
First teuthid cephalopod from the Lower Jurassic of South America (Neuquén Basin, Argentina)

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ABSTRACT

A new species of squid, *Teudopsis jeletzkyi* n. sp., is described from the Toarcian (Lower Jurassic) of the Los Molles Formation in Neuquen Province, central west Argentina. Fossil squids have thus far been unknown in the Mesozoic of South America. This species is the first record of the Order Teuthida in the Jurassic of South America.

KEYWORDS | Toarcian. Coleoidea. Teuthida. Neuquén Basin. Argentina.

INTRODUCTION

Teuthids are rare as fossils, mostly known from fine-grained sediments deposited under anoxic or otherwise restricted conditions. Known Jurassic records are from the Lower Jurassic, especially from the Toarcian of France (Deslongchamps, 1835; Guérin-Franiatte and Goussy, 1993), Germany (Zieten, 1832; Münster, 1843; Quenstedt, 1849; 1858), England (Tate and Blake, 1876; Crick, 1920; Doyle, 1990), and Canada (Hall, 1985; Hall and Neuman, 1989), the Lower Jurassic of Hungary (Nagy, 1958), and the Callovian of France (Fischer and Riou, 1982).

Presence of teuthids in the Mesozoic of the Southern Hemisphere was unknown until very recently. They were recorded from the Tithonian of the Longing Group Member at Longing Gap, Antarctic Peninsula (Doyle, 1991), and the Upper Albian of northwestern Queensland (Australia) (Wade, 1993). An earlier record from Queensland (Moore, 1870) was found to be an indeterminate bivalve fragment (Engeser and Phillips, 1986).

Teudopsis jeletzkyi n. sp. is the first teuthid species described from the Jurassic of South America, and also represents the first occurrence of this order in rocks of any age in South America. It should be mentioned, however, that teuthids ascribed to *Trachyteuthis* sp. (V. Covacevich identification, 1994), have been recorded from the Oxfordian of Cordillera Domeyko, Antofagasta (Chile; A. Rubilar, written communication).

GEOLOGICAL SETTING

The present specimens come from black shales of the Los Molles Formation, Neuquén Basin, west-central Argentina. The Neuquén Basin is a roughly oriented back-arc basin comprising a Mesozoic-Cenozoic sedimentary succession at least 7 km thick (see Legarreta and Uliana, 1996). Sedimentation began in the Triassic as volcanic and coarse-grained continental deposits, and from the Rhaetian onwards a narrow marine corridor was established in the northern area of the basin. This sea expanded in the Pliensbachian-Toarcian, producing a westwards prograding system and deep basin turbidites.

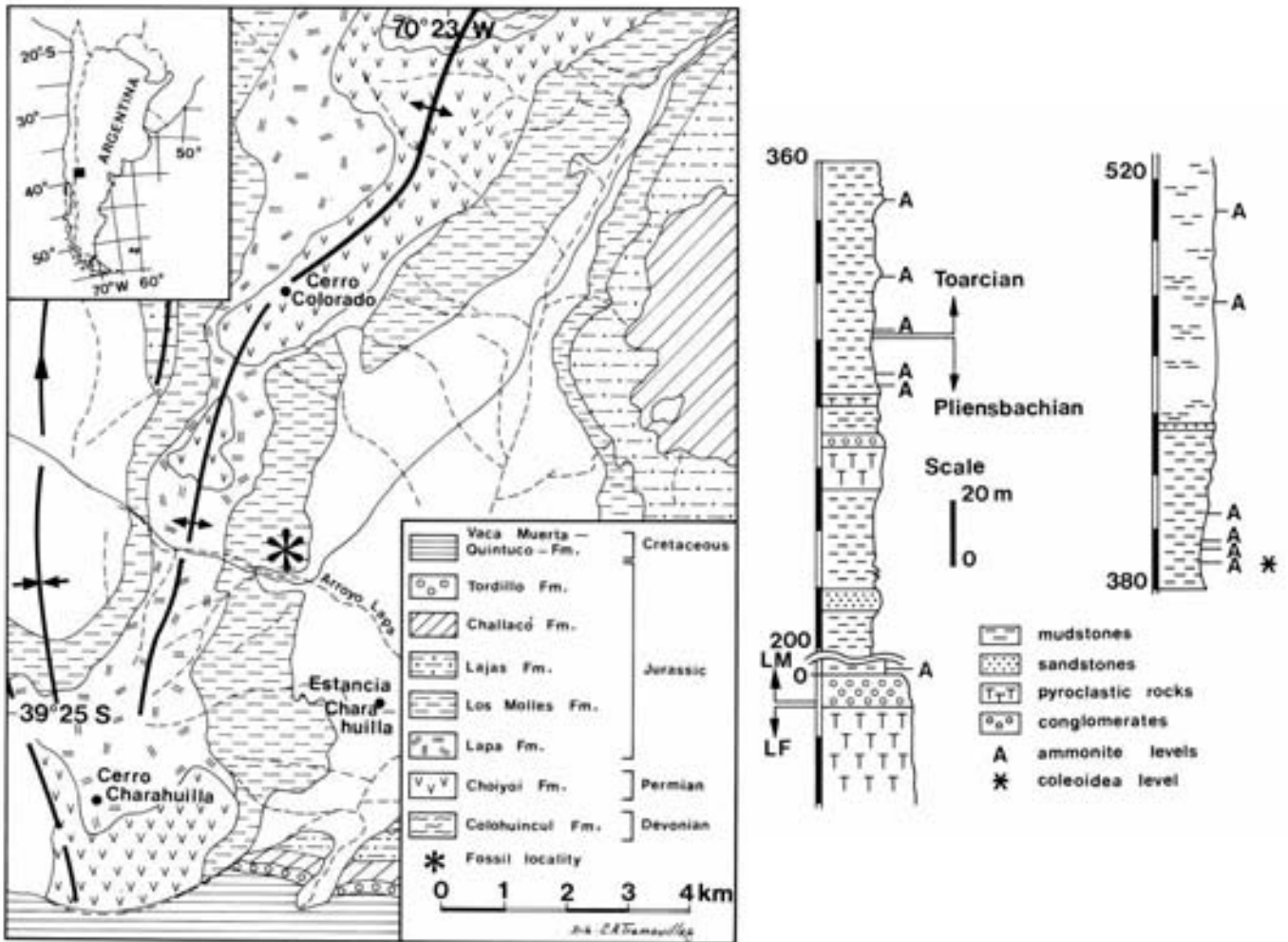


FIGURE 1 | Locality map and stratigraphical section at Arroyo Lapa, Neuquen Province, Argentina. Map modified after Gulisano and Gutiérrez Pleimling, 1995.

The teuthids here described came from Arroyo Lapa, a locality situated on the eastern slope of Sierra Chacaico, about 2.5 km north-west of Estancia Charahuilla and about 100 km south-west of the city of Zapala, in Neuquén Province (Fig. 1). The Sierra Chacaico is a north-south asymmetrical anticline, with a nucleus of Devonian metamorphics and Permian volcanics and Uppermost Triassic-Jurassic continental pyroclastics and conglomerates and marine strata as its western and eastern limbs. The Arroyo Lapa section is about 900 m thick and comprises the Uppermost Triassic-Lower Jurassic pyroclastics of the Lapa Formation, below, and the Pliensbachian- Aalenian outer shelf to basinal shales and mudstones of the Los Molles Formation, above. The specimens come from a bed of black shales, 380 m above the base of the Los Molles Formation exposed on the north bank of Lapa creek (Fig. 1). The associated fauna consists of poorly preserved impressions of ammonites, that can be identified as ?*Cleviceras* sp. About 4 m higher occurs *Harpoceras* cf. *falciferum* (SOWERBY), indicat-

ing the *Dactylioceras hoelderi* Andean Biozone, an approximate equivalent to the *Harpoceras falciferum* Standard Zone, Early Toarcian.

Faunal and sedimentological evidence point to these shales having accumulated in a dysaerobic environment lacking current- and wave induced circulation, where preservation of this type of structure might be expected. For more detailed analysis of the depositional environment of this unit see Gulisano and Gutiérrez Pleimling (1995).

SYSTEMATIC PALAEOLOGY

Order: Teuthida NAEF, 1916

Suborder: Mesoteuthina NAEF, 1921

(= Teudopsoidei Starobogatov, 1983)

Discussion: As explained by Jeletzky (1966, p. 39, 45) the Mesoteuthoidea Naef, 1921, were introduced in a

rank higher than the Family rank with a clear diagnosis and a list of subordinate families and genera. The name referred to a supposed intermediate evolutionary stage between the most primitive and the Recent teuthids. Although, Jeletzky (1966) recognized that the name has misleading evolutionary connotations, it was retained as a Suborder Mesoteuthina within the Teuthida “in a taxonomically emended and nomenclatorially corrected form”. The name was subsequently used among others by Engeser and Reitner (1986), Engeser and Bandel (1988), Hall and Neuman (1989) and Doyle (1990, 1993).

Nevertheless, the subordinal name “Teudopsoidei” was introduced by Starobogatov (1983, p. 6-7) as a replacement for Mesoteuthoidea Naef, 1921, without further explanation. This proposal, however, followed the criteria advocated by Starobogatov (1991) for the nomenclature of taxa at ranks above the family group, i.e. that “typified” taxa should replace “descriptive taxa” and that Suborders should end with the suffix “-oidei”. The new name was adopted by Doyle et al. (p. 5, 7), and other authors, but changed to Teudopsidina, as the “-ina” suffix is presently used in the Treatise on Invertebrate Paleontology for taxa at the Suborder level.

It is beyond the scope of this work to discuss this issue in detail, but it is worth mentioning that even if the International Code for Zoological Nomenclature (ICZN, 1999) does not include detailed provisions for Suprafamilial categories, the Mesoteuthina satisfy the few ICZN (1999, Art. 1.2.2) regulations for taxa at ranks above the family group. Furthermore, it is also relevant that even under Starobogatov’s (1991, pp. 13-14) recommendations Mesoteuthina seems to be an available name. Therefore, it is debatable the pertinence of Starobogatov’s (1983) proposal, especially when considering that stability is one of the ICZN main goals.

Family: Teudopsidae VAN REGTEREN ALTENA, 1949

Discussion: The Teudopsidae Van Regteren Altena, containing a single genus, *Teudopsis* DESLONGCHAMPS was placed in synonymy with the Palaeololiginidae Naef, 1921, by Engeser and Reitner (1986) on the grounds that presence of a free rhachis in the latter was too small a difference to justify separation at the family level. This conclusion was accepted by Hall and Neuman (1989) and also by Doyle (1990), although Doyle et al. (1994) separated them again, without further discussion. Hall and Neuman (1989) mentioned that Jeletzky (1966) has pointed to other differences between the two groups, such as the loss of the re-entrant-like character of the hyperbolar zones and the parallel-sided and much longer free rhachis in the Paleololiginidae. Although they uphold, Engeser and Reitner’s (1986) conclusion arguing that the gradual nature of these two families would seem to have

been implied by Naef (1922, fig. 55) when he illustrated the progressive narrowing of the anterior portion of the gladius and apparent derivation of a free rhachis. The same argument, however, was used by Jeletzky (1966, p. 45, fig. 5) to separate both families within an evolutionary trend where the Teudopsidae predated and were the root of several families, besides the Paleololiginidae. It seems therefore that Jeletzky’s (1966) conclusions should not be dismissed without a more detailed discussion.

GENUS *Teudopsis* DESLONGCHAMPS, 1835
(= *Beloteuthis* MÜNSTER, 1843, p. 59.)

Type species: *Teudopsis bunelii* DESLONGCHAMPS, 1835, by subsequent designation (Woodward, 1851-56, p. 69).

Diagnosis: Small to large, rhomboid to pyriform spoon-like gladius with posterior blade-like extension and rounded elliptical wings; median field restricted to well developed keel or mid rib; hyperbolar zones developed as weak deflection of the growth lines (Doyle, 1990).

Occurrence: Toarcian and Callovian of Europe (Naef, 1922; Fischer and Riou, 1982; Doyle, 1990; Guérin-Franiette and Goussy, 1993), Toarcian of North (Hall and Neuman, 1989) and South America

Discussion: Naef (1922, p. 142) placed under “*Beloteuthis*” MÜNSTER (1843), several species for which Deslongchamps (1835) had already introduced the name *Teudopsis*. *Beloteuthis* MÜNSTER (1843), was therefore considered a subjective synonym of *Teudopsis* by Van Regteren Altena (1949), a conclusion later upheld by Jeletzky (1966), Hall and Neuman (1989) and Doyle (1990).

Besides the type species, *T. bunelii* DESLONGCHAMPS, from the Toarcian of Courcy and Amayé-sur-Orne, Calvados (France) (Deslongchamps, 1835) and the “Saurian and Fish Bed” (*Harpoceras falciferum* Zone) of Alderton Hill, Gloucestershire (England) (Crick, 1920), *Teudopsis* includes the species *T. subcostata* (MÜNSTER, 1843) and *T. schuebleri* (QUENSTEDT, 1849), both from the Toarcian (*Harpoceras falciferum* Zone) Posidonienschiefer of Ohmden and Holzmaden (Germany) and Jet Rock Member of Whitby, North Yorkshire (England), *T. acuta* (MÜNSTER, 1843) from the Toarcian of Boll (Germany), *Teudopsis* sp. from the Lower Jurassic of Hungary (Nagy, 1958; see Engeser, 1988, 1990, and Doyle, 1990, p. 205 for specific affinities), *T. acuminensis* HALL and NEUMAN, 1989, from the Toarcian (*Harpoceras falciferum* Zone) Poker Chip Shale of the Fernie Formation (Canada), and *T. mortieri* GUÉRIN-FRANIATTE and GOUSPY (1993) from the Toarcian (*Dactylioceras tenuicostatum* Zone) of Fort

Mortier, Langres, Haute-Marne (France). Thus far only one species has been recorded later than the Toarcian, i.e. *Teudopsis* sp. from the Lower Callovian of Voulte-sur-Rhone (France) (Fischer and Riou, 1982). A *Teudopsis*, comparable to *T. subocostata*, was recorded by Smithe (1877) from the Upper Pliensbachian Marlstone Rock Bed, Churchdown, Gloucestershire (England). This could be the oldest record of *Teudopsis* (see Doyle, 1993, p. 233), but the specimen has not been traced (see Engeser and Phillips, 1986, p. 262), and according to D. Donovan (written comm. to R. Hewith) must be regarded as uninterpretable. A specimen from the Upper Jurassic/Lower Cretaceous Purbeck Beds of Dorset (England), described as *Teudopsis brodiei* CARRUTHERS (1871, p. 448, text-fig.) is in fact a remain of an indeterminate plant (Engeser and Phillips, 1986, p. 262).

Teudopsis jeletzkyi n. sp.

Figures 2 and 3

Diagnosis: Small species of *Teudopsis* characterised by a relatively wide gladius and long wings and lateral margins converging slowly into a rounded blade-like anterior margin.

Description: Material included in this species comprises two specimens. The holotype (MLP 31168a, Figs. 2A and 2B), is an incomplete gladius with most of wings and anterior portion missing, preserved with ventral surface exposed on bedding plane surface; outline pear-shaped, with maximum width ($W_m = 29.5$ mm) coincident with end of anterior wing at about mid-length, although slightly closer to posterior end; total length (L_m) (as reconstructed on Fig. 2B) about 57.5 mm, with lateral margins at anterior end slightly convex outwards and tapering gradually to a probably narrow rounded apex. Right wing partially preserved, prominent, broad, forming broadly rounded posterior margin and tapering strongly anteriorly and extending forward for 31.5 mm, reaching about half total length of gladius ($L_w/L_m = 0.55$); wing surfaces with faint straight striations converging with each other posteriorly, subparallel with lateral margin. Hyperbolic fields not visible. Median field reaches maximum width ($W_{mf} = 23.1$ mm) at about mid gladius; with a convexity along the mid-line, strong and relatively narrow anteriorly and becoming broader and less prominent towards the apex; curved growth lines on median field faint, subparallel to mid-line; shallow and narrow median groove corresponding to dorsal keel runs most of length of gladius on mid-line, although barely visible near anterior margin.

The second specimen (MLP 31168b, Figs. 3A and 3B) is an incomplete gladius, preserved as an external mould of a dorsal surface and exposed on bedding plane surface; outline pear-shaped, with maximum width ($W_m = 24.2$ mm) coincident with anterior end of wings, at about mid-

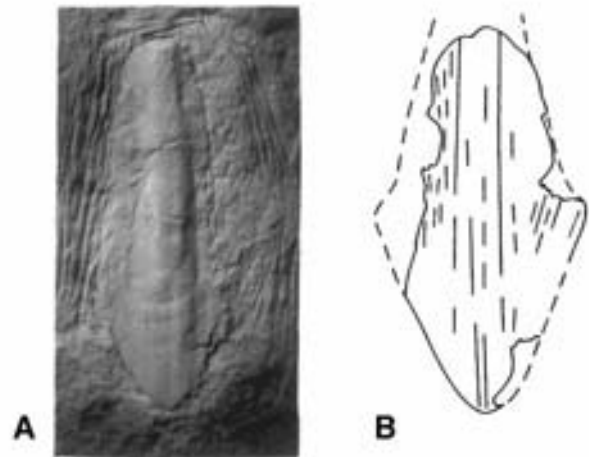


FIGURE 2. *Teudopsis jeletzkyi* n. sp., Arroyo Lapa. A) holotype, MLP 31168a. B) holotype, MLP 31168a. x1.

length; total length (L_m) about 68.1 mm, with lateral margins at anterior end slightly convex outwards and tapering gradually to a narrow rounded apex. Wings partially preserved, narrow and elongated, broad, forming broadly rounded posterior margin and tapering gradually anteriorly and extending forward (L_w) for 34.7 mm, reaching half total length of gladius ($L_w/L_m = 0.51$); wing surfaces with faint straight striations converging with each other posteriorly, subparallel with lateral margin. Hyperbolic zones poorly defined by indistinct asymptotes barely discernible. Median field reaches maximum width ($W_{mf} = 14.6$ mm) at about mid gladius; growth lines on median field faint, subparallel to mid-line; well developed, straight, round and smooth keel along length of gladius on mid-line, narrow at posterior end and broadening slightly towards anterior end.

Etymology: After my friend the late Jurij (Jura/George) Jeletzky (1915-1988), in recognition of his outstanding life-long contributions to the study of fossil Coleoidea.

Holotype: Specimen MLP 31168a, figured on figs. 2A-B, from the Los Molles Formation, *Dactylioceras hoelderi* Andean Biozone (~ *Harpoceras falciferum* Zone) of Arroyo Lapa, Neuquen Province, Argentina.

Other material examined: One specimen, MLP 31168b, figured on Figs. 3A and 3B, from same locality as the holotype.

Repository of type material: Departamento Paleozoología Invertebrados, Museo La Plata, Paseo del Bosque s/n, 1900 La Plata, Argentina.

Occurrence: The specimens were found *in situ* 380 m above the base of the Los Molles Formation, exposed on

the north bank of Lapa creek, about 100 km south-west of the city of Zapala, Neuquén Province (Fig. 1). *Dactylioceras hoelderi* Andean Zone (~ *Harpoceras falciferum* Standard Zone), Early Toarcian.

Discussion: This is a small species of *Teudopsis* characterised by the relatively wide gladius and long wings. Of the known species *T. bunelii* DESLONGCHAMPS (1835, p. 74, pl. 3, fig. 1, refigured in d'Orbigny, 1842, p. 38, pl. 1, fig. 1, and 1855, p. 360, pl. 20, fig. 1; Crick, 1920, p. 253, fig. 1 and plate B) differs by being larger and having poorly developed wings tapering gradually into median field and a rhachis extending slightly above the rest of the gladius. *T. subcostata* (MÜNSTER, 1843, p. 61, pl. 5, fig. 2, refigured in Naef, 1922, p. 142, text-fig. 53a; Quenstedt, 1849, p. 501, pl. 32, figs. 7-8, fig. 8 refigured in Chenu, 1859, p. 39, fig. 106; including "*T. leckenbyi*" BLAKE in Tate and Blake, 1876, p. 314, pl. 4, fig. 2, refigured in Doyle, 1990, p. 202, text-fig. 5B-C) differs in the larger size, rhomboid form and slightly shorter wings; *T. acuta* (MÜNSTER, 1843, p. 63, pl. 6, fig. 4, refigured in Naef, 1922, p. 148, fig. 54a) has shorter wings and a gladius that narrows more rapidly toward the anterior, forming a spike-like anterior; *T. cadominensis* HALL and NEUMAN (1989, p. 326, fig. 1) is larger, more slender ($Lm/Wm = 4.62$ vs. $1.94 - 2.8$) and has shorter wings ($Lw/Lm = 0.49$ vs. $0.51 - 0.55$); *T. mortieri* GUERIN-FRANIATTE and GOUSPY (1993, p. 186, pl. 2, fig. 2) is also larger, more slender ($Lm/Wm = 5.3$ vs. $1.94-2.8$) and with a free rhachis.

The closest species is *T. schuebleri* (QUENSTEDT, 1849, p. 499, pl. 32, figs. 14-15, fig. 15 refigured in Chenu, 1859, p. 38, fig. 102; Quenstedt, 1858, p. 243, pl. 34, fig. 9; including "*T. bollensis*" ZIETEN, 1832, p. 49, pl. 37, fig. 1, refigured in Naef, 1922, p. 144, text-fig. 53b, and Chenu, 1859, p. 39, fig. 105; "*T. ampullaris*" MÜNSTER, 1843, p. 60, pl. 6, fig. 1, refigured in Chenu, 1859, p. 38, fig. 101, and d'Orbigny, 1842, p. 156, pl. 14, fig. 2; "*T. cuspidatus* Simpson" BLAKE in Tate and Blake, 1876, p. 314, pl. 4, fig. 3, refigured in Doyle 1990, p. 201, text-figs. 4A,C), having close Lw/Lm ($0.41 - 0.51$ vs. $0.51 - 0.55$), but differing in being larger and slender ($Lm/Wm = 2.93 - 3.25$ vs. $1.94 - 2.8$) and having margins converging more rapidly in a more pointed blade-like anterior margin.

CONCLUDING REMARKS

Prior to the present study published teuthid records were unknown from South America. Presence of teuthids in the Mesozoic of the Southern Hemisphere was only known from the Tithonian of the Antarctic Peninsula (Doyle, 1991), and the Upper Albian of Australia (Wade, 1993). In the Northern Hemisphere a few records are known from the Jurassic of Cuba, the Upper Cretaceous of the Western Interior (USA), and Lebanon and the Toar-

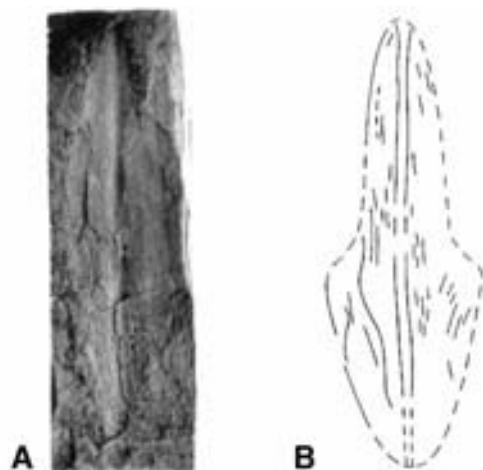


FIGURE 3 | *Teudopsis jeletzkyi* n. sp. Arroyo Lapa. A) paratype, MLP 31168b. B) paratype, MLP 31168b. x1.

cian of Canada, whilst other records are from Europe, mostly from France, Germany and England (see Doyle, 1991 and references therein).

As pointed out by Doyle (1991) there are too few records to draw definite conclusions about the paleobiogeography of Mesozoic teuthids, although the discovery of fossil teuthids from Gondwana suggests that the observed European bias is artificial and probably due to fragility of the remains and to a greater intensity of study in space and time. The disparate geographical records of *Teudopsis*, now known from Europe, Canada and Argentina, matches those of other Mesozoic teuthids and confirms Doyle's (1991) conclusion that they are a possible indicator of a formerly more widespread distribution. This is especially true for the Early Toarcian, when European and East Pacific teuthids, similarly to ammonoids, exhibited strong similarities, whilst preservation was enhanced by the presence of widespread organic-rich facies, resulting from a global oceanic anoxic event (Jenkyns, 1988).

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REFERENCES

- Carruthers, W., 1871. On some supposed vegetable fossils. Quarterly Journal of the Geological Society of London, 27, 443-448.
- Chenu, J.C., 1859. Manuel de Conchyliologie et de Paléontologie Conchyliologique. Paris, Ed. V. Masson, Tome Premier, i-vii + 1-97.
- Crick, G.C., 1920. On some Dibranchiate Cephalopods from the Upper Lias of Gloucestershire. Proceedings of the Cotteswold Naturalists Field Club, 20, 249-256.
- Deslongchamps, E., 1835. Mémoire sur les Teudopsides, animaux fossiles, voisins des Calmars. Bulletin de la Société Linnéenne de Normandie, Mémoire, 5, 68-78.
- Doyle, P., 1990. Teuthid Cephalopods from the Lower Jurassic of Yorkshire. Palaeontology, 33, 193-207.
- Doyle, P., 1991. Teuthid cephalopods from the Upper Jurassic of Antarctica. Palaeontology, 34, 169-178.
- Doyle, P., 1993. Mollusca: Cephalopoda (Coleoidea). In: Benton, M.J. (ed.). The Fossil Record 2, London, Chapman and Hall, 229-236.
- Doyle, P., 1994. Teuthid cephalopods from the Upper Jurassic of Antarctica. Palaeontology, 34, 169-178.
- Doyle, P., Donovan, D.T., Nixon, M., 1994. Phylogeny and Systematics of the Coleoidea. The University of Kansas, Paleontological Contributions, 5, 1-15.
- Engeser, T., 1988. Fossilium Catalogus 1: Animalia. Pars 130: Vampyromorpha ("Fossile Teuthiden"). Amsterdam, Kugler Publications, 167 pp.
- Engeser, T., 1990. Phylogeny of the fossil coleoid Cephalopoda (Mollusca). Berliner Geowissenschaftliche Abhandlungen, Abh. A 124, 123-191.
- Engeser, T., Bandel, K., 1988. Phylogenetic Classification of Coleoid Cephalopods. In: Wiedman, J., Kullman, J. (eds.). Cephalopods, Present and Past. 2nd International Cephalopod Symposium, Tübingen, Germany, E. Schweizerbart'sche Verlags., 105-115.
- Engeser, T., Phillips, D., 1986. Redescription of two specimens previously recorded as fossil teuthids (Coleoidea, Cephalopoda). Bulletin of the British Museum (Natural History), (Geol.), 40, 259-264.
- Engeser, T., Reitner, J., 1986. Coleoidenreste aus der Oberkreide des Libanon im Staatlichen Museum für Naturkunde in Stuttgart. Stuttgarter Beiträge zur Naturkunde, B, 124, 1-15.
- Fischer, J.-C., Riou, B., 1982. Les Teuthoïdes (Cephalopoda, Dibranchiata) du Callovien inférieur du la Volte-Sur-Rhône (Ardèche, France). Annales de Paléontologie, 68, 295-325.
- Guérin-Franiatte, S., Goussy, C., 1993. Découverte de Céphalopodes Teuthides (Coleoidea) dans le Lias Supérieur de Haute-Marne, France. Geobios, MS15, 181-189.
- Gulisano, C.A., Gutiérrez Pleimling, A.R., 1995. The Jurassic of the Neuquén Basin. a) Neuquén province. Secretaría de Minería de la Nación, Publicación, 158, 111 pp.
- Hall, R.L., 1985. *Paraplesioteuthis hastata* (Münster), the first teuthid squid recorded from the Jurassic of North America. Journal of Paleontology, 59, 870-874.
- Hall, R.L., Neuman, A.G., 1989. *Teudopsis cadominensis*, a new Teuthid squid from the Toarcian (Lower Jurassic) of Alberta. Journal of Paleontology, 63, 324-327.
- Jeletzky, J.A., 1966. Comparative morphology, phylogeny, and classification of the fossil Coleoidea. The University of Kansas, Paleontological Contributions, Mollusca, 7, 162 pp.
- Jenkyns, H.C., 1988. The early Toarcian (Jurassic) anoxic event: Stratigraphic, sedimentary, and geochemical evidence. American Journal of Science, 288, 101-151.
- Legarreta, L., Uliana, M., 1996. The Jurassic succession in west-central Argentina: stratal patterns, sequences and paleogeographic evolution. Paleogeography, Paleoclimatology, Paleocology, 120, 303-330.
- Moore, Ch., 1870. Australian Mesozoic Geology and Palaeontology. Proceedings of the Geological Society, 26, 226-261.
- Münster, G., 1843. Über zwei neue Arten von Sepia. Beiträge zur Petrefactenkunde, pt. 6, Beyreuth, 100 pp.
- Naef, A., 1916. Systematische Übersicht der mediterranen Cephalopoden. Pubblicazioni della Stazione Zoologica di Napoli, 1, 11-19.
- Naef, A., 1921. Die Cephalopoden. In Flora e Fauna del Golfo di Napoli, Berlin, ed. Friedländer, Monograph 35, pt. 1, vol. 1. 148 pp.
- Naef, A., 1922. Die Fossilen Tintenfische. Eine Paläozoologische Monographie. Jena, ed. G. Fischer, 322 pp.
- Nagy, I.Z., 1958. *Teudopsis subacuta* n.sp. A Mecseki Liászból. Földtani Közlöny, 88, 240-242.
- Orbigny, A. d', 1842. Paléontologie française; Terrains Jurassiques, I, Céphalopodes. Paris, ed. Masson, 642 pp.
- Orbigny, A. d', 1855. Mollusques, vivants et fossiles. Paris, ed. Gide, 605 pp.
- Quenstedt, F.A., 1846-49. Petrefactenkunde Deutschlands, 1. Die Cephalopoden. Tübingen, ed. Fues, 581 pp.
- Quenstedt, F.A., 1858. Der Jura. Tübingen, ed. Laupp, 842 pp.
- Regteren Altena, C.O. Van, 1949. Teyler's Museum. Systematic catalogue of the palaeontological collection. Sixth supplement (Teuthoidea). Archives du Musée Teyler, 10, 53-62.
- Smithe, F., 1877. On the Middle Lias of North Gloucestershire. The Spinatus Zone. Proceedings of the Cotteswold Naturalists' Field Club, 6 (for 1876), 349-405.
- Starobogatov, Ya.I., 1983. Phylogeny of Cephalopoda. In: Starobogatov, Ya.I., Nesis, K.N., (eds.). Taxonomy and Ecology of Cephalopoda. Scientific Papers, Leningrad, USSR Academy of Sciences, Zoological Institute, 8-12.
- Starobogatov, Ya.I., 1991. Problems in the Nomenclature of Higher Categories. Bulletin of Zoological Nomenclature, 48, 6-18.
- Tate, R., Blake, J.F., 1876. The Yorkshire Lias. London, ed. Van Voorst, 475 pp.
- Wade, M., 1993. New Kelaenida and Vampyromorpha: Cretaceous squids from Queensland. Memoir of the Association of Australasian Paleontologists, 15, 353-374.
- Woodward, S. P., 1851-56. Manual of the Mollusca. London, Weale, 488 pp.
- Zieten, C. H. von, 1830-32. Die Versteinerungen Württembergs. Expedition des Werkes unserer Zeit. Stuttgart, 102 pp.

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