Journal of Paleontology, 90(5), 2016, p. 910–922

0022-3360/16/0088-0906
doi: 10.1017/jpa.2016.110

Journal of PALEONTOLOGY
A JOURNAL OF THE PALEONTOLOGICAL SOCIETY

Callovian and Oxfordian (Jurassic) teuthids (Coleoidea, Cephalopoda) from Chile

Alberto C. Riccardi

División Paleozoología Invertebrados, Museo de La Plata, 1900 La Plata, Buenos Aires, Argentina ⟨riccardi@fcnym.unlp.edu.ar⟩

Abstract.—Coleoid specimens from the Jurassic of northern Chile are included in two different species of *Trachyteuthis*, i.e., *T. covacevichi* Fuchs and Schultze, 2008 and *T. chilensis* n. sp., and in a new genus and a new species, *Pseudoteudopsis perezi* n. gen. n. sp. The specimens described and figured are from two different areas in northern Chile. Those referred to *Pseudoteudopsis perezi* n. gen. n. sp. came from a locality north of Calama and are associated with ammonites indicating the lower Callovian uppermost *bodenbenderi* to lowermost *proximum* zones (≈ *gracilis* Standard Zone) of the Andean ammonite zonation. Those described as *T. covacevichi* and *T. chilensis* n. sp. came from the Cordillera de Domeyko, northeast of Taltal, and are associated with ammonites indicating the middle Oxfordian *transversarium* Zone.

Introduction

Thus far there have been few publications on Mesozoic material from the Southern Hemisphere assigned to teuthids (Schultze, 1989; Doyle, 1991; Riccardi, 2005; Rubilar and Pérez d'A, 2006) or vampyropods (Wade, 1993; Fuchs, 2006a; Fuchs and Schultze, 2008). These were based on a few representatives of the families Teudopsidae and Trachyteuthididae and came, from older to younger, from the Toarcian of Argentina (Riccardi, 2005), the Callovian (Rubilar and Pérez d'A., 2006) and Oxfordian (Schultze, 1989; Rubilar and Pérez d'A., 2006; Fuchs, 2006a; Fuchs and Schultze, 2008) of Chile, the Tithonian of the Antarctic Peninsula (Doyle, 1991), and the upper Albian of northwestern Queensland, Australia (Wade, 1993).

The Callovian and Oxfordian material from Chile came, respectively, from NW Cerro Jaspe and the Cordillera de Domeyko, Antofagasta Region (Fig. 1). The Callovian material consists of one specimen that was described and figured as *Trachyteuthis* sp. by Rubilar and Pérez d'A. (2006, p. 113, fig. 2C); the Oxfordian included two specimens that were also described and figured as *Trachyteuthis* sp. (Rubilar and Perez d'A., 2006, p. 113–114, figs. 2A, 2B, 2D). Two additional specimens from the Cordillera de Domeyko were later described as *Trachyteuthis covacevichi* Fuchs and Schultze (2008, p. 43, figs. 3–5). On the other hand, one specimen previously figured by Schultze (1989, pl. 1, fig. 2) as '*Plesioteuthis* sp.' was not refigured, and its repository remains unknown. A reappraisal of the whole collection is presented here, with new descriptions and figures, and the material is included in two different species of *Trachyteuthis, T. covacevichi* Fuchs and Schultze, 2008 and *T. chilensis* n. sp. and in a new genus and new species, *Pseudoteudopsis perezi* n. gen. n. sp.

Material and geological setting

The specimens here described and figured come from two different areas in northern Chile (Fig. 1).

North of Calama, Antofagasta Region.—One gladius from a locality south of Quebrada Quinchamale, ~5 km northwest of Cerro Jaspe, was collected by Andrew Tomlison in 2005 and deposited at the Servicio Nacional de Geología y Minería (SNGM–1849), Santiago, Chile - SERNAGEOMIN. It was figured (Rubilar and Pérez d'A., 2006, fig. 2C) as '*Trachyteuthis* sp.' and is here described and refigured as *Pseudoteudopsis perezi* n. gen. n. sp. (see Fig. 4.1–4.3 in Systematic paleontology). Ammonites identified as *Rehmannia (R.)* cf. *paucicostata* (Tornquist, 1898) and *Neuqueniceras antipodum* (Tornquist, 1898) were recovered from the same level (Rubilar and Pérez d'A., 2006, p. 113) indicating reference to the lower Callovian uppermost *bodenbenderi* to lowermost *proximum* zones of the Andean ammonite zonation (cf. Riccardi and Westermann, 1991; Riccardi, 2008).

Cordillera de Domeyko, northeast of Taltal.—The material consists of four specimens, three of which are included in *T. covacevichi* and one in *T. chilensis* n. sp. (see the following). They were collected by Vladimir Covacevich † (then at SERNAGEOMIN) and/or Hans-Peter Schultze (Kansas University) in March 1994, and deposited in the paleontological collection of the SERNAGEOMIN (SNGM–8245 to 8248).

The material of *T. covacevichi* came from Quebrada del Profeta, H. P. Schultze collection (Holotype, original MNHN, SGO.PI.6437a, b, figured by Fuchs and Schultze, 2008, p. 43, figs. 3, 4; plaster cast SNGM–8245, here figured in Fig. 2.1); Cerro Islote, V. Covacevich collection (SNGM–8248; figured by Rubilar and Pérez d'A., 2006, fig. 2D; here figured in Fig. 2.3); and Quebrada Sandón, H.P. Schultze, and V. Covacevich collection (original MNHN, SGO.PI.6438, figured by Fuchs and Schultze, 2008, fig. 5; plaster cast SNGM–8245, here figured in Fig. 2.5).

The only specimen of *T. chilensis* n. sp. came from Quebrada del Profeta, V. Covacevich collection (SNGM–8246;

Figure 1. Locality map, Antofagasta Region, Chile.

figured by Rubilar and Pérez d'A., 2006, fig. 2A, 2B, as '*Trachyteuthis* sp.' and refigured here in Fig. 3.1).

Ammonites referred by V. Covacevich (SERNAGEOMIN internal report, 1995) to the genera *Mirosphinctes* Schindewolf, 1926, *Euaspidoceras* Spath, 1931, *Cubaspidoceras* Myczyński, 1976, and '*Perisphinctes*' Waagen, 1869 were found at the same levels, indicating an Oxfordian age (see Rubilar and Perez, d'A., 2006). Fuchs and Schultze (2008, p. 44) labeled the type horizon of *T. covacevichi* as "uncertain (probably *cordatum* zone), early Oxfordian" without much elaboration although, from the stratigraphic accounts of the Quebrada del Profeta section given by Chong and Förster (1976, p. 147), Schultze (1989, p. 186), Gygi and Hillebrandt (1991, p. 142) and Hillebrandt et al. (2012, p. 67), the specimens of *T. covacevichi* from Quebrada del Profeta level '10' (cf. Schultze, 1989, p. 186, pl. 1, fig. 2; Fuchs, 2006a, pl. 14, fig. F; Fuchs and Schultze, 2008, figs. 3, 4; here Fig. 2.1, 2.2) were found together with ammonites belonging to the subgenera *Antilloceras* Wierzbowski, 1976, and *Gregoryceras* Spath, 1924, which characterize the middle Oxfordian *transversarium* Zone, and ~6 m above a level with *Caracoliceras dunkeri* (Steinmann, 1881), ascribed to the lower–middle Oxfordian uppermost Cordatum to Plicatilis Zones.

This fauna occurs in concretions, which also contain fishes, crustaceans, bivalves, and *Lingula* (cf. Schultze, 1989), within a succession of black sandy shales interbedded with fine-grained calcareous sandstones and thin limestone layers. Paleoenvironmental interpretations indicate dysaerobic shallow waters similar to those of the Posidonien Schiefer of southern Germany (cf. Chong and Förster, 1976; Schultze, 1989).

The specimens from Cerro Islote (Rubilar and Pérez d'A., 2006, fig. 2D; here Fig. 2.3, 2.4) and Quebrada Sandon (Fuchs and Schultze, 2008, fig. 5; here Fig. 2.5) are most likely from the same level, i.e., equivalent to the middle Oxfordian *transversarium* Zone (cf. Gygi and Hillebrandt, 1991).

Repository and institutional abbreviations.—Sgo–PI, Paleontología Invertebrados, Museo Nacional de Historia Natural, Santiago de Chile, Chile. SNGM, Colección Paleontológica Servicio Nacional de Geología y Minería (SERNAGEOMIN), Santiago de Chile, Chile.

Systematic paleontology

Abbreviations for morphologic terms and dimensions (cf. Fuchs and Larson, 2011, fig. 1).—GL = gladius length; GW = maximum gladius width; $GW_{1/2\ GL}$ = gladius width at half GL; GW_{HZ} = gladius width at anterior end of hyperbolar zone (HZ); GW_{LF} = gladius width at anterior end of lateral fields (LF); HZL = hyperbolar zone length; LFL = lateral fields length; A_{ia} = angle of diverging inner asymptotes; A_{ga} = angle of diverging granulate area.

Subclass Coleoidea Bather, 1888
Order ?Teuthida Naef, 1916
Family Trachyteuthididae Naef, 1921

Remarks.—Evolutionary history and classification at the ordinal level of coleoids is still highly debated (see Lindgren et al., 2012 and references therein). Thus, as no new information on this issue is added by the material here described and a discussion on higher-level taxonomy of gladius-bearing coleoids is beyond the scope of this paper, the Trachyteutididae are here tentatively placed in the order Teuthida, following traditional views on the group systematics (cf. Naef, 1922; Jeletzky, 1966).

It should be mentioned, however, that a three-part gladius with broad median field and wings (lateral fields), which was originally used to link fossils with modern teuthids, has been considered a plesiomorphic structure, which probably evolved at least four times in extant lineages and, therefore, is not a reliable character for determining relationships (see Young et al., 1998; Vecchione et al., 1999). The one feature that would allow correct systematic assignment of teuthids is the arm crown (presence or absence of tentacles or filaments), but it is rarely preserved in the fossil record, except for a handful of exceptional ('Lagerstatten') localities (see Donovan and Fuchs, 2016), and when they are preserved (as in *Mastigophora* Owen, 1856 and *Plesioteuthis* Wagner, 1859), they are subject to different interpretations (e.g., Naef, 1922; Jeletzky, 1966; Bandel and Leich, 1986; Young et al., 1998; Vecchione et al., 1999; Fuchs, 2006a, b, 2014; Fuchs et al., 2007; Fuchs and Larson, 2011; Klug et al., 2005, 2015; Donovan and Fuchs,

https://doi.org/10.1017/jpa.2016.110 Published online by Cambridge University Press

2016). Thus, relationships of families based only on gladii remain uncertain at present (Donovan et al., 2003).

Genus *Trachyteuthis* Meyer, 1846
(= *Coccoteuthis* Owen, 1855; ?*Voltzia* Schevill, 1950)

Type species.—*Trachyteuthis ensiformis* Meyer, 1846, Tithonian, Solnhofen, Germany, by monotypy (see Donovan, 1995) [= *T. hastiformis* (Rüppell, 1829)]

Other species.—*Trachyteuthis latipinnis* (Owen, 1855) from the Kimmeridge Clay of England and Tithonian of Germany; *T. zhuravlevi* Hecker and Hecker (1955) from the Tithonian of the Lower Volga region, Russia; *T. willisi* Wade (1993) from the Albian of Australia; *T. nusplingensis* Fuchs, Engeser, and Keupp (2007) from the upper Kimmeridgian of southern Germany; *T. teudopsiformis* Fuchs, Engeser, and Keupp (2007) from the lower Tithonian of southern Germany; *T. covacevichi* Fuchs and Schultze (2008) from the Oxfordian of Chile; *T. bacchiai* Fuchs and Larson (2011) from the Cenomanian of Lebanon; and possibly ?*T. palmeri* (Schevill, 1950) from the Oxfordian of Cuba. Another Cretaceous record has been reported, but not figured, from the Aptian of Germany (Engeser and Reitner, 1985).

Diagnosis.—Trachyteuthid gladius with a hyperbolar zone length/gladius length ratio of 0.34–0.52. Anterior gladius end rounded or weakly pointed (modified from Fuchs and Larson, 2011, p. 816; see Remarks)

Occurrence.—Most records of *Trachyteuthis* are from the lower Tithonian lithographic limestones of Solnhofen and Nusplingen, southern Germany, from which at least 50 specimens have been preserved in different museums (Fuchs et al., 2007, p. 576; according to D. Fuchs [personal communication, March 28, 2016], this number refers to the specimens used for morphometric comparisons, and there are ~10 times more accumulated in museums and private collections); ~23 of these were figured between 1825 and 2006, and until 2007 were considered (but see the following) to belong in a single species, *T. hastiformis*. A few additional specimens were also mentioned and/or figured from other regions in the Northern Hemisphere: three from the Tithonian of Russia (Trautschold, 1866; Hecker and Hecker, 1955), nine from the Kimmeridgian–Tithonian of England (Owen, 1855; Donovan, 1977; Hewitt and Wignall, 1988), (?) one from the Aptian of Germany (Engeser and Reitner, 1985), four from the Cenomanian of Lebanon (Fuchs, 2006b, 2007; Fuchs and Larson, 2011), and (?) two from the Oxfordian of Cuba (Schevill, 1950). Eleven *Trachyteuthis* specimens are known from the Southern Hemisphere: five from the Oxfordian of Chile (Schultze, 1989; Rubilar and Perez d'A., 2006; Fuchs and Schultze, 2008), one from the lower Tithonian of Antarctica (Doyle, 1991), and five from the Albian of Australia (Wade, 1993).

Remarks.—As noted by Doyle et al. (1994, p. 11) and Donovan (1995, p. 1), *Trachyteuthis* was proposed by Meyer (1846, p. 598) on the basis of at least two specimens for which he introduced two specific names, of which only one, *T. ensiformis*, is valid (International Commission on Zoological Nomenclature [ICZN], 1999, Art. 12.2.7) as the name was accompanied by reference to an unnamed specimen figured by Münster (1846, pl. 9, fig. 3). *T. ensiformis* is, therefore, the type species of *Trachyteuthis* Meyer, and *T. hastiformis* Rüppell, 1829 is a senior synonym. As Meyer (1846, p. 598) identified his own material with Münster's (1846) figure, it is clear that the type series contained more than one specimen, and Münster's specimen was, therefore, designated lectotype of the species (cf. Doyle et al., 1994, p. 11; Donovan, 1995, p. 2). Meyer (1846) did not mention, and was probably unaware of, the fact that Münster's (1846, pl. 9, fig. 3) specimen had been figured, together with another three specimens, under the name '*Sepia linguata*' by d'Orbigny (1839, in Férussac and d'Orbigny, 1835–1848, p. 292, pl. 16, fig. 3, a slightly reduced mirror image of Münster, 1846, pl. 9, fig. 3). Since then, most subsequent authors have accepted that *T. ensiformis* Meyer, 1846, is a (junior) subjective synonym of *T. hastiformis*, a conclusion that does not invalidate the availability of Meyer's (1846) specific name (ICZN, 1999, Art. 10.6).

Although the holotype—by monotypy—of *T. hastiformis* was figured by Rüppell (1829, pl. 3, fig. 2), it is worth mentioning that Rüppell (1829, p. 9) indicated that the first figured specimen of the species (cf. also d'Orbigny, 1839, in Férussac and d'Orbigny 1835–1848, p. 290) is probably represented by a drawing by the eighteenth-century copper engraver G.W. Knorr, which was included without identification in a monograph by Walch (1768–1773, pl. 22, fig. 2), who considered it a fish remain, an identification that was upheld by Germar (1826, p. 109). Another specimen of this species (see Fuchs et al., 2007, p. 579) was figured by König (1825, pl. 17, fig. 201) as '*Sepia prisca*,' and although this name constitutes the senior available name (ICZN, 1999, Art. 12.2.7), it should be considered a nomen oblitum and Rüppell's (1829) younger name, *T. hastiformis*, a nomen protectum (ICZN, 1999, Art. 23.9.1 and 23.9.2).

Münster (1837) introduced another seven new specific names—*S. obscura*, *S. linguata*, *S. regularis*, *S. gracilis*, *S. venusta*, *S. antiqua*, and *S. caudata*—but they have been considered nomina nuda as they lacked descriptions and/or illustrations or any other indication that could validate them (cf. ICZN, 1999, Art. 12). d'Orbigny (1839, in Férussac and d'Orbigny, 1835–1848), however, on the basis of Münster's unpublished notes and drawings (cf. Wagner, 1860, p. 759; Fuchs et al., 2007, p. 575), described and figured '*S. antiqua*,' '*S. caudata*,' and '*S. linguata*,' the last one including the material referred by Münster (1837) to the three remaining specific names. Only '*Sepia venusta*' was regarded an 'anomalous form' of a different species. Thus, d'Orbigny (1839, in Férussac and d'Orbigny 1835–1848; cf. also d'Orbigny, 1845), validated the three mentioned names, and became their author, as he was the first to publish them in a way that satisfies the criteria of availability (ICZN, 1999, Art. 50), although he clearly stated that he thought that all the specimens included under these specific names were in fact different growth stages and/or damaged representatives of a single species, i.e., *Sepia hastiformis* Rüppell.

It is worth mentioning that other specimens introduced by Münster (1837) as nomina nuda, i.e., *S. obscura*, *S. regularis*, *S. gracilis*, were placed by d'Orbigny (1839, in Férussac and d'Orbigny, 1835–1848, p. 292; 1845, p. 162) in *S. linguata*. As the name of this species, even if regarded as a synonym of *T. hastiformis*, also complies with the criteria of availability (ICZN, 1999, Art. 11), one of the syntypes should be selected as lectotype whenever the original collection is restudied.

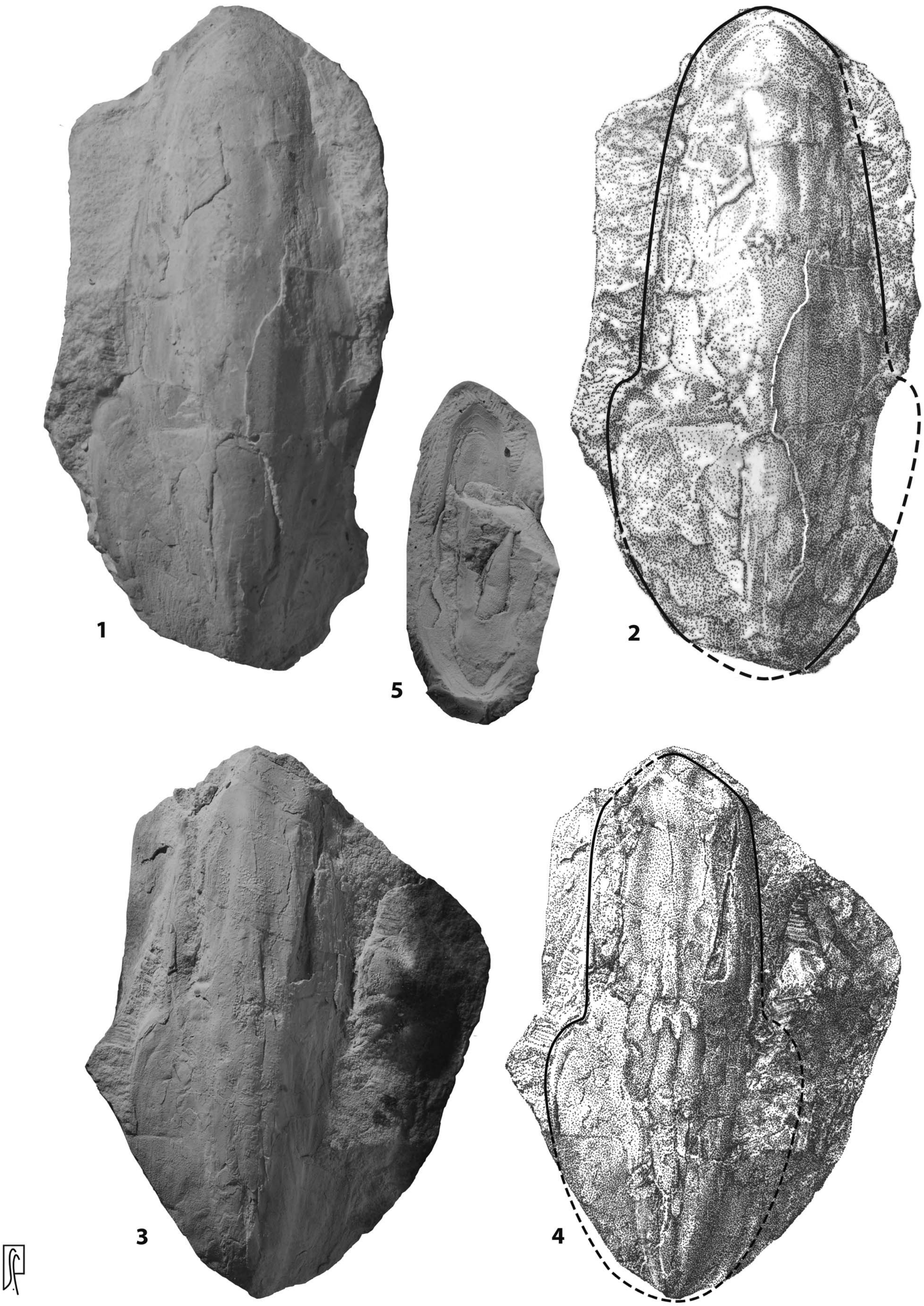
Almost all specimens included in *T. hastiformis* are from the lower Tithonian lithographic limestones of Solnhofen and Nusplingen, southern Germany. However, as a result of a morphological comparison by Fuchs et al. (2007, p. 576), based on at least 50 specimens from those localities deposited in different museums, *Trachyteuthis hastiformis* was restricted to specimens with coarse and irregular dorsal granulation and a median field with a spindle-shaped elevation, a feature first noted by Wagner (1860, p. 755). Two new species were also recognized, i.e., *T. nusplingensis* Fuchs, Engeser, and Keupp, 2007, and *T. teudopsiformis* Fuchs, Engeser, and Keupp, 2007. *T. nusplingensis* was characterized by a flat dorsal gladius and regular and fine granulation, whereas *T. teudopsiformis* was said to have a gladius median field with a pronounced median keel, narrow granulation restricted to the posterior keel, and sharply pointed anterior gladius. According to Fuchs et al. (2007, p. 588), reliable comparisons with *Trachyteuthis* representatives from other localities and stratigraphic levels are difficult or impossible, as in most cases morphological knowledge is antiquated or based on only a few poorly preserved specimens. In the opinion of Fuchs et al. (2007), all those specimens should be considered as *Trachyteuthis* sp. until additional records and morphological features justify specific distinctions.

On the basis of the mentioned diagnostic features, especially the presence or absence of spindle-shaped elevation on the median field of the gladius, besides the lectotype only ~10 of the ~23 figured specimens assigned to *T. hastiformis* between 1829 and 2006 should remain in this species (i.e., d'Orbigny, 1839, in Férussac and d'Orbigny, 1835–1848, pl. 14, fig. 2, pl. 16, fig. 1; Meyer, 1855, pl. 19, figs. 1, 2—var. *media* and *minor* of Wagner, 1859—; Rietschel, 1977, fig. 6; Bandel and Leich, 1986, figs. 14–16; Donovan, 1995, fig. 1; Fuchs, 2006a, pl. 14, figs. B, C), while ~13 should be excluded (i.e., d'Orbigny, 1839, in Férussac and d'Orbigny, 1835–1848, p. 290, pl. 14, fig. 1; pl. 15, figs. 1, 3; d'Orbigny, 1845, pl. 5, fig. 4, pl. 6, fig. 1; Quenstedt, 1849, pl. 31, fig. 25; Pictet, 1854, pl. 48, fig. 3; Zittel, 1885, fig. 710; Crick, 1896, pl. 14; Naef, 1922, fig. 51; Donovan, 1977, figs. 8, 9; Doyle, 1991, text-figs. 2A, B). For the latter there are at least two additional names available besides *T. linguatus*: *T. latipinnis* (Owen, 1855) and *T. zhuravlevi* (Hecker and Hecker, 1955). Resolution of this issue must await future studies of the European material.

Coccoteuthis, with *C. latipinnis* as type species, was introduced by Owen (1855, p. 125, pl. 7) for two specimens from the Kimmeridge clay of England. Owen (1855, p. 125) compared his material with several specimens from the Tithonian of Solnhofen, figured by König (1825, pl. 17, fig. 201) as '*Sepia prisca*,' by Rüppell (1829, p. 9, pl. 3, fig. 2) as '*Sepia hastiformis*,' by d'Orbigny (1839, in Ferussac and d'Orbigny, 1835–1848, pl. 14, figs. 1, 2) as '*Sepia antiqua* Münster,' and undesignated by Münster (1846, pl. 9, fig. 1), although he mentioned that *C. latipinnis* was broader in proportion to its length, a feature apparently shared by material from southern Germany, as exemplified by a specimen figured by Quenstedt (1849, p. 493, pl. 32, fig. 1) as *T. hastiformis*. Owen (1855) was apparently unaware of Meyer's (1846) proposal of *Trachyteuthis,* with *T. ensiformis* as type species, for part of Münster's (1846) material. Wagner (1860) proposed the synonymy of *Trachyteuthis* Meyer, 1846 and *Coccoteuthis* Owen, 1855, although he retained the latter as a senior synonym mentioning that figures and description were only given by Meyer in 1855. A similar view was taken by Keferstein (1866, p. 1441), Trautschold (1866, p. 15), and Crick (1896, p. 440), but Zittel (1885, 1895) took the opposite view, as did Naef (1922, p. 138) and all subsequent authors.

Trachyteuthus zhuravlevi (Hecker and Hecker, 1955) was introduced for one specimen from the Tithonian of Ulyanovsk (= Simbirsk) province, originally described as "*Coccoteuthis hastiformis* Rüpp." by Trautschold (1866, p. 15, pl. 4), and two other specimens (Hecker and Hecker, 1955, p. 40, pl. 2, figs. 2-3, text-figs. 4, ?5 [reproduced in part by Krymholts, 1958, pl. 71, fig. 3] + ?1) from the Tithonian of Pugachyov, Saratov province, also in the lower Volga River region. *T. zhuravlevi* is very similar to *T. hastiformis*, but according to Hecker and Hecker's (1955) interpretation of a specimen of this last species figured by Quenstedt (1849, pl. 31, fig. 25), it would differ in a narrow median band having granulae and keel, whereas in *T. hastiformis* they would cover the total median field of the gladius. In fact, both species appear to differ in the presence or absence of a spindle-shaped elevation on the gladius median field, a feature regarded by Fuchs et al. (2007, p. 579) as diagnostic for *T. hastiformis* (see the preceding).

Voltzia, with *V. palmeri* as type species, was introduced by Schevill (1950, p. 99, pl. 23, figs. 1–3) for two specimens from the Oxfordian of Cuba. According to Shevill (1950, p. 99) differences with *Trachyteuthis* were in the more prominent and chevron-shaped growth lines of the central field and the presence of a ventral "convex axial deposit smaller than but resembling the phragmocone of *Sepia*." Schevill (1950, p. 100) considered that "there is no close relationship between *Voltzia* and *Trachyteuthis*," noting differences in proportions and stressing the presence of a "modified phragmocone" as an essential contrast with regard to representatives of the latter as well as to "a series of Solnhofen-Eichstätt teuthoids" he had the opportunity to examine. The paratype, which was not figured, was said to have only two-thirds of the anterior part preserved, while the holotype, as described and figured by Schevill (1950, pl. 23, fig. 1) lacks the posterior margin and the right lateral field, whereas the left lateral field is not clearly visible. Moreover, Schevill's (1950, p. 99–100) description mentions, "dorsal surface tuberculate, more finely toward edges," a feature that is not clearly visible in the figure, especially with regard to arrangement and regularity. However, as all dorsal features of the anterior part and median field described and figured by Schevill (1950, pl. 23, figs. 1–3) do not differ from those known in *Trachyteuthis*, and even if the existence of a ventral phragmocone-like 'deposit' remains doubtful (cf. Waage, 1965, p. 17) and cannot be checked because the type material is missing from the collections of the Museum of Comparative Zoology, Cambridge, USA (cf. Jeletzky, 1966, p. 107), *Voltzia* has been considered, tentatively (Jeletzky, 1966, p. 45, 107;


1
2
3
4
5

Donovan, 1977, p. 31) or definitely (Riegraf, 1995, p. 151; Fuchs et al., 2007, p. 579), a synonym of *Trachyteuthis*. It could also be considered a nomen dubium (ICZN, 75.5, G).

Although the hyperbolar zone length/gladius length ratios of these species has been considered diagnostic for *Trachyteuthis* (Fuchs et al., 2007), i.e., HZL/GL = 0.40–0.45, they differ from those shown by *T. covacevichi* (HZL/GL = 0.45–0.52) and the new species *T. chilensis* n. sp. (HZL/GL = 0.34), recognized in the following. Thus, an emendation to the diagnosis of *Trachyteuthis* seems to be necessary (see the preceding).

Trachyteuthis covacevichi Fuchs and Schultze, 2008
Figure 2.1–2.5

1989 *Plesioteuthis* sp.; Schultze, p. 186, pl. 1, fig. 2

2006 *Trachyteuthis* sp.; Fuchs, 2006a, pl. 14, fig. F

pars 2006 *Trachyteuthis* sp.; Rubilar and Pérez d'A., fig. 2D, non figs. 2 A, 2B (= *Trachyteuthis chilensis* n. sp., see below), non fig. 2C (= *Pseudoteudopsis perezi* n. gen. n. sp., see the following).

2008 *Trachyteuthis covacevichi* Fuchs and Schultze, p. 43, figs. 3A–3C, 4 (Fuchs, 2006a, pl. 14, fig. F refigured), 5.

Holotype.—Specimen consisting of an almost complete gladius, SGO.PI. 6437a–b, here refigured in Figure 2.1.

Diagnosis.—Gladius with a hyperbolar length/gladius length ratio of 0.40–0.52. Anterior gladius end more or less rounded (modified from Fuchs and Schultze, 2008, p. 42; see Remarks).

Occurrence.—Middle Oxfordian *transversarium* Zone of Quebrada del Profeta, Antofagasta Region, Chile. As explained in the preceding section on Material and geological setting, the type horizon was referred to the Oxfordian by Rubilar and Pérez, d'A. (2006) due to the presence of the ammonite genera *Mirosphinctes* Schindewolf, *Euaspidoceras* Spath, *Cubaspidoceras* Myczynski, and ‘*Perisphinctes*’ Waagen, and labeled as “uncertain (probably cordatum zone), early Oxfordian,” without other considerations, by Fuchs and Schultze (2008, p. 44). However, as mentioned in the preceding Material and geological setting section, the specimens of *T. covacevichi* from Quebrada del Profeta level ‘10’ were found together with ammonites belonging to the subgenera *Antilloceras* Wierzbowski and *Gregoryceras* Spath, which characterize the middle Oxfordian *transversarium* Zone.

Description.—The holotype (Fig. 2.1, 2.2) is a three-dimensional uncompressed gladius with an elongate outline in which the posterior margin and the right lateral field have not been preserved. It has an inferred length (GL) of ~124.2 mm. Maximum gladius width (GW) = 58.2 mm at maximum expansion of the wing’s lateral fields, about 76.6 mm of gladius length measured from the anterior end. Gladius width decreases steadily toward the anterior margin, amounting to 45.6 mm at half of gladius length and 25.8 mm at 14.5 mm of the anterior margin. From there, the margin converges into a weakly rounded frontal tip. Median field is longitudinally and transversally arcuate, with maximum convexity in the gladius posterior end. Inner asymptotes separating the median field from the hyperbolar zones are clearly visible and diverge at an angle of 40°, whereas limit between the hyperbolar zone and lateral field is transitional. The gladius surface shows three successive layers partially exposed; the granulated dorsal (outer) layer is poorly represented and barely visible in a few patchy remnants on the gladius anterior right side and on the median field left slope at 65 mm of the anterior margin. The dorsal surface of the relatively thick intermediate layer shows ~18–20 growth lines of alternating strength per cm; on the median field they are strongly concave and projected toward the posterior margin to become almost parallel to the lateral margins on both sides of the median field. At about 83 mm of gladius length, measured from the anterior end, growth lines bend first outward and then backward, following the expansion of the lateral wings, forming the hyperbolar zone (HZ) and the related (inner) asymptote and merging gradually with the lateral field outer margin. Growth lines are weakly visible on the inner wall layer. Longitudinal ridges are also present on the outer surface of the intermediate layer along the median field, four of which (two, 0.11 mm apart, on each side of the median plane) are well visible in the posterior half of the gladius, coinciding with the point where the growth lines start to be parallel to the lateral margins; ridges of each pair are ~0.11 mm apart and diverge from the posterior margin end forming an angle of 15°. The area between both pairs of ridges and the axis of the median field is weakly depressed.

The second specimen (SNGM–8248; Fig. 2.3, 2.4) included in this species is also a three-dimensional uncompressed gladius with an elongated outline in which the posterior margin and anterior part of the right lateral field have not been preserved. It is smaller than the holotype and has an inferred length (GL) of 102 mm. Maximum gladius width (GW = 48 mm) corresponds to the maximum expansion of the lateral fields of the wings at about 59.2 mm of gladius length measured from the anterior end. Gladius width decreases steadily toward the anterior margin, amounting to 33.8 mm at half of gladius length and 27.6 mm at 10.2 mm of the anterior margin. From there, the margin converges into a weakly rounded frontal tip. Median field is longitudinally and transversally arcuate, with maximum transversal convexity in the gladius posterior end. Inner asymptotes separating the median field from the hyperbolar zones are clearly visible at the angle of convergence of the arcuate median field and the flat lateral wings and diverge

Figure 2. *Trachyteuthis covacevichi* Fuchs and Schultze, 2008, middle Oxfordian (*transversarium* Zone), Antofagasta Region, Chile. (**1, 2**) Holotype (plaster cast, SNGM-8245), Quebrada del Profeta, H.P. Schultze collection (original SGO.PI 6437): (**1**) dorsal view of plaster cast (coated with ammonium chloride); (**2**) same as (**1**) (drawing with gladius reconstructed outline). (**3, 4**) Nearly complete gladius, Cerro Islote, V. Covacevich collection (SNGM-8248): (**3**) dorsal view (coated with ammonium chloride); (**4**) same as (**3**) (drawing with gladius reconstructed outline). (**5**) Juvenile gladius (rubber cast of internal mold, SNGM-8247; original, SGO.PI 6438), Quebrada Sandón, H.P. Schultze and V. Covacevich collection. All figures 0.90x.

https://doi.org/10.1017/jpa.2016.110 Published online by Cambridge University Press

Table 1. Measurements in millimeters for *Trachyteuthis covacevichi* Fuchs and Schultze, 2008. GL = gladius length; GW = maximum gladius width; $GW_{1/2\ GL}$ = gladius width at half GL; GW_{HZ} = gladius width at anterior end of hyperbolar zone (HZ); GW_{LF} = gladius width at anterior end of lateral fields (LF); HZL = hyperbolar zone length; LFL = lateral fields length; A_{ia} = angle of diverging inner asymptotes; A_{ga} = angle of diverging granulate area. Values in parentheses = relation of each dimension to GL.

	GL	GW	$GW_{1/2GL}$	GW_{HZ}	GW_{LF}	HZL	LFL	GW/HZL	A_{ia}	A_{ga}
Holotype SGNM-8245	124.2	58.2 (0.47)	45.6 (0.37)	47.8 (0.38)	54.8 (0.44)	56.5 (0.45)	54.3 (0.44)	1.03	40°	15°
SNGM-8248	~102	48 (0.47)	33.8 (0.33)	33.8 (0.33)	44.7 (0.44)	53.1 (0.52)	48.8 (0.48)	0.90	40°	
SNGM-8247	54.3	24.8 (0.46)	18 (0.33)	17.6 (0.32)	24 (0.44)	22.8 (0.42)	21 (0.39)	1.08		

with an angle of 40°, whereas limit between the hyperbolar zone and lateral field is less pronounced and only visible on the gladius posterior right side. The gladius surface shows successive layers partially exposed but not clearly differentiated due to preservation; the granulated dorsal (outer) layer is poorly represented and barely visible in a few patchy remnants on the median field. The dorsal surface of what appears to be the intermediate layer shows some barely visible growth lines on some parts of the median field and on the lateral fields. Longitudinal protuberances like ridges are also present on both sides of the median field and are well visible in the gladius middle region. The areas between both ridges and the axis of the median field are slightly depressed.

A small juvenile gladius (SGO.PI.6438, SNGM–8247; Fig. 2.5) is preserved as a three-dimensional external mold exposing half of the gladius anterior part, left wing lateral field, and posterior margin, whereas other parts of the mold are filled with sediment. It has a length (GL) of 54.3 mm. The inferred maximum gladius width (GW = 24.8 mm) is on the maximum expansion of the wings' lateral fields, at about 37 mm of gladius length measured from the anterior end. Gladius width decreases steadily toward the anterior margin, amounting to 18 mm at half of gladius length and 10.8 mm at 6 mm of the anterior margin. From there the margin converges into a triangular frontal tip. The gladius anterior half is longitudinally and transversally arcuate. The gladius surface shows barely visible growth lines parallel to the margins in the left wing and close to the anterior, lateral and posterior margins (see Table 1).

Material.—The holotype, one plaster cast of a small (juvenile) gladius (SGO. –PI.6438) from tributaries north of Quebrada del Profeta, and three nearly complete gladii from a concretionary level, Quebrada del Profeta (SNGM–8245), Cerro Islote (SNGM–8248), and Quebrada Sandon (SNGM–8247), middle Oxfordian *transversarium* Zone, Antofagasta Region, Chile.

Remarks.—Some rather small differences between holotype dimensions reported by Fuchs and Schultze (2008, p. 43) and those recorded here could be because preservation prevents accurate measurements. The difference in recorded $GW_{1/2GL}$ (38 vs. 45.6 mm) could be due to reconstruction of missing parts. Difference in LFL values (38 vs. 54.3) is probably related to different interpretations of structure limits. The new specimen figured here (Fig. 2.3, 2.4) indicates that the 0.40–0.45 hyperbolar zone length/gladius length ratio given by Fuchs and Schultze (2008, p. 42) in the species diagnosis should be enlarged to 0.40–0.52.

As indicated by Fuchs and Schultze (2008, p. 45), the gladius of *T. covacevichi* differs from those of *T. hastiformis* and *T. nusplingensis*, from the Tithonian of southern Germany, by being relatively wider (GW/GL = 0.46–0.47 vs. 0.35–0.39) and more compact (LFL/GL = 0.39–0.48 vs. 0.32–0.35; GW_{HZ}/GL = 0.30–0.38 vs. 0.27–0.28). It also lacks the spindle-shaped elevation in the median field of *T. hastiformis.* As mentioned in the preceding, its gladius is also wider and more compact than that of *T. chilensis* n. sp. Comparison with *T.* cf. *hastiformis* from the Tithonian of Antarctica (Doyle, 1991, p. 172, text-fig. 2A, 2B) is hindered by the poor preservation of the Antarctic material.

Trachyteuthis chilensis new species
Figure 3.1–3.3

pars 2006 *Trachyteuthis* sp.; Rubilar and Pérez d'A., fig. 2A, 2B, non fig. 2C (= *Pseudoteudopsis perezi* n. gen. n. sp., see below); non Fig. 2D (= *Trachyteuthis covacevichi* Fuchs and Schultze, 2008; see the preceding).

Holotype.—The almost complete gladius with counterpart of anterior region, SNGM–8246, here figured in Figure 2.1–2.3, middle Oxfordian, Quebrada del Profeta, Antofagasta, Chile.

Diagnosis.—Compressed gladius of medium size with elongated outline, weakly rounded frontal tip, and pointed posterior margin, median field laterally limited by two weakly raised blunt ridges that diverge from the posterior to the anterior margin at an angle of about 20°, passing inward into two shallow depressions bordering on both sides a rounded weak elevation along the median field, granulae on dorsal surface regularly arranged following the anterior margin.

Occurrence.—Thus far species only known from the middle Oxfordian *transversarium* Zone of Quebrada del Profeta, Antofagasta Region, Chile.

Description.—The holotype is a compressed gladius with an elongated outline where the posterior margin and the left and partly the right lateral fields have not been preserved. It has an inferred length (GL) of ~221 mm. Maximum gladius width (GW = ~ 75.3 mm) corresponds to the maximum expansion of the wings' lateral fields at about 150.8 mm of the gladius length measured from the anterior end. Gladius width decreases steadily toward the anterior margin, amounting to 55.8 mm at half of gladius length and 38 mm at 17.6 mm of the anterior margin. From there, the margin converges into a weakly rounded frontal tip. On both sides along the median field are two weakly raised blunt ridges (indicated with X and X' in Fig. 3.2) that diverge from the posterior to the anterior margin at an angle of about 20° and are clearly visible at about half of gladius length; outward they are limited by a flat marginal area, and inward they pass

https://doi.org/10.1017/jpa.2016.110 Published online by Cambridge University Press

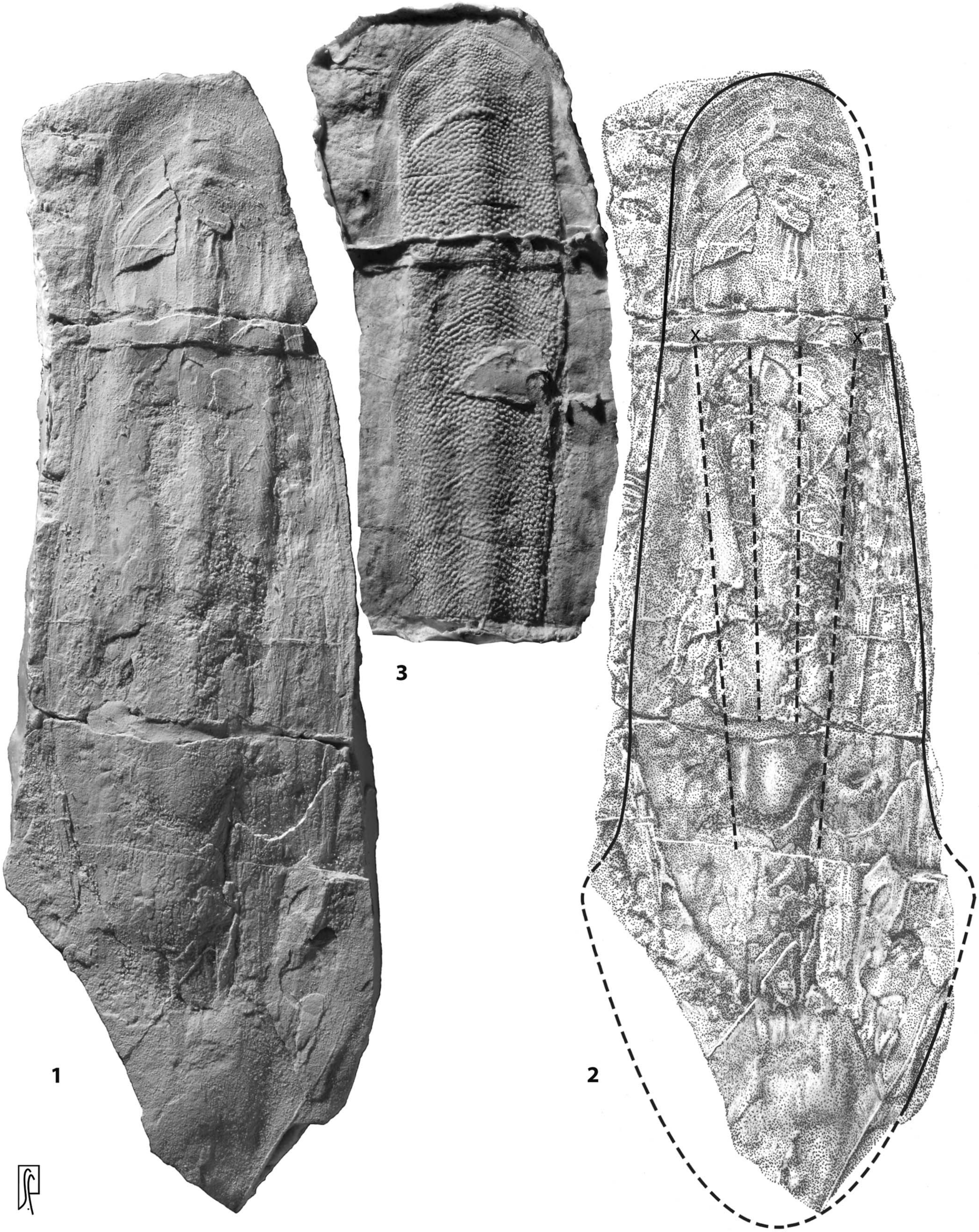


Figure 3. *Trachyteuthis chilensis* n. sp., Holotype (SNGM-8246, V. Covacevich collection), middle Oxfordian (*transversarium* Zone), Quebrada del Profeta, Antofagasta Region, Chile. (**1**) Gladius dorsal view (coated with ammonium chloride), 1x; (**2**) same as (**1**) (drawing with gladius reconstructed outline), 1x; (**3**) dorsum counterpart (rubber cast) showing median field granulated area, 0.90x. X–X´ = lateral ridges along median field.

https://doi.org/10.1017/jpa.2016.110 Published online by Cambridge University Press

Table 2. Measurements in millimeters for *Trachyteuthis chilensis* n. sp. GL = gladius length; GW = maximum gladius width; $GW_{1/2\ GL}$ = gladius width at half GL; GW_{HZ} = gladius width at anterior end of hyperbolar zone (HZ); GW_{LF} = gladius width at anterior end of lateral fields (LF); HZL = hyperbolar zone length; LFL = lateral fields length; A_{ia} = angle of diverging inner asymptotes; A_{ga} = angle of diverging granulate area. Values in parentheses = relation of each dimension to GL.

	GL	GW	$GW_{1/2GL}$	GW_{HZ}	GW_{LF}	HZL	LFL	GW/HZL	A_{ia}	A_{ga}
Holotype SNGM- 8246	~221	? 75.3 (0.34)	55.8 (0.25)	? 61.4 (0.28)	? 73.0 (0.33)	? 75.3 (0.34)	? 63.9 (0.29)	1.00	40°	10°

into two shallow depressions bordering on both sides a rounded weak elevation along the median field; depressions fade away anteriorly, where the median field becomes flat, and posteriorly where it is bluntly arched. An inner asymptote separating the median field from the hyperbolar zone is barely visible on the posterior right side, and the limit between the hyperbolar zone and the lateral field is marked by a very weak ridge. The estimated inner asymptote angle amounts to about 40°. The gladius surface shows three successive layers partially exposed; the granulated dorsal (outer) layer is poorly represented and barely visible in a few patchy remnants, e.g., on the gladius anterior right side and on the median field right depression at about half of the gladius length. The dorsal surface of the intermediate layer shows growth lines near the anterior margin, where they are strongly concave on the median field and projected toward the posterior margin to become almost parallel to the lateral margins; they are of alternating strength, the stronger amounting to about four per centimeter, while the weaker are barely visible. Very weak longitudinal ridges are also present on the outer surface of the intermediate layer along the lateral margins. A counterpart of the gladius anterior region (Fig. 2.3), with a length of 116.4 mm, shows the imprint of the dorsal gladius surface, where granulae are clearly exposed; they are regularly arranged following the growth lines of the median field and the shape of the gladius anterior margin; they reach their maximum size on the median line between 20 and ~60 mm of the anterior margin to become smaller toward the anterior, posterior, and lateral margins. The rounded weak elevation along the median field is clearly visible along the total gladius length, whereas the weak left ridge and concave depression are restricted to an area at about half of the gladius length (see Table 2).

Etymology.—From Chile, country of provenience of the holotype.

Material.—Holotype, SNGM–8246.

Remarks.—*Trachyteuthis chilensis* resembles *T. hastiformis* in the general outline, but differs in the absence of a spindle-shaped elevation in the gladius median field, in the regular arrangement and size variation of granulae, and perhaps, as reconstructed here, in the more elongated gladius with more pointed posterior and rounded anterior margins. It should be noted, however, that the presence in the middle part of the gladius of *T. chilensis* of a weak rounded elevation with two shallow depressions on either side could represent an incipient development of the spindle-shaped elevation that characterizes the younger species. Comparison with *T.* cf. *hastiformis* from the Tithonian of Antarctica (Doyle, 1991, p. 172, text-fig. 2A–2B) is hindered by the poor preservation of the Antarctic material.

Trachyteuthis chilensis differs from *T. latipinnis* (Owen, 1855) by being smaller (GL = ~221 mm vs. ~308 mm) and by the more elongated outline of the gladius and median field, the more rounded and flat gladius anterior margin, and the more regular granule arrangement.

Comparison with *T. zhuravlevi* Hecker and Hecker, 1955 is made difficult by the incomplete and poor preservation of the Russian specimens, although one of them (Hecker and Hecker, 1955, pl. 2, fig. 2, text-fig. 4; Krymholts, 1958, pl. 71, fig. 3) appears to have a broader gladius posterior margin and a narrower median field.

Trachyteuthis covacevichi has a smaller (GL = 54.3–124.2 mm vs. ~221 mm), relatively wider (GW/GL = 0.46–0.47 vs. 0.34), and more compact gladius (LFL/GL = 0.39–0.48 vs. 0.29; $W_{HZ}/_{GL}$ = 0.32–0.38 vs. 0.28).

Comparison with *T.* (?) *palmeri* (Schevill, 1950; p. 99, pl. 23, figs. 1, 2), from the Oxfordian of Cuba, is hindered by the incomplete preservation of the Cuban specimens—which are lost—where the lateral fields, hyperbolar zones, and tubercles are missing or are not clearly visible in the figures. Some proportions look rather similar, although the Cuban species appears to differ from *T. chilensis* in being smaller (GL = 197 mm vs. 221 mm) and broader ($GW_{1/2GL}$ = 0.28 vs. 0.25) and having a more anteriorly pointed gladius.

Genus *Pseudoteudopsis* new genus

Type species.—*Pseudoteudopsis perezi* new species, by monotypy.

Diagnosis.—As for the species.

Occurrence.—Thus far only known from the Callovian of the Antofagasta Region, Chile.

Etymology.—*Pseudo* (Gr.), meaning false, and *Teudopsis* (*Teuthis,* Gr., calamar; *øps,* Gr., appearance), referring to the false similarity with *Teudopsis* Deslongchamps, 1835.

Remarks.—*Pseudoteudopsis* n. gen. resembles *Teudopsis* Deslongchamps, 1835 in the pronounced median keel, but the latter is characterized by gladius margins converging rather rapidly in a pointed blade-like or spike-like anterior margin or a free rhachis (cf. Fuchs and Weis, 2010). Moreover, *Pseudoteudopsis* n. gen. differs in its elongated outline with rounded posterior and anterior margins, flat and poorly developed wings, presence of granulae on the dorsal surface, and an entire median keel of almost the same width from the posterior to the anterior margin.

https://doi.org/10.1017/jpa.2016.110 Published online by Cambridge University Press

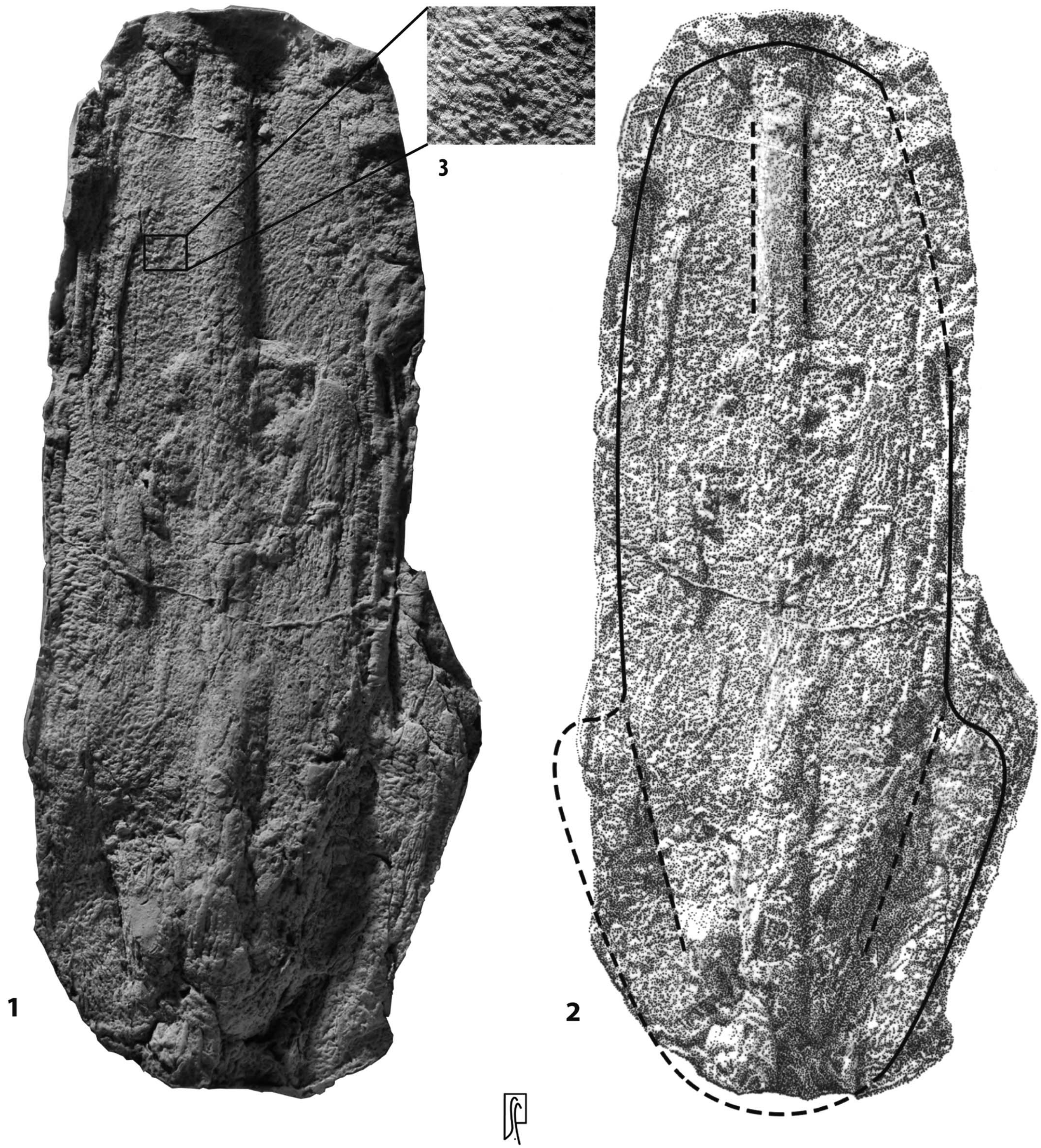


Figure 4. *Pseudoteudopsis perezi* n. gen. n. sp. Holotype, SNGM-1849, A. Tomlinson collection, lower Callovian (uppermost *bodenbenderi* to lowermost *proximum* Zones), Quebrada Quinchamale, northwest of Cerro Jaspe, Antofagasta province, Chile. (**1**) Rubber cast of external mold (coated with ammonium chloride); (**2**) same as (**1**) (drawing with gladius reconstructed outline); (**3**) detail of (**1**), external mold showing granulate area. (**1, 2**) 1x; (**3**) 4x.

Pseudoteudopsis perezi new species
Figure 4.1–4.3

pars 2006 *Trachyteuthis* sp.; Rubilar and Pérez d'A., fig. 2C; non fig. 2A, 2B (= *Trachyteuthis chilensis* n. sp., see the preceding), non fig. 2D (= *Trachyteuthis covacevichi* Fuchs and Schultze, 2008; see the preceding).

Holotype.—A three-dimensional external mold of a gladius of which a rubber cast is figured in Figure 4.1, 4.2, collected by

https://doi.org/10.1017/jpa.2016.110 Published online by Cambridge University Press

Table 3. Measurements in millimeters for *Pseudoteudopsis perezi* n. gen. n. sp. GL = gladius length; GW = maximum gladius width; $GW_{1/2\ GL}$ = gladius width at half GL; GW_{HZ} = gladius width at anterior end of hyperbolar zone (HZ); GW_{LF} = gladius width at anterior end of lateral fields (LF); HZL = hyperbolar zone length; LFL = lateral fields length; A_{ia} = angle of diverging inner asymptotes; A_{ga} = angle of diverging granulate area. Values in parentheses = relation of each dimension to GL.

	GL	GW	$GW_{1/2GL}$	GW_{HZ}	GW_{LF}	HZL	LFL	GW/HZL	A_{ia}	A_{ga}
Holotype SNGM- 1849	169	71 (0.42)	52.5 (0.31)	51.9 (0.31)	68.6 (0.40)	65.3 (0.39)	~59 (0.35)	1.08	50°	

Andrew Tomlison in 2005 and deposited at the SERNAGEOMIN (SNGM–1849), lower Callovian.

Diagnosis.—Elongated outline with rounded posterior and anterior margins, flat and poorly developed wings, presence of granulae on the dorsal surface, and a pronounced median ridge of almost the same width from the posterior to the anterior margin.

Type horizon.—Lower Callovian uppermost *bodenbenderi* to lowermost *proximum* zones, south of Quebrada Quinchamale, ~5 km northwest of Cerro Jaspe.

Description.—The holotype is represented by a three-dimensional external mold of a gladius with an elongated outline where the posterior margin and the left lateral wing are not preserved. It has an inferred length (GL) of 169 mm. Maximum gladius width (GW = 71 mm) on maximum expansion of the wings' lateral fields, at about 114.5 mm of gladius length measured from the anterior end. Gladius width decreases steadily toward the posterior margin with 51.5 mm at the beginning of the hyperbolar zones, from which the inner asymptotes continue bordering a relatively prominent median field, which reaches 22.4 mm in width just before forming a rounded posterior tip. Inner asymptotes diverge with an angle of 50° and separate the median field from the hyperbolar zone, which is not differentiated from the lateral fields. The gladius margins converge gradually toward the anterior margin reaching 32.9 mm in width just before forming a blunt anterior margin with a very small radius of curvature. Median field is flat in the gladius anterior half and becomes progressively more arcuate toward the posterior margin. The internal mold shows some patchy shell remnants and areas with irregular granulae and longitudinal fine ridges subparallel to gladius margin. Along the median line there is a prominent rounded ridge with a rather uniform width of ~9.3 mm from the posterior to anterior margin (see Table 3).

Etymology.—After my colleague and friend the late Ernesto Pérez d'Angelo (1932–2013), who promoted the initiation of this study, in recognition of his life-long contributions to the paleontology of Chile.

Material.—The holotype.

Remarks.—*Pseudoteudopsis perezi* n. sp. resembles *Teudopsis* sp. described by Fischer and Riou (1982, p. 15, pl. 3, fig. 7) from the lower Callovian of Voulte-sur-Rhône, France, in the presence of a prominent median keel having a similar width from the posterior to the anterior margin. The French specimen—a doubtful *Teudopsis* according to Fuchs and Weis (2010, p. 355)—is poorly preserved and consists of the posterior half of the gladius median field, in which the lateral wings are not visible. Its inclusion in *Teudopsis* was assumed (Fischer and Riou, 1982, p. 16) because the strong obliquity of the growth lines suggested a pointed rhachis. This specimen appears to differ from *Pseudoteudopsis perezi* n. gen. n. sp. in the pointed rhachis and the fact that the median keel is formed by 4–5 narrower ridges, but poor preservation prevents a close comparison.

A species of *Trachyteuthis* with a median keel, i.e., *Trachyteuthis teudopsiformis* Fuchs, Engeser, and Keupp (2007, p. 584, fig. 6) from the lower Tithonian of southern Germany, differs in the relatively broader gladius, more developed wings, and less prominent median keel that becomes wider and flattened toward the anterior margin.

Conclusions

As a result of this study, all known coleoid specimens from the Jurassic of Chile, representing the largest non-European coleoid collection outside Europe, are described and figured and referred to the Trachyteuthididae. An early Callovian specimen, the only one of that age known outside Europe, is referred to a new genus and species, *Pseudoteudopsis perezi* n. gen. n. sp. The genus *Trachyteuthis* Meyer, 1846 is represented by two middle Oxfordian species, *T. covacevichi* Fuchs and Schultze, 2008 and *T. chilensis* n. sp. The status of the different species of *Trachyteuthis* is reviewed. *T. latipinnis* (Owen, 1855) and *T. zhuravlevi* (Hecker and Hecker, 1955), originally described from Great Britain and Russia, respectively, are accepted as valid species. '*Voltzia palmeri*' (Schevill, 1950) from the Oxfordian of Cuba could be considered a poorly known species of *Trachyteuthis* or a nomen dubium. For *Trachytetuhis* type species, *T. hastiformis* (Rüppell, 1829), all specimens previously figured are reviewed, listing those that could and could not belong in the species. For the latter, it is concluded that at least one additional name is available, i.e., *T. linguatus* (d'Orbigny, 1839, in Férussac and d'Orbigny, 1835–1848).

Acknowledgments

The late E. Pérez d'A. and A. Rubilar R. made the specimens deposited at SERNAGEOMIN available for this study. A. Rubilar R. also contributed with field information and useful suggestions to improve this paper. Drawings were prepared by S. Faiad. Reviews by L. Doguzhaeva and D. Fuchs and comments by Editor J. Jin and Associate Editor D. Work improved the manuscript. The author is solely responsible for any existing mistakes. Laboratory research was financed by the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Argentina.

References

Bandel, K., and Leich, H., 1986, Jurassic Vampyromorpha (dibranchiate cephalopods): Neues Jahrbuch für Geologie und Paläontologie, Montashefte, v. 1986, p. 129–148.

Bather, F.A., 1888, Shell-growth in Cephalopoda (Siphonopoda): Annals and Magazine of Natural History, v. 6, p. 421–427.

Chong, G., and Förster, R., 1976, *Chilenophoberus atacamensis*, a new decapod crustacean from the middle Oxfordian of the Cordillera de Domeyko, northern Chile: Neues Jahrbuch für Geologie und Paläontologie, Monatshefte, v. 1976, p. 145–156.

Crick, G.C., 1896, On a specimen of *Coccoteuthis hastiformis*, Rüppell, sp., from the Lithographic Stone, Solenhofen, Bavaria: Geological Magazine, v. 3, p. 439–443.

Deslongchamps, E., 1835, Mémoire sur les Teudopsides, animaux fossiles, voisins des Calmars: Bulletin de la Société Linnéenne de Normandie, Mémoire, v. 5, p. 68–78.

Donovan, D., 1977, Evolution of the dibranchiate Cephalopoda: Symposia of the Zoological Society of London, v. 38, p. 15–48.

Donovan, D., 1995, A specimen of *Trachyteuthis* (Coleoidea) with fins from the Upper Jurassic of Solnhofen (Bavaria): Stuttgarter Beiträge zur Naturkunde, v. B235, p. 1–8.

Donovan, D.T., and Fuchs, D., 2016, Fossilized soft tissues in Coleoidea: Treatise Online, Number 73, Part M, Chapter 13: 1-30.

Donovan, D.T., Doguzhaeva, L.A., and Mutvei, H., 2003, Two pairs of fins in the Late Jurassic coleoid *Trachyteuthis* from southern Germany: Berliner Paläobiologische Abhandlungen, v. 3, p. 91–99.

d'Orbigny, A., 1845, Paléontologie Universelle des Coquilles et des Mollusques, Paris, Gide et Cie., 320 p.

Doyle, P., 1991, Teuthid cephalopods from the Upper Jurassic of Antarctica: Palaeontology, v. 34, p. 169–178.

Doyle, P., Donovan, D.T., and Nixon, M., 1994, Phylogeny and systematics of the Coleoidea: The University of Kansas, Paleontological Contributions, v. 5, p. 1–15.

Engeser, T., and Reitner, J., 1985, Teuthiden aus dem Unterapt ("Töck") von Helgoland (Schleswig-Holstein, Norddeutschland): Paläontologische Zeitschrift, v. 59, p. 245–260.

Férussac, A.E. d'Audebard de, and d'Orbigny, A., 1835–1848, Histoire Naturelle Générale et Particulière des Céphalopods Acétabulifères Vivants et Fossils, Paris, A. Lacour, 361 p.

Fischer, J.-C., and Riou, B., 1982, Les Teuthoïdes (Cephalopoda, Dibranchiata) du Callovien inférieur du la Voulte-Sur-Rhône (Ardèche, France): Annales de Paléontologie, v. 68, p. 295–325.

Fuchs, D., 2006a, Fossil erhaltungsfähige Merkmalskomplexe der Coleoidea (Cephalopoda) und ihre phylogenetische Bedeutung: Berliner Paläobiologische Abhandlungen, v. 8, p. 1–115.

Fuchs, D., 2006b, Morphology, taxonomy and diversity of vampyropod coleoids (Cephalopoda) from the Upper Cretaceous of Lebanon: Memorie della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano, v. 34, p. 1–28.

Fuchs, D., 2007, Coleoid cephalopods from the Plattenkalks of the Late Jurassic of southern Germany and the Late Cretaceous of Lebanon—A faunal comparison: Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, v. 245, p. 59–69.

Fuchs, D., 2014, First evidence of *Mastigophora* (Cephalopoda: Coleoidea) from the early Callovian of La Voulte-sur-Rhône (France): Göttingen Contributions to Geosciences, v. 77, p. 21–27.

Fuchs, D., and Larson, N., 2011, Diversity, morphology, and phylogeny of coleoid cephalopods from the Upper Cretaceous Plattenkalks of Lebanon—Part II: Teudopseina: Journal of Paleontology, v. 85, p. 815–834.

Fuchs, D., and Schultze, H.-P., 2008, *Trachyteuthis covacevichi* n. sp., a Late Jurassic Palaeopacific coleoid cephalopod: Fossil Record, v. 11, p. 39–49.

Fuchs, D., and Weiss, R., 2010, Taxonomy, morphology and phylogeny of Lower Jurassic teudopseid coleoids (Cephalopoda): Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, v. 257, p. 351–366.

Fuchs, D., Engeser, T., and Keupp, H., 2007, Gladius shape variation in coleoid cephalopod *Trachyteuthis* from the Upper Jurassic Nusplingen and Solnhofen Plattenkalks: Acta Palaeontologica Polonica, v. 52, p. 575–589.

Germar, E.F., 1826, Ueber die Versteinerungen von Solenhofen. Deutschland, geognostisch-geologisch dargestellt, mit charten und Zeichnungen: Eine Zeitschrift herausgegeben von Ch. Keferstein, v. 4, p. 89–110.

Gygi, R.A., and Hillebrandt, A. von, 1991, Ammonites (mainly *Gregoryceras*) of the Oxfordian (Late Jurassic) in northern Chile and time-correlation with Europe: Schweizerische Paläontologische Abhandlungen, v. 113, p. 137–185.

Hecker, E.L., and Hecker, R.F., 1955, Remains of Teuthoidea from the Upper Jurassic and Lower Cretaceous of the Lower Volga area: Voprosy Paleontologii, v. 2, p. 36–44 [in Russian].

Hewitt, R.A., and Wignall, P.B., 1988, Structure and phylogenetic significance of *Trachyteuthis* (Coleoidea) from the Kimmeridge Clay of England: Proceedings of the Yorkshire Geological Society, v. 47, p. 149–153.

Hillebrandt, A., von, Kossler, A., and Gröschke, M., 2012, *Caracoliceras*, a new Oxfordian (Upper Jurassic) ammonite genus from northern Chile: Revue de Paléobiologie, v. VS8, p. 65–81.

International Commission on Zoological Nomenclature (ICZN) 1999, International Code of Zoological Nomenclature, London, International Trust for Zoological Nomenclature, 306 p.

Jeletzky, J.A., 1966, Comparative morphology, phylogeny, and classification of fossil Coleoidea: The University of Kansas, Paleontological Contributions, Mollusca, v. 7, p. 1–162.

Keferstein, W., 1866, Kopftragende Weichthiere (Malacozoa cephalophora), *in* Keferstein, W.M., and Bronn, H.G., Dr. H.G. Bronn's Klassen und Ordnungen der Weichthiere (Malacozoa) in Wort und Bild, Leipzig und Heidelberg, C.F. Winter´sche Verlagshandlung, 1500 p.

Klug, C., Schweigert, G., Dietl, G., and Fuchs, D., 2005, Coleoid beaks from the Nusplingen Lithographic Limestone (Upper Kimmeridgian, SW Germany): Lethaia, v. 38, p. 173–192.

Klug, C., Fuchs, D., Schweigert, G., Röper, M., and Tischlinger, H., 2015, New anatomical information on arms and fins from exceptionally preserved *Plesioteuthis* (Coleoidea) from the Late Jurassic of Germany: Swiss Journal of Palaeontology, v. 134, p. 245–255.

König, C.D.E., 1825, Icones Fossilium Sectiles: Centuria prima, London, G.B. Sowerby, p. 1–4.

Krymholts, G.Y., 1958, Subclass Endocochlia, *in* Orlov, Yu. A., ed., Fundamentals of Paleontology, 6, Mollusca, Cephalopoda, Moscow, p. 145–178 [In Russian].

Lindgren, A.R., Pankey, M.S., Hochberg, F.G., and Oakley, T.H., 2012, A multi-gene phylogeny of Cephalopoda supports convergent morphological evolution in association with multiple habitat shifts in the marine environment: Evolutionary Biology, v. 12, p. 1–15.

Meyer, H. von, 1846, Trachyteuthis ein neues Sepien-Genus von Solenhofen: Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefakten-Kunde, Mittheilungen, v. 1846, p. 598.

Meyer, H. von, 1855, *Trachyteuthis ensiformis* aus dem lithographischen Schiefer in Bayern: Palaeontographica, v. 4, p. 106–109.

Münster, G., 1837, Mineralogische Vorträge aud der Versammlung Deutscher Naturforscher und Ärzte, Jena 1836, Sektion für Geognosie, Geographie und Mineralogie: Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefaktenkunde, v. 1837, p. 252.

Münster, G., 1846, Ueber die schalenlosen Cephalopoden des oberen Juragebirges, der lithographischen Kalschiefer in Bayern: Beiträge zur Petrefaktenkunde, v. 7, p. 51–65.

Myczyński, R., 1976, A new ammonite fauna from the Oxfordian of the Pinar del Rio province, western Cuba: Acta Geologica Polonica, v. 26, p. 261–297.

Naef, A., 1916, Systematische Übersicht der mediterranen Cephalopoden: Publicazioni della Stazione Zoologica di Napoli, v. 1, p. 11–19.

Naef, A., 1921, Die Cephalopoden. *in* Flora e Fauna del Golfo di Napoli, Monograph, v. 35: Berlin, Friedländer, 148 p.

Naef, A., 1922, Die Fossilen Tintenfische, Eine Paläozoologische Monographie, Jena, G. Fischer Ed., 322 p.

Owen, R., 1855, Notice of a new species of an extinct genus of Dibranchiate Cephalopod (*Coccoteuthis latipinnis*) from the upper Oolithic Shales at Kimmeridge: Quarterly Journal of the Geological Society of London, v. 11, p. 124–125.

Owen, R.A., 1856, Description of cephalopods. *in* Descriptive Catalogue of the Fossil Organic Remains of Invertebrate Contained in the Museum of the Royal College of Surgeons of England, London, Taylor & Francis, p. 260.

Pictet, F.-J., 1854, Traité de Paléontologie, ou Histoire Naturelle des Animaux Fossils, Volume 2, Paris, J.-B. Baillière, 727 p.

Quenstedt, F.A., 1846–1849, Petrefactenkunde Deutschlands, 1, Cephalopoden, Tübingen, Fues, 581 p.

Riccardi, A.C., 2005, First teuthid cephalopod from the Lower Jurassic of South America (Neuquén Basin, Argentina): Geologica Acta, v. 3, p. 179–184.

Riccardi, A.C., 2008, The marine Jurassic of Argentina: A biostratigraphic framework: Episodes, v. 31, p. 326–335.

Riccardi, A.C., and Westermann, G.E.G., 1991, Middle Jurassic ammonoid fauna and biochronology of the Argentinean-Chilean Andes, Part IV, Bathonian-Callovian Reineckeiidae: Palaeontographica, v. A216, p. 111–145.

Riegraf, W., 1995, Cephalopoda dibranchiate fossiles (Coleoidea), *in* Westphal, F., ed., Fossilium Catalogus, I: Animalia, Amsterdam, Kugler Publications, 411 p.

Rietschel, S., 1977, Ein Belemnitentier mit Weichteilerhaltung und Rostrum im Senckenberg: Natur und Museum, v. 107, p. 121–130.

Rubilar, A.R., and Pérez d'A., E., 2006, Nuevos restos fósiles de téuthidos (Cephalopoda, Coleoidea) en Chile: XI Congreso Geológico Chileno, Actas, v. 2, p. 113–116.
Rüppell, E., 1829, Abbildung und Beschreibung einiger neuen oder wenig gekannten Versteinerungen aus der Kalkschieferformation von Solenhofen, Frankfurt a. M., H.L. Brönner, p. 3–12.
Schevill, W.E., 1950, An Upper Jurassic sepioid from Cuba: Journal of Paleontology, v. 24, p. 99–101.
Schindewolf, O.H., 1926, Zur Systematik der Perisphincten: Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, v. 55, p. 497–517.
Schultze, H.P., 1989, Three-dimensional muscle preservation in Jurassic fishes of Chile: Revista Geológica de Chile, v. 16, p. 183–215.
Spath, L.F., 1924, On the Blake collection of ammonites from Kachh, India: Memoirs of the Geological Survey of India, Palaeontologia Indica, N.S., v. 9, no. 1, p. 1–29.
Spath, F.L., 1927–1933, Revision of the Jurassic cephalopod fauna of Kachh (Cutch): Memoirs of the Geological Survey of India, Palaeontologia Indica, N.S., v. 9, no. 2, 945 p.
Steinmann, G., 1881, Zur Kenntniss der Jura und Kreideformation von Caracoles (Bolivia): Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, v. 1, p. 239–301.
Tornquist, A., 1898, Der Dogger am Espinazito-Paß: Palaeontologische Abhandlungen, Neue Folge, v. 8, p. 3–69.
Trautschold, H., 1866, Zur Fauna des russischen Jura: Bulletin Société Impériale des Naturalistes de Moscou, v. 39, p. 1–24.
Vecchione, M., Young, R.E., Donovan, D.T., and Rodhouse, P.G., 1999, Reevaluation of coleoid cephalopod relationships based on modified arms in the Jurassic coleoid *Mastigophora*: Lethaia, v. 32, p. 113–118.
Waage, K.M., 1965, The Late Cretaceous coleoid cephalopod *Actinosepia canadensis* Whiteaves: Postilla Peabody Museum of Natural History, Yale University, v. 94, p. 1–33.
Waagen, W., 1869, Die Formenreihe des Ammonites subradiatus: Geognostisch-Paläontologische Beiträge, v. 2, p. 181–256.
Wade, M., 1993, New Kelaenida and Vampyromorpha, Cretaceous squid from Queensland: Memoir of the Association of Australasian Paleontologists, v. 15, p. 353–374.
Wagner, A., 1859, Revision der bisherigen systematischen Bestimmungen der fossilen Ueberreste von nackten Dintenfischen aus dem süddeutschen Juragebirge: Gelehrte Anzeigen k. bayerischen Akademie der Wissenschaften, Mathematisch-physikalische Klasse, v. 48, no. 34, p. 274–278.
Wagner, A., 1860, Die fossilen Ueberreste von nackten Dintenfische aus dem lithographischen Schiefer und dem Lias des süddeutschen Juragebirges: Abhandlungen der königlich bayerischen Akademie der Wissenschaften Historischen Classe, v. 8, p. 751–821.
Walch, J.E.I., 1768–1773, Die Naturgeschichte der Versteinerungen zur Erläuterung der Knorrischen Sammlung von Merkwürdigkeiten der Natur: Nürnberg, P.J. Felße, v. 1, 187 p.; v. 2, no. 1, 184 p.; v. 2, no. 2, 303 p.; v. 3, 235 p.; v. 4, 128 p.
Wierzbowski, A., 1976, Oxfordian ammonites of the Pinar del Rio province (western Cuba); their revision and stratigraphical significance: Acta Geologica Polonica, v. 26, p. 137–260.
Young, R.E., Vecchione, M., and Donovan, D.T., 1998, The evolution of coleoid cephalopods and their present biodiversity and ecology, *in* Payne, A.I.L., Lipiński, M.R., Clarke, M.R., and Roeleveld, M.A.C., eds., Cephalopod biodiversity, ecology and evolution: African Journal of Marine Science, v. 20, p. 393–420.
Zittel, K.A. von, 1885, Handbuch der Palaeontologie, II Band: Mollusca und Arthropoda, Munich und Leipzig, R. Oldenberg, 893 p.
Zittel, K.A. von, 1895, Grundzüge der Paläontologie (Paläozoologie), Munich und Leipzig, R. Oldenberg, 976 p.

Accepted 3 June 2016