phragmocone deposits' similar to those of *Sepia*. Donovan (1977) questioned the distinction of the nominal genera *Voltzia* and *Trachyteuthis*, but went further in suggesting that *Trachyteuthis* was a true sepiid, attributing the lack of phragmocone to solution of the delicate aragonite plates after burial. In one specimen of *Trachyteuthis* from Solenhofen (BMNH 83730), Donovan reported fragments attributable to phragmocone debris as a 'lag' beneath the shell. After sectioning, I found that this specimen revealed no further debris beneath the dorsal shield, and no indication of an extensive phragmocone development, and as such this evidence is not unequivocal. No traces of phragmocone were found in the Antarctic specimen, which is preserved as a thin shield < 1 mm thick, built of successive lamellae. An ink sac is present in this specimen, and though slightly displaced, it is found directly beneath the thin gladius, without any trace of intervening phragmocone plates.

Hewitt and Wignall (1988) have studied the mineralogy of *Trachyteuthis* specimens from the English Kimmeridge Clay, and have determined that its original mineralogy was francolite, rather than aragonite. These authors used this as additional evidence against sepiid affinities of *Trachyteuthis*, arguing that one would expect a sepiid 'cuttlebone' to be aragonitic, rather than

phosphatic. The Antarctic specimen described below is also phosphatic, but the possibility of diagenetic replacement of original aragonite cannot be ruled out, especially since specimens of the thin-shelled ammonite *Haploceras* and belemnoid *?Belemnoteuthis* (both originally aragonitic) are found as crushed, phosphatic films in the Nordenskjöld Formation.

In summary, it seems probable that despite the close morphological similarities between the shells of *Trachyteuthis* (= *Voltzia*) and *Sepia*, the absence of a proven phragmocone and the possible original phosphate shell mineralogy of the former suggest that assignment to the Teuthida rather than to the Sepiida is more correct.

Range. Definite records from the Lower Oxfordian to Tithonian of southern West Germany (Bavaria), England (Dorset, North Yorkshire), USSR (Volga region), Cuba (Viñales region) and Antarctica (Graham Land). A single doubtful record from the Lower Aptian of northern West Germany (Heligoland).

Trachyteuthis cf. *hastiformis* (Rüppell, 1829)

Text-figs 2A, B and 4

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| cf. *1829 | <i>Sepia hastiformis</i> Rüppell, p. 9, pl. 3, fig. 2. |
| cf. v. 1855 | <i>Coccoteuthis latipinnis</i> Owen, p. 124, pl. 7. |
| cf. v. 1896 | <i>Coccoteuthis hastiformis</i> Rüppell; Crick, p. 439, pl. 14. |
| cf. 1922 | <i>Trachyteuthis hastiformis</i> (Rüppell); Naef, p. 137, text-fig. 51. |
| cf. v. 1977 | <i>Trachyteuthis</i> sp. Donovan, p. 32, text-figs 8 and 9. |
| cf. v. 1988a | <i>Trachyteuthis hastiformis</i> (Rüppell); Engeser, p. 82, text-fig. 1c. |
| cf. 1988b | <i>Trachyteuthis hastiformis</i> (Rüppell); Engeser, p. 59. [Full and extensive synonymy given]. |
| v. 1988 | fossil teuthid; Anonymous, p. 15, text-fig. 6. [Colour photograph of specimen described below]. |

Type specimen (of *Trachyteuthis hastiformis*). Holotype, Senckenberg Museum, Frankfurt-am-Main, register number XI 1328. Lower Tithonian, Solenhofen Limestone, Mühlheim, Bavaria, West Germany.

Material. One specimen, BAS D.9007.33, uppermost Longing Member, Nordenskjöld Formation (Whitham and Doyle 1989, p. 6). Longing Gap, Graham Land, Antarctic Peninsula. Preserved intact in a carbonate concretionary horizon yielding the ammonite *Virgatospinctes rotundidoma* Uhlig of Tithonian age (Whitham and Doyle, 1989, text-fig. 6f).

Description. The single specimen collected comprises the majority of the median field of a small (total preserved length 90.5 mm) *Trachyteuthis* gladius. It is preserved in a carbonate concretion allowing three-dimensional preservation, in a formation that otherwise yields compressed fossils. The specimen consists of two parts, naturally split by freeze-thaw action. These represent ventral and dorsal surfaces of the gladius divided cleanly along shell lamellae, the two parts united are less than 1 mm thick.

The dorsal fragment (Text-fig. 2B) is the most recognizable of the two as *Trachyteuthis*. It exhibits (in negative, as it is the undersurface of the topmost part of the gladius) a median field with a narrow (width 23.4 mm) central region composed of a series of closely spaced pustules arranged in arcuate arrays which correspond to growth lines. A central ridge or median keel is present. The median field is completed by relatively smooth lateral areas ('*Seiteplatte*' of Naef 1922, text-fig. 51). These are incomplete, but display some longitudinal striation. Finally, there are displaced fragments of a probable wing present at the left posterior of the shell.

The ventral fragment (Text-fig. 2A) is less easily recognizable as representative of *Trachyteuthis*, as there are no pustules or definable field areas present. The fragment consists of an almost smooth shield with some traces of arcuate growth lines in the central area. Part of the lateral area of the median field is definable in the right anterior of the specimen, and fragments of a wing in the left posterior. This portion of the gladius very clearly shows the lamellar construction of the gladius and, where successive lamellae have exfoliated, neither it nor the underlying matrix displays any evidence of phragmocone deposits. The presence of an ink sac is indicated by a dull black mass up to 5 mm thick beneath the ventral portion of the gladius in the right posterior of the fragment (Text-fig. 2A).



TEXT-FIG. 2. *Trachyteuthis cf. hastiformis* (Rüppell). Specimen D.9007.33, Tithonian, Longing Member, Nordenskjöld Formation, Longing Gap. Ventral and dorsal fragments of naturally split gladius, $\times 1$. A, ventral fragment showing the ink sac beneath the thin lamellae of the shell. B, dorsal fragment showing the characteristic pustules of the median field. Abbreviations: MA, median asymptote; MF, median field; MK, median keel; Sp, 'Seiteplatte'; W, wing. A reconstruction of the gladius is given in Text-figure 4.

Remarks. This specimen is clearly representative of the genus *Trachyteuthis*, and is very close to specimens from the Kimmeridge Clay of England and the Solenhofen Limestone of West Germany. However, its small size, which may indicate that it is a juvenile, and its incomplete preservation, allow only tentative assignment to the species *Trachyteuthis hastiformis* (Rüppell). *Trachyteuthis palmeri* (Schevill) (Lower Oxfordian, Cuba) and *T. zhuravlevi* Hecker and Hecker (Lower Volgian, Volga region, USSR) are poorly known, and differ only in their greater width and elongate form, respectively.

Suborder KELAENINA Starobogatov, 1983
 Family MÜNSTERELLIDAE Roger, 1952
 MÜNSTERELLID gen. et sp. nov.

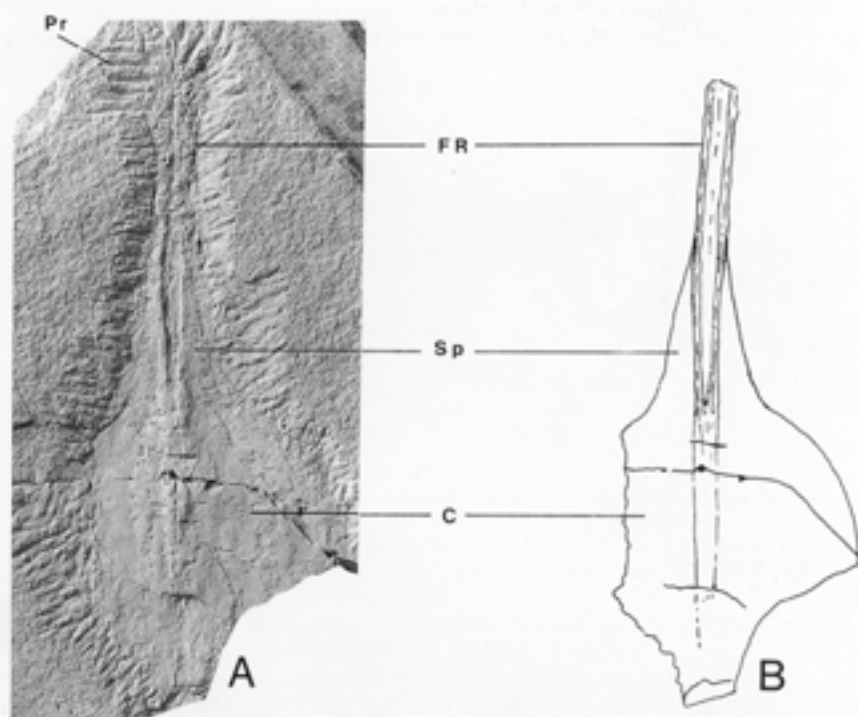
Text-figs 3A, B and 4

Material. A single specimen, BAS D.9008.3, found loose in the uppermost Longing Member (approximately equivalent horizon to BAS D.9007.33), Nordenskjöld Formation, Longing Gap, Graham Land, Antarctic Peninsula. Associated *Virgatosphinctes* and *Retroceramus* specimens indicate a Tithonian age.

Description. The specimen consists of a gladius with a preserved length of 82.5 mm, comprising a broad spoon-shaped conus with a rhachis extending anteriorly from it (Text-fig. 3A).

The spoon-shaped conus is incomplete, but has an approximate maximum width of 37 mm. It is preserved flattened with no indications of concentric or other growth lines upon its dorsal surface. The median field of the gladius is developed as a rhachis, commencing as a median ridge or raised area in the posterior of the gladius, then extending anterior of the conus. The median field is completed by smooth lateral outgrowths ('*Seiteplatte*') which accompany the rhachis for half of its length and up to 60 mm of the total length of the gladius, and indistinct surface features on the conus indicate the possible position of the median asymptotes which border the median field (Text-fig. 4).

The rhachis diverges anteriorly at an angle of approximately 5° , and expands to a maximum width of 4 mm. As the rhachis expands, it divides anteriorly from its original raised area on the conus to produce two laterally placed ridges with an intervening, smoother area. There is some indication of a weak median keel in the centre of this region, but preservation is too poor for this to be unequivocal.

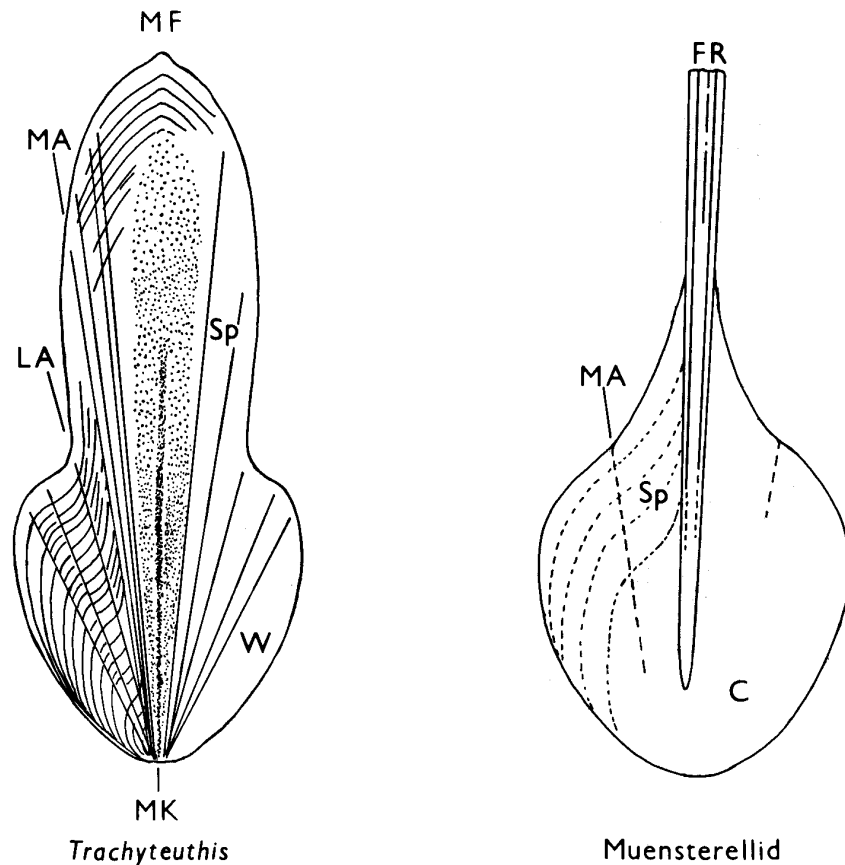


TEXT-FIG. 3. Muensterellid gen. et sp. nov. Specimen D.9008.3, Tithonian, Longing Member, Nordenskjöld Formation, Longing Gap. A, dorsal view of gladius $\times 1$. B, sketch representation of same view, $\times 1$. Abbreviations: C, conus; FR, free rhachis; Pr, preparation marks; Sp, '*Seiteplatte*'. A reconstruction of the gladius is given in Text-figure 4.

Remarks. The unusual divided form of the rhachis, and apparent absence of growth lines in this specimen, initially gave rise to doubts about its actual cephalopod affinities. However, despite this, the regular form of the conus and its relationship with the rhachis confirm that this specimen undoubtedly represents a (new) teuthid taxon, and it is certainly not representative of any known non-cephalopod mollusc, plant (cf. Engeser and Phillips 1986) or even fish (P. Forey, pers. comm. 1987).

The form of the specimen discussed most closely resembles taxa of the Muensterellidae (Kelaenina). Specifically, the presence of a 'free rhachis' distinguishes it from otherwise similar specimens of *Palaeololigo* Naef (Palaeologinidae, Mesoteuthina), which have a broader median field. Of the Muensterellidae, the Tithonian genera *Listroteuthis* Naef and *Muensterella* Schevill are closest, especially the former which has a similar conus shape. The only other muensterellid with a divided rhachis is the Campanian form *Tusoteuthis* Logan (= *Kansasteuthis* Miller and Walker; see Nicholls and Isaak 1987, p. 734). The gladius of *Tusoteuthis* has a leaf-shaped conus with a robust 'free rhachis' starting immediately from its anterior. The rhachis does not diverge significantly to the anterior, and is much more robust than that of the present specimen. Difference of rhachis design in otherwise similar spoon-shaped gladii of Recent squid was noted by Toll (1988), illustrating the potential for variability in this feature. The rhachis of the Recent family Bathyteuthidae would seem to be analogous to the Antarctic specimen, having lateral rods joined by a central U-shaped area.

The only Prototeuthina which approaches the present specimen is the genus *Maioteuthis* Reitner and Engeser (Plesioteuthididae). *Maioteuthis* has a much reduced conus and an extremely long and



TEXT-FIG. 4. Suggested reconstructions of the Antarctic teuthids, not to scale. *Trachyteuthis* redrawn after Naef (1922, fig. 51). Abbreviations: C, conus; LA, lateral asymptote; MA, median asymptote; MF, median field; MK, median keel; Sp, 'Seiteplatte'; W, wing.

narrow median field which divides anteriorly to present a weak median keel (Reitner and Engeser 1982, text-fig. 2). The Antarctic specimen resembles *Maioteuthis* only in having a divided median field with a faintly developed median keel, but differs greatly in possessing a spoon-like conus with an anteriorly extensive 'free rhachis', demonstrating its muensterellid affinities.

In summary, the overall form of the gladius (conus and rhachis) of this specimen would support the erection of a new genus within the Muensterellidae. However, the single specimen available does not permit the formal designation of a new taxon.

PALAEOBIOGEOGRAPHICAL CONSIDERATIONS

There are too few records to provide any definite conclusions about the palaeobiogeography of Mesozoic teuthids. However, the discovery of fossil teuthid gladii from Gondwana is significant in illustrating that the present observed European bias is artificial, induced to some extent by the fragility of the remains and a greater intensity of study in western Europe. Therefore, some primary observations are presented here.

In addition to its European (England, West Germany) occurrences (see Engeser 1988*b* and references therein), the genus *Trachyteuthis* is recorded from the Lower Volgian of the USSR (Volga region) (Hecker and Hecker 1955), the Lower Oxfordian of western Cuba (as *Voltzia*) (Schevill 1950) and now the Tithonian of Antarctica. The majority of these specimens are remarkably similar to the western European representatives, especially the Antarctic example, suggestive of an almost worldwide distribution for *Trachyteuthis* in the Late Jurassic, transgressing boreal and Tethyan realm boundaries observed in other marine groups. Cretaceous trachyteuthids are represented only by a possible *Trachyteuthis* from the Lower Aptian of Heligoland (northern Germany) (Engeser and Reitner 1985) and Upper Cretaceous records from the Lebanon (e.g. *Libanonteuthis* Kretzoi) and North America (e.g. *Actinosepia* Whiteaves) (Engeser 1988*b*).

The Muensterellidae have similarly disparate geographical records. *Muensterella* and associated genera (i.e. *Listroteuthis* Naef, *Calaenoteuthis* Naef) are presently known only from the Lower Tithonian of West Germany (see Engeser 1988*b*). The Antarctic muensterellid, described from sediments of similar age, has many points in common with these European genera, and like *Trachyteuthis*, is a possible indicator of a formerly more widespread distribution. Cretaceous muensterellids are relatively rare, but there is some indication of less centred distribution pattern than is presently observed. Thus, while *Tusoteuthis* (? = *Kansasteuthis*, *Niobarateuthis* and *Enchoteuthis*) is only recorded from the Upper Cretaceous of North America (Nicholls and Isaak 1987), two undescribed Australian teuthid specimens with affinity to *Tusoteuthis* are preserved in the BMNH collections. These specimens, from the Lower Cretaceous (Albian) of Queensland, Australia, (BMNH C.59211, C.59276) resemble *Tusoteuthis*, but are larger, possessing a ribbed conus and multiple grooved free rhachis, and undoubtedly represent a new taxon.

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