

An Early Triassic gladius associated with soft tissue remains from Idaho, USA—a squid-like coleoid cephalopod at the onset of Mesozoic Era

LARISA A. DOGUZHAeva, ARNAUD BRAYARD, NICOLAS GOUEMAND,
LAUREL J. KRUMENACKER, JAMES F. JENKS, KEVIN G. BYLUND, EMMANUEL FARA,
NICOLAS OLIVIER, EMMANUELLE VENNIN, and GILLES ESCARGUEL



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We describe an Olenekian (Early Triassic) “fossil squid” belonging to the oldest complex Mesozoic marine biota collected in the Lower Shale unit of the Lower Triassic Thaynes Group in Idaho, USA. The studied specimen shows a tapered structure embedded in a cylindrical soft body. Morphological, ultrastructural and geochemical features of the specimen suggest that it corresponds to an internally-shelled cephalopod exhibiting a tapered micro-laminated gladius with rachis, narrow median and lateral fields and a large conus; a pair of posterior large fin-supported cartilages and fins; ventral and dorsal mantle band-shape structures, the dorsal one being cartilaginous; mantle patches; a stomach containing undigested arm-hooks and sheet-like pieces of potential flooded ink. Coupled SEM/EDS analyses show that (i) arm-hooks and ink were pseudomorphed by nanoparticles (less than 0.6 μm in diameter) of carbon, (ii) gladius and soft tissues were substituted by granules of calcium phosphate, (iii) cartilage canalicula's were partially filled with calcium phosphate grains and crystals of Zn- and S-containing minerals. The specimen was hence probably fossilized due to metabolism of P- and C-accumulating bacteria. Based on this specimen, *Idahoteuthis parisiana* Doguzhaeva and Brayard gen. et sp. nov. and Idahoteuthidae Doguzhaeva and Brayard fam. nov. are erected. This family is characterized by an elongated, cylindrical, dorsally cartilaginous muscular mantle; well-developed, about 0.2 mantle length, rounded anteriorly and acute posteriorly, fin-supported cartilages and similarly shaped two fins at conical mantle termination, and thin slender gladius with narrow median and lateral fields, rachis and breviconic conus. This family assumedly falls in Myopsida (Decabrachia). A streamlined body, large fin-supported cartilages and eroded arm-hooks in the stomach of *Idahoteuthis* Doguzhaeva and Brayard gen. nov. suggest that this was a maneuverable cannibal predator that dwelled in the subequatorial shallow sea of the west coast of Pangaea.

Key words: Cephalopoda, Coleoidea, phylogeny, gladius, soft tissue preservation, Triassic, USA, Idaho.

Larisa A. Doguzhaeva [larisa.doguzhaeva@gmail.com; larisa.doguzhaeva@nrm.se], Department of Palaeobiology, Swedish Museum of Natural History, P.O. Box 50007, SE-10405 Stockholm, Sweden.

Arnaud Brayard [arnaud.brayard@bourgogne.fr], Emmanuel Fara [emmanuel.fara@u-bourgogne.fr], and Emmanuelle Vennin [Emmanuelle.vennin@u-bourgogne.fr], Biogéosciences UMR6282, CNRS, Univ. Bourgogne Franche-Comté, 6 Boulevard Gabriel, 21000 Dijon, France.

Nicolas Goudemand [nicolas.goudemand@ens-lyon.fr], Université de Lyon, ENS de Lyon, CNRS, Université Claude Bernard Lyon 1, Institut de Génomique Fonctionnelle de Lyon, UMR 5242, 46 Allée d'Italie, F-69364 Lyon Cedex 07, France;

Laurel J. Krumenacker [lkrumenacker@gmail.com], Department of Earth Sciences, Montana State University, P.O. Box 173480, Bozeman, Montana 59717-3480, USA.

James F. Jenks [jenksjimruby@gmail.com], 1134 Johnson Ridge Lane, West Jordan, Utah 84084, USA.

Kevin G. Bylund [kevin@ammonoid.com], 140 South 700 East, Spanish Fork, Utah 84660, USA.

Nicolas Olivier [nicolas.olivier@univ-lyon1.fr], Institute of Functional Genomics of Lyon, ENS Lyon-CNRS 5242-INRA USC 1370, 46 allée d'Italie, 69364 Lyon Cedex 07, France.

Gilles Escarguel [Gilles.Escarguel@univ-lyon1.fr], Laboratoire d'Ecologie des Hydrosystèmes Naturels et Anthropisés, UMR CNRS 5023, Université Claude Bernard Lyon 1, 27-43 Boulevard du 11 novembre 1918, 69622 Villeurbanne Cedex, France.

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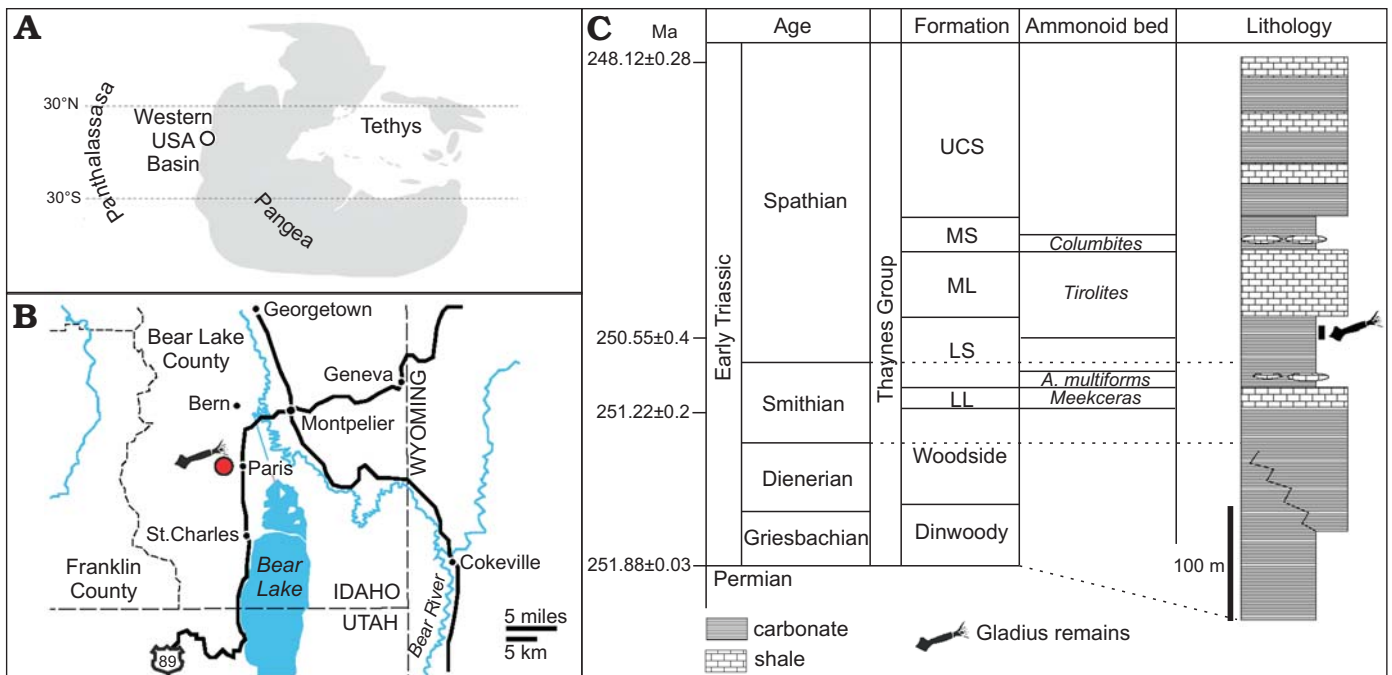


Fig. 1. **A.** Palaeogeographic map of the western USA basin during the Early Triassic. **B.** Present-day location of the studied exposure. **C.** Synthetic stratigraphical and lithological succession of the Bear Lake area (after Romano et al. 2013) with position of the studied specimen. Ammonoid zonation after Jenks et al. (2013) and Jattiot et al. (2016). Stratigraphy follows the main units defined by Kummel (1954). Radiometric ages after Galfetti et al. (2007) and Burgess et al. (2014). Abbreviations: LL, Lower Limestone; LS, Lower Shale; ML, Middle Limestone; MS, Middle Shale; UCS, Upper Calcareous Siltstone.

Introduction

A ~250.6 Myr-old middle Olenekian (= early Spathian, Early Triassic) complex marine ecosystem named the Paris Biota, has been recently discovered in southern Idaho, USA (Brayard et al. 2017). One of the most intriguing specimens of this exceptional fossil assemblage is represented by an elongated structure interpreted as a coleoid gladius associated with soft tissues (Brayard et al. 2017: fig. 4G). This gladius is the oldest one that reveals similarities to gladii of some extant coleoid taxa and therefore it can serve as a basis to propose a new scenario on the evolutionary development of a gladius. Based on this specimen, *Idahoteuthis parisiana* gen. et sp. nov. and Idahoteuthidae Doguzhaeva and Brayard fam. nov. are erected and their systematic position is analyzed. The preservation of the non-biomineralized structures, a gladius, arm-hooks and sheet patches of a potential ink in the stomach, mantle and fin-supported cartilages, as well as the position of this coleoid in the Early Triassic food web are also discussed.

Institutional abbreviations.—NRM, Swedish Museum of Natural History, Stockholm, Sweden; UBGD, Université de Bourgogne, Géologie Dijon, France.

Geological setting

The gladius specimen comes from the Lower Shale unit of the Lower Triassic Thaynes Group, west of the city of Paris,

Bear Lake County, southeastern Idaho, western USA (Fig. 1; Brayard et al. 2017: figs. 1–4). This unit is represented by alternating limestone and shale beds, which were deposited during the middle Olenekian in the shallow Western USA Basin. This epicontinental sea was connected to the Panthalassic Ocean to the west and located at a near equatorial position on the western margin of Pangea (Fig. 1). Exposures containing this specimen are approximately 20 m thick and consists of mainly grey to blue, thin-bedded silty limestone, deposited in a distal upper offshore environment on a very flat platform. The early Spathian (base of the middle Olenekian) ammonoid *Tirolites* abundantly occurs throughout these exposures (Brayard et al. 2017). A radiometric age of about 250.6 Mya (i.e., only about 1.3 Mya after the end-Permian mass extinction) is assigned to the immediately overlying Middle Limestone unit and was obtained from the coeval *Tirolites*–*Columbites* beds in South China (Galfetti et al. 2007; Jenks et al. 2013).

Material and methods

The studied specimen is ca. 48.7 mm long and ca. 7.4 mm large fossil embedded in a compact silty limestone split into two slabs (Figs. 2A, 3). The specimen is compressed because of compaction and deformed according to original differences in morphology and composition observed between its anterior, middle and posterior parts (Figs. 2, 3). This specimen displays non-biomineralized structures, the original dislocation and symmetry of which may be changed.

Considering its tapered end (Figs. 2A, 3) as indicating the anterior part, the specimen is exposed on its left side (Fig. 2A). The tapered end is likely folded and compressed due to compaction (Figs. 2A, 3). The middle part of the left side of the gladius is removed that allows to see the material beneath (Figs. 2A, C, 4). The middle part of the specimen is cylindrical in shape (Fig. 2A); one side (dorsal; at the top on pictures) being more straight and less deformed than the opposite one (ventral; at the bottom on pictures). The latter shows a wavy outline indicative of elastic soft tissue deformations (Fig. 2A). The posterior end of the specimen shows a flattened triangular structure (Fig. 2) and a pair of pear-like structures with a metallic luster (Fig. 2A). At the anterior end of the specimen (Fig. 2A₁), an uncertain organic structure distantly resembling longitudinally fractured coleoid-type jaws is present (see Doguzhaeva et al. 2007b: figs. 11.1A, B, 11.7A, 11.8A–F; Doguzhaeva and Mapes 2017: figs. 2A, B, 3A, B for comparison). It is formed by set of long curved, black interrupted lines, some of which are jointed and form a beak-like structure (Fig. 2A₁).

The specimen was studied using a Nikon S522249 light microscope and a Wild M400 light photomicroscope. Ultrastructural and elemental analyses were carried out by means of a Scanning Electron Microscope Hitachi-4300 equipped with an energy dispersive spectrometer (EDS) at the Swedish Museum of Natural History in Stockholm. Ultrastructures were examined under magnifications up to 70 000, using a gold coating (Figs. 4–9). Elemental analyses (SOM: table 1, Supplementary Online Material available at http://app.pan.pl/SOM/app63-Doguzhaeva_et_al_SOM.pdf) were performed at an accelerated voltage of 15 kV, and we used energy calibration as measured on standard minerals of known accuracy. EDS analyses were made on several points of each morphological structure and matrix (SOM: table 1). All elements were analyzed and no peak was omitted. The contents of the elements are given in per cent to total weight.

Results

Morphology and ultrastructure.—The studied specimen shows the following structures; their initial location and symmetry may have been modified because of various potential postmortem deformations.

Gladius: The total length of the exposed part of the gladius is 42.2 mm, and the total preserved length of the fossil is 48.7 mm. The actual length of the gladius is likely longer as the length of the rachis (a free continuation of the median field) is incomplete (Figs. 2A₁, 3). The gladius is slender, tapered, with three narrow longitudinal areas (median and lateral fields), a rachis, and a relatively long conus that is ~0.15% of the gladius length (without the rachis) (Fig. 2A₁). The gladius structure exhibits five preserved parts: (i) a short piece of a broken rachis, (ii) an anterior tapered part (Figs. 2A, 3), (iii) a dorsal, thin longitudinal fracture between the tapered part and the end of the conus (Fig. 2A), (iv) a conus

(Fig. 2), and (v) a displaced tiny ~3 mm long fragment of an apical part (Fig. 2C). It shows three narrow fields that are broadly rounded anteriorly; the median one being slightly longer than lateral fields (Fig. 2C₂). The gladius is thin-walled, micro-laminated, non-biomineralized and may have been constituted by chitin (Fig. 9C).

Fin-supported cartilages: These are large, about 0.15% of the gladius length, paired, pear-like structures adjacent to the conus (Fig. 2A). They are formed by a canalicular cartilage (Bairati et al. 1987) characterized by a well developed matrix and the canalicular network made of canals with individualized walls (Figs. 5–7, 8A).

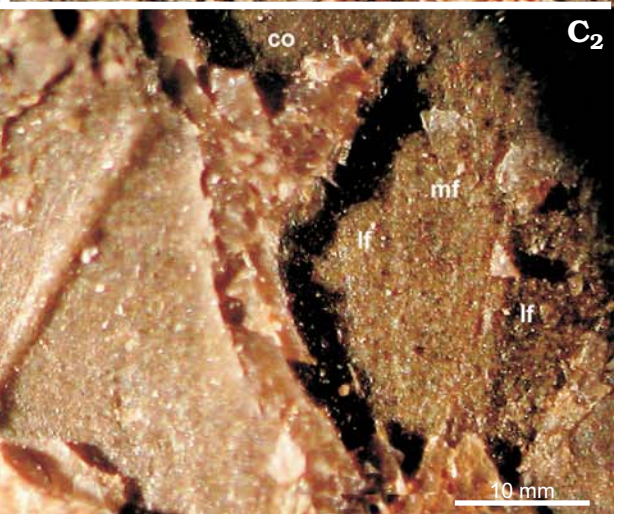
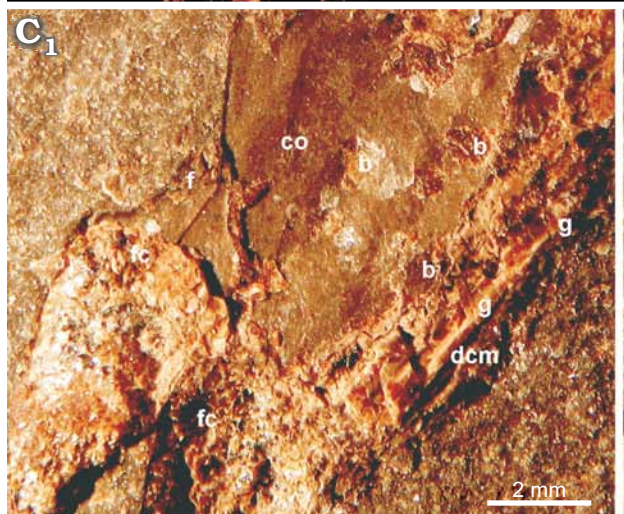
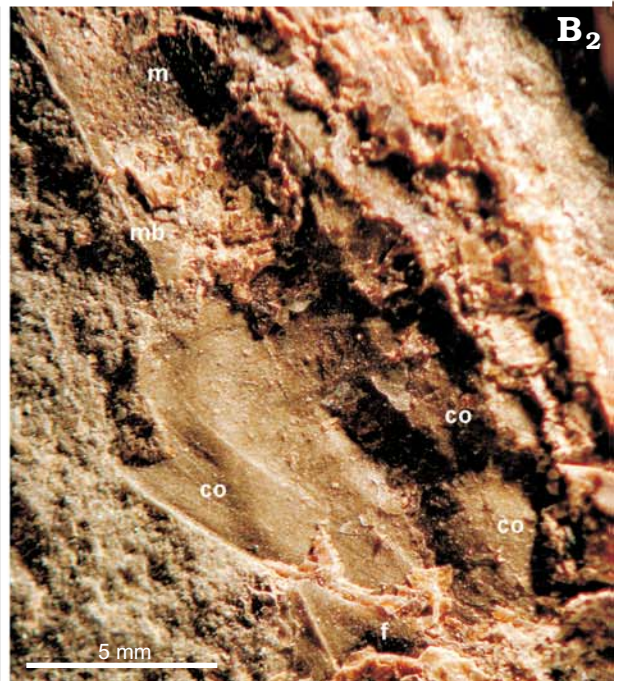
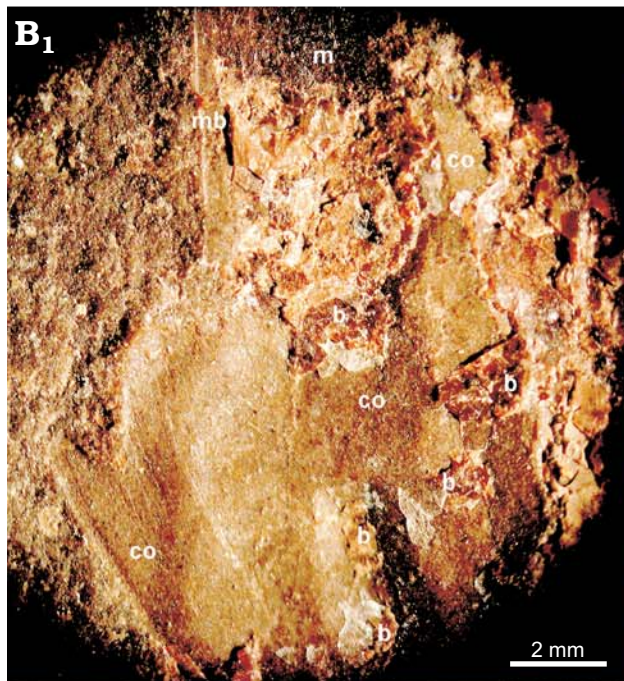
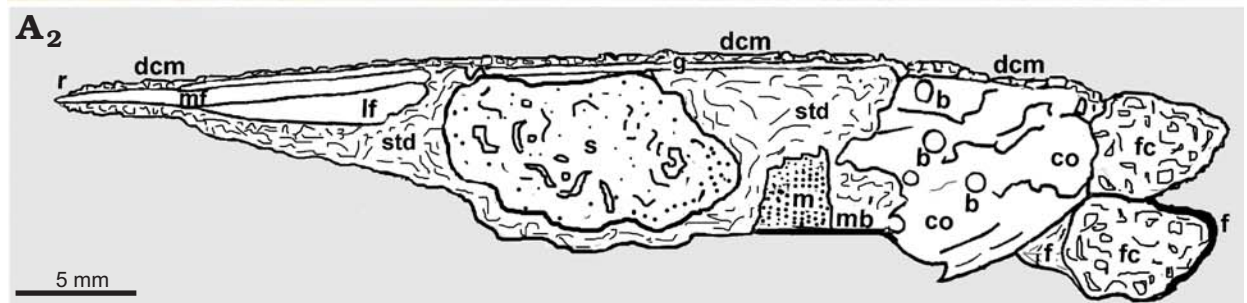
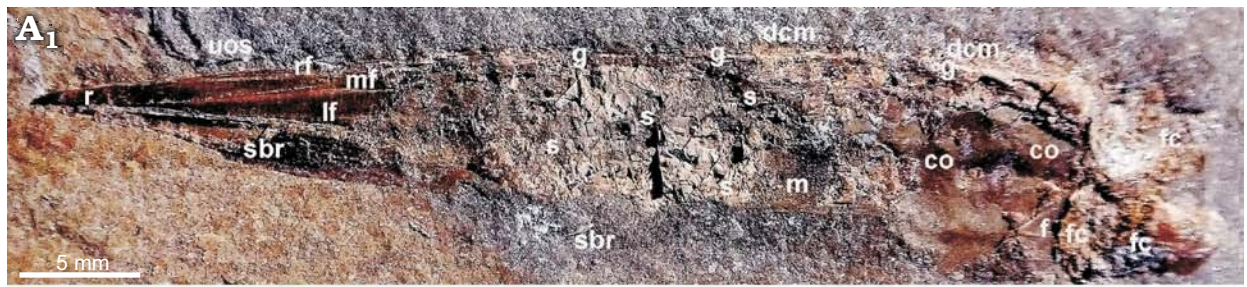
Fins: These are ~10 mm long, partially preserved paired non-biomineralized structures located near the posterior end of the conus. They surround the pear-shaped canalicular cartilages. They are ~0.2 of the preserved length of the specimen (Fig. 2A).

Stomach: This structure corresponds to a large, oval, fractured sac located in the central part of the specimen, close to its ventral side (Fig. 2A). It exhibits a lighter color than the surrounding material and provides access to numerous inclusions. The stomach shows a broken folded edge on its ventral side, excepting on the posterior part where it adjoins a preserved fragment of the band-like mantle structure that may have protected it. The stomach is, however, not broken dorsally and laterally. It contains diverse, supposedly undigested hard remains as well as soft tissue debris; about ten arm hooks and tiny black sheet patches of ink material are identified (Figs. 4, 9A, B, D, F). For comparison, the stomach described in the Late Cretaceous “fossil squid” *Dorateuthis* contains undigested fish remains (Lukeneder and Harzhauzer 2004).

Arm-hooks: These are found accumulated in the stomach (Fig. 4) and are not observed around the specimen. They are ~2–2.4 mm in maximum size (distance between the distal end of the basement and the acute tip of the hook), black, compressed, fractured, eroded, and lack of typical luster. They have a relatively long and thick basement and display a nearly straight, thick shaft inclined towards a strongly curved and long hook (for comparisons see Rieber 1970; Kulicki and Szaniawski 1972; Engeser and Clarke 1988; Doguzhaeva et al. 2007a: fig. 6.6; Doguzhaeva et al. 2007c: figs. 2B, C, 5A; Doguzhaeva et al. 2010a: figs. 6, 8; Doguzhaeva et al. 2010b: figs. 6A–E, 9C, D).

Mantle: Along the ventral side, the mantle is represented by a short portion of a straight band continuing from the conus forward along the body (Fig. 2A, B) and an adjacent patch with thin wavy longitudinal ridges (Fig. 2B). On the dorsal side of the specimen, it is represented by a dark wavy cartilaginous band, consisted from a canalicular cartilaginous (Figs. 2A₂, 7, 8) (for comparison see Doguzhaeva et al. 2007b: figs. 11.2C, 11.3–11.6, 11.7A–D; Doguzhaeva and Mapes 2018: figs. 2.6, 3.2, 3.3, 4.1–4.6).

Soft body remains: This category comprises non-biomineralized remains attached to the gladius anteriorly (Figs. 2A, 3).



Soft tissue debris: Sporadically-dispersed soft tissue remains are identified because of their micro-granular ultrastructure and plastic deformation typical for fossilized non-biomineralized material (Fig. 9A, B, D, E, F). They are preserved between the folded sides of the gladius (for comparison see Doguzhaeva et al. 2007c: figs 6.8–6.11; Doguzhaeva et al. 2010b: figs. 2–9).

Ink: Despite the fact that the ink sac is not preserved, potential flooded ink is irregularly disseminated in the specimen as tiny pieces of black sheets (Figs. 4A, 9A, B). Similar black sheets of flooded ink were observed in some specimens of the Late Triassic coleoid *Phragmoteuthis*, while some other specimens show flask-shape ink sacs (Doguzhaeva et al. 2007c: figs. 2A, 3B, C). The patches of black sheets were especially identified in the stomach. Like the arm-hooks, they consist of carbon micro-granules (Fig. 9A) (for comparison see Doguzhaeva et al. 2004: figs. 1A–C, 2A, B; Doguzhaeva et al. 2007c: figs. 3B, C, 6B, E).

Bite marks: These marks are rounded or oval, irregularly spaced pits about 1–2 mm in diameter largely observed in the conus (Fig. 2A₂, B₁, C₁).

The uncertain organic structure: This structure consists of dark chitinous laminas (Fig. 2A₁). It distantly resembles a longitudinally sectioned coleoid beak (for comparison see Doguzhaeva et al. 2006: figs. 2, 7A–C, 8; Klug et al. 2010: figs. 2A–H; Doguzhaeva and Mapes 2017: figs. 2A, B, 3).

Original composition and fossilization of the specimen (SEM/EDS data).—Gladius: The gladius shows a micro-laminated ultrastructure (Fig. 9C) and is uniformly dominated by calcium phosphate: calcium is about 20–28%; phosphorus is 3–13%, oxygen is 35–50%, and carbon is 10–17% (SOM: table 1). At some places, the gladius is weakly silicified (silicon is up to about 2%) and contains antimony (up to 8%), iodine (about 3%) and sodium, platinum, and magnesium (less than 1%). The gladius lacks sulfur and iron (SOM: table 1). This chemical composition points towards a diagenetic phosphatization of chitin, which is in living coleoids also micro-laminated (Doguzhaeva and Mutvei 2006: figs. 4A–G, 5B). Chitinous fossil gladii have been the place for fossilization processes mediated by phosphorus-accumulating bacteria, which enhance the preservation of gladii as phosphatized pseudomorphs (Doguzhaeva and Mutvei 2003), especially in anoxic paleoenvironments (see Weaver et al. 2011). An experimental study on the micro-laminated pen of *Loligo* showed that an alkaline treatment changes porosity, wettability, swelling and the crystalline packing of β -chitin by means of intercalation of water mole-

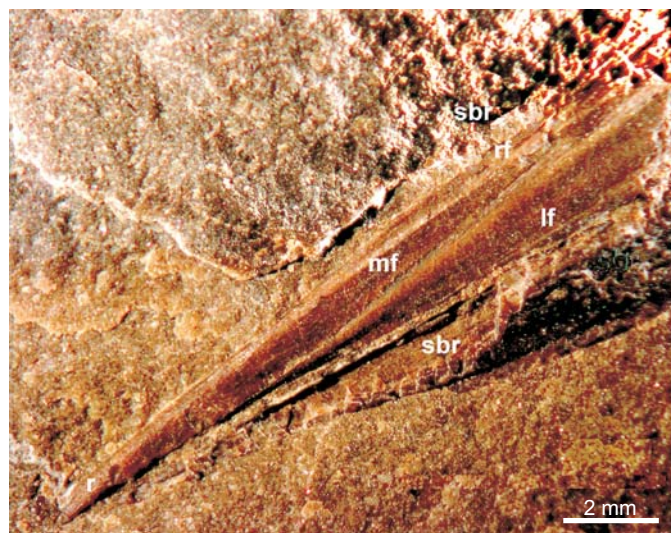


Fig. 3. Coleoid cephalopod *Idahoteuthis parisiana* Doguzhaeva and Brayard gen. et sp. nov. (holotype, UBGD 30545); middle Olenekian, Early Triassic; Idaho, USA; a folded tapered anterior part of the gladius with a rachis, and narrow median and acute left and right lateral fields. Abbreviations: lf, left lateral field; mf, median field; rf, right lateral field; sbr, soft body remains.

cules between the chitin laminas (Ianiro et al. 2014). Similar ways of degradation of the studied gladius may have preceded its diagenetic phosphatization.

Fin cartilages: The external coating of fin cartilages shows highly variable values of carbon (about 13–40%), oxygen (about 8–48%), phosphorus (up to 9%), sulfur (up to 28%), calcium (from less than 1–22%), and zinc (up to about 50%). It also contains antimony (about 6%), mercury (up to about 4%), iodine (about 2%), silicon (up to 2%) and sodium, aluminum, and iron (less than 1%) (SOM: table 1). The cartilage matrix (its original elastic components were likely elastin and collagen) is uniformly dominated by calcium phosphate, like the gladius: calcium is about 20–28%, phosphorus is up to 12%, oxygen is 36–47%, antimony is 6–9%, iodine is less than 3%, sodium, magnesium, and aluminum are less than 1% (SOM: table 1). However, the cartilage matrix shows small amounts of zinc (up to 1.2%), sulfur (up to 0.4%), potassium (up to 0.6%), and iron (up to 0.9%) which are not detected in the gladius. The canal wall exhibits a composition similar to the surface coating while the canal filling shows large content of zinc (up to 63.5%) and sulfur (up to 19%); carbon is up to about 47%, oxygen is 1–48%, and calcium is 1–24%. Besides, there are mercury (up to about 7%), platinum (up to about 5%), silicon (up to about 6%), antimony (2–6%), sodium (up to about 3%),

← Fig. 2. Coleoid cephalopod *Idahoteuthis parisiana* Doguzhaeva and Brayard gen. et sp. nov. (holotype, UBGD 30545); middle Olenekian, Early Triassic; Idaho, USA. UBGD 30545. **A.** Overall view of the specimen showing the anteriorly tapered gladius embedded in soft tissues and uncertain organic structure positioned at its tapered end. Photograph (A₁) and explanatory drawing (A₂). **B.** Conus (B₁) and its counterpart (B₂) showing the outer and inner surfaces, respectively, as well as adjacent part of soft body to show a band-like mantle structure bordering a body ventrally and continuing from the conus forward and a mantle coating the ventral side of the body and showing a mantle rippled pattern (see A₂). **C.** Posterior portion of the specimen showing position (C₁) and structure (C₂) of tiny fragment of the apical gladius showing three narrow slowly expended fields with rounded anterior outlines. Abbreviations: b, bite mark; co, conus; dcm, dorsal cartilaginous mantle; f, fin; fc, fin cartilage; g, gladius; lf, left lateral field; m, mantle; mb, mantle band-like structure; mf, median field; r, rachis; rf, right lateral field; s, stomach; sbr, soft body remains; std, soft tissue debris; uos, uncertain organic structure.

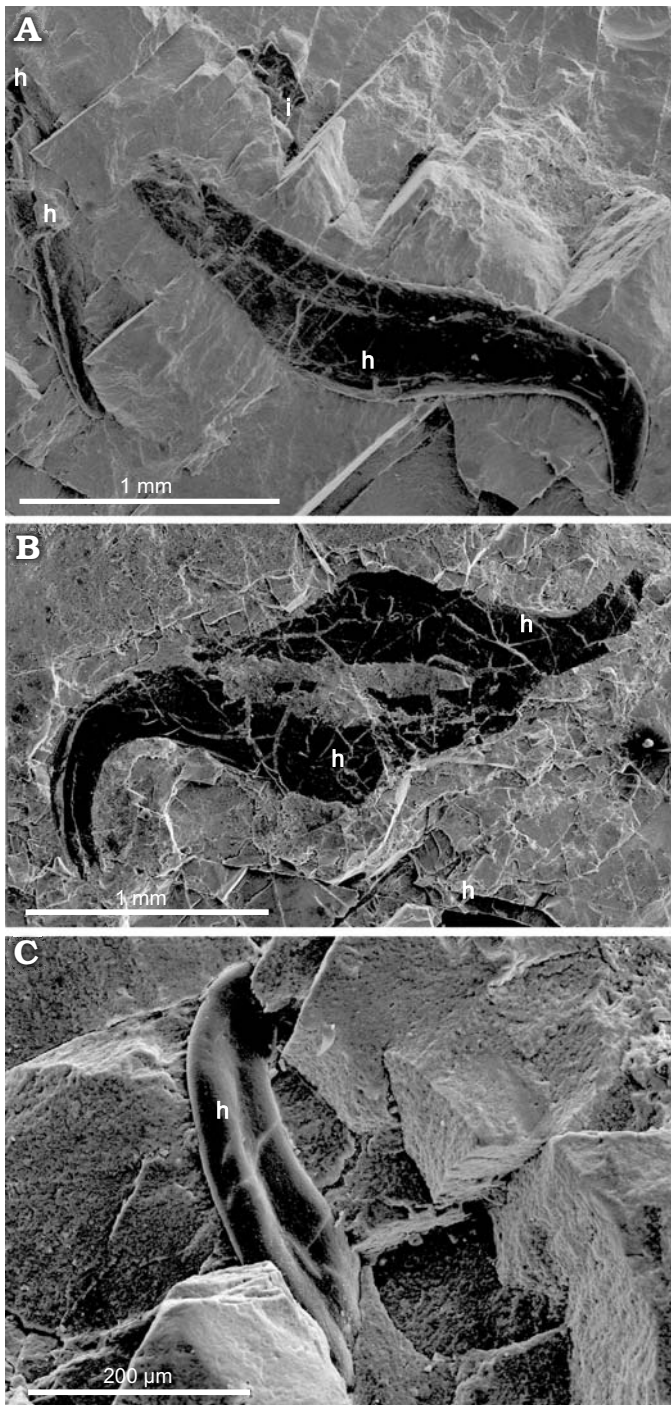


Fig. 4. Coleoid cephalopod *Idahoteuthis parisiana* Doguzhaeva and Brayard gen. et sp. nov. (holotype, UBGD 30545); middle Olenekian, Early Triassic; Idaho, USA; arm-hooks in the stomach. **A.** A well exposed arm-hook with deformed shaft and a broken distal end of the basement, tip not exposed; another arm-hook less visible and fractured. **B.** Three deformed arm-hooks. **C.** A deformed arm-hook showing a depression along the compressed shaft. Abbreviations: h, arm-hook; i, ink sheet-like patch.

phosphorus (up to 3%), iron (up to 3%), iodine (up to about 2%), aluminum (up to about 2%), magnesium (about 1%), and potassium (less than 1%). Thus, EDS data indicate that fin cartilages, which have a more complex in vivo histological structure, show a more diversified, diagenetic chemical

composition than the micro-laminated gladius, including a specific distribution of heavy metals.

Matrix adjoining the gladius: The matrix shows values of carbon similar to those of the gladius (about 17%) while the oxygen content is slightly higher (63% against 51%) and the maximum values of phosphorus are twice lower than in the gladius (about 6% against 13% in the gladius; SOM: table 1), potentially indicating differential fossilization and diagenetic pathways. Calcium is highly variable (4–23%) but its highest values are only slightly lower than in the gladius (about 28%). Silicon maximum values are five times higher than in the gladius. Potassium, sodium, and sulfur, which are absent in the gladius, are detected in the matrix but values remain anecdotal (less than 1%). Antimony and iodine are slightly lower in the contacts than in the gladius in the matrix but values remain anecdotal (7% and 2% against 8% and 3%, respectively). The composition of the matrix adjoining the gladius was thus probably in situ poorly influenced by the decay of soft tissues.

Arm-hooks: They are uniformly dominated by high carbon content (about 70%). Oxygen is about 25%, calcium 3%, and chromium 1% (SOM: table 1). This composition points towards a fossilization by means of carbonization. The carbonization of arm-hooks was previously reported in the Late Triassic *Phragmoteuthis* (Doguzhaeva et al. 2007c). The differing composition of the observed chitin structures, like the gladius and the arm-hooks, may result from minor variations of their original chemical composition, as well as the potential different packing of the chitin sheets and the crystalline packing of β -chitin. This observation agrees with the micro-granules of carbon found in the Late Triassic *Phragmoteuthis*, which are smaller in the arm-hooks than in the gladius suggesting some ultrastructural differences (Doguzhaeva et al. 2007c).

Ink: Observed potential ink tiny patches show high content of carbon (up to about 46%) and oxygen (up to about 44%), and low content of calcium (up to 6%), phosphorus (up to 3%), titanium (up to 3%), and sulfur (about 2%) (SOM: table 1). Therefore, the ink (originally melanin) was fossilized by means of carbonization, like the arm-hooks. The ink is the only substance showing a peak of titanium. This may correspond to observations in vivo on melanin from coleoid ink, which absorbs heavy metals (Chen et al. 2009).

Overall, the SEM/EDS analyses (SOM: table 1) highlight the main diagenetic processes responsible for preservation of the organic matter-rich structures; they are: (i) phosphatization of the gladius, cartilages, mantle, stomach mass and soft tissue debris, (ii) zinc-sulfur mineralization of the canalicular system in fin cartilages, and (iii) carbonization of arm hooks and ink. In addition to zinc, the absorption of heavy metals such as platinum, mercury, and titanium occurred during the fossilization of the non-biomineralized structures (SOM: table 1). The observed differential soft tissue preservation could result from the combined effects of the metabolism of anaerobic P-, C-, and S-accumulating bacteria and seawater potentially characterized by a high

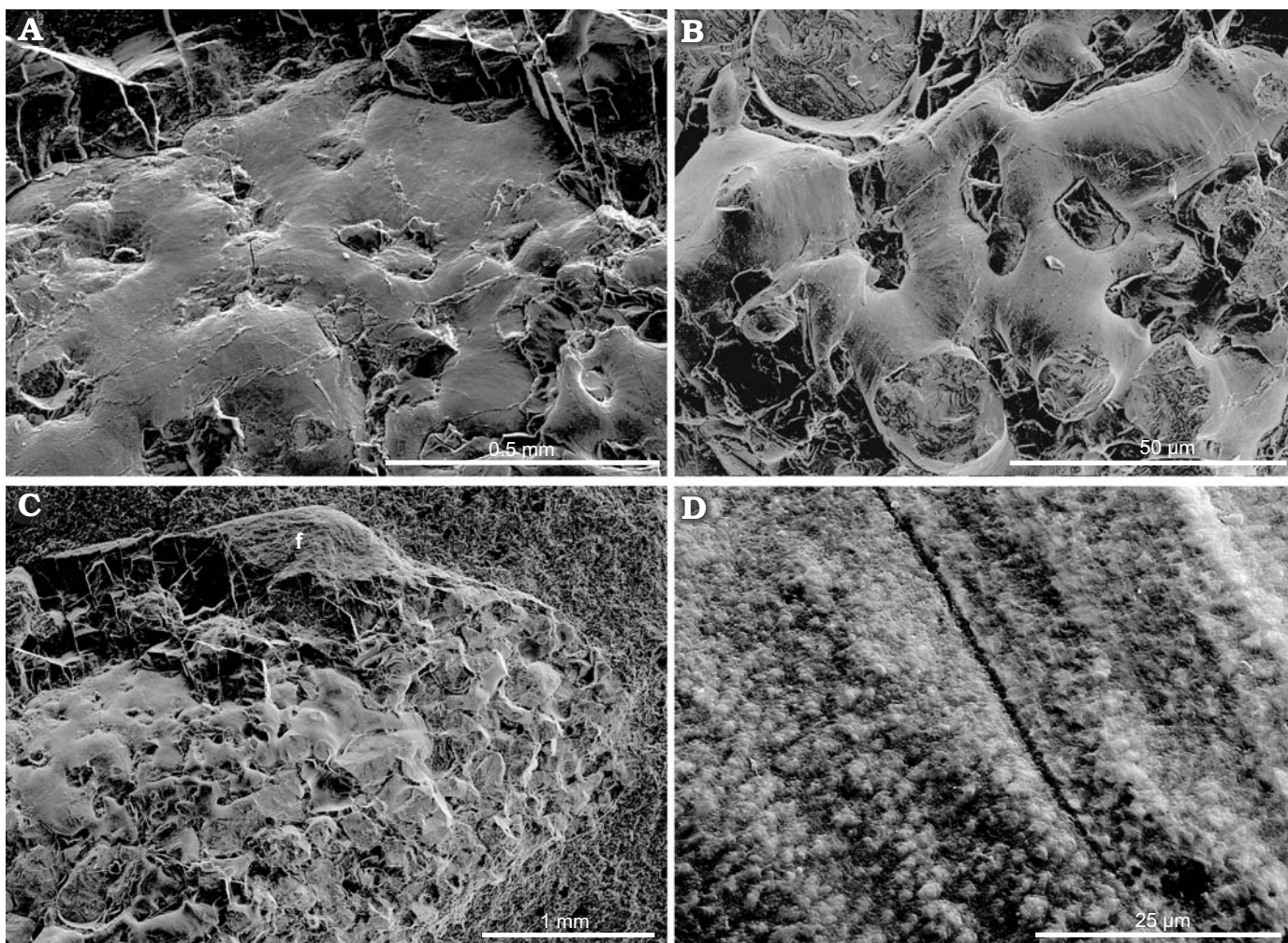


Fig. 5. Coleoid cephalopod *Idahoteuthis parisiana* Doguzhaeva and Brayard gen. et sp. nov. (holotype, UBGD 30545); middle Olenekian, Early Triassic; Idaho, USA; fin-supported cartilages. The surfaces of fractured cartilages (A–C), outer surface (D). Abbreviation: f, fin.

content of sulfur and heavy metals. These observations are in accordance with previous experimental studies showing, e.g., the capacity of the invertebrate cartilage tissues to form hydroxyapatite (Eilberg et al. 1975), and the demonstrated in vivo adsorption and absorption of heavy metals by soft tissues of modern coleoids (see Miramand and Guary 1980; Smith et al. 1984; Chen et al. 2009; Jamil et al. 2014).

Systematic palaeontology

Class Cephalopoda Cuvier, 1797

Subclass Coleoidea Bather, 1888

Superorder Decabrachia Boettger, 1952

?Order Myopsida d'Orbigny, 1841

Family *Idahoteuthidae* Doguzhaeva and Brayard nov.

Type genus: *Idahoteuthis* Doguzhaeva and Brayard gen. nov.; see below, monogeneric.

Diagnosis.—Cylindrical, stream-line, dorsally cartilaginous muscular mantle; two well-developed, ca. 0.2–0.3

mantle length, pear-shape fin-supported cartilages and fins at conical mantle termination; thin slender gladius with narrow median and lateral fields, rachis; breviconic conus as long as fin-supported cartilages and fins.

Geographic and stratigraphic range.—Middle Olenekian (early Spathian) Lower Shale unit of the Lower Triassic Thaynes Group; west of the city of Paris, Bear Lake County, southeastern Idaho, western USA.

Genus *Idahoteuthis* Doguzhaeva and Brayard nov.

Type species: *Idahoteuthis parisiana* Doguzhaeva and Brayard gen. et sp. nov., see below, monotypic.

Etymology: Named after the state of Idaho, USA where the specimen was found.

Diagnosis.—Slender gladius; maximum width/length ratio, ca. 0.2, in middle part; long, narrow, anteriorly angulated lateral fields; median and lateral keels; conus large, ca. 0.25 gladius length without rachis length.

Remarks.—At the juvenile stage, the gladius is narrow, with three narrow fields each of which shows a broadly rounded anterior outline (Fig. 2C). The median field is slightly lon-

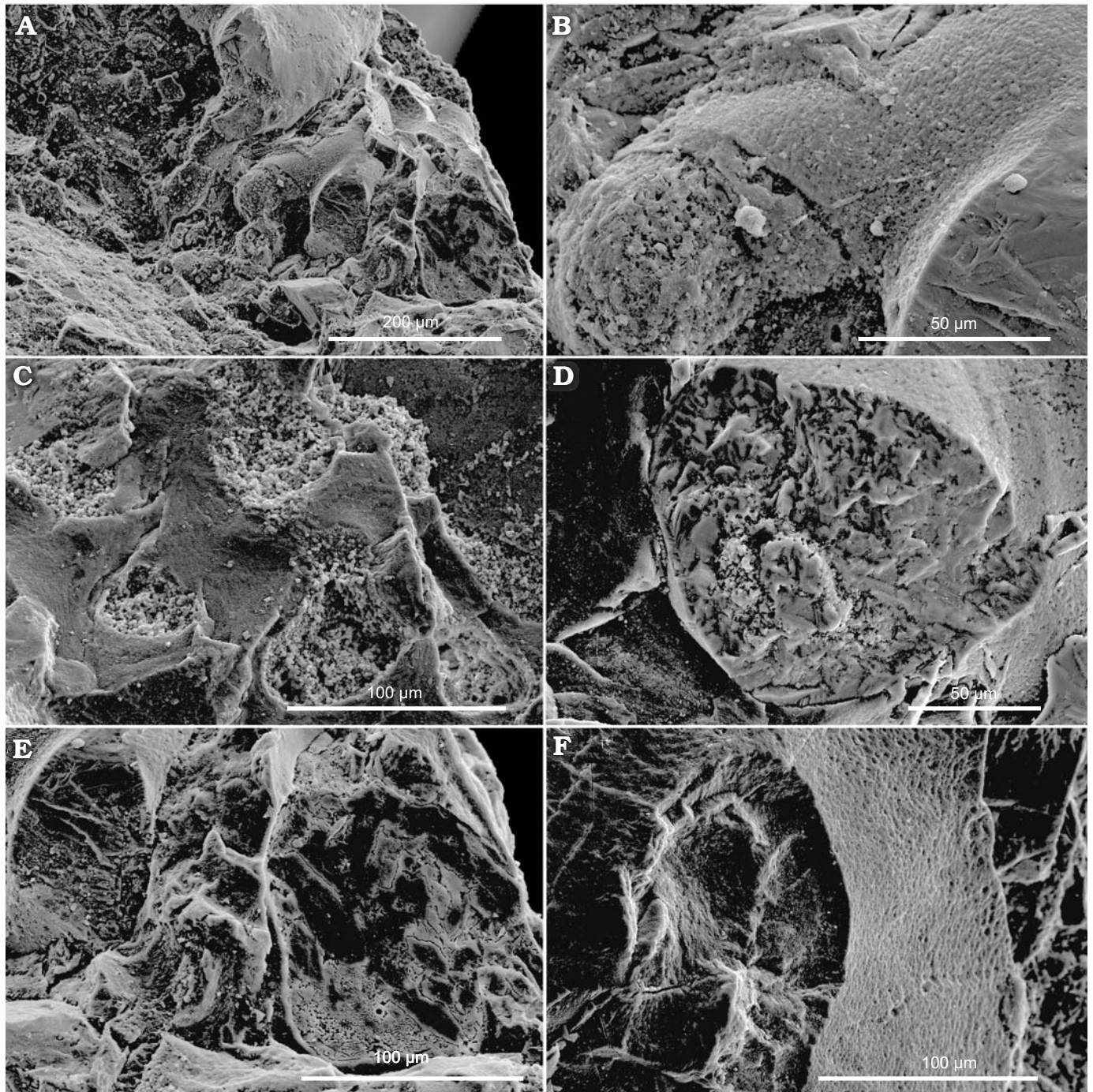


Fig. 6. Coleoid cephalopod *Idahoteuthis parisiانا* Doguzhaeva and Brayard gen. et sp. nov. (holotype, UBGD 30545); middle Olenekian, Early Triassic; Idaho, USA; views on the canalicular structure of fin-supported cartilages (A–D).

ger that lateral fields. This morphology suggests that the rachis and anteriorly tapered median and angulated lateral fields appeared at later ontogenetic stage. The new family *Idahoteuthidae* assumedly falls in the order *Myopsida*. Extant myopsids are neritic, often dwelling in very shallow waters, or are upper slope demersal species; many species are also efficient swimmers (Vecchione and Young 2008). Combined observed features in *Idahoteuhs* gen. nov. and comparisons with present-day coleoids therefore suggest that members of *Idahoteuthidae* had a streamlined body, a

micro-laminated ultrastructure and a non-biomineralized, supposedly chitinous composition of gladius providing a light and flexible skeleton, as well as well-developed fin cartilages favoring effective maneuvering in swimming.

Idahoteuthis parisiانا Doguzhaeva and Brayard
sp. nov.

Figs. 2–9.

Etymology: Named after the city of Paris, Idaho (USA), where the specimen was found.

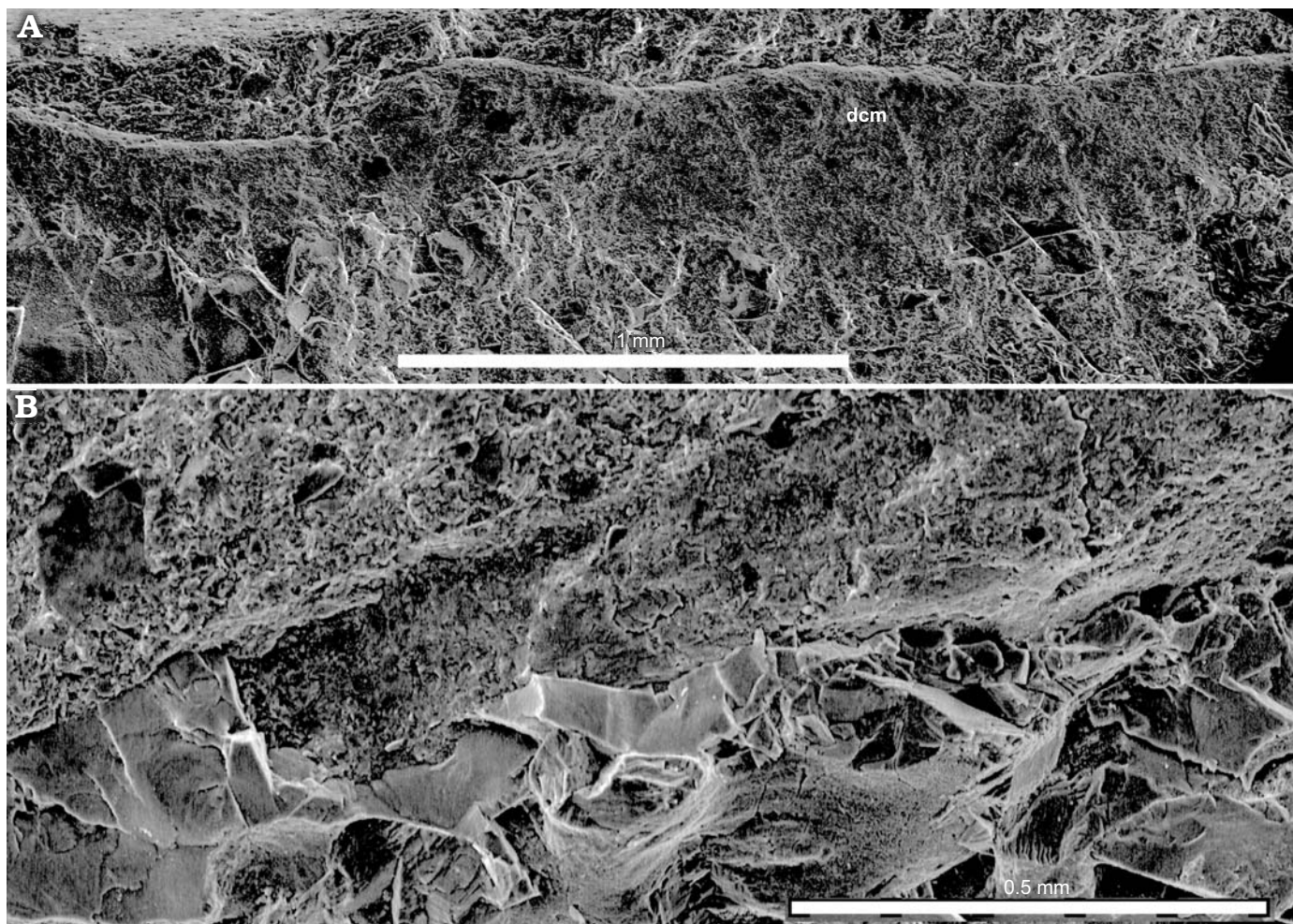


Fig. 7. Coleoid cephalopod *Idahoteuthis parisiana* Doguzhaeva and Brayard gen. et sp. nov. (holotype, UBGD 30545); middle Olenekian, Early Triassic; Idaho, USA; cartilaginous mantle band-shape structure on the dorsal side of soft body. Overview (A) and detail of analicular cartilage (B). Abbreviation: dcm, dorsal cartilaginous mantle.

Holotype: UBGD 30545. The specimen is exposed on two split surfaces of the broken concretion. It is compressed because of compaction and strongly deformed according to original differences in morphology and composition observed between its anterior, middle and posterior parts. It reveals a multi-way fossilization resulted in different preservation of chitin gladius, and arm hooks and soft tissue remains..

Type horizon: Early Triassic, middle Olenekian (early Spathian).

Type locality: West of the city of Paris, southeastern Idaho, western USA.

Diagnosis.—Tapered, slender, ca. 40–50 mm long, gladius with maximum width/length ratio, ca. 0.2, in its middle part; narrow median field with rachis; narrow, anteriorly angulated long lateral fields; median and lateral keels; conus large, ca. 0.25 gladius length without rachis length.

Description.—The holotype is a 48.7 mm long specimen showing non-biomineralized structures. Its anterior, central and posterior parts are differently deformed. The middle part of the gladius is embedded in soft body that retains its cylindrical shape in the middle part of the specimen; the cephalic area is not preserved (Fig. 2A). The gladius is thin-walled, micro-laminated, flexible, diagenetically phos-

phatized and apparently originally chitinous (SOM: table 1; Fig. 9C). It is ca. 42.2 mm long, anteriorly tapered and exhibits a large conus at its posterior end (Figs. 2, 3). The median field is narrow and anteriorly ended by a free rachis (Figs. 2A, 3). The extremity of the rachis is broken and its actual length is unknown; the measured length is about 4 mm. The lateral fields are narrow, long, and acute anteriorly (Fig. 2A₁). The conus is ca. 8.3 mm long, that is ca. 0.25 of the gladius length (Fig. 2A, C₁). The posterior extremity of the conus approximately corresponds to the top of the V-shape “sinus” between fins (Fig. 2C). The conus shows a small lateral tooth-like structure (Fig. 2A₂, B, C₁). The smooth outer surface of the gladius is exposed in its most anterior tapered part (Fig. 2A), in the conus (Fig. 2A₁, C₁) and in a tiny ~3 mm apical part of the gladius that is displaced from its original position and seen in the marginal part of the conus (Fig. 2C). The apical gladius has slowly expanded narrow median and two lateral fields with broadly rounded anterior outline; the central field being slightly longer and broader than lateral ones. This highlights the presumed ontogenetic transformation of the rounded frontal outline of

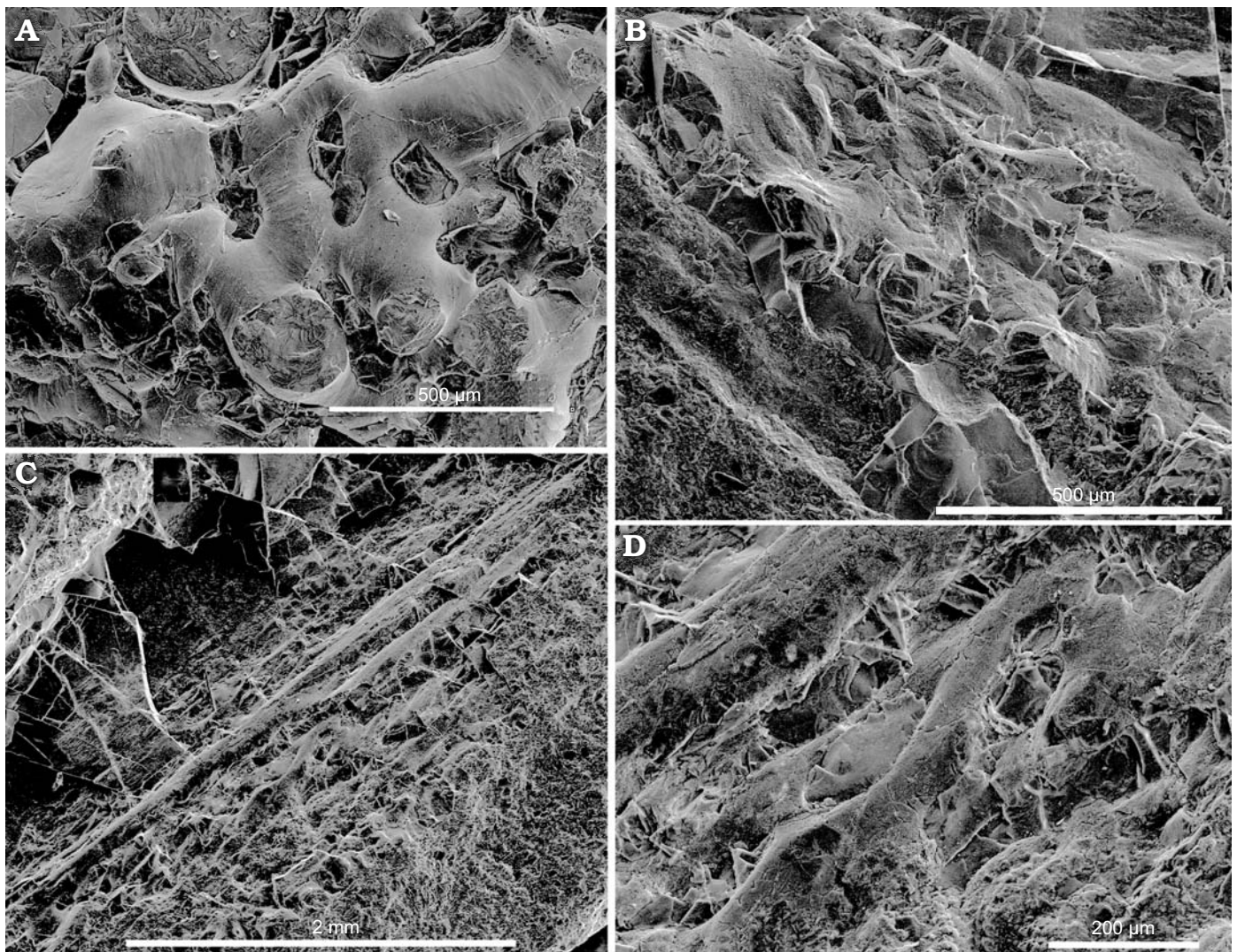


Fig. 8. Coleoid cephalopod *Idahoteuthis parisiana* Doguzhaeva and Brayard gen. et sp. nov. (holotype, UBGD 30545); middle Olenekian, Early Triassic; Idaho, USA. **A**. Canalicular cartilage of fin-supported structure. **B–D**. Cartilaginous mantle band-shape structure on dorsal side showing a canalicular type of cartilage.

the juvenile gladius into the tapered frontal outline in later ontogenetic stages. It is worth noting that the ontogenetic stage that would be characterized by a *Loligosepia*-type gladius showing a broad triangular median field, is missing in the ontogeny of *Idahoteuthis parisiana* Doguzhaeva and Brayard gen. et sp. nov. In the middle part, the gladius is deformed in a way that its sides are brought together and overlap one another. Because the left half of the gladius is broken and removed, soft tissue remains are exposed there (Fig. 2A, B). This part of the specimen is occupied by a large, oval, phosphatized stomach (Fig. 2A₁). Due to compaction, the latter likely looks larger, than it was originally. The stomach exhibits a lighter color than other structures in this area. It has a gently folded periphery along the ventral side but it is less deformed along the dorsal side (Fig. 2A). The stomach contains irregularly dispersed deformed arm hooks, ten of which have been found on a fracture plan (Fig. 4). It is worth to note that the stomach of the Late Cretaceous “fossil squid” *Dorateuthis* contained the undigested fish

remains (Lukeneder and Harzhauzer 2004). In addition to the arm hooks, the exposed surface of the stomach displays scattered tiny, black sheet fragments of potential flooded ink. Like the arm hooks, ink exhibits a micro-globular ultra-structure and a carbon composition (Fig. 9A; SOM: table 1). Posteriorly, a pair of pear-like, fin-supported cartilages and fins complete the specimen (Figs. 2A, C₁, 5, 6, 8A). They adjoin the conus; both being approximately equally long. The mantle is exposed like a ventral band-shape structure extending from the conus along the ventral margin of the soft body (Fig. 2A₂, B). It might provide postmortem fixation of the cylindrical shape of the body on the ventral side where other supporting structures were missing. The ventral mantle is also represented by a patch preserved in front of the conus; it has thin, wavy longitudinal ridges (Fig. 2B). On the dorsal side, the gladius is coated by a band-shape structure of thin cartilaginous mantle (Figs. 2A₂, C₁, 7, 8). This cartilage tissue is canalicular (Figs. 7B, 8), like in fin cartilages (Figs. 5C, 6, 8A). Additionally, sporadical-

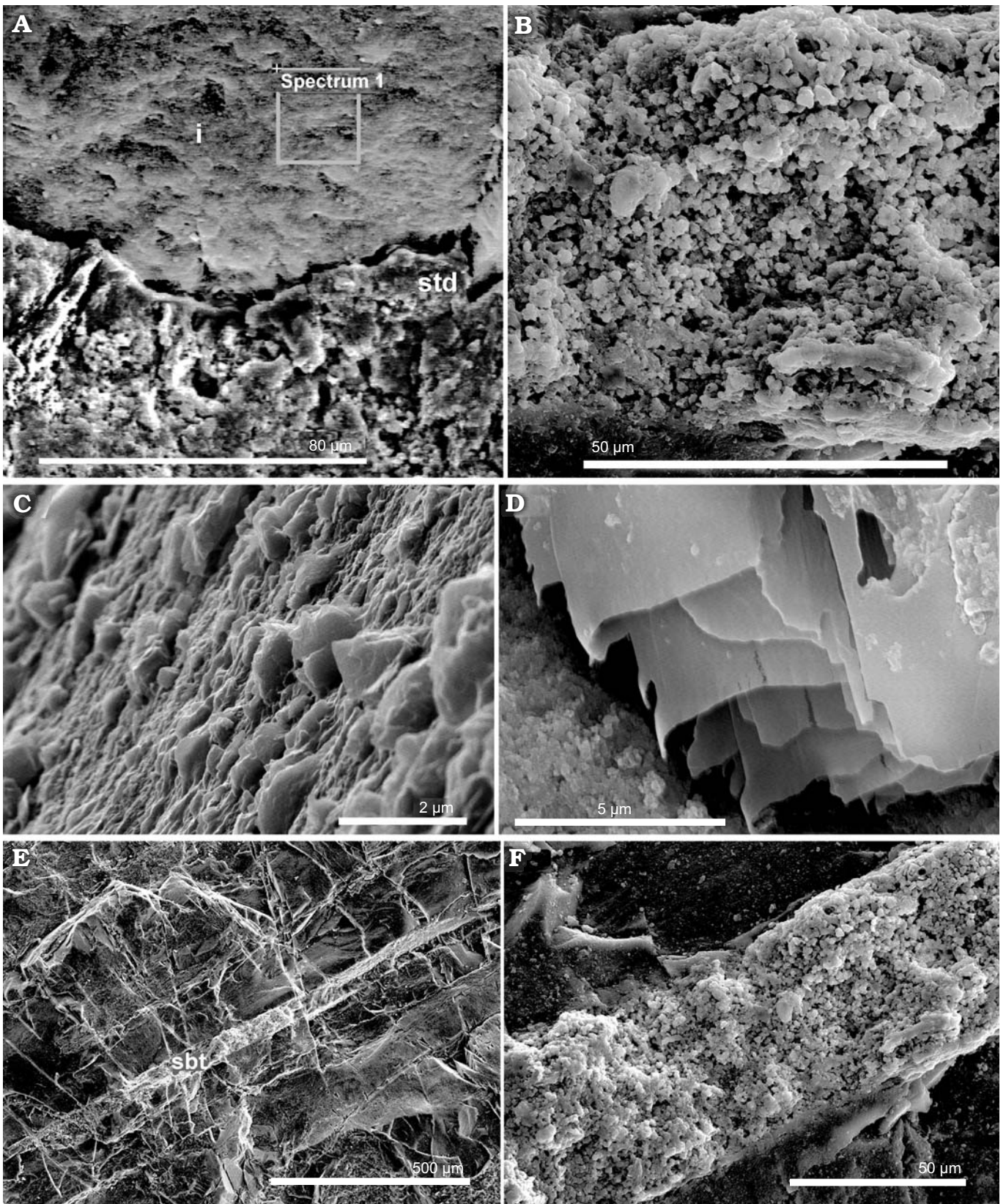


Fig. 9. Coleoid cephalopod *Idahoteuthis parisiiana* Doguzhaeva and Brayard gen. et sp. nov. (holotype, UBGD 30545); middle Olenekian, Early Triassic; Idaho, USA; globular ultrastructure of non-biomineralized structures. **A.** Sheet-like patch of flooded ink (top) and soft tissue debris (bottom); a site of the geochemical analysis is marked with a square. **B.** Undetermined long soft tissue piece showing a micro-granular ultrastructure on the dorsal side of the soft body. **C.** Micro-laminated ultrastructure of the gladius. **D.** Undetermined non-biomineralized micro-laminated fragment from the stomach. **E.** A linear fragment of soft tissue on dorsal side of the body. **F.** Micro-globular ultrastructure. Abbreviations: i, ink sheet-like patch; sbt, soft body tissues; std, soft tissue debris.

ly-dispersed mantle debris are identified by their plastic micro-deformation and micro-granular ultrastructures typical for fossilized non-biomineralized materials (Fig. 9A, E, F; for comparison see Doguzhaeva et al. 2004b: figs. 2A, B; Doguzhaeva et al. 2007a: figs. 6.7A–E; Doguzhaeva et al. 2007b: figs. 11.3–11.7; Doguzhaeva et al. 2010b: figs. 2–9).

Stratigraphic and geographic range.—Type locality and horizon only.

Discussion

Phylogenetic implications.—Naef (1922) suggested that the evolutionary development of the gladius started based on a broad *Loligosepia*-type gladius progressively narrowing, with a median field reducing up to a thin rib or rachis leading to the narrow gladius of extant taxa. In this way, Jeletzky (1966) considered the Suborder Loligosepiina Jeletzky, 1965 as the stem group of modern oegopsid and myopsid squids. Morphological similarities between the gladius of the Early Jurassic *Loligosepia*, characterized by a broad triangular median field (see Fuchs and Weis 2008; Donovan and Boletzky 2014), and extant squid *Thysanoteuthis* were also interpreted as evidence of an ancestor-descendant relationship between these two genera by Starobogatov (1983). These similarities were oppositely considered as having no phylogenetic value by Nesis (1992). Young et al. (1998) assumed that the gladius appeared at least four times in extant taxa Vampyromorpha, Oegopsida, Myopsida, and Sepiolidae. Vecchione et al. (1999) also suggested that a three-part gladius with a broad median field and wings has no value for determining phylogenetic relationships. Later, Kröger et al. (2011) endorsed this view. Fuchs et al. (2013) described a *Loligosepia* specimen showing eight, rather than ten, arms in an arm crown. Since this discovery, loligosepiids have been considered separately from modern Decabrachia (Fuchs et al. 2013) and Donovan and Boletzky (2014) suggested that *Loligosepia* lies near the origin of Recent Octobrachia during the Early Jurassic. Following this view, fossil gladius with a *Loligosepia*-type gladius fall in Octobrachia rather than Decabrachia. This might be the case for the Middle Triassic *Reitnertheuthis* and the Late Triassic *Germanoteuthis* in which the median field is breviconic and triangular (Schweigert and Fuchs 2012). Contrary to these two Middle and Late Triassic genera, the Early Triassic *Idahoteuthis* Doguzhaeva and Brayard gen. nov. may fall in Decabrachia because of its narrow median field. Narrow gladius are well documented in e.g., younger *Plesioteuthis* from the Late Jurassic (Donovan and Toll 1988; Fuchs et al. 2007, 2015; Klug et al. 2010, 2015). Based on morphological similarities with gladius of extant squids (Ommastrephidae) (i.e., a narrow and long rachis, median and lateral keels, and the conus), *Plesioteuthis* was considered as the rootstock of oegopsid squids (Jeletzky 1966; Donovan and Toll 1988). Based on recently recovered beaks *Plesioteuthis* was as-

signed to Decabrachia (Klug et al. 2010), however based on two pairs of fins and cirrate arms, *Plesioteuthis* has been assigned to octobrachiids (Klug et al. 2015).

A narrow gladius is also known in e.g., the Early Cretaceous *Nesisoteuthis*. Judging on a shape of growth lines, it has a pointed median field and is even more similar to ommastrephids than the Jurassic *Plesioteuthis*. However, whether *Nesisoteuthis* has a conus remains unknown as a single specimen of this genus is available and does not show a preserved posterior part (Doguzhaeva 2005: figs. 1A–C).

Idahoteuthis Doguzhaeva and Brayard gen. nov. is preceded by the Early Permian gladius-bearing coleoid *Glochinomorpha stifeli* (Gordon 1971) that shows limited morphological similarity with the other known gladius (Doguzhaeva and Mapes 2015: figs. 1–3). Recently obtained data on *Glochinomorpha* via ultrastructural and chemical approaches, however, suggests that: (i) the gladius appeared in the late Paleozoic, rather than in the Middle–Late Triassic, (ii) its appearance preceded Middle–Late Triassic phragmoteuthids still having a phragmocone, (iii) the biochemical development of shell material (sensu secretion of non-biomineralized, apparently chitinous, shell material as opposed to aragonite in the phragmocone of *Phragmoteuthis*) preceded its morphological transformation (sensu typical gladius structure with a limited number of longitudinal sectors and the presence of a conus), and (iv) the combination of the archaic gladius morphology and advanced gladius composition results from the asynchronous appearance of biochemical and morphological innovations in early evolutionary stages of squids (Doguzhaeva and Mapes 2015). Thus, a high evolutionary rate corresponding to the assumed morphologic transformation of the *Glochinomorpha*-type gladius (see Doguzhaeva and Mapes 2015: figs. 1A–H, 2–4) into a tapered, narrow *Idahoteuthis*-type gladius (Figs. 2A) have taken place during the Early Permian–Early Triassic interval. The Early Triassic occurrence of the *Idahoteuthis*-type gladius supports a scenario where gladius-bearing coleoids evolved independently from the proostracum-bearing belemnoids, including phragmoteuthids (see Doguzhaeva 2012). Even if *Phragmoteuthis*-type proostraca are found in older intervals than the middle Olenekian (see Rosenkrantz 1946), a direct evolutionary transformation of this shell type into a gladius would request the unlikely short-time combination of the following processes: (i) the elimination of a phragmocone comprising about 20 camerae, septa, septal necks, connecting rings and conotheca; (ii) the elimination of a soft siphuncle, including blood vessels and connecting tissues, running through approximately 20 camerae of the phragmocone; (iii) the re-organization of the soft tissues and muscular system; (iv) the development of physiological processes that can have enhanced secretion of chitin and associated proteins, instead of aragonite shell material; and (v) the appearance of a new locomotion system. Keeping this in mind, a direct transformation of the *Phragmoteuthis*-type shell into an *Idahoteuthis*-type gladius is hardly conceivable in a relatively short geological time interval. For the same

reasons, the *Phragmoteuthis* lineage can hardly be considered, in our opinion, as the rootstock of Decabrachia or Octobrachia (Fuchs and Iba 2015).

To sum up, the earliest known gladii are presently known due to the Early Permian *Glochinomorpha* and the Early Triassic *Idahoteuthis*. Contrary to *Glochinomorpha*-type gladius, the *Idahoteuthis*-type gladius exhibits advanced morphological characters: three narrow longitudinal fields and a conus that are developed in extant Myopsida and Oegopsida. Based on molecular data, the divergence time for Myopsida appears close to the Late Permian/Early Triassic interval (Strugnell et al. 2006). The divergence time for Decabrachia is older (Strugnell et al. 2006), which is in agreement with the Late Carboniferous occurrence of the spirulid *Shimanskya* (Doguzhaeva et al. 1999).

Implications for Early Triassic food webs.—Numerous arm hooks have been collected in coprolites from the same exposures where *Idahoteuthis* Doguzhaeva and Brayard gen. nov. was found. Thus, in the middle Olenekian of the western USA basin, some coleoids were a prey for indeterminate predators, likely large-sized vertebrates such as fishes or ichthyosaurs (Brayard et al. 2017). For instance, chondrichthyan remains corresponding to specimens of about 1 m in length are common in some coeval exposures from Idaho (Romano et al. 2013). Ichthyosaur remains are also known from neighboring localities, and can have also been potential hunters for coleoids (Brayard et al. 2017). A strong prey-predator trophic relationship between coleoids and vertebrates thus may have existed during the middle Olenekian, at least in the Western USA basin. Based on the chitinous, thin-walled, tapered narrow gladius indicative of a streamlined body, the well-developed fin cartilages, the posterior fins, and the arm-hooks in the stomach, *I. parisiana* Doguzhaeva and Brayard gen. et sp. nov. was probably well adapted for active swimming and may have also been a small size predator inhabiting the subequatorial shallow warm sea on the west coast of Pangaea. Overall, the presence of eroded and deformed arm-hooks in the stomach of *Idahoteuthis* (Fig. 4) suggests cannibalism among Early Triassic coleoids, as frequently encountered in extant squids (Ibáñez and Keyl 2010). Such trophic links among coleoids and between coleoids and other taxa highlight the multi-layered marine trophic network in the subequatorial warm shallow water marine environment of the west coast of Pangaea soon after the end-Permian mass extinction.

Conclusions

An Olenekian (Early Triassic) small size squid *Idahoteuthis parisiana* Doguzhaeva and Brayard gen. et sp. nov. and Idahoteuthidae Doguzhaeva and Brayard fam. nov. are described on the basis of a narrow, tapered, thin-walled gladius embedded in cylindrical body showing a pair of fins, large fin-supported cartilages, a dorsal cartilaginous band-

like mantle structure, ventral non-cartilaginous band-like mantle structure and a stomach containing undigested arm hooks and flat patches of ink. The family Idahoteuthidae assumedly belongs to order Myopsida.

Idahoteuthis parisiana evidences the fossil squids inhabited the subequatorial warm shallow sea on the west coast of Pangaea in the Early Triassic; they were mobile predators, but also a prey for larger predators, including coleoids. Cannibalism of *I. parisiana* is deduced from the stomach content comprising undigested arm hooks. The micro-laminated lifetime chitin material of the gladius, microenvironments linked to diverse microbial blooms, and transient anoxic/disoxic conditions are considered as the main potential factors leading to the formation of the multiple fossilization types of the gladius and soft tissue body remains.

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References

- Bairati, A., De Biasi, S., Cheli, F., and Oggioni, A. 1987. The head cartilage of cephalopods. I. Architecture and ultrastructure of the extracellular matrix. *Tissue cell* 19: 673–685.
- Bather, F.A. 1888. Shell-growth in Cephalopoda (Siphonopoda). *Annals and Magazine of Natural History* 6: 421–427.
- Boettger, C.B. 1952. Die Stämme des Tierreichs in ihrer systematischen Gliederung. *Abhandlungen der Braunschweigischen Wissenschaftlichen Gesellschaft* 4: 238–300.
- Brayard, A., Krümenacker, L.J., Botting, J.P., Jenks, J.F., Bylund, K. G., Fara, E., Vennin, E., Olivier, N., Goudemand, N., Saucède, T., Charbonnier, S., Romano, C., Doguzhaeva, L., Thuy, B., Hautmann, M., Stephen, D.A., Thomazo, C., and Escarguel, G. 2017. Unexpected Early Triassic marine ecosystem and the rise of the Modern evolutionary fauna. *Science Advances* 3: e1602159.
- Chen, S., Xue, C., Wang, J., Feng, H., Wang, Y., Ma, Q., and Wang, D. 2009. Adsorption of Pb (II) and Cd (II) by squid *Ommastrephes bartramii* melanin. *Bioinorganic Chemistry and Applications* 2009: 901563.
- Cuvier, G. 1797. *Tableau élémentaire de l'histoire naturelle des animaux*. 710 pp. Baudouin, Paris.
- Doguzhaeva, L.A. 2005. A gladius-bearing coleoid cephalopod from the Aptian of Central Russia. *Mitteilungen des Geologisch-Paläontologischen Institutes der Universität Hamburg* 89: 41–48.
- Doguzhaeva, L.A. 2012. The original composition of the pro-ostracum of

- an early Sinemurian belemnite from Belgium deduced from mode of fossilization and ultrastructure. *Palaeontology* 55: 249–260.
- Doguzhaeva, L.A. and Mutvei, H. 2003. Gladius composition and ultrastructure in extinct squid-like coleoids: *Loligosepia*, *Trachyteuthis* and *Teudopsis*. *Revue de Paléobiologie* 22: 877–894.
- Doguzhaeva, L.A. and Mapes, R.H. 2015. Arm hooks and structural features in the Early Permian *Glochinomorpha* Gordon 1971, indicative of its coleoid affiliation. *Lethaia* 48: 100–114.
- Doguzhaeva, L.A. and Mapes, R.H. 2017. Beak from the body chamber of the Early Carboniferous (Visean) shelled longiconic coleoid (Cephalopoda) from Arkansas, USA. *Lethaia* 50 (4): 540–547.
- Doguzhaeva, L.A. and Mapes, R.H. 2018. A new late Carboniferous coleoid from Oklahoma, USA: implications for the early evolutionary history of the subclass Coleoidea (Cephalopoda). *Journal of Paleontology* 92 (2): 157–169.
- Doguzhaeva, L.A. and Mutvei, H. 2006. Ultrastructural and chemical comparison between gladii in living coleoids and Aptian coleoids from Central Russia. *Acta Universitatis Carolinae—Geologica* 49: 83–93.
- Doguzhaeva, L.A., Mapes, R.H., and Mutvei, H. 1999. A Late Carboniferous spirulid coleoid from the southern mid-continent (USA): Shell wall ultrastructure and evolutionary implications. In: F. Oloriz and F.J. Rodriguez-Tovar (eds.), *Advancing Research on Living and Fossil Cephalopods*, 47–57. Kluwer Academic Plenum Publishers, New York.
- Doguzhaeva, L.A., Mapes, R.H., and Mutvei, H. 2004. Occurrence of ink in Paleozoic and Mesozoic coleoids (Cephalopoda). *Mitteilungen des Geologisch-Paläontologischen Institutes der Universität Hamburg* 88: 145–156.
- Doguzhaeva, L.A., Mapes, R.H., and Mutvei, H. 2007a. A Late Carboniferous coleoid cephalopod from the Mazon Creek Lagerstätte (USA), with a radula, arm hooks, mantle tissues, and ink. In: N.H. Landman, R.A. Davis, and R.H. Mapes (eds.), *Cephalopods Present and Past. New Insights And Fresh Perspectives*, 121–143. Springer, The Netherlands.
- Doguzhaeva, L.A., Mapes, R.H., and Mutvei, H. 2007b. The preservation of body tissues, shell, and mandibles in the ceratitid ammonoid *Austrotrachyceras* (Late Triassic), Austria. In: N.H. Landman, R.A. Davis, and R.H. Mapes (eds.), *Cephalopods Present and Past: New Insights and Fresh Perspectives*. 221–238. Springer, Dordrecht.
- Doguzhaeva, L.A., Mapes, R.H., and Mutvei, H. 2010a. Evolutionary patterns of Carboniferous coleoid cephalopods based on their diversity and morphological plasticity. In: K. Tanabe, Y. Shigetani, T. Sasaki, and H. Hirano (eds.), *Cephalopods Present and Past*, 171–180. Tokai University Press, Tokyo.
- Doguzhaeva, L.A., Mapes, R.H., Bengtson, S., and Mutvei, H. 2010b. A radula and associated cephalic remains of a Late Carboniferous coleoid from Idaho, USA. *Ferrantia* 59: 37–50.
- Doguzhaeva, L.A., Summesberger, H., and Mutvei, H. 2006. A unique Upper Triassic coleoid from the Austrian Alps reveals proostracum and jaw ultrastructure. *Acta Universitatis Carolinae—Geologica* 49: 69–82.
- Doguzhaeva, L.A., Summesberger, H., Mutvei, H., and Brandstaetter, F. 2007c. The mantle, ink sac, ink, arm hooks and soft body debris associated with the shells in Late Triassic coleoid cephalopod *Phragmo-teuthis* from the Austrian Alps. *Palaeoworld* 16: 272–284.
- Donovan, D.T. and Boletzky, S.V. 2014. *Loligosepia* (Cephalopoda: Coleoidea) from the Lower Jurassic of the Dorset coast, England. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 273: 45–63.
- Donovan, D.T. and Toll, R.B. 1988. The gladius in coleoid (Cephalopoda) evolution. In: M.R. Clarke and E.R. Trueman (eds.), *The Mollusca, Paleontology and Neontology of Cephalopods* 12, 89–101. Academic Press, San Diego.
- Eilberg, R.G., Zuckerberg, D.A., and Person, N.J.P. 1975. Mineralization of invertebrate cartilage. *Calcified Tissue Research* 19: 85–90.
- Engeser, T. and Clarke, M.R. 1988. Cephalopod hooks, both recent and fossil. In: M.R. Clarke and E.R. Trueman (eds.), *The Mollusca, Paleontology and Neontology of Cephalopods* 12, 133–151. Academic Press, San Diego.
- Fuchs, D. and Iba, Y. 2015. The gladiuses in coleoid cephalopods: homology, parallelism, or convergence? *Swiss Journal of Palaeontology* 134: 187–197.
- Fuchs, D. and Weis, R. 2008. Taxonomy, morphology and phylogeny of Lower Jurassic loligosepiid coleoids (Cephalopoda). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 249: 93–112.
- Fuchs, D., Iba, Y., Tischlinger, H., and Klug, C. 2015. The locomotion system of Mesozoic Coleoidea (Cephalopoda) and its phylogenetic significance. *Lethaia* 49: 433–454.
- Fuchs, D., Keupp, H., and Schweigert, G. 2013. First record of a complete arm crown of the Early Jurassic coleoid *Loligosepia* (Cephalopoda). *Paläontologische Zeitschrift* 87: 431–435.
- Fuchs, D., Klinghammer, A., and Keupp, H. 2007. Taxonomy, morphology and phylogeny of plesiot euthid coleoids from the Upper Jurassic (Tithonian) Plattenkalks of Solnhofen. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 245: 239–252.
- Galfetti, T., Bucher, H., Ovtcharova, M., Schaltegger, U., Brayard A., Brühwiller, T., Goudemand, N., Weissert, H., Hochuli, P.A., and Guodun, F.C.K. 2007. Timing of the Early Triassic carbon cycle perturbations inferred from new U-Pb ages and ammonoid biochronozones. *Earth and Planetary Science Letters* 258: 593–604.
- Gordon, M. Jr. 1971. Primitive squid gladii from the Permian of Utah. *US Geological Survey Professional Paper* 750C: C34–C38.
- Ianiro, A., Di Giosia, M., Fermani, S., Samori, C., Barbalinardo, M., Valle, F., Pellegrini, G., Biscarini, F., Zerbetto, F., Calvaresi, M., and Falini, G. 2014. Customizing properties of β -chitin in squid pen (gladius) by chemical treatments. *Marine Drugs* 12: 5979–5992.
- Ibáñez, C. and Keyl, F. 2010. Cannibalism in cephalopods. *Reviews in Fish Biology and Fisheries* 20: 123–136.
- Jamil, T., Lias, K., Norsila, D., and Syafinaz, N.S. 2014. Assessment of heavy metal contamination in squid (*Loligo* spp.) tissues of Kedah-Perlis waters, Malaysia. *The Malaysian Journal of Analytical Sciences* 18: 195–203.
- Jattiot, R., Brayard, A., Fara, E., and Charbonnier, S. 2015. Gladius-bearing coleoids from the Upper Cretaceous Lebanese Lagerstätten: Diversity, morphology, and phylogenetic implications. *Journal of Paleontology* 89:148–167.
- Jeletzky, J.A. 1965. Taxonomy and phylogeny of fossil Coleoidea (= Dibranchiata). *Geological Survey of Canada Papers* 65: 72–76.
- Jeletzky, J.A. 1966. Comparative morphology, phylogeny and classification of fossil Coleoidea. *Paleontological Contributions, University of Kansas, Mollusca* 7: 1–16.
- Jenks, J., Guex, J., Hungerbühler, A., Taylor, D., and Bucher, H. 2013. Ammonoid biostratigraphy of the early Spathian Columbites parisianus zone (Early Triassic) at Bear Lake Hot Springs, Idaho, USA. *New Mexico Museum of Natural History and Science* 61: 268–283.
- Klug, C., Fuchs, D., Schweigert, G., Röper, M., and Tischlinger, H. 2015. New anatomical information on arms and fins from exceptionally preserved *Plesiot euthis* (Coleoidea) from the Late Jurassic of Germany. *Swiss Journal Palaeontology* 134: 245–255.
- Klug, C., Schweigert, G., and Dietl, G. 2010. A new *Plesiot euthis* with beak from the Kimmeridgian of Nusplingen (Germany). *Ferrantia* 59: 73–77.
- Kröger, B., Vinther, J., and Fuchs, D. 2011. Cephalopod origin and evolution: a congruent picture emerging from fossils, development and molecules. *BioEssays* 33: 602–613.
- Kulicki, C. and Szaniawski, H. 1972. Cephalopod arm hooks from the Jurassic of Poland. *Acta Palaeontologica Polonica* 17: 379–426.
- Kummel, B. 1954. Triassic stratigraphy of southeastern Idaho and adjacent areas. *U.S. Geological Survey Professional Paper* 254: 165–194.
- Lukeneder, A. and Harzhauser, M. 2004. The Cretaceous coleoid *Dora-teuthis syriaca* Woodward: morphology, feeding habits and phylogenetic implications. *Annalen des Naturhistorischen Museums in Wien* 106 A: 213–225.
- Miramand, P. and Guary, J.C. 1980. High concentrations of some heavy

- metals in tissues of the Mediterranean octopus. *Bulletin of Environmental Contamination and Toxicology* 24: 783–788.
- Naef, A. 1922. Die fossilen Tintenfische. Ein paläozoologische Monographie. 322 pp. Fischerverlag, Jena.
- Nesis, K.N. 1992. The diamondback squid, *Thysanoteuthis rhombus* Trotschel, 1857: a “living fossil”? *Ruthenica* 2: 91–103.
- d’Orbigny, A. 1835–1843. Mollusques. In *Voyage dans l’Amérique Méridionale* 50: 1–758.
- Rieber, H. 1970. *Breviconoteuthis breviconus* (Reis), ein Phragmoteuthide aus der Mittleren Trias des Monte San Giorgio (Kanton Tessin Schweiz). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 7: 415–421.
- Romano, C., Kogan, I., Jenks, J., Jerjen, I. and Brinkmann, W. 2013. *Saurichthys* and other fossil fishes from the late Smithian (Early Triassic) of Bear Lake Country (Idaho, USA), with a discussion of saurichthyid palaeogeography and evolution. *Bulletin of Geosciences* 87: 543–570.
- Rosenkrantz, A. 1946. Hook-bearing cephalopods from the East Greenland Permian. *Meddelelser fra Dansk Geologisk Forening* 11: 160–161.
- Schweigert, G. and Fuchs, D. 2012. First record of a true coleoid cephalopod from the Germanic Triassic (Ladinian). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 266: 19–30.
- Smith, J.D., Plues, L., Heyraud, M., and Cherry, R.D. 1984. Concentrations of the elements Ag, Al, Ca, Cd, Cu, Fe, Mg, Pb and Zn, and the radionuclides ²¹⁰Pb and ²¹⁰Po in the digestive gland of the squid *Nototodarus gouldi*. *Marine Environmental Research* 13: 55–68.
- Starobogatov, Y.I. 1983. The system of the Cephalopoda [in Russian]. In: J.I. Starobogatov and K.N. Nesis (eds.), *Sistematika i ekologiya golo-vonogih molluskov*, 4–7. Zoological Institute USSR Academy of Sciences, Leningrad.
- Strugnell, J., Jackson, J., Drummond, A.J., and Cooper, A. 2006. Divergence time estimates for major cephalopod groups: evidence from multiple genes. *Cladistics* 22: 89–96.
- Vecchione, M., Young, R.E., Donovan, D.T., and Rodhouse, P. 1999. Re-evaluation of coleoid cephalopod relationships based on modified arms in the Jurassic coleoid *Mastigophora*. *Lethaia* 32: 113–118.
- Vecchione, M. and Young, R.E. 2008. *Myopsida Naef, 1916*. *The Tree of Life Web Project* (version 21 April 2008) <http://tolweb.org/Myopsida/52670/2008.04.21>
- Young, R.E., Vecchione, M., and Donovan, D. 1998. The evolution of coleoid cephalopods and their present biodiversity and ecology. *South African Journal of Marine Sciences* 20: 393–420.
- Weaver, P.G., Doguzhaeva, L.A., Lawver, D.R., Tacker, R.C., and Ciampaglio, C.N. 2011. Characterization of organics consistent with β-chitin preserved in the Late Eocene cuttlefish *Mississaeptia mississippiensis*. *PLoS ONE* 6 (11): e28195.