

Trachyteuthis covacevichi n. sp., a Late Jurassic Palaeopacific coleoid cephalopod

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Abstract

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A new early Oxfordian coleoid cephalopod, *Trachyteuthis covacevichi* n. sp., is described from northern Chile. It represents the first Late Jurassic Palaeopacific vampyropod and thus considerably extends the palaeogeographic distribution of trachyteuthids. In general, *Tr. covacevichi* n. sp. possesses a gladius typical for the genus, but wider than in other species. Similarities between *Tr. covacevichi* n. sp., *Tr. palmeri* from the Oxfordian of Cuba and *Tr. sp.* from the Kimmeridgian of Europe confirm a Caribbean Seaway between the Tethys and the Palaeopacific during Late Jurassic times. Morphologically, the wide gladius of *Tr. covacevichi* n. sp. supports a close phylogenetic relationship between *Teudopsis* and *Trachyteuthis*.

Introduction

In general, the fossil record of coleoid cephalopods is poor. This is chiefly due to their reduced internal shell. In the scientific history of fossil coleoids, comprehensive studies concerning morphology, evolution, diversity and distribution appeared only sporadically over a long time period. Only two major monographs on fossil coleoids published by Naef (1922) and Jeletzky (1966) exist. However, increased interests in the last twenty years of coleoid research provided a series of additional information that significantly influenced our ideas about the palaeobiology of the Coleoidea (Bandel & Leich 1986; Doguzhaeva 1996, 2000; Doguzhaeva et al. 1999; Haas 2002; Donovan et al. 2003; Fuchs et al. 2003; Klug et al. 2005; Fuchs 2006a, b, c).

The morphological understanding of some coleoid groups such as the trachyteuthids has been particularly improved (Doyle 1991; Doguzhaeva & Mutvei 2003; Donovan et al. 2003; Klug et al. 2005; Fuchs 2006a). It has been shown that this group had an almost cosmopolitan distribution and a comparatively great longevity

from the Middle Jurassic to the latest Cretaceous (Fuchs 2006a, b). Particularly during Jurassic times, they have been a diverse and abundant group at least in the Tethys realm. Numerous specimens have been identified as trachyteuthids from the Callovian of England (Martill & Hudson 1994), the Oxfordian of Cuba (Schevill 1950), the Kimmeridgian of England (Hewitt & Wignall 1988) and Germany (Klug et al. 2005), and from the Tithonian of Germany (Fuchs 2006a and references therein), Russia (Hecker & Hecker 1955) and Antarctica (Doyle 1991). In contrast, only a handful of records have been available from the Palaeopacific; all from the Oxfordian of Chile (Schultze 1989; Fuchs 2006a; Rubilar & Pérez d'A. 2006).

These specimens from the Jurassic of Chile were collected during an expedition sponsored by the National Geographic Society and conducted by members of the Museum of Natural History, University of Kansas, Lawrence, Kansas, USA (G. Arratia, H.-P. Schultze, K. Shaw, J. Chorn) with V. Covacevich (Servicio Nacional de Geología y Minería, Santiago, Chile) as guest in 1994. Since this material has never been considered

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previously in a taxonomic context, it is the aim of the present paper to describe the Chilean material.

Geological setting

The fossil localities in ravines north of Quebrada del Profeta, Sierra Varas, Cordillera de Domeyko (Fig. 1) have been discovered by Guillermo Chong, Universidad del Norte, Antofagasta, Chile, in the 1960s and visited by the junior author in 1978 and 1994 (for more details see Schultze 1989, figs 1, 2 and Arratia & Schultze 1999, figs 1, 14). The Jurassic is folded tectonically so that the fossil horizons are repeated in the ravines from east to west (Schultze 1989, fig. 2). Schultze (1989, fig. 3) gave a section through the sequence showing the occurrence of ten horizons with concretions in black sandy shales. The coleoid-bearing concretions were collected from the main fossil bearing horizon 10. These concretions are calcareous (Schultze 1989, fig. 18) and occur in calcite-containing sandy shales. In contrast, the three-dimensionally preserved fossils within the concretions are phosphatic. Soft tissues are preserved in calcium phosphate (fluorapatite) in these concretions (Schultze 1989, fig. 20). Schultze (1989) argued that the phosphatisation of the muscle tissue of fishes must have occurred before they were imbedded, because muscle pieces are distributed irregularly like bones in concretions with disarticulated fishes (Schultze 1989, pl. 4, fig. 3). Ammonites are preserved with their siphuncles. Soft tissue occurs also in association with coleoid cephalopods (see below). In contrast, calcitic or aragonitic bivalve shells are poorly preserved.

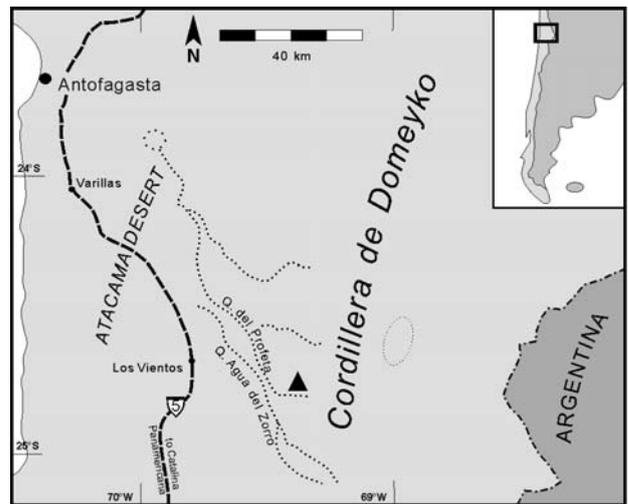


Figure 1. Map of South America with detail of the Cordillera de Domeyko in Chile. The geographic position of the exposures north of Quebrada del Profeta is marked by a black triangle.

Most of the fishes are complete and must have been imbedded relatively quickly. Disarticulated fishes and especially all the disarticulated crustacean remains indicate a longer interval on the sediment, which passed prior to the formation of the concretions. The parts of disarticulated specimens are not current-aligned and thus, currents did probably not affect the sediment surface. The ammonites are free of epizoans, and the bivalves are not attached to any ammonites; thus, there is no direct indication that they were drifted into this depositional environment.

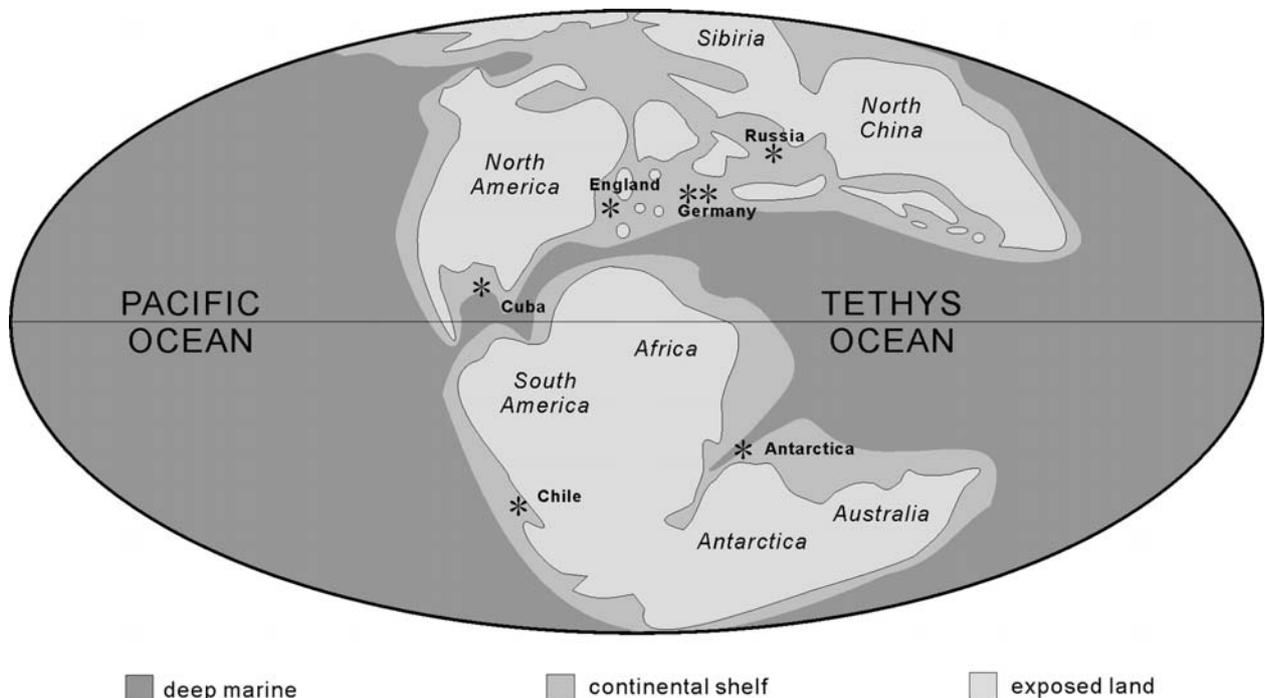


Figure 2. Scheme of the palaeogeographic situation during Late Jurassic times (modified after Smith et al. 1994). Records of *Trachyteuthis* are marked by asterisks.

Palaeogeographic maps for the Oxfordian place the Chilean locality close to the western margin of Gondwana (Fig. 2). The fishes indicate a near-coast environment (pycnodontiform and semionotid) with some open-sea elements (pachycormid fishes, ichthyosaurs). The clusters of oysters and the occurrence of decapod crustaceans point to shallow water depths, possibly below 30 m and certainly above 100 m.

Associated fauna

Common fossils at the locality are bony fishes (actinopterygians; Arratia & Schultze 1999): the pycnodontiform *Gyrodus* sp. (Kriwet 2000), the semionotid *Lepidotes* sp. (Arratia, 1987; Arratia & Cione 1996), *Hypsocormus*-like pachycormids (Arratia 1987), the possible stem teleosts *Atacamichthys* (figured as amii-form in Arratia 1987) and Teleost sp. 1 (Arratia & Schultze 1999), and teleosts, Varasichthyidae (*Varasichthys*, *Bobbichthys*, *Domeykos*, *Protoclupea*; Arratia & Cione 1996), Chongichthyidae (*Chongichthys*; Arratia & Cione 1996), as well as Teleostei incertae sedis (?*Pholidophorus domeykanus*; Arratia & Cione 1996). Few reptile bones have been discovered, these are common in corresponding horizons in Quebrada de San Pedro near Caracoles (crocodiles and ichthyosaurs) at the northern end of the Cordillera de Domeyko.

A single specimen of the decapod crustacean *Chilenophoberus atacamensis* Chong & Förster, 1976 was described as a unique occurrence (Chong & Förster 1976). In reality, *Chilenophoberus* is the most common fossil at these localities, not as complete specimens (Arratia 1987, pl. 3, fig. 1), but in form of disarticulated parts of carapaces, abdomens, telsons and uropods (Schultze 1989, pl. 1, fig. 4), which were mistakenly interpreted as shrivelled fish scales. The ammonites (*Perisphinctes* sp., *Euaspidoceras* sp. and other; Schultze 1989, pl. 1, fig. 5) have not yet been described properly. Bivalves (oysters and “*Posidonia*”; Schultze 1989, pl. 1, fig. 3) are poorly preserved. Coleoid cephalopods were discovered in 1978 (Schultze 1989, pl. 1, fig. 2) and 1994 (described here). Only one single lingulid brachiopod has been found. In addition, algae occur (Schultze 1989, pl. 1, fig. 1).

Like today, Northern Chile was positioned at the western margin of the South American continent during Jurassic times (Fig. 2). An area cladogram and the interrelationships of varasichthyids (Arratia 1994) indicate a connection between the Palaeopacific coast of Chile and Cuba through the open straight between North and South America in the early Late Jurassic. The varasichthyids migrated through the western Tethys to Europe in the Late Jurassic (Arratia 1994). The pycnodontid genus *Gyrodus* shows the same distribution as the varasichthyids. The genus *Gyrodus* occurs along the eastern maritime coast of South America and in westernmost parts of the Tethys (Cuba), with a later expansion to Europe (Kriwet 2000).

Systematic Palaeontology

Subclass **Coleoidea** Bather, 1888

Superorder **Vampyropoda** Boletzky, 1992

Order **Octobranchia** Fioroni, 1982

Suborder **Teudopseina** Starobogatov, 1983

Families included. Trachyteuthididae Naef, 1921, Teudopseidae Regteren Altena, 1949, Palaeololiginidae Naef, 1921, and Muensterellidae Roger, 1952.

Family **Trachyteuthididae** Naef, 1921

Type genus. *Trachyteuthis* Meyer, 1846

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

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

Remarks. Systematically, *Trachyteuthis* was placed in various coleoid groups. Rüppell (1829), who described the type species *Trachyteuthis hastiformis*, and several other workers from that time, regarded the remains as a sepiid cuttlebone owing to the presence of characteristic dorsal granulations. Owen (1855) considered *Trachyteuthis* to be intermediate between sepiids and teuthids. Naef (1922) and Jeletzky (1966) put *Trachyteuthis* along with the so-called “fossil teuthids”, whereas Donovan (1977) assigned it again to the sepiids. Bandel & Leich (1986) introduced an alternative idea. Since *Trachyteuthis* and other “fossil teuthids” such as *Plesiotеuthis* and *Lep-totheuthis* never show more than eight arms, these authors regarded them as early members of the vampyropod order Vampyromorpha Robson, 1929, the sister taxon of the Octobranchia (Octopoda + Cirroctopoda). Recent discoveries of well-preserved *Trachyteuthis* with two pairs of fins supported vampyropod relationships (Donovan et al. 2003). Furthermore, Haas (2002) and Bizikov (2004) claimed that gladius vestiges of Recent octopods and cirroctopods evolved through the gradual reduction of teudopseid-like gladii, which means that Teudopseina represent a stem-group of the Octobranchia.

The presence of two pairs of fins, eight arms, cirri and arm web as well as the absence of a chambered phragmocone led us to place *Trachyteuthis* within the Vampyropoda and the argumentation of Haas (2002) and Bizikov (2004) convinced us to assume affiliations to the Octobranchia rather than to the Vampyromorpha.

The Late Cretaceous genus *Libanoteuthis* Kretzoi, 1942 is regarded to be a junior synonym of *Glyphiteuthis* Reuss, 1854 (Fuchs 2006b).

***Trachyteuthis* Meyer, 1846**

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, p. 11).

Diagnosis. Gladius with a hyperbolar zone length/gladius length ratio of 0.40–0.45. Anterior gladius end more or less arcuated.

Species included. *Tr. hastiformis* (Rüppell, 1829), *Tr. latipinnis* (Owen, 1855), *Tr. zhuravlevi* Hecker & Hecker, 1955, *Tr. palmeri* (Schevill, 1950), *Tr. nusplingensis* Fuchs et al. (2007), *Tr. teudopsiformis* Fuchs et al. (2007), *Tr. willisi* Wade, 1993, *Tr. covacevichi* n. sp.

Stratigraphic and geographic range. Middle Jurassic (Callovian) to Late Cretaceous (Cenomanian); Europe, Central Russia, Cuba, Chile, Antarctica, Australia and Lebanon.

Remarks. Meyer (1846) introduced the genus *Trachyteuthis* without detailed descriptions or illustrations.

Crick (1896) therefore proposed that *Trachyteuthis* Meyer, 1846 is a junior subjective synonym of *Coccoliteuthis* Owen, 1855, because a full description of *Trachyteuthis* by Meyer (1855) was published slightly after the erection of *Coccoliteuthis* by Owen (1855). However, the bibliographic reference to plate 9, fig. 3 in Münster (1846) is valid after the ICZN (Art. 12). Most recent workers therefore considered *Coccoliteuthis* to be a junior subjective synonym of *Trachyteuthis* (Engeser 1988; Doyle 1991; Doyle et al. 1994; Donovan 1995; Riegraf et al. 1998). *Voltzia* Schevill, 1950 is a junior subjective synonym, too.

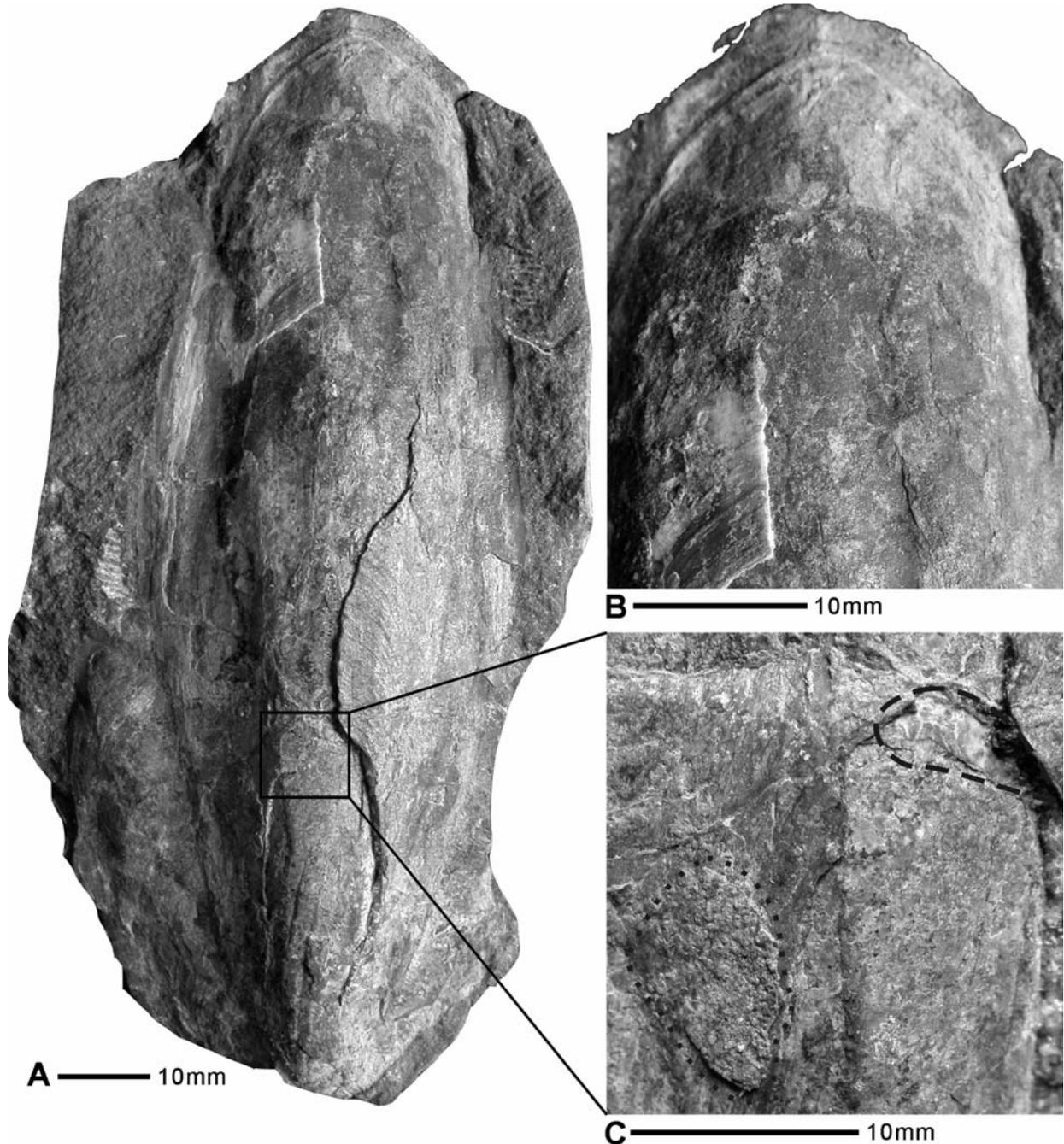


Figure 3. *Trachyteuthis covacevichi* n. sp. from Cordillera de Domeyko, Chile. **A.** Specimen SGO.PI.6437a (part), gladius in dorsal view; **B.** Detail of **A**, showing the anterior third of the gladius; **C.** Detail of **A**, showing three gladius layers; dotted line – dorsal (outer) granulated layer; dashed line – ventral (inner) layer.

***Trachyteuthis covacevichi* n. sp.**

Figures 3–5

1989 *Plesiotheuthis* sp. Schultze: pl. 1, fig. 2.2006 *Trachyteuthis* sp. Fuchs a: pl. 14, fig. F.2006 *Trachyteuthis* sp. Rubilar & Pérez d'A.: fig. 2A–B, C.

Derivation of name. In honour of the late Vladimir Covacevich, geologist and invertebrate palaeontologist of the Servicio Nacional de Geología y Minería de Chile, who was member of the field party in 1994.

Holotype. Specimen SGO.PI.6437a + b (Figs 3–4), deposited in the Museo Nacional de Historia Natural, Santiago (Chile).

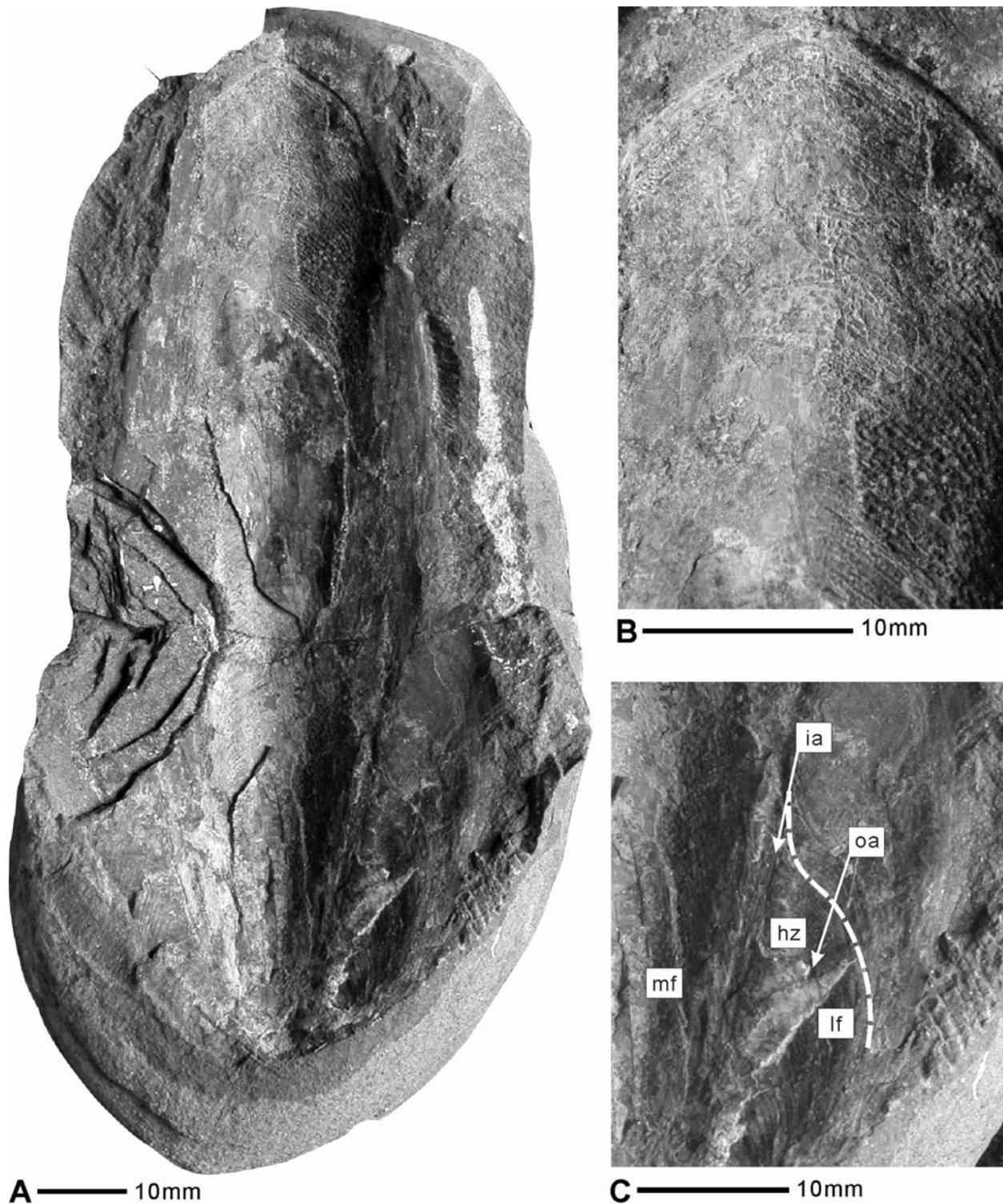


Figure 4. *Trachyteuthis covacevichi* n. sp. from Cordillera de Domeyko, Chile. **A.** Specimen SGO.PI.6437b (counterpart), gladius in ventral view; **B.** Detail of **A**, showing dorsal imprints of the granulae; **C.** Detail of **A**, showing the course of growth increments; **ia** – inner asymptote, **hz** – hyperbolar zone, **lf** – lateral field, **mf** – median field, **oa** – outer asymptote, dashed line – growth increment.

Type locality. Tributaries north of Quebrada del Profeta, Sierra de Varas, Cordillera de Domeyko, northern Chile.

Type horizon. Uncertain (probably *cordatum* zone); early Oxfordian, Late Jurassic.

Additional material. One specimen, SGO.PI.6438 (Fig. 5).

Diagnosis. Gladius shape comparatively wide and compact, anterior end weakly pointed, granulated area diverge at an angle of 15 degrees.

Description. The material includes three-dimensionally uncompressed gladii. The holotype consists of part (SGO.PI.6437a, Fig. 3) and counterpart (SGO.PI.6437b, Fig. 4). The gladius of the holotype is in an excellent condition (only outermost margins of the lateral fields are partly missing). It was embedded on the venter. Specimen SGO.PI.6438 preserves a juvenile gladius of



Figure 5. *Trachyteuthis covacevichi* n. sp. from Cordillera de Domeyko, Chile. Specimen SGO.PI.6438, gladius seen in dorsal view.

52 mm length (Fig. 5). It is in very bad condition showing no relevant characters.

The gladius of the holotype has a total length of 125 mm. Median field, hyperbolar zones and lateral fields are clearly distinguishable owing to growth lines visible on both part and counterpart (Fig. 4A, C). Hyperbolar zone is 55 mm, the lateral field 38 mm in length. Hyperbolar zone is gently curved. Gladius width is 38 mm at half of the gladius length (approximately the anterior end of the hyperbolar zone) and 50 mm at the anterior end of the lateral field. Maximum gladius width is 56 mm (morphometric indices are given in Table 1). Inner asymptotes that delimit the hyperbolar zones from the median field, are well marked by ridges; they diverge with an angle of 40 degrees. Outer asymptotes are indistinct.

Imprints of the dorsal gladius surface are visible on specimen SGO.PI.6437b. Especially the anterior third of this specimen shows distinct imprints of granulae typical for *Trachyteuthis* (Fig. 4B). Granulae are arranged in accordance with growth increments as seen in SGO.PI.6437a (Fig. 3B). The arcuated growth lines reflect the weakly pointed anterior gladius end. The granulated area forms a comparatively broad band diverging from posterior to anterior at an angle of 15 degrees. A median keel or line is absent.

The sturdy gladius consists of three main layers. The ventral layer generally adheres to the part (Fig. 3A–C); the dorsal granulated layer to the counterpart (Fig. 4A, B). Small pieces of the granulated dorsal layer can be also seen on the part (Fig. 3B, C). The intermediate layer, which is the thickest layer, is exposed on both parts. Its inner surface is almost smooth. Growth lines are very weak, but distinct longitudinal ridges are crossing the growth lines (Fig. 4A). By contrast, the outer surface of the intermediate layer displays distinct growth increments (Fig. 3B).

Though we did not analyse the mineralogy, the gladius is most probably preserved in francolite. A primary aragonitic gladius composition appears unlikely, because aragonitic shells have been dissolved in Oxfordian deposits of the Cordillera de Domeyko. It is more probable that the original gladius composition was chitinous (Doguzhaeva et al. 2003; Fuchs 2006a).

One can easily recognize the natural inflection of the gladius because of its three-dimensionality. The median field shows a remarkable longitudinal as well as transversal convexity. This convexity is stronger in the posterior part than in the anterior. The flexion decreases at the transition from the hyperbolar zone to the lateral fields. The lateral fields follow the longitudinal inflection of the median field, but not the transversal direction.

Most of the soft tissue is dissolved except for mantle musculature that is preserved in a very few places, and imprints of the ink sac.

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

Table 1. Comparison of morphometric indices and some other gladius characters between *Tr. hastiformis*, *Tr. nusplingensis*, *Tr. teudopsiformis* and *Tr. covacevichi* n. sp.

Measurements	<i>Tr. hastiformis</i>	<i>Tr. nusplingensis</i>	<i>Tr. teudopsiformis</i>	<i>Tr. covacevichi</i> n. sp.
hyperbolar zone length/gladius length HZL/GL	0.39–0.4	0.36	?	0.44
lateral field length/gladius length LFL/GL	0.34–0.35	0.32	?	0.4
gladius width at the anterior end of the hyperbolar zones/gladius width GW_{hz}/GL	0.27–0.28	0.27	?	0.3
gladius width at anterior end of the lateral fields/gladius width GW_{lf}/GL	0.34–0.35	0.34	?	0.4
maximum gladius width/gladius length GW_{max}/GL	0.35–0.37	0.39	?	0.45
gladius width at the half gladius length/gladius width $GW_{1/2gl}/GL$	0.26–0.27	0.27	?	0.3
maximum gladius width/hyperbolar zone length GW_{max}/HZL	0.87–0.93	1.05	?	1.01
angle of diverging inner asymptotes A_{ia}	40°	40°	43°	40°
angle of diverging granulated area A_{ga}	\	12°	restricted to keel	15°
granulation	coarse, irregular	fine, regular	coarse, regular	fine, regular
keel	absent	absent	present	absent
spindel-shaped deformation on the median field	present	absent	absent	absent
preservation	± flattened	± flattened	± flattened	3-dimensional

Discussion. The specimens illustrated in Rubilar & Pérez d'A. (2006, fig. 2A–B, D), have been collected at the same locality by the same field crew. We have not yet investigated these specimens in detail, but they are most probably identical with *Tr. covacevichi* n. sp. The Callovian gladius shown in Rubilar & Pérez d'A. (2006, fig. 2C) bears a strongly pronounced median keel and apparently lacks the dorsal granulation. It might be identical with *Teudopsis jeletzkyi* from the Callovian of Argentina (Riccardi 2005).

In general, the gladius outline of *Tr. covacevichi* n. sp. is very similar to that of *Tr. hastiformis* (Fig. 6A, E) and *Tr. nusplingensis* (Fig. 6B, F). However, gladii from the Solnhofen and Nusplingen Limestones are more or less flattened; gladius shape comparisons between flattened and three-dimensional gladii are therefore problematic. Lengths and particularly widths obtained from flattened gladii are highly depending on the rate of compaction since the gladii have been originally flexed. Width-length ratios (GW_{max}/GL , $GW_{1/2gl}/GL$ and GW_{hz}/GL , see Table 1 for explanations) given for flattened specimens are therefore only approximate (tentatively too wide), whereas measurements obtained from three-dimensional gladii are more accurate. Nevertheless, the high width-length ratios obtained from *Tr. covacevichi* n. sp. indicate a wider gladius than in *Tr. hastiformis* or *Tr. nusplingensis* (Fig. 6, Tab. 1). Also the ratios LFL/GL and HZL/GL are higher in *Tr. covacevichi*, suggesting generally a more compact gladius shape. Apart from the outline, the gladius of *Tr. covacevichi* n. sp. can be clearly distinguished from *Tr. hastiformis* by the lack of the spindle-shaped deformation that is characteristic for the median field of *Tr. hastiformis* (Fuchs 2006a; Fuchs et al. 2007). The granulation of *Tr. nusplingensis* is very si-

milar to *Tr. covacevichi* n. sp., but the granulated area of the former diverges at a smaller angle (Fig. 6, Tab. 1).

Tr. teudopsiformis from Solnhofen can be easily distinguished from *Tr. covacevichi* n. sp. by an extremely narrow granulated area that is restricted to a median keel.

The shape of the anterior gladius margin in *Tr. covacevichi* n. sp. shows close similarities to contemporary *Tr. palmeri*, but a precise comparison is difficult because lateral fields, hyperbolar zones as well as details about the granulation are still unknown in *Tr. palmeri*. It is likewise difficult to compare *Tr. covacevichi* n. sp. and Callovian *Tr.* sp. (Martill & Hudson 1994), the oldest known trachyteuthid. However, it seems that *Tr.* sp. displays higher LFL/GL and HZL/GL-ratios than our specimens (own observation).

Determination of differences between *Tr. covacevichi* n. sp. and other species of *Trachyteuthis*, *Tr. cf. hastiformis* from Antarctica, *Tr. zhuravlevi* from Russia, *Tr.* sp. from Helgoland, *Tr. willisi* from Australia, and *Tr. cf. hastiformis* from Lebanon, are problematic, because they have been identified by very few fragmentary specimens that offer only parts of the granulated area or imprints of the dorsal gladius surface. Distinctive characters as listed in Table 1 are thus unknown from these specimens.

The general gladius shape of *Tr. covacevichi* n. sp. is very close to the Toarcian genus *Teudopsis*, but the former can be easily distinguished by the possession of dorsal granulation and the absence of a pronounced median keel. *Tr. covacevichi* n. sp. clearly differs from Late Cretaceous genera *Glyphiteuthis* and *Actinosepia* by having higher LFL/GL- and HZL/GL-ratios, a less pointed anterior margin and by a planar median field without keel.

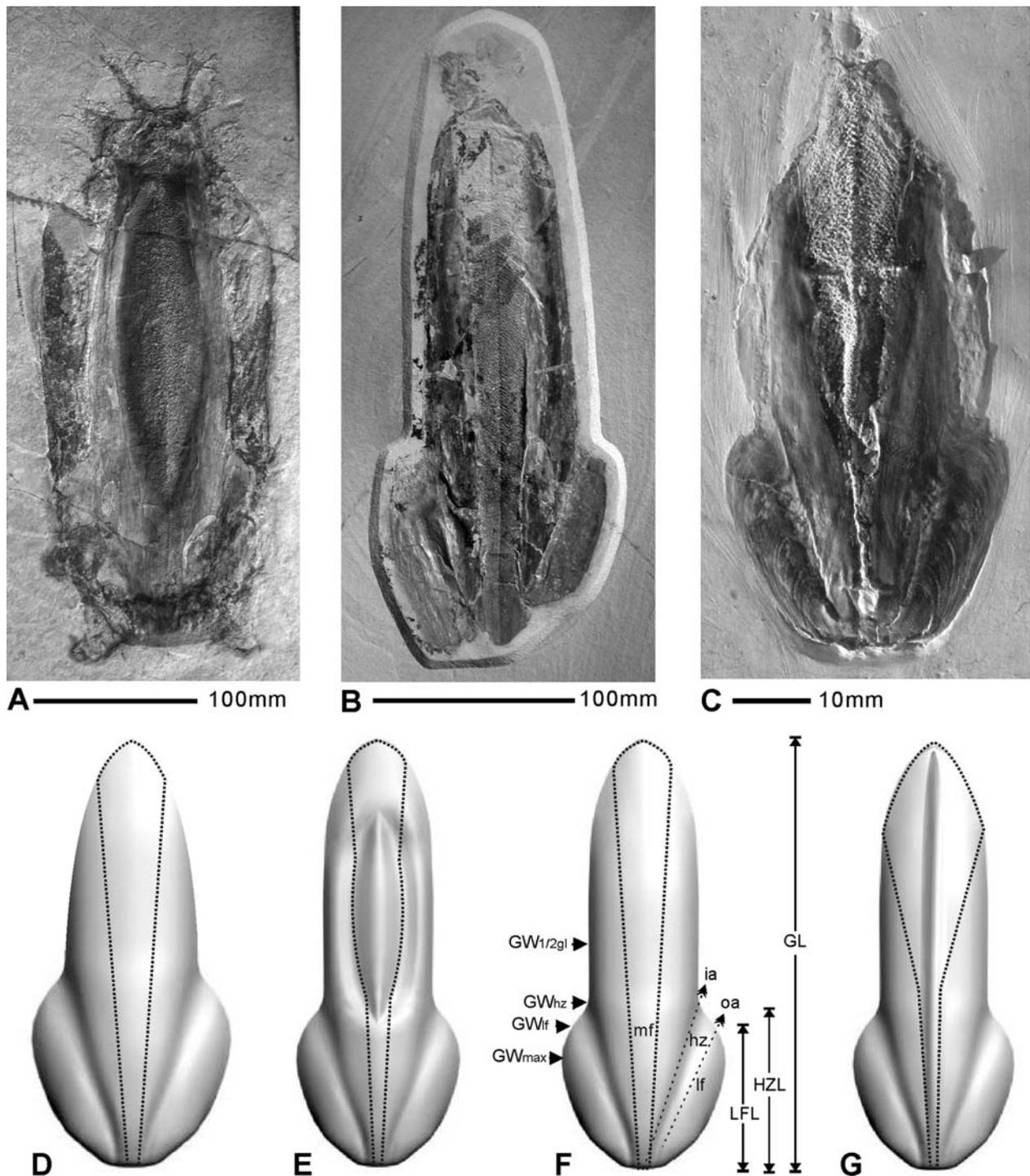


Figure 6. **A.** *Trachyteuthis hastiformis* (Rüppell, 1829) from Solnhofen (SOS 5762, Jura Museum Eichstätt), note the spindle-shaped elevation on the median field; **B.** *Trachyteuthis nusplingensis* Fuchs et al. (2007) from Nusplingen (SMNS 63596, Staatliches Museum für Naturkunde Stuttgart); **C.** *Trachyteuthis teudopsiformis* Fuchs et al. (2007) from Solnhofen (G 1306061, Museum Berger, Eichstätt); **D.** 3D reconstruction of the gladius of *Trachyteuthis covacevichi* n. sp.; **E.** 3D reconstruction of *Trachyteuthis hastiformis*; **F.** 3D reconstruction of *Trachyteuthis nusplingensis*; **G.** 3D reconstruction of *Trachyteuthis teudopsiformis*; **GL** – gladius length; **GW_{1/2gl}** – gladius width at the half gladius length; **GW_{hz}** – gladius width at the anterior end of the hyperbolar zone; **GW_{lf}** – gladius width at the anterior end of the lateral field; **GW_{max}** – maximum gladius width; **HZL** – hyperbolar zone length; **hz** – hyperbolar zone; **ia** – inner asymptote; **LFL** – lateral field length; **lf** – lateral field; **mf** – median field; **oa** – outer asymptote.

Conclusions

Most Jurassic vampyropods have been reported from the Tethyan realm (Fig. 7). To date, only three taxa have been recorded from outside the Tethys. Toarcian *Teudopsis cadominensis* and *Paraplesioteuthis hastata* are known from the Western Interior Basin of North America (Hall 1985; Hall & Neuman 1989). Similarities with their western Tethys coevals indicate a marine connection between Tethys and Palaeopacific via the Arctic Sea (Hall 1985; Hall & Neuman 1989). *Teudopsis jeletzkyi* from the Callovian of Argentina is the only record from the Southern Palaeopacific during the Toarcian. Hence, *Tr. covacevichi* n. sp. represents the second Jurassic and the first Late Jurassic vampyropod from the Palaeopacific. The record of *Tr. covacevichi* n. sp. indicates a wide palaeogeographic distribution of trachyteuthids during the Jurassic period, which supports earlier assumptions concerning a worldwide distribution of ancestral coleoids (Doyle 1991).

Phylogenetically, the compact gladius shape of *Tr. covacevichi* n. sp. supports the idea that trachyteuthids developed from *Teudopsis*-like forms during the early Middle Jurassic (Fuchs 2006a; Fuchs et al. 2007). In the light of this, *Tr. covacevichi* n. sp. retained a comparatively wide and anteriorly pointed gladius (Fig. 7). Unfortunately, it is still uncertain if the stratigraphically oldest record of *Trachyteuthis* from the Callovian of England, exhibits a more primitive gladius shape.

As the rarity of coleoids in the fossil record is certainly a diagenetic artefact induced by their poor preservational potential, conclusions on their palaeobiogeography have to be drawn with reservation. However, the close similarity between *Tr. palmeri* from the Oxfordian of Cuba, *Tr. covacevichi* n. sp. from the Oxfordian of Chile, and *Trachyteuthis* from the European Kimmeridgian confirms a Caribbean seaway between the Tethys and the Palaeopacific starting with the Middle Jurassic. With respect to the results presented herein, further conclusions about the place of origin of trachyteuthids depend on the detailed gladius morphology of the English Callovian *Trachyteuthis*. As North American *Teudopsis cadominensis*, South American *Teudopsis jeletzkyi* and European *Teudopsis subcostata* are very similar, the origin of trachyteuthids might have occurred in the Palaeopacific or in the Tethys. If the poorly known gladius shape of the Callovian *Trachyteuthis* from England links *Teudopsis* and *Trachyteuthis*, a migration of trachyteuthids from the Tethys to the Palaeopacific in the early Middle Jurassic is conceivable. If *Tr. covacevichi* n. sp. is more primitive than the Callovian species, however, it is also conceivable that *Trachyteuthis* originated in the southern Palaeopacific and migrated to the Tethys. In the latter case, the distribution would correspond to that of the fishes of the Cordillera de Domeyko, Chile, and Vinales, Cuba (Arratia 1994; Kriwet 2000). The faunal association indicates a shallow coastal marine

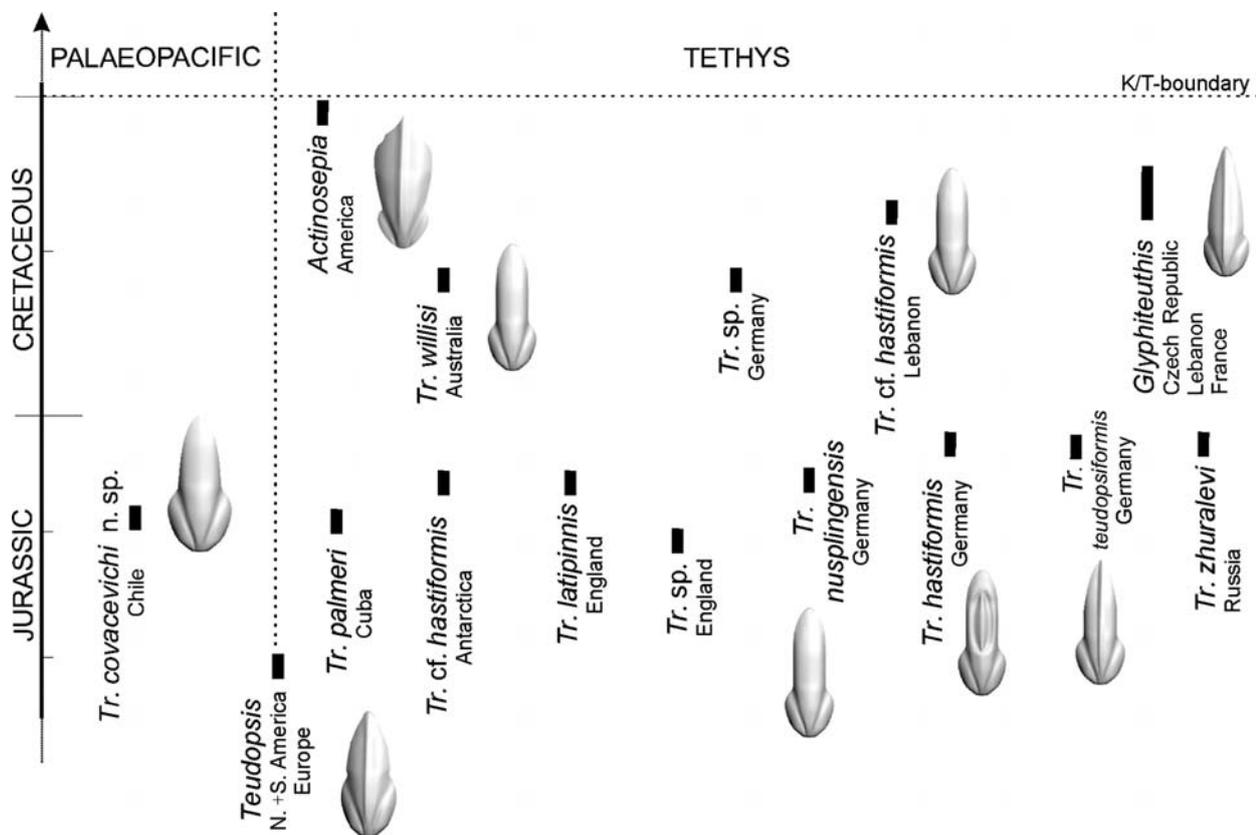


Figure 7. Stratigraphic and geographic records of trachyteuthids and some teudopsids.

habitat for *Tr. covacevichi* n. sp. The same palaeoenvironment is also assumed for other trachyteuthids from the tethyal realm.

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