Berliner Paläobiol. Abh.	03	091-099	Berlin 2003

TWO PAIRS OF FINS IN THE LATE JURASSIC COLEOID *TRACHYTEUTHIS* FROM SOUTHERN GERMANY

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ABSTRACT

A specimen of the Upper Jurassic coleoid *Trachyteuthis* showing two pairs of posterior lobate fins is described. It is the only known coleoid with two pairs of fins in the adult apart from the Recent *Grimalditeuthis*. A four-finned ancestral state of Vampyromorpha is hypothesized.

Keywords: *Trachyteuthis*, fins, phylogeny

INTRODUCTION

Recent coleoids have a single pair of fins, the exception being the incirrate octopods which have none. Possession of a single pair of fins in some fossil genera, such as *Plesioteuthis* (Naef 1922), *Mastigophora* (Donovan 1983) is therefore not a character which is useful in elucidating phylogeny, since it appears to be plesiomorphic. Consequently there has been little or no discussion of the significance of fins in phylogeny. *Trachyteuthis* is now shown to be unique among fossil coleoids in that its fins form two pairs. The genus is unusual in other respects, the gladius and the arm crown, and the fins now serve to emphasise its isolation among fossil and Recent coleoids.

PREVIOUS WORK

Crick (1896) described a small individual (gladius length 95 mm) in the British Museum (Natural History) (no. C.5775) which he claimed to show impressions of the fins (Fig. 1a). He recognised anterior boundaries of the fins about three-fifths of the distance from the posterior to the anterior end of the gladius, and posterior boundaries a few mm from the posterior end. The condition of the specimen has deteriorated since Crick wrote his account and the features which he described as fins are now difficult to see. Crick's interpretation is unlikely in the light of later work.

Naef (1922, p. 139, fig. 52) gave a reconstruction showing a single large fin on each side extending almost the whole length of the body (Fig. 1b). This was stated to be based on Crick (1896) but is not supported by Crick's description. Bandel and Leich (1986, Fig. 20) also offered a reconstruction with fins extending the whole length of the muscular mantle (Fig. 1c).

Frickhinger (1994, p. 88, fig. 132) illustrated a specimen in the possession of Interfoss which was described as "mit Fangarmen, Flossen und Spur" (with arms, fins and impression). The illustration shows two fins about half way along the body of the animal, the left hand one being apparently complete, the right hand one being fragmentary and less convincing. The head of this specimen has been detached from the body and it is possible that the fins have also been displaced.

Donovan (1995) described a specimen in the Teyler Museum, Haarlem, Netherlands, interpreted as showing a single pair of posterior, subterminal, lobate

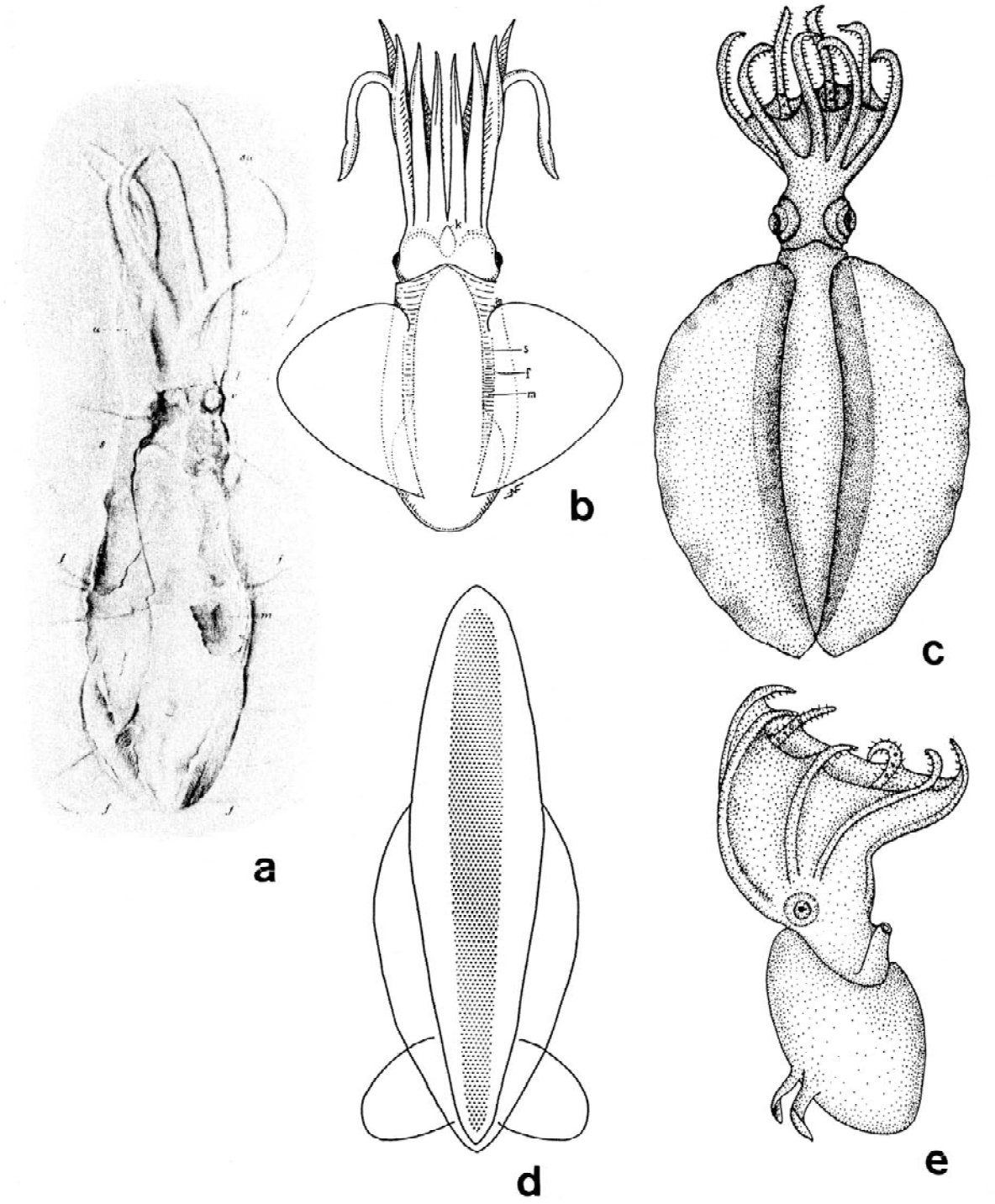

Fig. 1 **a** *Trachyteuthis* (specimen BM(NH) C5775) as figured by Crick (1896), x 0.64. *f* indicates fins. **b**, Restoration of soft parts of *Trachyteuthis* by Naef (1922). Note the decabrachian arm crown. **c**, Restoration of soft parts of *Trachyteuthis* by Bandel and Leich (1986). Arm crown is somewhat similar to that of *Vampyroteuthis*. **d**, Fins of *Trachyteuthis* superimposed on outline of gladius (Donovan 1995). **e**, *Vampyroteuthis*, drawing from Bandel and Leich (1986) after Chun

fins (Fig. 1d). An alternative interpretation in the light of the specimen here described is that two overlapping fins are present on the right hand side of the fossil. This appears to have been the first description to describe the detailed structure of the fins, which showed branching bundles of muscle fibres similar to those of Recent squids.

MATERIAL

The specimen described here is preserved in the Palaeozoological collections of the Swedish Natural History Museum, Stockholm, no. 98280. It is from the Solnhofen Formation (Lithographic Limestone) of Eichstätt, Germany. It is of Upper Jurassic (Lower Tithonian) age, Zone of *Hybonoticeras hybonotum*. The exact locality and horizon are not known.

The specimen is the lower slab of the part and counterpart which originally constituted the complete specimen, the whereabouts of the upper slab is unknown. The rock matrix shows laminations < 1 mm thick. The fossil consists of the impression of the dorsal surface of the animal. A small portion of the gladius remained (now removed), the rest of the gladius being presumably attached to the missing upper slab. The anterior end of the impression is damaged, the posterior end is not clear. The preserved length of the gladius is 330 mm. The maximum width of the median field is 95 mm and the greatest width across the lateral fields (wings) is about 118 mm. The gladius length when complete is estimated at about 380 mm.

TAXONOMY

The type species of *Trachyteuthis* was discussed by Donovan (1995). Examples from the Solnhofen limestone are usually referred to the earliest species to be described, *Trachyteuthis hastata* (Rüppell, 1829). Many later specific names have been proposed, reviewed by Wagner (1860). Gladii vary in shape as well as size but there is no modern study of variation in the genus which might indicate whether one or more species are present.

DESCRIPTION OF THE SPECIMEN

The present specimen falls near the upper size limit for the species. There is no question that the animal was fully grown. The impression shows the dorsal surface of the gladius. The characteristic tuberculate central area has a maximum width of 42 mm near the anterior end. Smooth areas on either side of the gladius impression mark the extent of soft tissue, presumably after compression by burial. The boundaries of the smooth areas are sharp. The total width across the smooth areas is variable but is about 140 mm. There is no trace of the transversely striated muscular mantle which is sometimes preserved with the Solnhofen fossil coleoids.

MODE OF PRESERVATION OF FINS

The impression of the tuberculate central area of the gladius is clear which suggests that the dorsal surface of the gladius was already partly exposed by decay of the soft tissues covering it. However the most posterior part of the tuberculate area is not seen which shows that it was still covered by soft tissue. This interpretation is supported by the impressions of the fins which are clearest near the posterior end. The fact that the muscle bundles are seen, as in the example described by Donovan (1995), may indicate that the integument of the fins had also decayed, although the muscular structure is occasionally visible in illustrations of living squids (e.g. *Pterygioteuthis*, Chun 1910, pl. 12, figs 1, 2, 4), perhaps because the fins are transparent and not pigmented.

DESCRIPTION OF THE FINS

The fossil preserved the impression of the dorsal surface of the animal (Fig. 2a). The left side as seen is therefore the actual right side and is so referred to below.

The anterior pair are about 65-70 mm (actual right) and 55 mm (actual left) long, measured obliquely (Figs 2b, 3). Their proximal ends, presumed attachment sites, are a few mm from the margin of the central tuberculate area of the gladius. The (actual) left appears further from the tuberculate area than the right, probably due to incomplete preservation (Fig. 3). Bundles of muscle fibres are about 0.5 mm wide near the base of the fin and thinner near the distal end. The striations are approximately parallel to the margins of the fin.

Of the posterior pair the (actual) right is the better preserved and appears nearly complete (Figs 2a, 3). Proximally the muscle bundles are thicker than those of

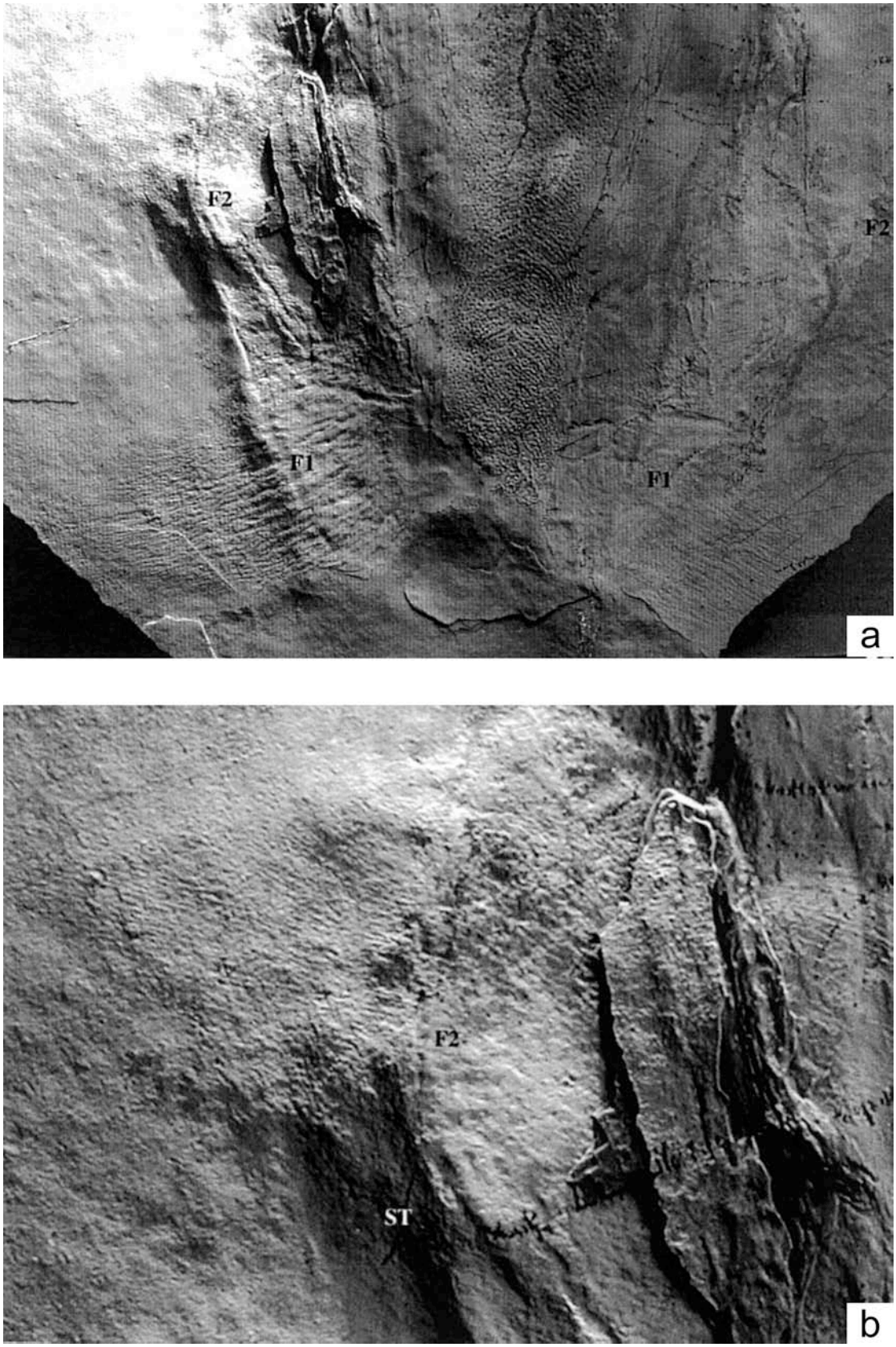

Fig. 2 *Trachyteuthis*, Solnhofen Formation, near Eichstätt, Bavaria. Swedish Museum of Natural History, Stockholm, no. 98280. **a**, Posterior part of specimen, x 0.9. **b**, Detail of anterior right fin, x 2.1. F1 = posterior fins. F2 = anterior fins. ST = soft tissue with different orientation from fin muscles

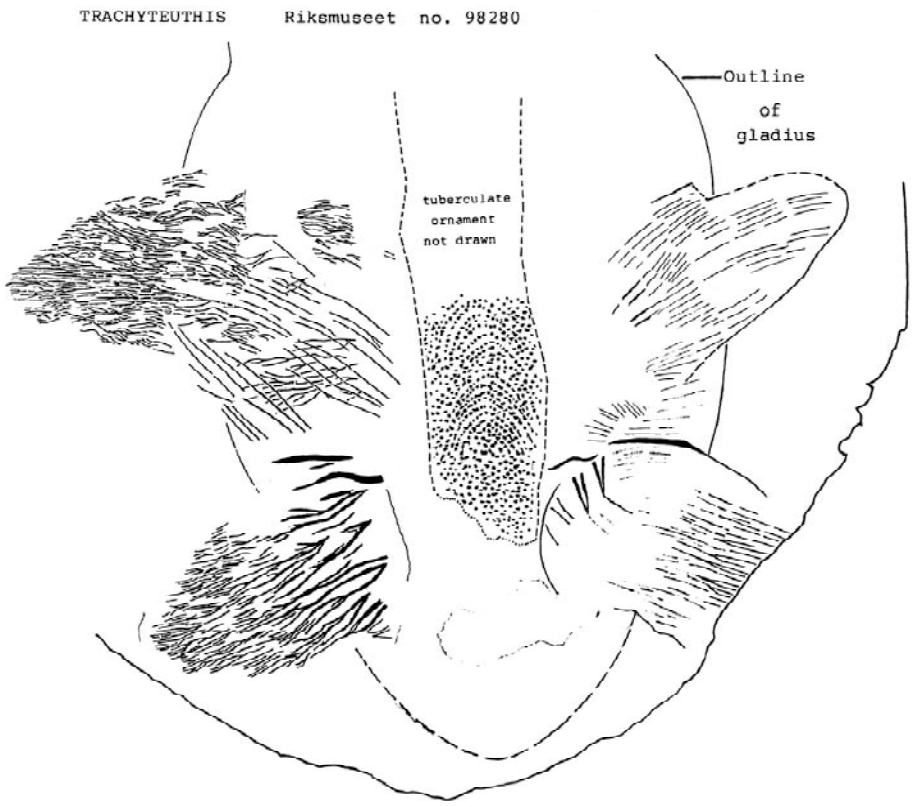

Fig. 3 Drawing of specimen shown in Fig. 2

the anterior fins, up to about 1.5 mm across and they divide into narrower branches. The shape of the fin appears more pointed than the anterior pair but this may be a matter of incomplete preservation. The (actual) left posterior fin is less well preserved but was presumably similar to the right. Its distal end is truncated by the edge of the slab.

Attachment and position

The posterior end of the gladius is not seen but its approximate position may be restored (Fig. 3). The fins were attached over a distance of about 95 mm about 40 mm from the posterior end. The fins were attached to the dorsal surface of the animal. The anterior pair attach at, or close to, the margin of the tuberculate area of the gladius. The posterior pair appear to have been attached a few mm outside the tuberculate area. Attachment to the dorsal surface of the gladius would correspond with the situation described by Naef (1922, Fig. 7 & p. 35) for his ”Allgemeine Ausgangsform der Dibranchiaten” (i.e. his hypothetical ancestral form of the dibranchiates) (his Fig.7a). Though it is not possible to say whether a ”Flossenwurzeltasche” (fin root pocket) was present (Naef´s Fig. 7, b, c) as opposed to direct attachment via a fin cartilage (Naef´s Fig, 7a).

Function

The function of fins in swimming was briefly considered by Clarke (1988, pp. 207, 208) who recognised eight types within Coleoidea as a whole. *Trachyteuthis* possessed a well-developed muscular mantle and was therefore capable of jet propulsion. The function of the fins was perhaps for stabilisation, or control of attitude, rather than for primary propulsion.

COMPARISON WITH RECENT COLEOIDS

In many Recent squids the single pair of fins lies at the posterior end of the body and in some families (e.g. Histioteuthidae, Psychroteuthidae; Nesis 1987) they extend beyond the hinder end of the body. More rarely the fins lie a short distance from the posterior end (e.g. *Pickfordiateuthis*, *Pterygioteuthis*, *Pyroteuthis*; Nesis 1987). In cirrate octopods the fins may lie half-way along the body.

Pickford (1940, p. 174) wrote that in

Vampyroteuthis "The fins rest directly on the shell sac whose wall is thickened to form what appear to be cartilaginous supports. In other living dibranchiates, the fin cartilages, although probably derived developmentally from the shell sac, are completely separated from it in the adult animal." Clarke (1988, p. 208) wrote that the fins in *Vampyroteuthis* have a "well-developed muscular band in the anterior margin attached to the broad pen".

PHYLOGENY AND SYSTEMATICS

Several characters have been considered by authors as useful in determining the affinities of *Trachyteuthis*. These include gladius morphology, gladius composition and fins.

Gladius morphology

Rüppell (1829) placed the Upper Jurassic gladius now assigned to *Trachyteuthis* in the genus *Sepia*, because of the resemblance of the dorsal surface to that of the cuttle-bone, noting that it differed from living species by the heart-shaped expansion of the posterior third. Naef (1922) explained this resemblance as a convergence, and (Naef 1921) included his new family Trachyteuthidae in his Suborder Teuthoidea along with the Recent squids.

Donovan (1977), also influenced by the strong resemblance of the dorsal surface to that of *Sepia*, returned to Rüppell's position and considered *Trachyteuthis* as a close relative and ancestor of Recent Sepia. This did not find general acceptance. Bandel and Leich (1986) placed *Trachyteuthis*, along with *Plesioteuthis* and *Leptoteuthis*, in Vampyromorpha, chiefly on the basis of the presence of a web uniting the bases of the arms. *Trachyteuthis* has generally been placed close to other Jurassic teuthids with pointed gladii such as *Palaeololigo* and *Teudopsis* (Doyle *et al.* 1994, Engeser website 1998 [http://userpage.fu-berlin.de /~palaeont/fossilcoleoidea/welcome.html]).

Gladius composition

Gladii of *Trachyteuthis* from both the Solnhofen Formation of Bavaria and the Kimmeridge Clay of southern England, the two sources of the majority of specimens, are now composed of francolite, a fluorapatite mineral with composition $Ca_5(PO_4,CO_3)_3(F,OH)$ (Hewitt & Wignall 1988). These authors concluded that the original gladius "was largely composed of a laminar fabric of chitinous material, with a crystalline material concentrated in folded layers over the median dorsal surface." They postulated that the crystalline material was the mineral brushite, $CaHPO_4.ZH_2O$. They stated that original phosphatic mineralogy made unlikely the affinity between *Trachyteuthis* and Sepiidae which had been postulated by Donovan (1977).

In fact Mesozoic fossil gladii from several different families are composed of francolite (Hewitt *et al.* 1983, Hewitt and Whyte 1990, unpublished analyses). Original phosphatic mineralogy is unlikely because Recent molluscs invariably secrete calcium carbonate. Hewitt and Jagt (1999, pp. 321, 322) included further study of the ultrastructure of *Trachyteuthis* and write of francolite replacement of aragonite in *Loligosepia* and *Trachyteuthis*. In fact Bandel and Leich (1986, p. 145) had already written of the "originally spherulitic aragonitic structure" in *Trachyteuthis*.

It is probable that these Mesozoic gladii were largely chitinous, and it is an unresolved question whether the present francolitic mineralogy replaces aragonite or not. In any case gladius composition is not useful in determining affinity.

Fins

Donovan (1995) described a specimen of *Trachyteuthis* showing a posterior subterminal pair of lobate fins. These were quite different from the fins which extend the whole length of the body in Sepiidae, and did not support his earlier (Donovan 1977) interpretation.

SIGNIFICANCE OF FINS FOR PHYLOGENY AND TAXONOMY OF COLEOIDS

Among living coleoids the Decabrachia and the cirrate octopods have a single pair of fins. *Grimalditeuthis*, a rare monotypic squid genus, has a single pair of fins in the young but appears to be unique among Recent coleoids in having two pairs in the adult (Clarke in

Sweeney *et al.* eds, 1992, pp. 181, 182). The extra pair in the adult is anterior to the juvenile pair and is described by Clarke (1988, p. 108) as secondary. Clarke (1988) also refers to additional "secondary" fins in larval *Chiroteuthis*. The implication is that these second pairs are late evolutionary developments and not relics of an ancestral state.

Juvenile *Vampyroteuthis* has a pair of fins which are resorbed and replaced by a pair anterior to it in the adult (Pickford 1949, 1950), so that for a brief period of the life history two pairs are present. The phylogenetic significance of this has not been discussed. One interpretation could be that there was an ancestral state with two pairs throughout ontogeny. If this is so, then it can be united with *Trachyteuthis* in a clade with the unique apomorphy, among coleoids, of two pairs of fins.

Vampyroteuthis was originally thought to be a cirrate octopod. After the discovery of the filaments (modified arm pair II) it was placed in a separate Suborder Vampyromorpha (Robson 1929), later an Order (e.g. Clarke & Trueman 1988). It was for long considered intermediate between octopods and decapods, but a sister-group relationship with Octopoda (i.e. Cirrata + Incirrata) was demonstrated by Young and Vecchione (1996) and has been accepted, these two clades forming the Octobrachia (Sweeney & Roper 1998).

The pivotal features supporting the elevation of *Vampyroteuthis* to ordinal level are the broad gladius that reaches the full mantle length, and the retractile filaments. Pickford (1949), describing the gladius of *Vampyroteuthis*, drew attention to the close resemblance of this delicate shell to the gladius of the Prototeuthoidea and Mesoteuthoidea of Naef (1922), the latter including *Trachyteuthis*. However, Vecchione *et al.* (1999, p. 117) suggest that a three-part gladius with broad median field and wings (lateral fields) is plesiomorphic for neocoleoids and therefore has no value for determining relationships. According to Young, Vecchione and Donovan (1998) the gladius probably evolved at least four times in extant lineages (Vampyromorpha, Oegopsida, Myopsida and Sepiolidae).

According to these authors the arm crown (presence or absence of tentacles or filaments) is the character which allows correct systematic assignment of teuthids. However, *Mastigophora* (Vecchione *et al.* 1999) and possibly *Plesioteuthis* (Naef 1922, p. 118) are the sole extinct genera with tentacles so far known. Relationship of all other families based only on gladii must remain uncertain at present.

Returning to consideration of a *Trachyteuthis* - *Vampyroteuthis* clade, we must therefore consider two other characters: the gladius and the arm crown. The gladius of *Vampyroteuthis* resembles that of *Loligosepia*, not *Trachyteuthis*; the more specialized nature of the latter indicates that it could be a side branch, not an ancestor. As regards the arm crown, rare *Trachyteuthis* are known with arms preserved as impressions (Crick 1896; Bandel & Leich 1986). Crick counted eight arms. Bandel and Leich also assumed eight. Because one cannot be certain that all arms have left an impression, *Trachyteuthis* could have had ten arms, or it could have had eight, with or without filaments. If filaments were present, it is unlikely that they would ever be found fossil.

Two possible relationships of *Vampyroteuthis* and *Trachyteuthis* are shown in Fig. 4.

CONCLUSIONS

A relationship is postulated between *Vampyroteuthis* and *Trachyteuthis* as the only two coleoids (ignoring *Chiroteuthis* and *Grimalditeuthis*, see above) which have two pairs of fins at any stage in the life history. This would imply a two-pair state as primitive in Octobrachia. Whether the two-pair state existed further back in the ancestry (i.e. in the ancestors of all Neocoleoidea, or of all Coleoidea) cannot be determined on present evidence.

ACKNOWLEDGEMENTS

We are greatly indebted to Martin Stein of Philipps-Universität, Marburg, Germany for scanning the images used in this study. To Eva Norrman for technical help and advice; to Stefan Bengtson for help with transmitting images; and to Toby Stiles for processing and printing images. Doguzhaeva acknowledges grants from the Swedish Academy in 2000 and 2001 to support her visits to the

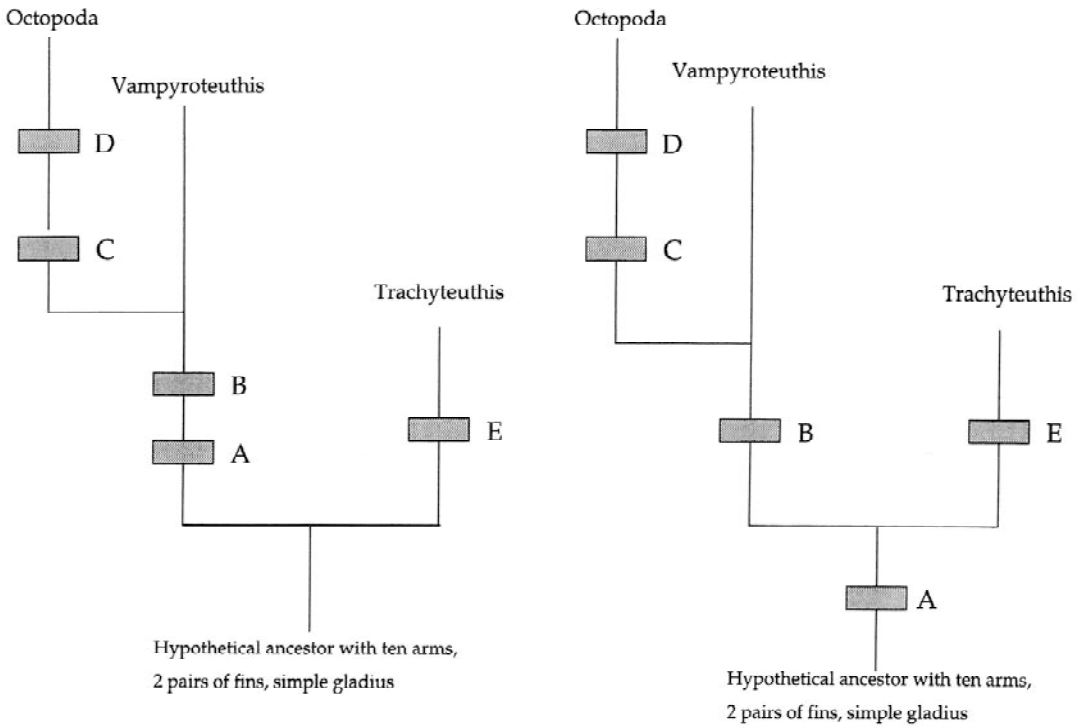

Fig. 4 Possible relationships of *Vampyroteuthis* and *Trachyteuthis*. Letters denote character states as follows: **A**, Arm pair II specialized as filaments. **B**, Posterior pair of fins suppressed in adult. **C**, Posterior pair of fins lost. **D**, Filaments lost. **E** Specialized gladius of *Trachyteuthis* type

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Received: 21 November 2002 / Accepted: 2 April 2003