Gladius shape variation in coleoid cephalopod *Trachyteuthis* from the Upper Jurassic Nusplingen and Solnhofen Plattenkalks

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Although the fossil record of coleoid cephalopods is generally poor, the Upper Jurassic Nusplingen and Solnhofen Plattenkalks have provided numerous well-preserved coleoids. *Trachyteuthis hastiformis*, a comparatively large vampyropod coleoid, was previously known to represent the sole species of its genus in Nusplingen and Solnhofen. However, morphological comparisons based on 50 specimens from different museum collections revealed two additional species: *T. nusplingensis* sp. nov. and *T. teudopsiformis* sp. nov. Both species lack the distinct spindle-shaped elevation on the gladius median field typical for *T. hastiformis*. *T. nusplingensis* sp. nov. is clearly characterised by a smooth median field and a more or less regular granulation on the dorsal gladius surface, whereas *T. teudopsiformis* sp. nov. can be easily distinguished by the presence of a *Teudopsis*-like median keel and an extremely narrow granulation. Morphometric analyses have shown that length-width indices are ambiguous characters to differentiate between the three species. Phylogenetically, the keeled and anteriorly pointed *T. teudopsiformis* sp. nov. can be linked with the Early Jurassic genus *Teudopsis* and the Late Cretaceous genus *Glyphiteuthis*.

Key words: Cephalopoda, Coleoidea, Vampyropoda, *Trachyteuthis*, gladius, Kimmeridgian, Tithonian.

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Introduction

Trachyteuthis is an extinct genus of vampyropod coleoid with a stratigraphic occurrence from the Callovian (Middle Jurassic) to the Cenomanian (Late Cretaceous). The morphological knowledge of *Trachyteuthis* is based mainly on specimens from the Kimmeridgian Nusplingen and the Tithonian Solnhofen Plattenkalks (both Upper Jurassic). Thanks to the extraordinary preservation found in the Nusplingen and Solnhofen Plattenkalks, *Tr. hastiformis* (Rüppel, 1829) belongs to the best known fossil coleoids. Although *Tr. hastiformis* is generally considered to represent the only trachyteuthid in Nusplingen and Solnhofen, many additional species have been proposed in the past two hundred years of research; and indeed, gladii (singular gladius; the chitinous pen in the dorsal mantle) seem to vary in shape and size. If we do not want to assume each state of preservation to be a separate species, it is urgently necessary to conduct a comparative morphological study which might reveal whether one or more species existed. It was therefore the aim of the present study to examine the detailed gladius morphology of *Trachyteuthis* based on a high number of specimens.

Institutional abbreviations.—G, Museum Bérger, Eichstätt, Germany; MARKA, Markgrafenmuseum, Ansbach, Germany; MB.C, Museum für Naturkunde, Berlin, Germany; BMNH, Natural History Museum London, UK; PIMUZ, Paläontologisches Institut und Museum, Universität Zürich, Switzerland; SMF, Senkenberg Museum, Frankfurt/Main, Germany; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany; SOS, Jura Museum, Eichstätt, Germany.

Historical background

Knorr (1773: pl. 22: 2) was the first to illustrate an example of *Trachyteuthis*. He identified it as fish remains. Rüppell (1829: 9) is credited with being the first to fully describe *Sepia hastiformis* from the Solnhofen area. Rüppell (1829) and many subsequent palaeontologists considered the preserved remnants to be a fossil cuttlebone of *Sepia*. Eight years later Münster (1837) recognised eight species (*S. hastiformis*, *S. obscura*, *S. regularis*, *S. linguata*, *S. gracilis*, *S. venusta*, *S. caudata*, and *S. antiqua*) in the Solnhofen Plattenkalks but gave neither descriptions nor illustrations of these species. Count G.G. Münster was in poor health and provided his unpublished drawings and descriptions to Alcide d'Orbigny who finally published them in a series of publications (Férrussac and d'Orbigny 1835–48, d'Orbigny 1845–46). Count Münster died in 1844 before he could complete his work, and Wilhelm Dunker, the editor of the seventh volume of the "Beiträge zur

Petrefaktenkunde", finally published again an incomplete manuscript by Münster (Münster 1846). In Férrussac and d'Orbigny (1835–48), d'Orbigny revised Münster's ideas and presented *Sepia hastiformis*, *S. antiqua*, *S. caudata*, *S. lingulata*, and *S. venusta*, although he mentioned that specific distinctions are mainly due to ontogenetic differences or preservational artefacts. It is worth to note that d'Orbigny's knowledge was merely based on notes and drawings by Münster. He had never investigated original material.

In the meantime, Meyer (1846) recognised the morphological differences between fossil and living forms and erected the genus *Trachyteuthis*. He disregarded older publications and distinguished two species, *T. ensiformis* and *T. oblonga* from the Solnhofen Plattenkalks, but without giving detailed descriptions and illustrations. Almost ten years later Meyer (1855) provided an extensive description of *T. ensiformis*.

Owen (1855) was the first to report a "sepiid-like cuttlebone" in the Kimmeridge Clay of England, *Coccoteuthis latipinnis* Owen, 1855. He suggested that *Coccoteuthis*, which is identical with *Trachyteuthis*, is intermediate between Sepiidae and Loliginidae.

Wagner (1860), who re-examined Münster's specimens, discussed generic and specific names circulating in the literature and concluded that each species is identical with *S. hastiformis*. In the following years *Trachyteuthis* was variously treated as a diverse genus or as monospecific. However, during the twentieth century only *Trachyteuthis hastiformis* achieved general acceptance (Naef 1922; Jeletzky 1966; Donovan 1977; Bandel and Leich 1986; Engeser 1988; Doyle et al. 1994; Haas 2002; Donovan et al. 2003).

The systematic affiliation of *Trachyteuthis* was long under debate. Naef (1922) and Jeletzky (1966) put *Trachyteuthis* along with so-called "fossil teuthids", whereas Donovan (1977) assigned it to sepiids. Later on, Bandel and Leich (1986) introduced an alternative idea. Since *Trachyteuthis* and other "fossil teuthids" such as *Plesioteuthis* and *Leptotheuthis* never show more than eight arms, Bandel and Leich (1986) regarded them as early members of the Vampyromorpha. A discovery of two pairs of fins recently supported vampyropod affiliations of *Trachyteuthis* (Donovan et al. 2003).

Material and methods

Between 2002 and 2005 more than 20 different museum collections were visited. A total number of 50 specimens from the Upper Jurassic Plattenkalks of Nusplingen and Solnhofen labelled as *Trachyteuthis* were investigated. The studied material included the type species of *Trachyteuthis*, *Trachyteuthis ensiformis* Meyer, 1846 and the holotype of *Trachyteuthis hastiformis* (Rüppell, 1829). Apart from these "German" specimens we had also the opportunity to investigate specimens of *Trachyteuthis* from the Callovian and Kimmeridgian of England, the Oxfordian of Chile, the

Table 1. Comparative measurements of type specimens of *Trachyteuthis hastiformis, Trachyteuthis nusplingensis* and *Trachyteuthis teudopsiformis*. Note that not preserved indices are omitted. Abbreviations: A_{ia}, angle of diverging inner asymptotes; A_{ga}, angle of granulated area; GL, gladius length; $GW_{1/2gl}$, gladius width at half way along the gladius length; GW_{hz}, gladius width at the anterior limit of the hyperbolar zone; GW_{lf}, gladius width at the anterior limit of the lateral field; GW_{max}, maximum gladius width; HZL, hyperbolar zone length; LFL, lateral field length.

Measurements	*Trachyteuthis hastiformis* (Rüppell, 1829)			*Trachyteuthis nusplingensis* sp. nov.	*Trachyteuthis teudopsiformis* sp. nov.
	SMF IX1328 (holotype)	MARKA1 (original of Meyer 1846)	SOS 5762	SMNS 63596 (holotype)	G 130606 (holotype)
GL	225 + x mm	295+ x mm	325 mm	280+3 mm (interpolated)	70+x mm (incomplete)
HZL	?	?	125±2 mm	100+3 mm (interpolated)	30 mm
LFL	?	?	109±2 mm	90 mm	26 mm
GW_{hz}	?	?	87±2 mm	77 mm	25 mm
GW_{lf}	?	?	108±2 mm	97 mm	33 mm
GW_{max}	?	?	113±2 mm	109 mm	37 mm
$GW_{1/2gl}$	?	?	83±2 mm	75 mm	?
A_{ia}	?	?	40°	40°	43°
A_{ga}	\	\	\	12°	restricted to keel
HZL/GL	?	0.39–0.42	0.39–0.4	0.36	?
LFL/GL	?	?	0.34–0.35	0.32	?
$GW_{hz/GL}$	?	?	0.27–0.28	0.27	?
$GW_{lf/GL}$	?	?	0.34–0.35	0.34	?
$GW_{max/GL}$	?	?	0.35–0.37	0.39	?
$GW_{1/2gl/GL}$	?	?	0.26–0.27	0.27	?
$GW_{max/HZL}$	?	?	0.87–0.93	1.05	?
Granulation	coarse, irregular	coarse, irregular	coarse, irregular	fine, regular	narrow
Spindel-shaped elevation	present	present	present	absent	absent

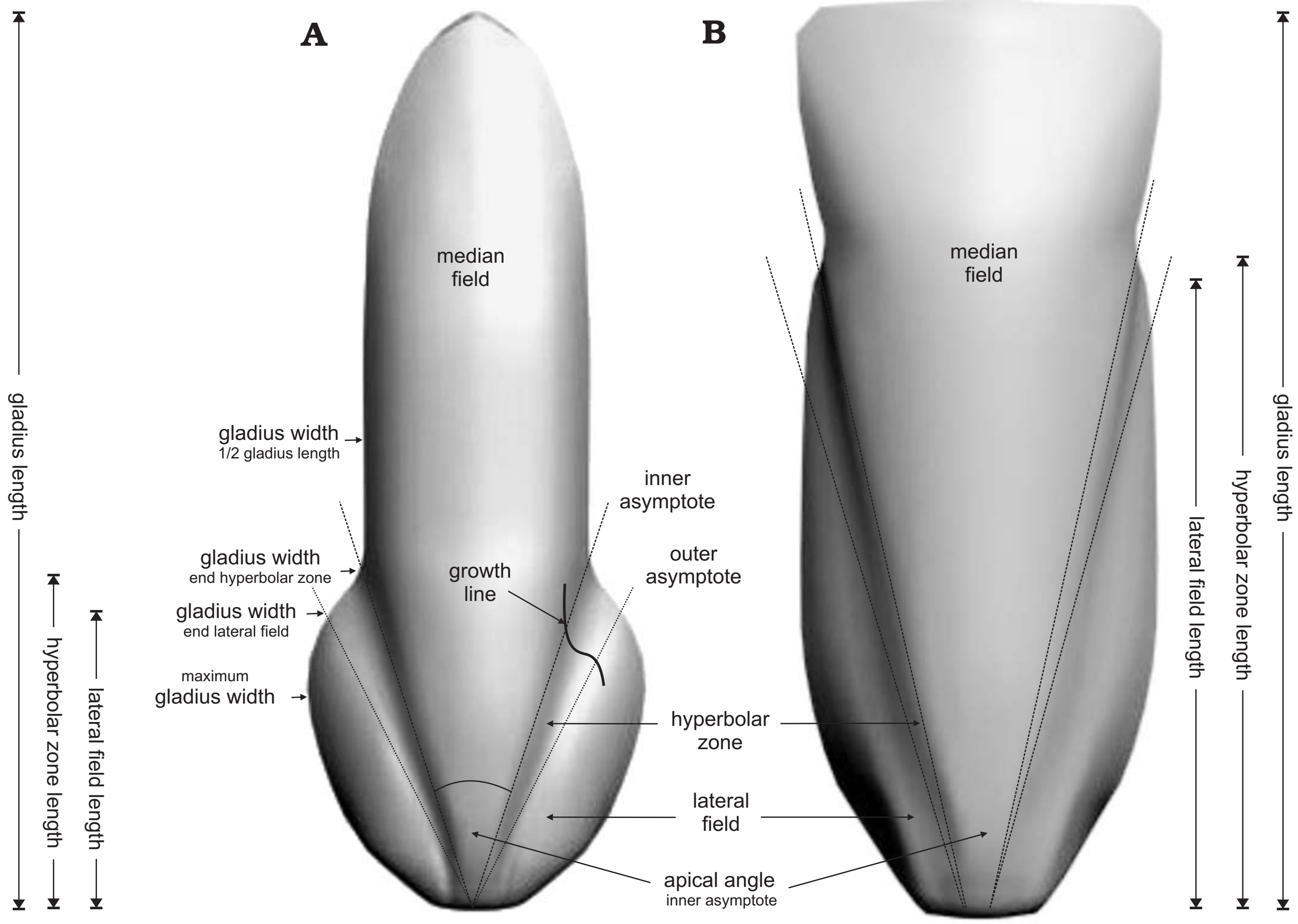


Fig. 1. Morphology, terminology and measurements of a vampyropod gladius. **A**. *Trachyteuthis*. **B**. *Loligosepia*.

Aptian of Heligoland (Northern Germany) and Australia, and the Cenomanian–Santonian of Lebanon.

General morphology, terminology, and measurements of Mesozoic gladii.—The gladius (Fig. 1) is a sturdy, but flexible chitinous structure within the dorsal mantle known to occur in the living Vampyromorpha, Oegopsida, Myopsida, and Sepiolida. The gladius is commonly regarded as a derivation of the proostracum, a dorsal extension of the body chamber of belemnoid coleoids (Naef 1922: 104; Jeletzky 1966: 8; Fuchs 2006a: 46).

Naef (1922: figs. 47, 51) and Jeletzky (1966: 32, fig. 4) discussed the homologies between proostraca and fossil gladii in detail and provided a convincing terminology to describe gladius elements. With the help of *Phragmoteuthis bisinuata* (Belemnoidea) and *Loligosepia aalensis* (Vampyropoda), Naef (1922) and Jeletzky (1966) distinguished fields with different growth lines (Fig. 1): a parabolar median field, hyperbolar fields and parabolar lateral fields ["Konusfahnen" in Naef (1922); "wings" in Jeletzky (1966)]. The comparatively narrow hyperbolar fields separate median field and lateral fields. Where growth lines pass from parabolar to hyperbolar or from hyperbolar to parabolar more or less distinct lines or ridges are diverging. These are called inner (median) and outer (lateral) asymptotes. Since inner and outer asymptotes are difficult to determine in some taxa and thus the boundary between hyperbolar and lateral fields is not sharp, we prefer to use the term hyperbolar zone. In cross-section, the hyperbolar zone is generally formed as a more or less developed furrow between the median field and the lateral fields.

Posteriorly, the fields form a conus, which most probably represents a remnant of the former phragmocone. In loligosepiid and teudopseid gladii the ventral conus length is strongly reduced (spoon-shaped), whereas in prototeuthids the narrow gladii retain a ventrally closed (funnel-shaped) unchambered conus.

A teudopseid gladius, to which the gladius of *Trachyteuthis* belongs, is characterised by a pointed or rounded anterior gladius extremity. In contrast to a loligosepiid gladius, hyperbolar zones and lateral fields are shortened. The gladius of the family Trachyteuthididae can be easily identified by the possession of sepiid-like granules (tubercles) on the dorsal surface of the gladius.

A compilation of standardised measurements are given in Table 1 and illustrated in Fig. 1.

Results

Gladius morphology of *Trachyteuthis* from the Nusplingen and Solnhofen Plattenkalks.—As a first result we ascertain that a morphometrical study in combination with a statistical analysis is highly problematic, because reliable measurements of many specimens were ambiguous owing to their fragmental states of preservation (see Table 1). In these cases, the specimens could be identified as *Trachyteuthis* solely by the presence of its typical granulation on the dorsal surface of the gladius.

In the few cases where the gladius is almost complete, significant fluctuations in length-width-indices occurred. For example, the ratio of hyperbolar zone length/gladius length varied between 0.37 and 0.42, the ratio of maximum gladius width/gladius length even between 0.22 and 0.39. The range of values was always transitional, i.e., a distinct character distribution indicating the presence of distinguishable gladius outlines does not exist. The comparatively great variance is certainly due to different positions of embedding or to different rates of compaction. As the transversal curvature of the gladius is stronger than the longitudinal curvature, especially width indices depend strongly on the rate of compaction. Another reason for erroneous measurements was an insufficient preparation of the gladius. In the light of these potential measurement errors, using small differences in gladius shape has proved to be highly problematic.

Nevertheless, among the studied specimens we have found three different modifications in particular concerning the median field (Fig. 2):

Non-planar type (Fig. 2A).—In dorsal aspect, the non-planar type exhibits a distinct spindle-shaped elevation along the longitudinal axis of the median field. The outer margins of this enigmatic bulge are depressed below the rest of the median field. Gladii in ventral aspect show, vice versa, a spindle-shaped depression accompanied by a marginal elevation. In strongly compacted specimens, this structure is flattened and difficult to discern. The granulated area on the dorsal surface follows the outline of the spindle. The granules are comparatively coarse and more or less irregularly arranged.

Planar type (Fig. 2B).—The median field of this type is constantly curved without distinct elevations or depressions. The two legs of the narrow and cone-shaped granulated area are straight and sharply delimited from the smooth outer parts of the median field. It diverges under an angle of 12°. The granules are fine and more or less regularly arranged in anteriorly directed arches. Along the medial axis the granules form a slight ridge.

Keeled type (Fig. 2C).—This type might be easily mistaken as a representative of the Early Jurassic genus *Teudopsis*, because a well-developed prominent keel similar to that of the genus *Teudopsis* is present on the dorsal median field. The granulated area diverges under an extremely narrow angle. Posteriorly, the granulated area is restricted to the pronounced keel; anteriorly, it broadens. The anterior median field is distinctly pointed.

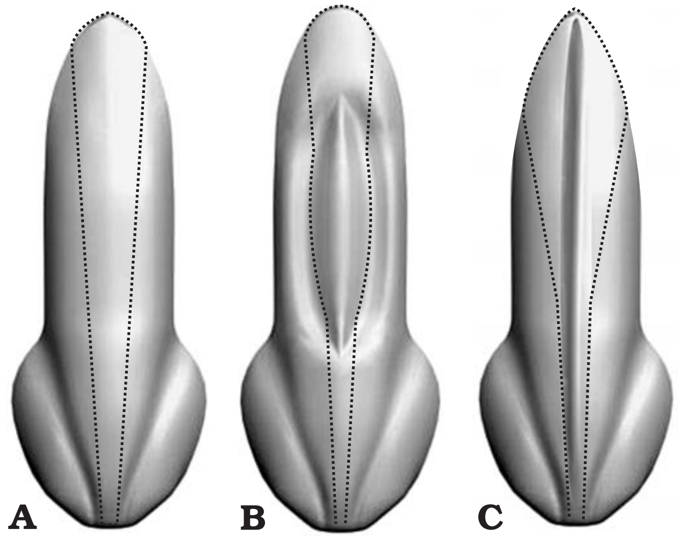


Fig. 2. Gladius shape variation in *Trachyteuthis*. **A**. Planar type. **B**. Non-planar type. **C**. Keeled type. The granulated area is marked by a pointed line.

The non-planar type is probably the most common type in the Solnhofen area. Only one specimen from Nusplingen might belong to this type. Until now the distribution of the planar type seems to be restricted to the Nusplingen Plattenkalks. The keeled type is rare (only four specimens are identified) and exclusively known from Eichstätt and Daiting (Solnhofen region, South Germany). We exclude a sexual dimorphism between the non-planar-and the keeled type from the Solnhofen region, because in this case we would expect a more balanced abundance.

Systematic palaeontology

Subclass Coleoidea Bather, 1888
Superorder Vampyropoda Boletzky, 1992
Order Octobrachia Häckel, 1866
Suborder Teudopseina Starobogatov, 1983

Emended diagnosis.—Gladius with clearly reduced and opened conus (spoon-shaped conus). Lateral fields and hyperbolar zones less than the half gladius length. Hyperbolar zones between lateral and median field as well-developed broad furrows. Anterior median field more or less pointed.

Families included.—Trachyteuthididae Naef, 1921, Palaeoloiginidae Naef, 1921, Teudopseidae Van Regteren Altena, 1949, and Muensterellidae Roger, 1952.

Remarks.—As mentioned above the phylogenetic and systematic position of the Teudopseina is controversial. Owing to remarkable similarities between a trachyteuthid gladius and sepiid cuttlebones, particularly neontologists doubt in vampyropod affinities. However, fossil evidences which could support sepiid affiliations (i.e., calcified phragmocone, ten arms) are unknown. Instead, the characters eight arms, two pairs of fins, interbrachial web, cirri, uniserial suckers and *Octopus*-like lower beak strongly support relationship with vampyropods (Bandel and Leich 1986; Donovan et al. 2003; Fuchs et al. 2003; Klug et al. 2004; Fuchs 2006a). One may argue that some of these characters might be interpreted as diagenetical artefacts, others as plesiomorphic within the Coleoidea and/or also as decabrachian features, but the combination is striking and convinced us to attribute Teudopseina to the vampyropod branch. Finally, both Haas (2002) and Bizikov (2004) claimed that the shell vestiges of Recent Octopoda and Cirroctopoda developed from a teudopseid gladius by reducing the median field. Following that assumption, Teudopseina would represent a stem-group of the Octobrachia.

Family Trachyteuthididae Naef, 1921

Type genus: *Trachyteuthis* Meyer, 1846; type species *Trachyteuthis ensiformis* Meyer, 1846; Tithonian (Late Jurassic), Solnhofen region, Southern Germany.

Emended diagnosis.—Teudopseid vampyropods with granules (tubercles) on the dorsal surface of the gladius.

Genera included.—*Trachyteuthis* Meyer, 1846; *Glyphiteuthis* Reuss, 1854; *Actinosepia* Whiteaves, 1897

Stratigraphic and geographic range.—Callovian (Middle Jurassic)–Maastrichtian (Late Cretaceous) of Europe, Central Russia, Lebanon, Cuba, Chile, Antarctica, Australia and North America.

Genus *Trachyteuthis* Meyer, 1846

(= subjective senior synonym of *Coccoteuthis* Owen, 1855; *Voltzia* Schevill, 1950)

Type species: *Trachyteuthis ensiformis* Meyer, 1846 (= junior subjective synonym of *Sepia hastiformis* Rüppell, 1829), Tithonian (Late Jurassic), Solnhofen region, Southern Germany; subsequently designated by Doyle et al. (1994: 11).

Emended diagnosis.—Gladius with hyperbolar zone length/gladius length ratio of 0.40–0.45. Anterior gladius end more or less arcuated.

Species included.—*Trachyteuthis hastiformis* (Rüppell, 1829); *Tr. latipinnis* (Owen, 1855); *Tr. zhuravlevi* Hecker and Hecker, 1955; *Tr. palmeri* (Schevill, 1950); *Tr. nusplingensis* sp. nov.; *Tr. teudopsiformis* sp. nov.

Stratigraphic and geographic range.—As for the family.

Remarks.—Crick (1896) proposed that *Trachyteuthis* is a junior subjective synonym of *Coccoteuthis* Owen, 1855 because a full description of *Trachyteuthis* by Meyer (1855) was slightly after the erection of *Coccoteuthis* by Owen (1855). Indeed, Meyer (1846: 598) introduced the genus *Trachyteuthis* without detailed descriptions or illustrations, but the bibliographic reference to pl. 9: 3 in Münster (1846) is valid according to ICZN (art. 12). The majority of workers therefore considered *Coccoteuthis* to be a junior subjective synonym of *Trachyteuthis* (Engeser 1988; Doyle 1991; Doyle et al. 1994; Donovan 1995; Riegraf et al. 1998; Donovan et al. 2003). *Voltzia* Schevill, 1950 is a junior subjective synonym, too.

Meyer (1846: 598) established two species of *Trachyteuthis*: *Tr. oblonga* and *Tr. ensiformis. Tr. oblonga* has neither a description nor a bibliographic reference and is therefore a nomen nudum (Engeser 1988). *Tr. ensiformis* was indicated in form of a bibliographic reference (Meyer 1846: 598). *Tr. ensiformis* is therefore available according to ICZN (art. 12). Meyer (1846) did not originally include *Sepia hastiformis* Rüppell, 1829 in his new genus *Trachyteuthis*. Many subsequent workers overlooked this fact (Bülow-Trummer 1920; Engeser 1988) and regarded *Sepia hastiformis* Rüppell, 1829 as the type species of *Trachyteuthis*. But Doyle et al. (1994) correctly re-established *T. ensiformis* as the type species of *Trachyteuthis* according to art. 67.2 of ICZN (2000).

Trachyteuthis hastiformis (Rüppell, 1829)

Figs. 3, 4.

1825 *Sepia prisca* sp. nov.; König 1825: pl. 27: 201 (nomen nudum).
1829 *Sepia hastiformis* sp. nov.; Rüppell 1829: 9–10, pl. 3: 2.
1837 *Sepia obscura* sp. nov.; Münster 1837: 252 (nomen nudum).
1837 *Sepia regularis* sp. nov.; Münster 1837: 252 (nomen nudum).
1837 *Sepia linguata* sp. nov.; Münster 1837: 252 (nomen nudum).
1837 *Sepia venusta* sp. nov.; Münster 1837: 252 (nomen nudum).
1837 *Sepia antiqua*; Münster 1837: 252 (nomen nudum).
1835–48 *Sepia hastiformis*; Férrussac and d'Orbigny 1835–48: pl. 16: 1, 2.
1835–48 *Sepia antiqua* Münster; Férrussac and d'Orbigny 1835–48: pl. 14: 1, 2.
1835–48 *Sepia caudata* Münster; Férrussac and d'Orbigny 1835–48: pl. 15: 1, 2.
1835–48 *Sepia linguata* Münster; Férrussac and d'Orbigny 1835–48: pl. 14: 3, pl. 15: 4, 5, pl. 16: 3.
1846 "without appellation"; Münster 1846: pl. 9: 3.
1846 *Trachyteuthis ensiformis*; Meyer 1846: 598.
1846 *Trachyteuthis oblonga* sp. nov.; Meyer 1846: 598 (nomen nudum).
1855 *Trachyteuthis ensiformis* sp. nov.; Meyer 1846: 106–109, pl. 19: 1.
1922 *Trachyteuthis hastiformis* Rüppell, 1829; Naef 1922: 137, figs. 51, 52.
1977 *Trachyteuthis hastiformis*; Rietschel 1977: fig. 6.
1986 *Trachyteuthis hastiformis* Rüppell, 1829; Bandel and Leich 1986: 140, figs. 14, 15.
1988 *Trachyteuthis hastiformis* Rüppell, 1829; Engeser 1988: 59.
1995 *Trachyteuthis sp.*; Donovan 1995: 2, figs. 1–4.
2003 *Trachyteuthis hastata* Rüppell, 1829; Donovan et al. 2003: 93, fig. 1.
2006 *Trachyteuthis hastiformis*; Fuchs 2006a: 52, text-fig. 3.6-4, pl. 14: A–C.

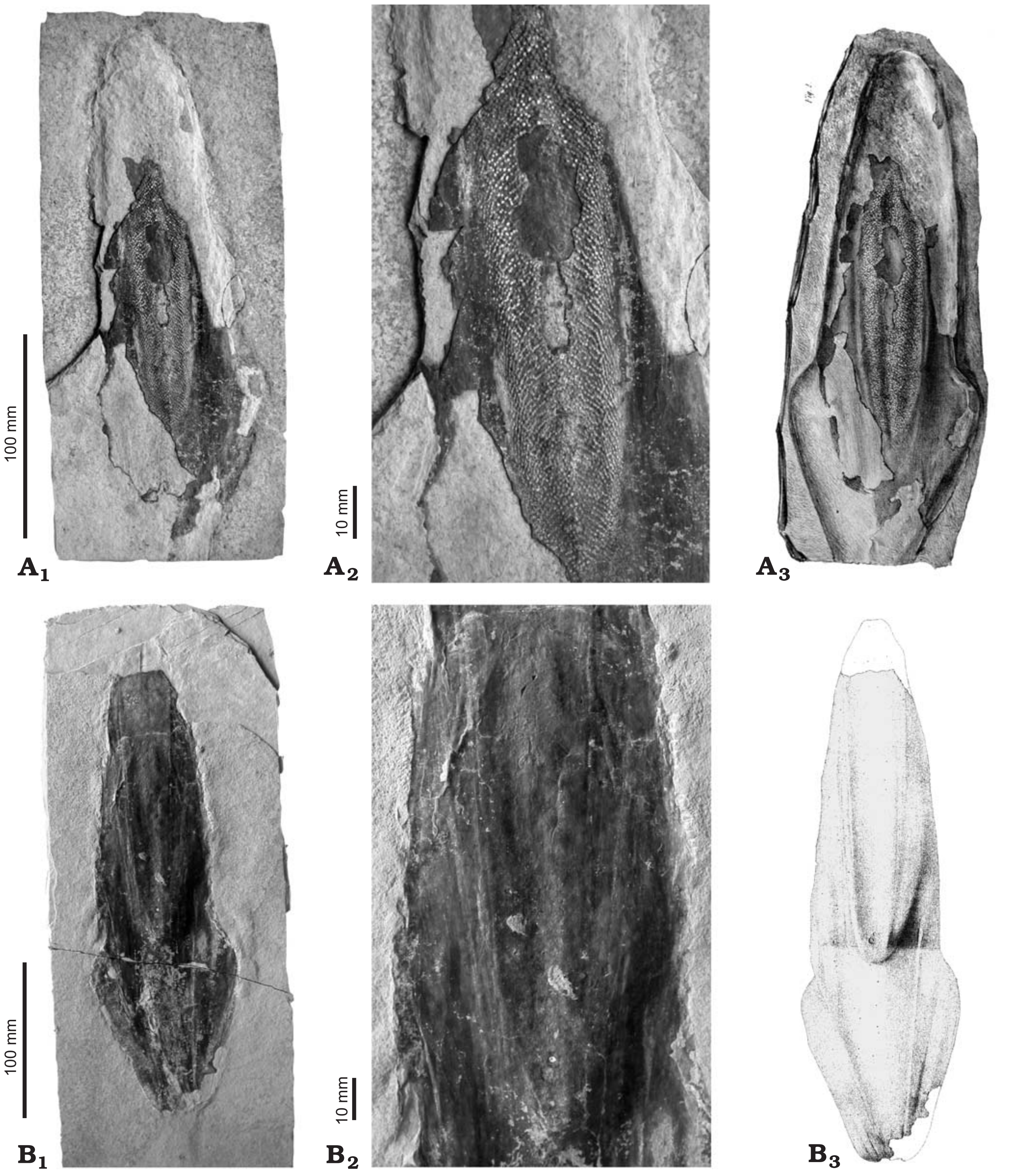
Holotype: SMF IX1328, original of Rüppell (1829: 9–10, pl. 3: 2).

Type locality: Mühlheim (Solnhofen area, Southern Germany).

Type horizon: Solnhofen Plattenkalks, Lower Tithonian, Solnhofen Formation (Malm zeta 2b), *Hybonoticeras hybonotum* Zone.

Diagnosis.—Gladius median field with a spindle-shape elevation. Dorsal granulation coarse and irregular.

Nomenclatural remarks.—As *Sepia prisca* König, 1825 (pl. 27: 201) remained unpublished, *Sepia hastiformis* Rüppell, 1829 has priority. *Sepia antiqua* Férrussac and d'Orbigny, 1835–48, *Sepia caudata* Férrussac and d'Orbigny, 1835–48 and *Sepia linguata* Férrussac and d'Orbigny 1835–48 are considered to be junior subjective synonyms of *Sepia hastiformis* Rüppell, 1829. After re-investigation of the originals of both Rüppell (1829) and Meyer (1855), we ascertain that



A₁ **A₂** **A₃** **B₁** **B₂** **B₃**

Fig. 3. Gladius of vampyropod coleoid *Trachyteuthis hastiformis* (Rüppell, 1829). **A**. Holotype (SMF IX1328), Lower Tithonian (*Hybonoticeras hybonotum* Zone), Mühlheim. A_1, lower slab with gladius in dorsal aspect; A_2, close-up of A_1 showing the granulated area within the spindle-shaped elevation, which is flattened but easily visible in outlines; A_3, original drawing of Rüppell (1829: pl. 3: 3). **B**. Specimen MARKM 1 (original of Meyer (1855: pl. 19: 1), Lower Tithonian (*Hybonoticeras hybonotum* Zone), Solnhofen area. B_1, gladius in ventral aspect; B_2, close-up of B_1 showing the spindle-shape structure; B_3, original drawing of Meyer (1855: pl. 19: 1).

Trachyteuthis ensiformis Meyer, 1846 is identical with *Sepia hastiformis* Rüppell, 1829. *Trachyteuthis ensiformis* Meyer, 1846 is therefore a junior subjective synonym of *Sepia hastiformis* Rüppell, 1829.

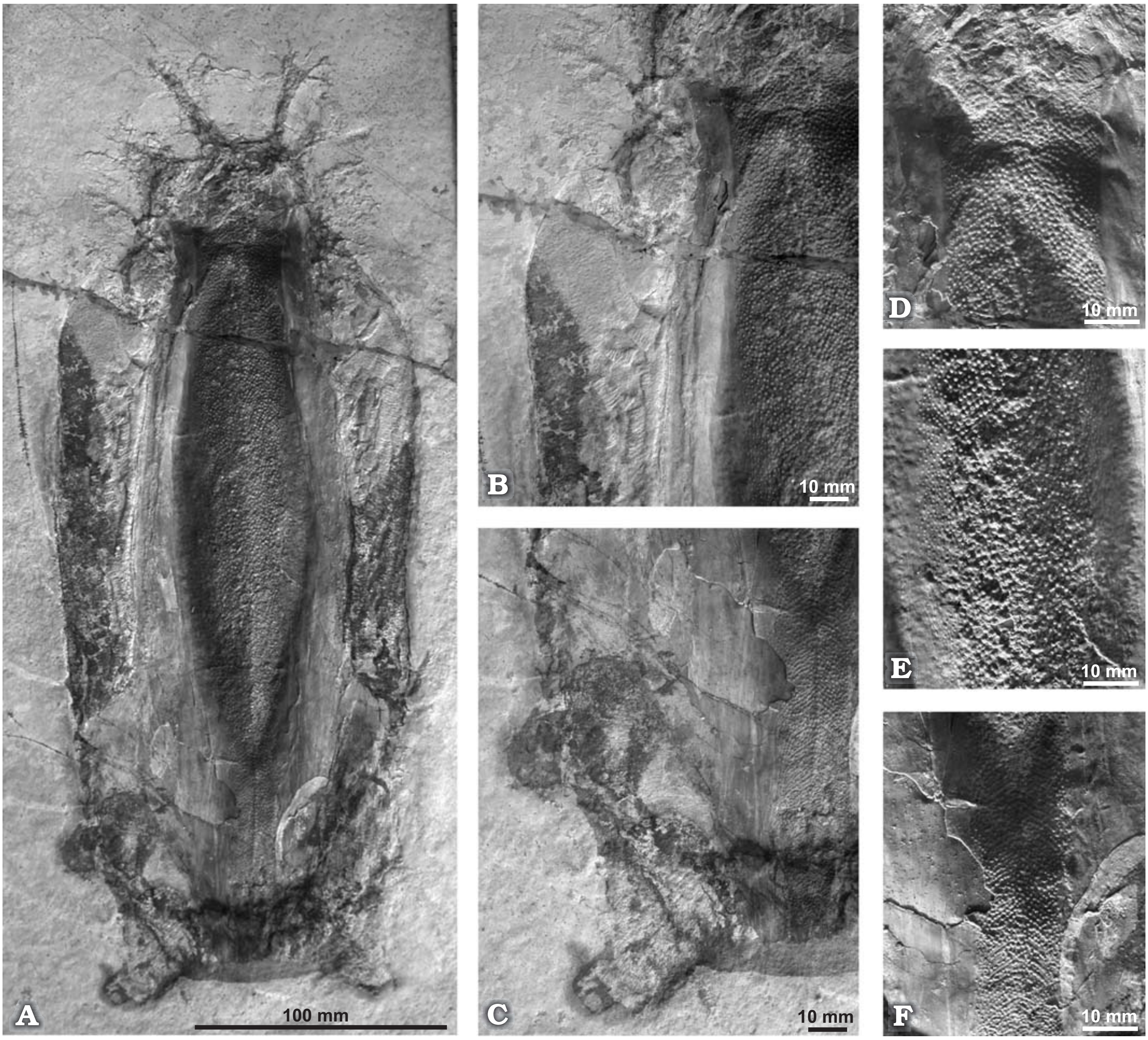


Fig. 4. Gladius of vampyropod coleoid *Trachyteuthis hastiformis* (Rüppell, 1829). Specimen SOS 5762, Lower Tithonian (*Hybonoticeras hybonotum* Zone), Sappenfeld (Solnhofen area). **A**. Dorsal view. **B**. Close up of A showing the anterior mantle margin. Note that the gladius protrudes from the latter. **C**. Close-up of A showing position and shape of the paired fins. **D**. Close-up of A showing the granules at the anterior third of the gladius. **E**. Close-up of A showing the granules at the middle third of the gladius. **F**. Close-up of A showing the granules at the posterior third of the gladius.

Re-description of the holotype.—The original of Rüppell (1829: pl. 3: 2) includes part and counterpart (Fig. 3A). The figured gladius represents the lower slab because the outline of the fossil is elevated above the bedding plane of the slab ("Sockelerhaltung", see Seilacher et al. 1976). Shell material is preserved partly on the lower and partly on the upper slab. The upper slab exhibits the rounded anterior gladius end and parts of the posterior median field, whereas the lower slab exposes the middle portion of the median field and the outline of the anterior extremity (Fig. $3A_1$). The gladius has a preserved length of 225 mm (Table 1). Neither lateral fields nor hyperbolar zones are visible. It seems that at least the left lateral field and hyperbolar zone are preserved on the lower slab but are still covered with sediment.

The lower slab displays the dorsal, the upper the ventral gladius surface. Where gladius material is missing on the upper slab imprints of the dorsal surface appear. Rüppell (1829: 10) described a "convex elevation". Indeed, a slight spindle-shaped elevation is recognisable on both slabs (Fig. $3A_2$). In dorsal view, this structure seems to be raised above the gladius surface, whereas the marginal parts of the "spindle" are depressed below the gladius surface. The elevation has a longitudinal ridge, which corresponds to the median line of the gladius.

As Rüppell (1829: 19) correctly stated, the granules are arranged in anteriorly directed parabolic lines (Fig. $3A_2$). But the granulation becomes more and more irregular at the anterior gladius half. From posterior to anterior, the fine granulation also becomes coarser (except the most anterior gladius end). Granules are finest at their outer margin and coarsest in the median line. The granulated area has its maximum width within the spindle-shaped area.

Both slabs clearly demonstrate that the gladius was laminated. Especially the lower slab shows that only the uppermost (dorsal) layer bears the granulation. Where this layer is exfoliated growth lines become visible.

Re-description of the specimen of Meyer (1855: 106–109, pl. 19: 1).—The gladius of Meyer's specimen (MARKA 1) exposed in ventral aspect has a preserved length of 295 mm (Table 1, Fig. 3B). Only 20–25 mm of the most anterior end is not preserved. Imprints of the dorsal tubercles are visible where gladius material is missing. Granules are irregularly arranged.

The outer margins of the gladius are imperfectly dissected. Length and width indices are therefore doubtful. However, as Meyer (1846: 107) correctly stated, the ratio of hyperbolar zone length to total gladius length is between 0.39 and 0.42.

Growth increments are not visible. One can see several diverging lines in the posterior portion, but inner and outer asymptotes are difficult to determine.

A spindle-shaped elevation, which is not mentioned by Meyer (1846), is present in the middle portion of the median field (Fig. $3B_2$). This structure, 70–80 mm in length and 20–30 mm in width, possesses a central depression along the median line. The posterior end of the spindle is more pronounced than the anterior. It commences approximately at the anterior end of the lateral field.

Further specimens of *Tr. hastiformis* with a distinct spindle-shaped elevation on the median field were previously figured in Rietschel (1977: fig. 6), Bandel and Leich (1986: fig. 15), Donovan (1995: fig. 1), Fuchs (2006a: fig. 3.6-4, pl. 14: A–C). Férrussac and d'Orbigny (1835–48) probably observed the same structure, because a spindle-shaped depression is clearly visible in their drawing of *Sepia antiqua* (pl. 14: 2).

Wagner (1860: 755) was apparently the first who reported this peculiar structure. He wrote on page 755 (translated from German): "From time to time a longitudinal bulge arises on the granulated surface representing a longitudinal furrow on the ventral side."

Description of a three-dimensionally preserved specimen of Tr. hastiformis.—A previously undescribed specimen (SOS 5762) from Sappenfeld (Solnhofen region) exhibits a complete gladius, which is 325 mm in total length and almost unflattened (Table 1, Fig. 4A). As mantle musculature covers the outermost margins of the gladius, length-width indices cannot be exactly determined. One can easily recognise that the spindle-shaped elevation is surrounded by a depression. The bulge is approximately 195 mm in total length (62% of the total gladius length). Its posterior end starts about 80 mm away from the posterior gladius end and shortly before lateral fields and hyperbolar zones expire. In cross-section the bulge is arquated (roof-shaped) with an indistinct ridge along the median line. The maximum width of the spindle measured half way along the total spindle length is 50–60 mm.

The alteration of the granules from posterior to anterior extremities is distinct (Fig. 4D–F). Posteriorly, the granulation is fine and regularly arranged in anteriorly directed parabolic lines (Fig. 4F). In this part, the granulated area linearly diverges with a very acute angle. When entering the spindle, the granulated area suddenly spreads out and follows the spindle (Fig. 4E). Simultaneously, granules become coarser and irregularly arranged. Granules located marginally within the depression are very small compared to those on the top of the bulge. Most anteriorly, where the spindle does not exist, the granulated area seems to diverge again linearly (Fig. 4D).

Apart from the gladius, the present specimen yields extraordinarily preserved details of soft tissues. The solid muscular mantle of this specimen is conserved in such a unique manner that the body outline of the animal and even the position of the gladius within the mantle can be easily reconstructed. The most characteristic feature is that the anterior gladius end distinctly protrudes from the anterior mantle margin (Fig. 4B). To a lesser extent this is also the case in Recent *Vampyroteuthis*. According to Bizikov (2004: 10, fig. 2), the circular mantle muscles in *Vampyroteuthis* attach to the ventral site of the gladius, except for the foremost rim.

In general, the body outline of *Trachyteuthis hastiformis* was cylindrical (bullet-shaped). The body is constantly 140 mm wide and posteriorly rounded. It seems that the lateral mantle is longer than the dorsal.

Posteriorly, one can see two pairs of lobate fins (Fig. 4C). This is well in accordance with previous observations made by Donovan (2002: fig. 1) and Donovan et al. (2003: fig. 2), who first reported the presence of two pairs of fins in *Trachyteuthis hastiformis.* Each of them is about 45–50 mm long. At their base the fins are about 20–25 mm in width. Striations of the muscle bundles are oriented parallel to the margins of the fin. Branching of muscle bundles as described by Donovan (2002) and Donovan et al. (2003) are not observed. Their position seems to be identical with those described in Donovan (2002) and Donovan et al. (2003). Both pairs were attached to the dorsal gladius surface (probably indirectly to the shell sac as in Recent vampyropods, see Bizikov 2004). The posterior pair was anchored to the rearmost part of the lateral field, whereas the anterior pair was attached to the middle part of the lateral field. Most probably the hyperbolar zone also served as an insertion site as in *Vampyroteuthis* (Bizikov 2004: fig. 51).

Stratigraphic and geographic range.—Known with certainty from the Lower Tithonian (Malm zeta 2–3) of the Solnhofen Plattenkalks (Southern Germany). *Tr. hastiformis* probably also occurred in the Kimmeridgian (Malm zeta 1) of Nusplingen (Southern Germany).

Trachyteuthis. nusplingensis sp. nov.

Fig. 5.

1846 "without appellation"; Münster 1846: pl. 9, 2.

2005 *Trachyteuthis hastiformis* Rüppell 1829; Klug et al. 2005: 179, figs. 6A, G, 7B, D, 13A.

2006 *Trachyteuthis* ?*spec.*; Fuchs 2006a: 52, pl. 14: D.

Derivation of the name: After the village of Nusplingen (Southern Germany).

Holotype: SMNS 63596; completely preserved gladius of an adult individual.

Paratypes: SMNS 63596, 65345, 63254;completely preserved adult gladii.

Type locality: Nusplingen quarry, South of Balingen (Germany).

Type horizon: Nusplingen Plattenkalks, Upper Kimmeridgian, (Malm zeta 1), *Hybonoticeras beckeri* Zone.

Diagnosis.—Dorsal gladius surface flat. Granulation regular and fine.

Morphologic differences between *Tr. nusplingensis* and *Tr. hastiformis* are small and thus difficult to determine in poorly preserved specimens, but in well preserved specimens they are distinct. *Tr. nusplingensis* lacks the spindle-shaped elevation on the median field described in *Tr. hastiformis*. In comparison to the coarse and irregular granulation in *Tr.*

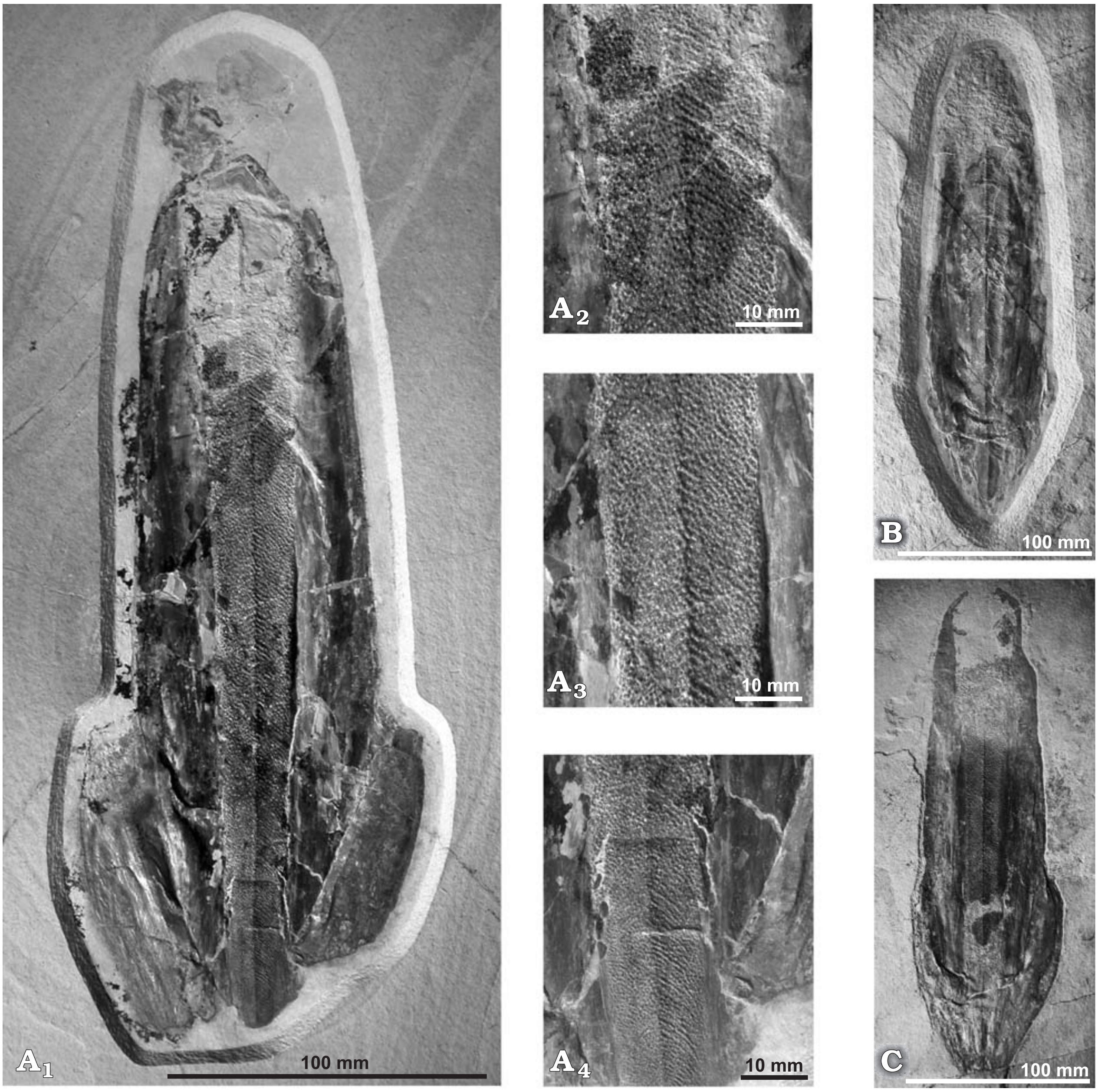


Fig. 5. Gladius of vampyropod coleoid *Trachyteuthis nusplingensis* sp. nov. **A**. Holotype (SMNS 63596), Upper Kimmeridgian (*Hybonoticeras beckeri* Zone), Nusplingen. A_1, gladius seen in dorsal aspect; A_2, close-up of A_1 showing the granules at the anterior third of the gladius; A_3, close-up of A_1 showing the granules at the middle third of the gladius; A_4, close-up of A_1 showing the granules at the posterior third of the gladius. **B**. Specimen SMNS 63259, Upper Kimmeridgian (*Hybonoticeras beckeri* Zone), Nusplingen, gladius seen in dorsal aspect. **C**. Specimen SMNS 65345, Upper Kimmeridgian (*Hybonoticeras beckeri* Zone), Nusplingen, gladius seen in dorsal aspect.

hastiformis, granulation in *Tr. nusplingensis* is fine and regularly arranged throughout the whole gladius length (Table 1).

Description of the holotype.—Specimen SMNS 63596 consists of an almost complete and nearly uncompacted gladius in dorsal view (Fig. 5A). Only a few millimetres of the rearmost part are missing (Table 1). The overall shape of the gladius seems to be identical to *T. hastiformis.* Since the gladius is only slightly compacted these measurements are valuable proxies reconstructing real gladius proportions, and the dorsal relief can easily be investigated. The hyperbolar zone forms a distinct furrow between the lateral fields and median field. The boundary between the hyperbolar zone and the median field is sharp, because the curvature of the median field is stronger than the lateral fields. Inner asymptotes are therefore well definable. Outer asymptotes indicating the transition from lateral fields into hyperbolar zones are discernable by weak growth lines.

After 50% of the total gladius length, the curvature of the median field decreases. Anteriorly, the median field is almost flat.

The granulated area diverges constantly at a narrow angle of 12°. Granules are arranged in anteriorly directed parabolic lines (Fig. $5A_2$–A_4). Their size increases from posterior to anterior. Most anteriorly preserved mantle musculature covers the granulated area. Outer tubercles have the same size as inner ones. Laterally and medially, they form an indistinct ridge throughout the gladius length.

Stratigraphic and geographic range.—Known only from the type locality.

Trachyteuthis teudopsiformis sp. nov.

Fig. 6.

2006 *Trachyteuthis (Teudopsis) spec.*; Fuchs 2006a: 52, pl. 14: E.

Derivation of the name: The species name refers to the close similarity to the Toarcian vampyropod genus *Teudopsis* Eudes-Deslongchamps, 1835.

Holotype: G 1306061; nearly complete gladius of an adolescent individual.

Paratype: MB.C 1002.4 (part) and PIMUZ 17826 (counterpart); fragmentary gladius of an adult individual.

Type locality: quarry Bérger, Blumenberg near Eichstätt (Southern Germany).

Type horizon: Solnhofen Plattenkalks, Lower Tithonian, Malm zeta 2–3, *Hybonoticeras hybonotum* Zone.

Material—G 1306061, MB.C 1002.4, PIMUZ 17826.

Diagnosis.—Gladius median field with a pronounced median keel. Granulation narrow, posteriorly restricted to the keel. Anterior gladius end sharply pointed.

Trachyteuthis teudopsiformis can be easily distinguished from other species of this genus by the possession of a *Teudopsis*-like prominent median keel, a comparatively narrow granulated area and a distinctly pointed anterior end (Table 1). Adult *Tr. teudopsiformis* has possibly longer hyperbolar zones compared to *Tr. hastiformis* or *Tr. nusplingensis* (juvenile representatives are extremely rare). The extraordinary clarity of growth lines might be a diagenetical artefact. If not, it is a further characteristical feature of *Tr. teudopsiformis*, because generally growth increments in *Tr. hastiformis* and *Tr. nusplingensis* are weakly developed.

Description of the holotype.—The gladius, which is seen in dorsal aspect, has a preserved length of 70 mm (Table 1, Fig. 6A). It is in an excellent condition except for the missing anterior part.

The most characteristic feature is the existence of a pronounced median keel, which increases in thickness from posterior to anterior. Most anteriorly it seems that the keel is flattened. A preservational interruption in the posterior third of the keel shows that the keel is solid (Fig. $6A_3$).

Another obvious character is the posterior granulation, which is restricted to the keel (Fig. $6A_3$). In the anterior half, the granulated area suddenly broadens (Fig. $6A_2$). Granules are coarse but regularly arranged in arcuated rows indicating a distinctly pointed anterior rim. As the total gladius length is uncertain and both hyberbolar zones and lateral fields are strongly flattened, determination of ratios is problematic. Although this specimen represents just an adolescent individual, we chose it for holotype, because gladius characters are best shown. Soft tissues are not preserved.

Description of the paratype.—The paratype (Fig. 6B, C) consists of part and counterpart (MB.C 1002.4 + PIMUZ 17826). Owing to the typical "Sockelerhaltung" in the Solnhofen Plattenkalks, MB.C 1002.4, the better preserved specimen (Fig. $6B_1$), can be determined as the upper slab. Hence, the gladius was embedded ventrally with the dorsal side above. As upper (outer, dorsal) gladius laminae adhere to MB.C 1002.4 and lower (inner, ventral) laminae to PIMUZ 17826 neither the dorsal gladius surface nor the ventral gladius surface are visible. However, in a few small places, where gladius material is missing, several imprints of granules are present in MB.C 1002.4 (Fig. $6B_2$). The gladius was partially compacted. In spite of this, both slabs display a *Teudopsis*-like median keel constantly increasing in width from posterior to anterior.

In contrast to both lateral fields and the left (anatomic right, due to the ventral view) hyperbolar zone, which are not preserved, preservation of the right (anatomic left) hyperbolar zone enables at least length measurements.

As lateral fields are missing, the maximum gladius width and the overall shape of the posterior gladius end remains uncertain, but a more or less obtuse end can be presumed. Although outer margins of the anterior top are fragmentary, dorsal imprints indicate a distinctly pointed anterior end. Extraordinarily preserved growth increments clearly confirm this assumption and even enable the gladius outline of earlier ontogenetic stages to be determined. Significant differences between ontogenetic younger and older stages can be found. At a gladius length of 70 mm the hyperbolar zone accounts for approximately 33% of the total gladius length. In ontogenetic older stages, e.g., at a gladius length of 180 mm, the same ratio increases up to 45%. This allometric mode of growth found in *Trachyteuthis teudopsiformis* is surprising

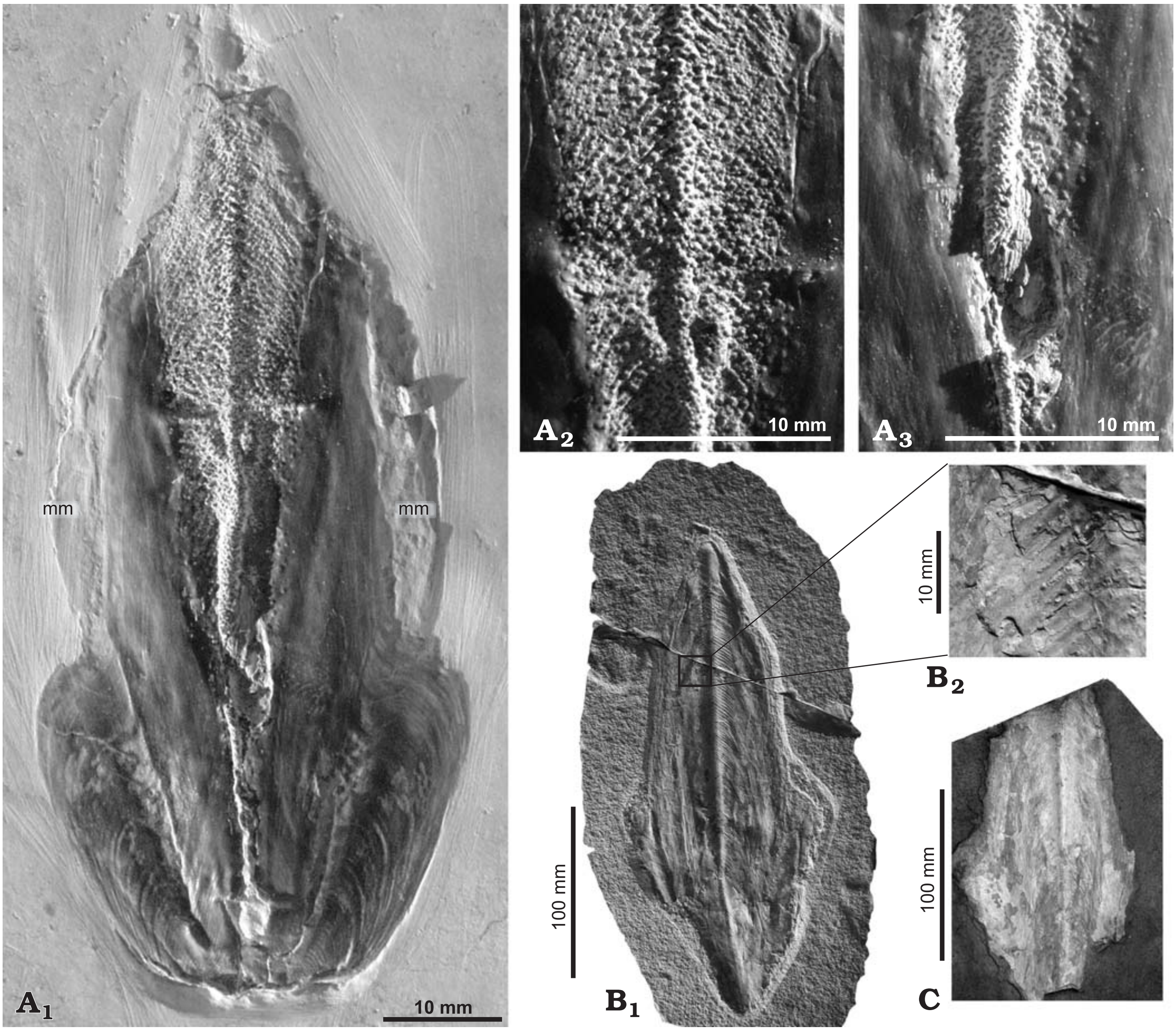


Fig. 6. Gladius of vampyropod coleoid *Trachyteuthis teudopsiformis* sp. nov. **A**. Holotype (G 1306061), Lower Tithonian (*Hybonoticeras hybonotum* Zone), Blumenberg. A_1, gladius seen in dorsal aspect; mm, mantle musculature; A_2, close-up of A_1 showing the granules at the anterior half of the gladius; A_3, close-up of A_1 showing the granules at the posterior half of the gladius. **B**. Paratype (MB.C.1002.4), Lower Tithonian (*Hybonoticeras hybonotum* Zone), Daiting. B_1, gladius seen in ventral aspect; B_2, close-up of B_1 showing imprints of dorsal granules. **C**. Counterpart of the paratype (PIMUZ17826), gladius seen in dorsal aspect.

because the gladii of plesioteuthids from Solnhofen grow isometrically (own observations).

As in the holotype, soft tissues are not preserved in the paratype.

Other possible examples of Trachyteuthis teudopsiformis.—At least one poorly preserved specimen from the Solnhofen region and previously studied by Naef (1922: fig. 52) also offer a distinct median keel in combination with anteriorly pointed growth lines. Naef (1922) reconstructed the fins by means of two different specimens; among them the specimen of Crick (1896: pl. 14). We re-investigated the other specimen (SOS 1425) and found weak evidence of a median keel (Fig. 7A, B). We are aware that identification of this specimen as *Tr. teudopsiformis* is only tentative due to a poorly preserved gladius.

Stratigraphic and geographic range.—Known only from the type locality.

Gladius morphology of *Trachyteuthis* from other localities

The oldest record of *Trachyteuthis* is known from the Callovian of Christian Malford, Wiltshire, England (Page 1991). The single specimen is badly preserved and provides little in-

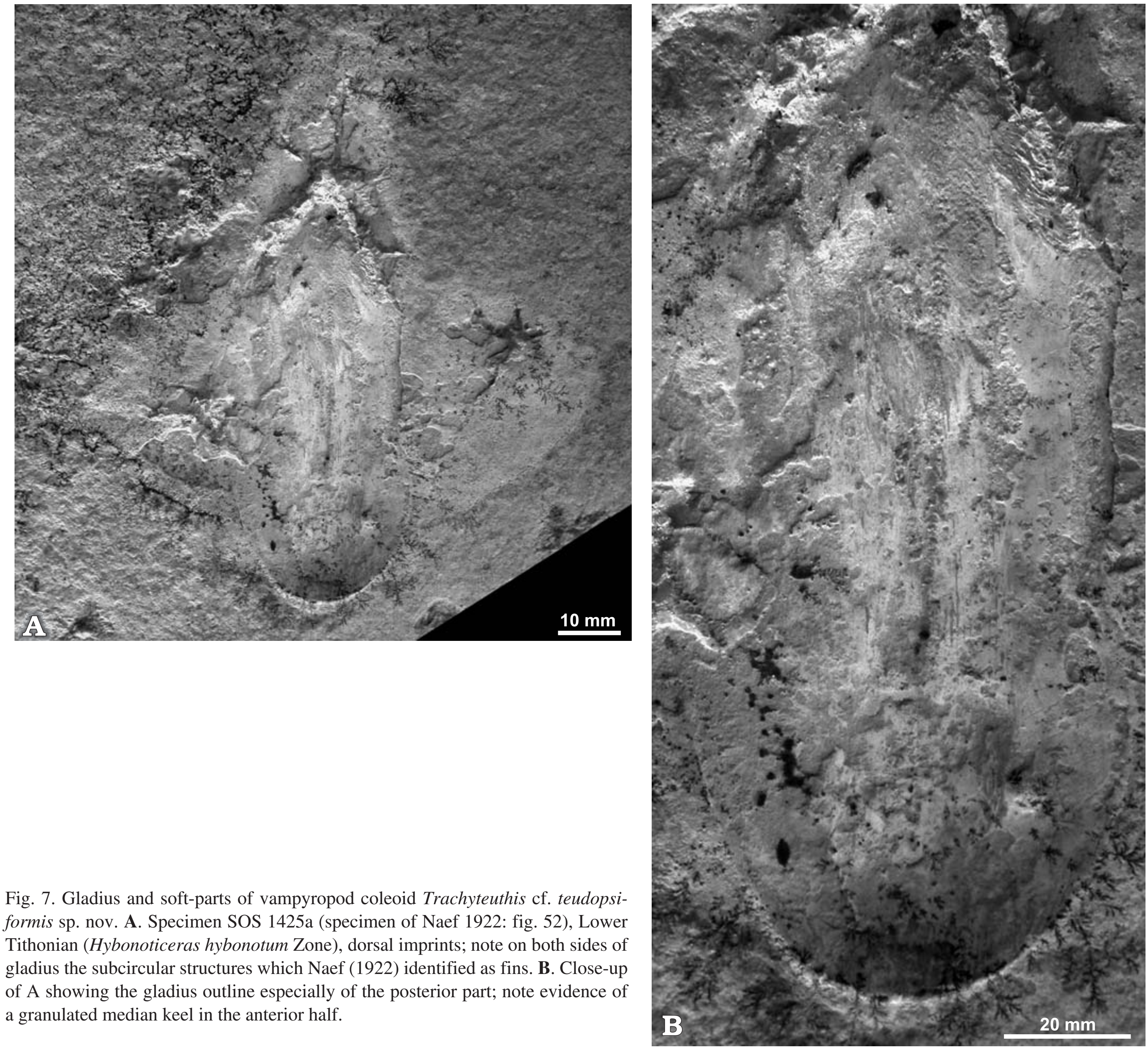


Fig. 7. Gladius and soft-parts of vampyropod coleoid *Trachyteuthis* cf. *teudopsiformis* sp. nov. **A**. Specimen SOS 1425a (specimen of Naef 1922: fig. 52), Lower Tithonian (*Hybonoticeras hybonotum* Zone), dorsal imprints; note on both sides of gladius the subcircular structures which Naef (1922) identified as fins. **B**. Close-up of A showing the gladius outline especially of the posterior part; note evidence of a granulated median keel in the anterior half.

formation. A comparison with specimens from Nusplingen and Solnhofen is therefore inappropriate.

Similar problems exist with *Trachyteutis* (*Voltzia*) *palmeri* (Schevill, 1950) from the Oxfordian of Cuba. Judged by the photographs given in Schevill (1950: pl. 23), the 3-dimensionally preserved gladius belongs to the planar type, but without re-investigation this evaluation is only tentative.

An uncompacted and complete gladius of *Trachyteuthis* from the Oxfordian of Chile shows also similarities to the planar *Trachyteuthis nusplingensis*, but is distinctly broader (Schulze 1989; Fuchs 2006a).

The few specimens of *Trachyteuthis* (*Coccoteuthis*) *latipinnis* (Owen, 1855) from the English Kimmeridge Clay of Speeton are probably identical with the non-planar *Trachyteuthis hastiformis*. The original of Owen (1855: pl. 7) displays rudiments of a spindle-shape elevation on the median field and coarse irregularly arranged granules are clearly visible.

In Tithonian times, *Trachyteuthis* is also known from the Russian Platform and from Antarctica. The Antarctic representative (*Trachyteuthis* cf. *hastiformis*) is represented by a single fragment of the median field (Doyle 1991: fig. 2). Doyle (1991: 172) described "…pustules arranged in arcuate arrays". This description rather indicates affiliations to planar *Trachyteuthis nusplingensis*. Knowledge about the Russian *Trachyteuthis zhuravlevi* is very poor (Hecker and Hecker 1955). At least the specimen figured on pl. I: 3 bears some resemblance to the planar type. However, in order to give a reliable assignment re-investigation is crucial.

Cretaceous records of *Trachyteuthis* are known from the Aptian of Heligoland, Germany (Engeser and Reitner 1985),

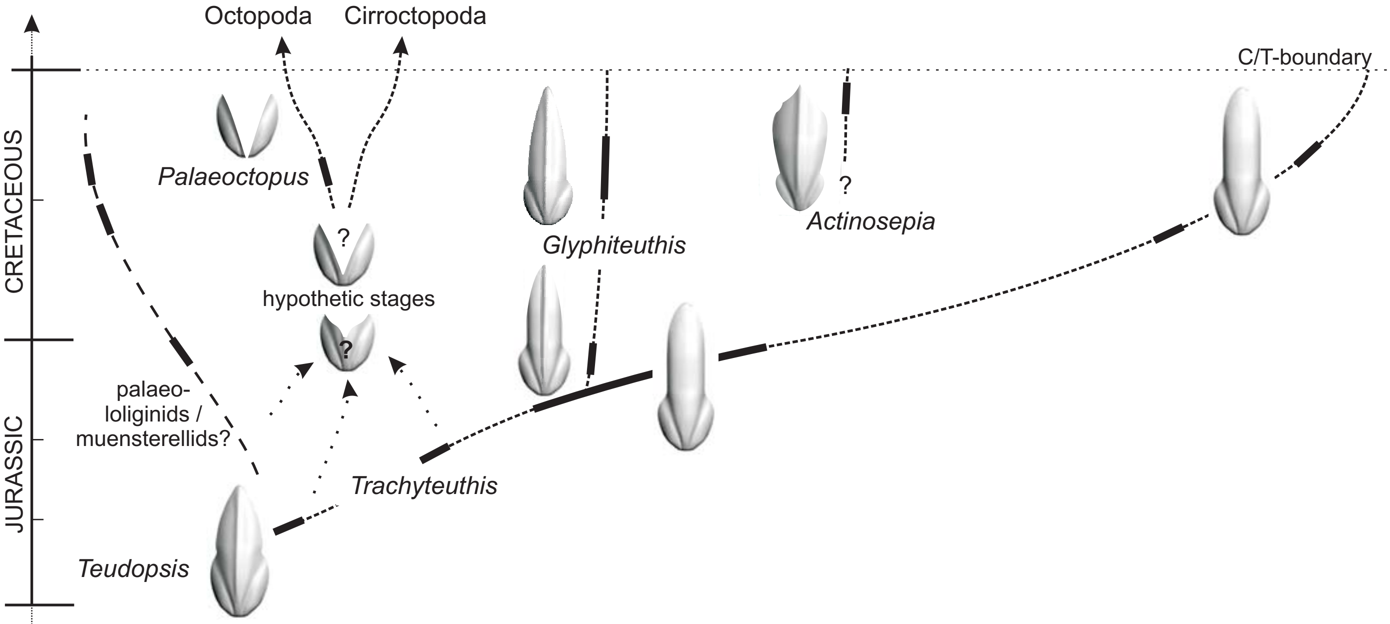


Fig. 8. Stratigraphic occurrence and possible phylogenetic relationships of fossil octobrachians.

the Albian of Queensland, Australia (Wade 1993), and the Cenomanian of Haqel, Lebanon (Fuchs 2006b). The gladius outline of each of these forms is very similar to *T. hastiformis* and *T. nusplingensis*. Distinctive characters separating them from Jurassic forms are, however, not observable due to a poor preservation.

Phylogenetic implications

First Haas (2002) and later Bizikov (2004) stated that both the U-shaped clasp in Recent cirroctopods and the paired stylets in octopods originated by the consequent reduction of the median field of an ancestral gladius. According to this, the paired structures in the posterior mantle sac of *Paleoctopus* from the Upper Cretaceous Plattenkalks of Lebanon represent the lateral fields and probably relicts of the hyperbolar zone. The interruption of the two halves in the median line indicates that the Late Cretaceous genus *Paleoctopus* already belongs to the octopod lineage. Consequently, divergence of Cirroctopoda and Octopoda must have been completed before Santonian times. Because of a comparatively wide median field Haas (2002) assumed a trachyteuthidid-like gladius to be the gladius from which the gradual reduction of the median field has been initialised. Based on the same ideas, Bizikov (2004) favoured a gladius which is similar to the older genus *Teudopsis*. The present record of *Trachyteuthis teudopsiformis* confirms both assumptions. The pointed anterior gladius end as well as the pronounced keel in *Tr. teudopsiformis* supports the derivation of trachyteuthidids from *Teudopsis*-like ancestors (Fig. 8). *Tr. teudopsiformis* can be seen as a connecting link between the Early Jurassic (Toarcian) genus *Teudopsis* and the Late Cretaceous genus *Glyphiteuthis* from the Turonian of Bohemia (Czech Republic; Reuss 1854; Kostak 2002) and Normandy (France; Lennier 1866). We re-investigated the type material of *Glyphiteuthis* from Bohemia and found very similar gladius characteristics (anterior gladius end pointed, narrow granulated area, pronounced dorsal keel). As recently suggested by Fuchs (2006b), *Glyphiteuthis* (= "*Libanoteuthis*") *libanotica* (Fraas, 1878) from the Cenomanian to Santonian Plattenkalks of Lebanon exhibits the same characters. The gladius of *Glyphiteuthis* can be distinguished from *Trachyteuthis* mainly by its shorter lateral fields.

The bizarre gladius of *Actinosepia canadensis* Whiteaves, 1897 from the Late Campanian and Maastrichtian of the Northern United States and Canada exhibits an entirely granulated median field that is sharply pointed, several dorsal keels and very short lateral fields (Whiteaves 1897; Waage 1965). Waage (1965) regarded *Actinosepia* as a trachyteuthid, but with respect to this enigmatic character combination phylogenetic affinities must remain uncertain.

If Octobrachia (Cirroctopoda + Octopoda) is derived from forms such as *Teudopsis* or *Trachyteuthis,* it is reasonable to consider the Teudopseina as the stem group of the Octobrachia. Loligosepiina (*Loligosepia*, *Geopeltis*, *Jeletzkyteuthis*), another group of Mesozoic coleoids with a gladius that is very similar to living *Vampyroteuthis* (broad triangular median field, very long lateral fields) is mostly placed on the vampyromorph lineage (Engeser 1988; Doyle et al. 1994; Haas 2002; Bisikov 2004; Fuchs 2006a).

Phylogenetic and systematic relationship of the Prototeuthina (*Paraplesioteuthis, Plesioteuthis, Dorateuthis*), the third group of gladius-bearing Mesozoic coleoids, is highly controversial and will be the subject of a separated study.

Conclusions

Among specimens from the Upper Jurassic Plattenkalks of Nusplingen and Solnhofen at least three morphospecies, *Tr. hastiformis, Tr. nusplingensis* and *Tr. teudopsiformis*, with different modifications of the median field can be distinguished. It remains uncertain whether *Tr. hastiformis* also occurs in the Nusplingen Plattenkalks or *Tr. nusplingensis* in the Solnhofen Plattenkalks, but we assume that this problem can be resolved in the course of further observations. Unfortunately, reliable comparisons with representatives of *Trachyteuthis* from other localities and stratigraphic levels are difficult or even impossible. Morphological knowledge of most is antiquated or based on only a few poorly preserved specimens. Following the morphospecies concept, each of them must be therefore considered as *Trachyteuthis sp.* until additional records improve our morphological understanding and eventually justify specific distinctions. The re-description of the holotype of *Tr. hastiformis* and the detailed descriptions of two new species of *Trachyteuthis* facilitate assignments of future records.

Although morphometric studies concerning the gladius outline have proved to be ambiguous due to insufficient preservation of most specimens, the general gladius outline of the genus *Trachyteuthis* seems to be absolutely firm until their extinction.

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