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A specimen of *Trachyteuthis* (Coleoidea) with fins from the Upper Jurassic of Solnhofen (Bavaria)

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With 4 figures

Summary

A specimen of the Upper Jurassic coleoid genus *Trachyteuthis* which has fin musculature preserved is described for the first time. The detailed arrangement of fin muscles is similar to that of living Coleoidea. The shape and location of the fin argues against *Trachyteuthis* being a sepiid. The type species of *Trachyteuthis* is discussed.

Zusammenfassung

Erstmals wird aus der Gattung *Trachyteuthis* (Coleoidea, Oberjura) ein Exemplar mit erhaltener Flossenmuskulatur beschrieben. Die bis in feine Details erkennbare Anordnung der Muskeln ähnelt der heute lebender Coleoiden (Tintenfische). Form und Lage der Flossen sprechen gegen eine Zugehörigkeit von *Trachyteuthis* zu den Sepien; die Familienzuordnung bleibt unsicher. Die Typusart von *Trachyteuthis* wird erörtert.

1. Nomenclature and systematics

The genus *Trachyteuthis* was proposed in an anonymous letter to the editor of the Neues Jahrbuch (Meyer, 1846), known to have been written by Hermann von Meyer, as stated in Meyer (1855). The genus was introduced as follows: „Die Schulpen, welche der in der lebenden Sepie am ähnlichsten sind, sind davon so sehr verschieden, daß sie in ein eigenes Genus gebracht werden müssen, das ich Trachyteuthis nenne. Die Sammlung zu Ansbach besitzt ausgezeichnete Schulpen zweier Spezies der Art, die ich als Trachyteuthis oblonga und T. ensiformis bezeichne; letzter scheint ein bei Münster (H. VII, t. 9, f. 3) abgebildetes Fragment anzugehören; erste Spezies ist in Münster's Heften nicht enthalten."

Trachyteuthis oblonga und *T. ensiformis* were both new specific names. *T. oblonga* is a nomen nudum and is thus not available. *T. ensiformis* is accompanied by an indication, in the form of the reference to Münster's figure, and is thus available and becomes the type species by monotypy. Doyle et al. (1994) designated *T. ensiformis* as type species but this action was, in fact, superfluous. Doyle et al. (1994) de-

signated the original of MÜNSTER (1846, pl. 9, fig. 3), the only figured syntype, as Lectotype of the type species.

Trachyteuthis hastiformis (RÜPPELL, 1829) was stated to be the type species by BÜLOW-TRUMMER (1920: 248), followed by ENGESER (1988: 58), but was not an originally included nominal species.

The genus *Coccoteuthis* was proposed by OWEN (1855) with the type species by monotypy *C. latipinnis* from the English Kimmeridge Clay. It is a subjective synonym of *Trachyteuthis*, as recognised by BÜLOW-TRUMMER (1920) and by ENGESER (1988). CRICK (1896) argued that *Coccoteuthis* was the correct name because MEYER did not fully describe his genus until 1855 (MEYER, 1855). As noted above, however, *Trachyteuthis* is valid with priority from 1846.

A number of different specific names were proposed for forms of *Trachyteuthis* from the Solnhofener Plattenkalk by nineteenth century authors. The number of species was reduced to five by BÜLOW-TRUMMER (1920) and to one by ENGESER (1988) who regarded all later names as synonyms of *T. hastiformis* (RÜPPELL, 1829). In the absence of a study of variation in *Trachyteuthis* from the Solnhofener Plattenkalk it is impossible to decide whether one or more species are present, although certainly most of the nineteenth century names will prove to be synonyms.

2. Soft parts of *Trachyteuthis*

General

Transversely striated muscular mantle tissue is fairly commonly observed in association with *Trachyteuthis* gladiuses. It is a plesiomorphic character for Coleoidea (KEAR et al., 1995).

Two specimens have been described with the arm crown preserved. One is in the British Museum (Natural History) Reg. no. C5775 and was described by CRICK (1896). It is further discussed below. The other was figured by ABEL (1922) and by MÜLLER (1963). It was stated to be in the Vienna University teaching collection by ABEL (1922) and in the Haus der Natur, Salzburg, by the firm of FRANZ WEIGERT (Neuburg an der Donau) who supply replicas. The first specimen shows seven or eight arms (CRICK thought eight) and the second at least five. In both specimens the arms are thinner and longer than in most living Sepiidae. Probable traces of suckers are visible in both specimens. There are no arm hooks. No tentacles have been observed in fossil *Trachyteuthis*.

Teyler Museum specimen

The specimen is preserved in matrix typical of the Solnhofener Plattenkalk, of Upper Jurassic (Lower Tithonian, "Zeta 2") stratigraphical age. This formation is variously dated between about -145 and -150 m. y. It occurs in a series of inter-reef basins extending over an area 50 km or more from east to west in Bavaria. The locality of the specimen is not recorded. It is numbered 6022 in the Teyler Museum, Haarlem, Netherlands, and was examined in February, 1990.

The specimen differs from the original figured specimen of *T. hastiformis* RÜPPELL (1829) in having a gladius with a narrower median tuberculate area, and wings which, although indistinct, appear to extend further along the sides of the gladius (Fig. 2). For this reason it is here regarded as *Trachyteuthis* sp. The specimen is unique in the writer's experience of examining examples of this genus in European museums

(London, Haarlem, Frankfurt, Munich, Stuttgart, Bonn, Eichstätt, Tübingen) in showing a clearly preserved posterior subterminal fin.

The fossil is raised above the surface of the slab which is probably the lower of the original two slabs. The whereabouts of the counterpart slab is unknown. The fossil is interpreted as the impression of the dorsal surface of the gladius (Fig. 1). The specimen as preserved is 365 mm long, but both anterior and posterior extremities of the gladius are missing.

On the right hand side of the gladius as seen, i. e. the left hand side of the gladius in its original orientation, a fin is clearly preserved. Part of the outline is faintly visible, rather more than half the outline is missing but the original shape can be restored with some confidence (Fig. 2). The fin was lobate, the length greater than the antero-posterior breadth.

The fin appears to have been attached ventral to the wing of the gladius. The musculature of the fin is preserved in detail (Figs. 3, 4). Near the line of attachment to the body the muscle bundles are up to about 1 mm in diameter (as preserved), but they rapidly branch into smaller units, which may branch further although some rejoining also occurs. The muscle bundles near the periphery of the fin are about 0.33 mm to 0.25 mm in diameter. There appears to have been a thickened anterior margin about 6 mm wide.

Anterior to the fin on the same side of the gladius traces of the muscular mantle are present. Transverse striations, characteristic of fossilized coleoid mantle (KEAR et al., 1995), are visible in some places. On the other side (left hand as seen) the thickened anterior margin of the other fin of the pair is seen. Fossilized soft tissue is seen posterior to this but detail is not easy to resolve.

Other possible examples of fins in *Trachyteuthis*

An undescribed and unregistered specimen in the British Museum (Natural History) shows indistinct traces of similar structures to those here described at the posterior end on the right side (left as seen on the specimen, which is a gladius seen from the underside).

CRICK (1896) described as *Coccoteuthis hastiformis* (RÜPPELL) var. *minor* WAGNER a specimen from the Solnhofener Plattenkalk in the British Museum (Natural History) (no. C5775) which he thought had traces of fins preserved. The specimen has been re-examined by the writer. The alleged fins are areas where the surface of the limestone slab adjoining the fossil is smoother than the usual surface of bedding planes in the Solnhofener Plattenkalk. These smooth areas are carefully described by CRICK but are not clearly shown in the illustration to his paper. There is no sign of muscle bundles such as those described here. In the writer's opinion the smooth areas do not represent fins, whatever their significance may be.

3. Discussion

Comparison with modern Decapoda

Fins of the shape described here for *Trachyteuthis* are not the commonest type in living Decapoda, but they are found in several groups – some sepiolids, some cranchiids, *Spirula*, some chiroteuthids, neoteuthids, and histioteuthids. These families

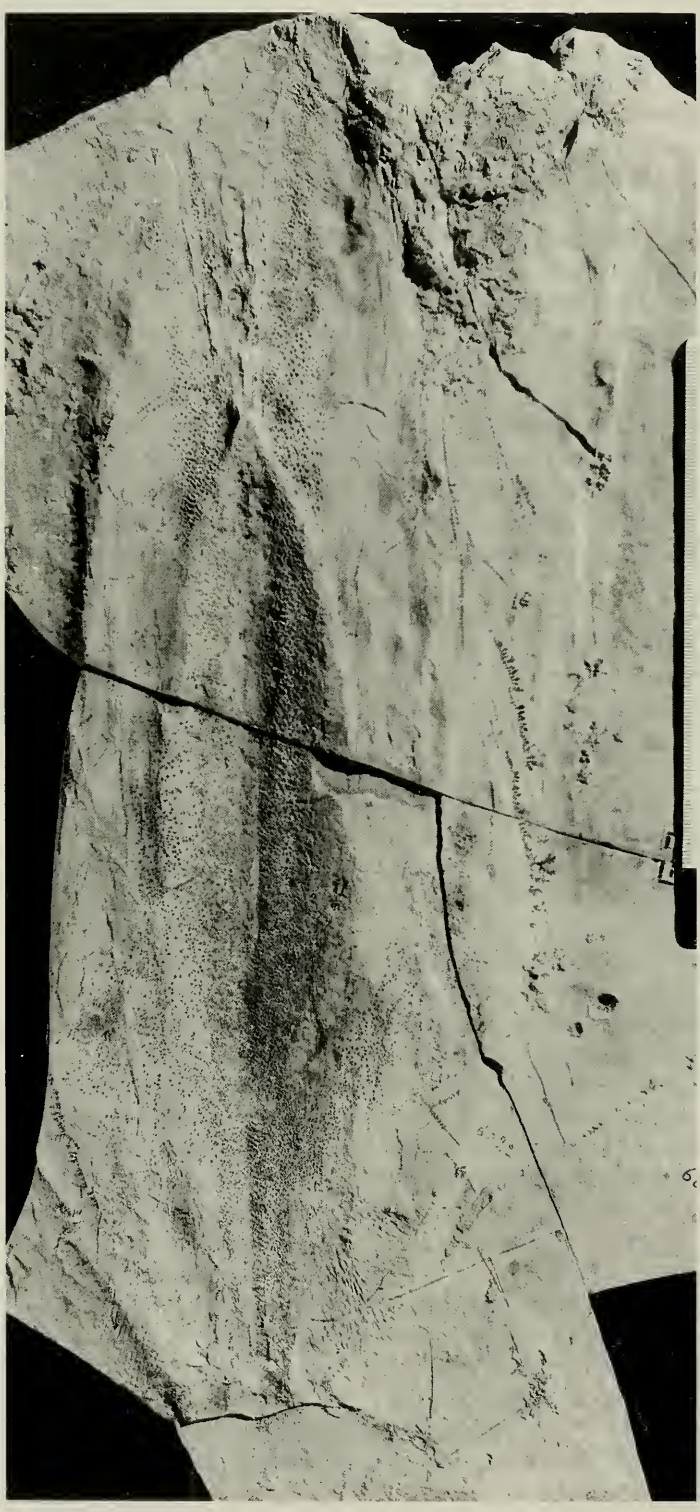

Fig. 1.
Trachyteuthis sp. from the Solnhofener Plattenkalk, Bavaria, Germany. Impression of dorsal surface of gladius with remains of soft tissues. Teyler Museum, Haarlem, Netherlands, no. 6022. – x0,5.

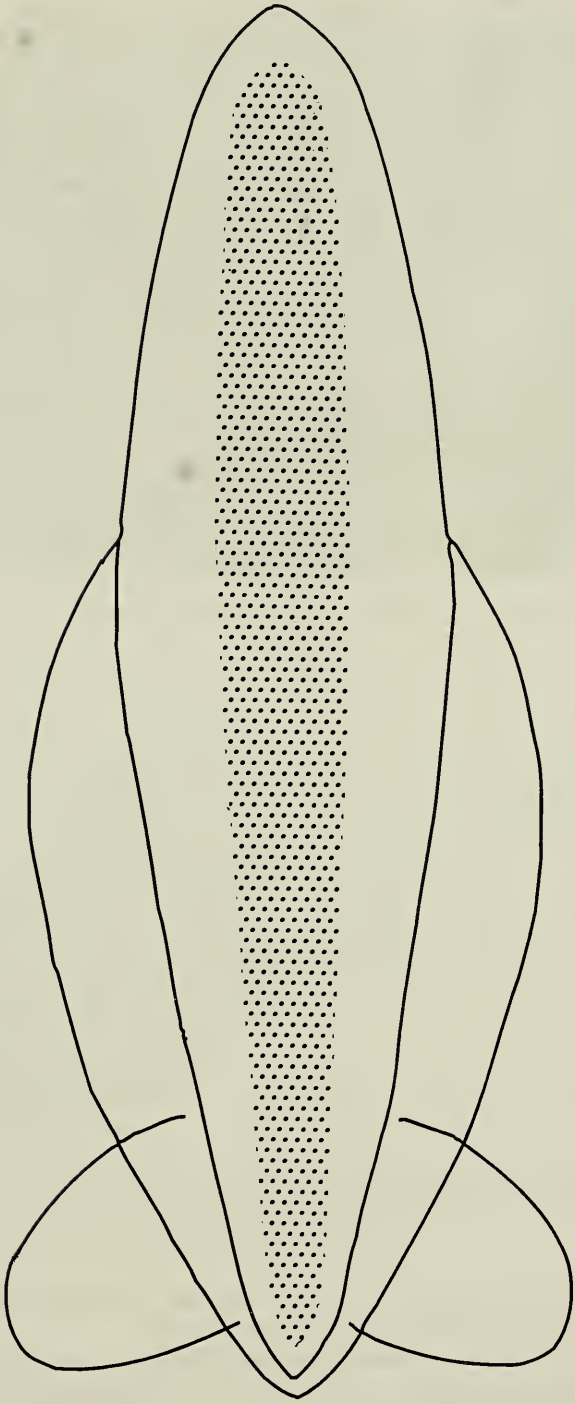

Fig. 2. Restored outline of the gladius of the specimen of *Trachyteuthis* sp. shown in Fig. 1. The outlines of the fins are shown. The shaded area represents the median tuberculate area of the gladius. – Ca. x0,45.

Fig. 3. Part of the specimen shown in Fig. 1, showing the posterior part of the gladius and fin. – x0,9.

Fig. 4. Slightly restored drawing of the musculature of the fin shown in Fig. 3. – x0,9.

are not regarded as closely related (CLARKE, 1988) and fin shape seems unlikely to be a "good" character for indicating phylogenetic affinity.

The musculature of decapod fins is not well described in the literature. DICK YOUNG has kindly examined the fin musculature of several species and reports as follows:

"I have examined briefly the fins of *Euprymna* (sepiolid), *Abralia* (oegopsid) and *Bathyteuthis* (oegopsid or myopsid). They all show a similar pattern. The fin muscle

bundles (fin rays) are wider near the attachment of the fin than at the periphery by roughly a factor of two. Since the bundles reach the edge of the fin perpendicular to this edge, the muscles must undergo a great deal of spreading. That is, the length of the attachment is far less than the distance around the periphery of the fin. To obtain the spread the fin rays subdivide and apparently become flatter. In following a single fin ray it can be seen to divide and converge at various points along its path. In spite of all this, the fins give the general impression of having highly parallel rays if not examined too closely. In fins such as those of *Vampyroteuthis* where some of the muscles are not numerous, the subdivision is more obvious."

This description exactly fits the muscle bundles or 'fin rays' observed in the present specimen of *Trachyteuthis*.

Affinities of *Trachyteuthis*

The present writer (DONOVAN, 1977: 31) interpreted *Trachyteuthis* as a member of Sepiida on the basis of the similarity between the dorsal surface of the gladius, with its median tuberculate area, and the dorsal surface of the cuttlebone of modern *Sepia*. Other authors before and since have rejected this view, regarding *Trachyteuthis* as a teuthid (JELETZKY, 1966) or a vampyromorph (ENGESER, 1988). It is true that none of the specimens shows any traces of a phragmocone on the ventral side, although this could be because the Solnhofen environment was unfavourable for the preservation of aragonite. The Oxfordian genus *Voltzia* SCHEVILL (1950), probably a junior subjective synonym of *Trachyteuthis*, was claimed to show a phragmocone in cross section, but this fossil needs re-study.

HEWITT & WIGNALL (1988) have also shown that there is a compositional difference, the *Trachyteuthis* gladius being composed of francolite as opposed to aragonite in the *Sepia* cuttlebone, though A. SEILACHER (personal communication) regards the francolite of the Solnhofen specimens as of early diagenetic origin. HEWITT & WIGNALL therefore also reject *Trachyteuthis* as a sepiid.

The fin adds to the list of differences between *Trachyteuthis* and living Sepiidae. All the latter have lateral fins which extend the whole length of the body. However, the fin structure here described is a plesiomorphic character for Coleoidea (see below) so that it does not help in deciding the affinities of *Trachyteuthis*.

Evolutionary implications

The arrangement of fin muscles here described is present in *Vampyroteuthis*, cirrate octopods and in decapods (YOUNG & VECCHIONE, in press; R. E. YOUNG, personal communication). It therefore is a plesiomorphic character assumed to have been already present in the common ancestors of living Coleoidea. The specimen here described shows that this fin structure was present at least as early as the Upper Jurassic (Lower Tithonian, about -145 to -150 m. y.).

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