

# A new late Carboniferous coleoid from Oklahoma, USA: implications for the early evolutionary history of the subclass Coleoidea (Cephalopoda)

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**Abstract.**—The limited record of the bactritoid-like coleoid cephalopods is here expanded due to discovery of a late Carboniferous (Moscovian) orthocone comprising a phragmocone and a body chamber with a proostracum-like structure, a sheath-like rostrum, an ink sac, and a muscular mantle preserved on top of the conch. The specimen comes from the Wewoka Formation in the vicinity of the city of Okmulgee, Oklahoma, which previously yielded an orthocone indicative of an evolutionary branch of the Carboniferous cephalopods described as the order *Donovaniconida* Doguzhaeva, Mapes, and Mutvei, 2007a within the subclass Coleoidea Bather, 1888. Here, we describe from that site a bactritoid-like coleoid, *Oklaconus okmulgeensis* n. gen. n. sp. in Oklaconidae n. fam. A broad lateral lobe of the suture line and a compressed conch with a narrowed dorsal side and a broadly rounded ventral side distinguish this genus from *Donovaniconus* Doguzhaeva, Mapes, and Mutvei, 2002b. The muscular mantle is preserved as a dense sheet-like structure, with a crisscross pattern and a globular-lamellar ultrastructure. Recent knowledge on the early to late Carboniferous coleoids is discussed. Carboniferous coleoids show a high morphological plasticity with a capacity for being altered to create the diverse combinations of ‘bactritoid’ and ‘coleoid’ structures. This could be the principle evolutionary driver of their radiation in the late Carboniferous.

## Introduction

Prior to the current century, the Late Triassic *Phragmoteuthis bisinuata* von Mojsisovics, 1882 (= *Belemnoteuthis* of Bronn, 1859; = *Acanthoteuthis* Suess, 1865) from the Austrian Alps was the oldest coleoid known to have an ink sac (Bronn, 1859; Suess, 1865; von Mojsisovics, 1882; Doguzhaeva et al., 2007c; Doguzhaeva and Summesberger, 2012). Recently, the oldest coleoids with ink sacs have been reported from the lower to upper Carboniferous of North America (Doguzhaeva et al., 2002c, d, 2003, 2004a, 2007a, 2010a; Mapes et al., 2010a, b; Mapes and Doguzhaeva, 2017). These taxa illuminate their high morphological diversity and evolutionary radiation in the late Carboniferous (Doguzhaeva et al., 2010a).

Flower and Gordon (1959) described the first Carboniferous coleoid genera (*Hematites*, *Paleoconus*, and *Bactritimimus*) that were referred to the order Aulacocerida Stolley, 1919 because of the presence of a robust rostrum covering the phragmocone. Since then, the Middle Pennsylvanian (Moscovian = Desmoinesian) deposits in Illinois (the Mazon Creek Lagerstätte) and Oklahoma (Deep Fork River locality) have been the world’s primary Carboniferous coleoid ‘producers’ of that age (Johnson and Richardson, 1966, 1968; Saunders and Richardson, 1979; Allison, 1987; Kluessendorf and Doyle, 2000; Doguzhaeva et al., 2002b, 2002c, 2007a, 2010b). Recently, the Carboniferous phragmocone-bearing coleoids have been assigned to four orders: Hematitida Doguzhaeva, Mapes, and Mutvei, 2002a; Donovaniconida; Aulacocerida, and Spirulida Pompeckj, 1912, all of which have a small marginal siphuncle, contrary to paracoleoids with a

broad central siphuncle (Doguzhaeva et al., 2017). The present paper is focused on a new late Carboniferous bactritoid-like coleoid from Oklahoma with an ink sac in the body chamber and a muscular mantle on top of the conch. The record of ink sacs in Carboniferous coleoids and a lack of the body chamber in *Hematites* and its significance for clarifying the origin of a proostracum in belemnoids are also discussed.

## Geological setting and environmental conditions

The studied specimen, as well as the earlier described bactritoid-like coleoid *Donovaniconus oklahomensis* Doguzhaeva, Mapes, and Mutvei, 2002b comes from the Wewoka Formation, Pennsylvanian, Desmoinesian (= late Carboniferous, Moscovian) in Oklahoma, USA. The Oklahoma occurrence is limited to the Deep Fork River locality ~5 km to the west of the community of Okmulgee on the western side of the Deep Fork Creek bridge on Oklahoma Highway 56 (see Mapes, 1979, locality P-6, p. 9–10, or locality OKD-10 of Boardman et al., 1994, SE1/4, SE1/4, sec. 10, T. 13N, R. 12E; Okmulgee Lake 7½’ quadrangle). The locality is a fossil-bearing shale bed with a single carbonate concretion layer. This layer yielded the coleoids *Donovaniconus* and *Oklaconus* n. gen. The concretions are always longer than thick (maximum and minimum length, ~150 mm and 450 mm, respectively, and ~70 mm thick). They commonly contain diverse ammonoids at all stages of growth, numerous juvenile bactritoids, rare orthoconic and coiled nautiloids, rare cephalopod beaks, the spat of bivalves and gastropods, and fish debris (see Mapes, 1979, locality P-6).

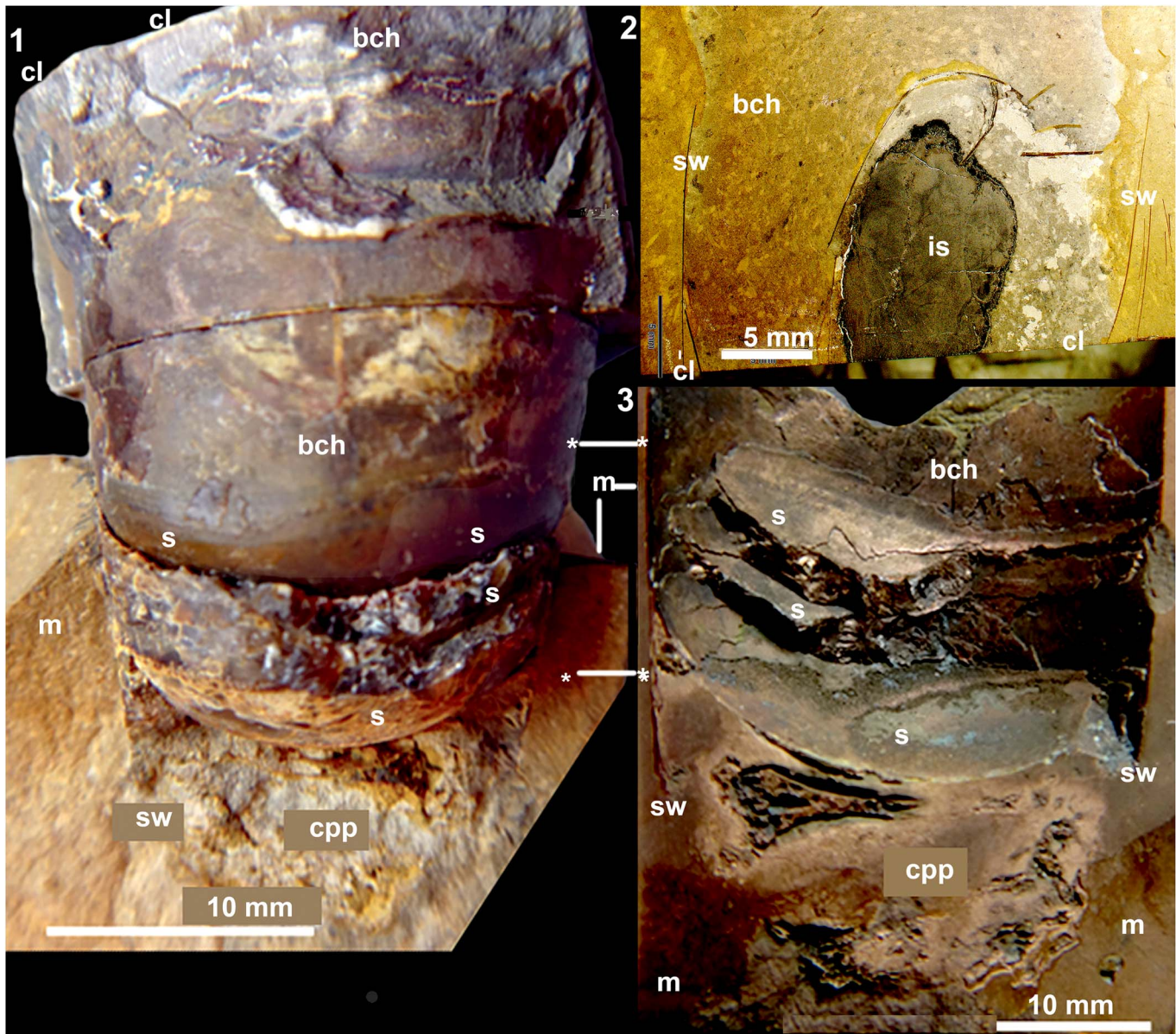
Approximately 1 in 100 concretions contains a bacritoid-like coleoid specimen (Doguzhaeva et al., 2003, p. 64). In total, more than 50 such coleoid specimens have been recovered over three decades of collecting by RM. Almost all of the specimens are fragmented phragmocones and partially crushed body chambers that are confined to single bedding planes in the concretions.

The fossil-bearing shale is the middle transgression-regression cycle of three that are present in the formation. According to Boardman et al. (1994, fig. 2, column B), this middle cycle is time equivalent to the Francis Creek Shale in Illinois, which is well known as the famous Mazon Creek Lagerstätte. The Wewoka carbonate concretion layer that yielded the studied specimen formed in offshore, middle to outer

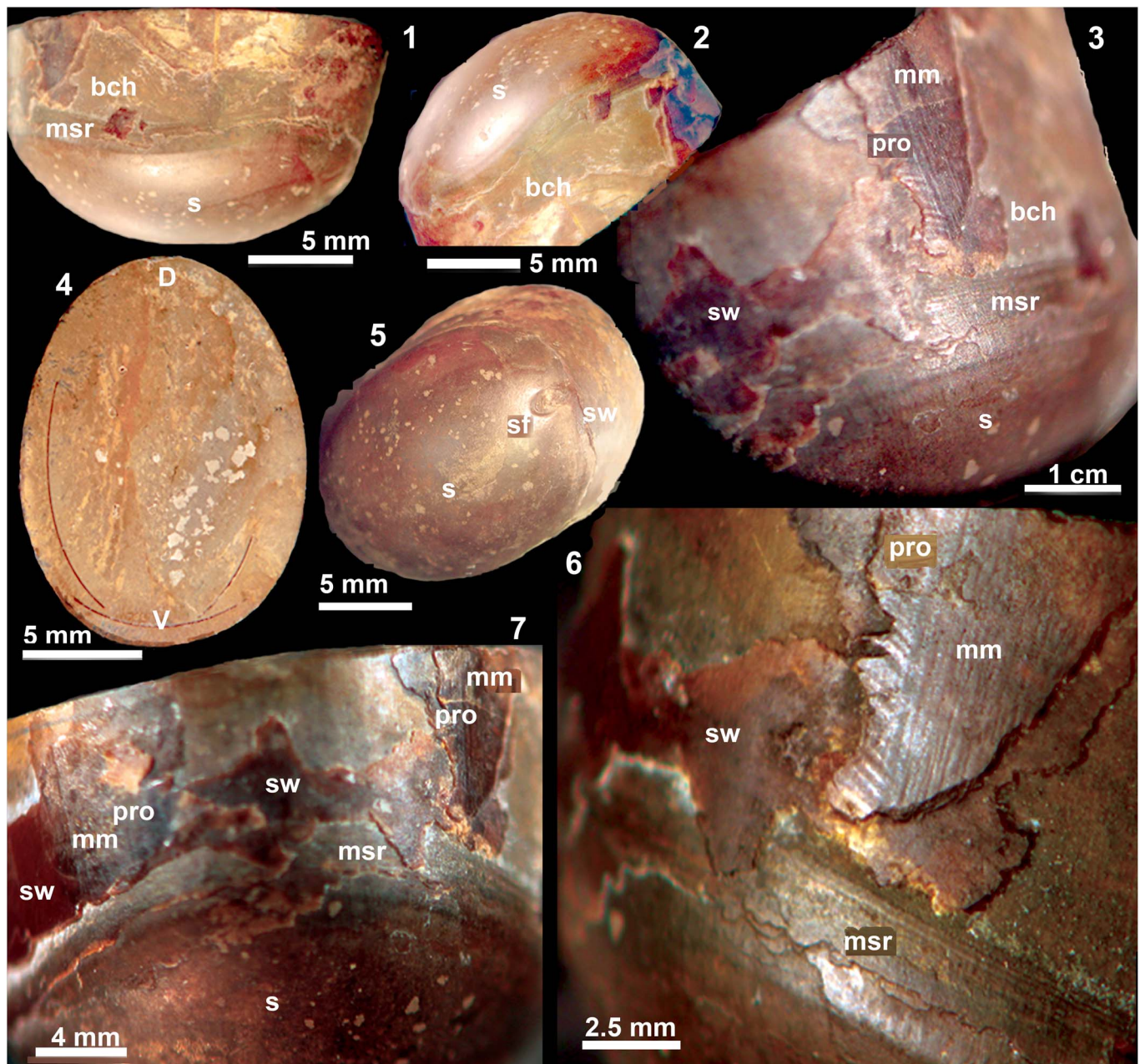
shelf, mud deposits. The layer was formed during the early phase of the cyclothem regression. Bottom oxygen level at the time of mud deposition and concretion formation was low to very low, as reflected in the lack of benthic fauna.

### Materials and methods

The studied specimen (AMNH 82600) was collected by RHM and investigated using the Hitachi S-4300 scanning electron microscope in the Department of Palaeobiology of the Swedish Museum of Natural History, Stockholm. It is a straight, ~85 mm long conch (Figs. 1, 2, 3) that was located on the edge of an ovoid, lens-like, carbonate concretion ~300 mm long and 60 mm thick. The conch preserves a long body chamber



**Fig. 1.** *Oklaconus okmulgeensis* n. gen. n. sp., AMNH 82600, Moscovian, Oklahoma, overview of three parts of the specimen: (1) the internal mold of the body chamber with exposed lateral aspect (top) and the partially preserved phragmocone (bottom); (2) body chamber section [a continuation of the body chamber in (1) to show the ink sac]; (3) inner surface of the body chamber (top) and partially preserved phragmocone (bottom) [counterpart of (1)]. bch = body chamber; cl = approximate corresponding levels of shell part in (1) and longitudinal section in (2); cpp = crushed apical portion of the phragmocone; is = ink sac; m = matrix; s = septum; sw = shell wall; \*-\* = approximate corresponding levels of shell part (1) and counterpart (3).

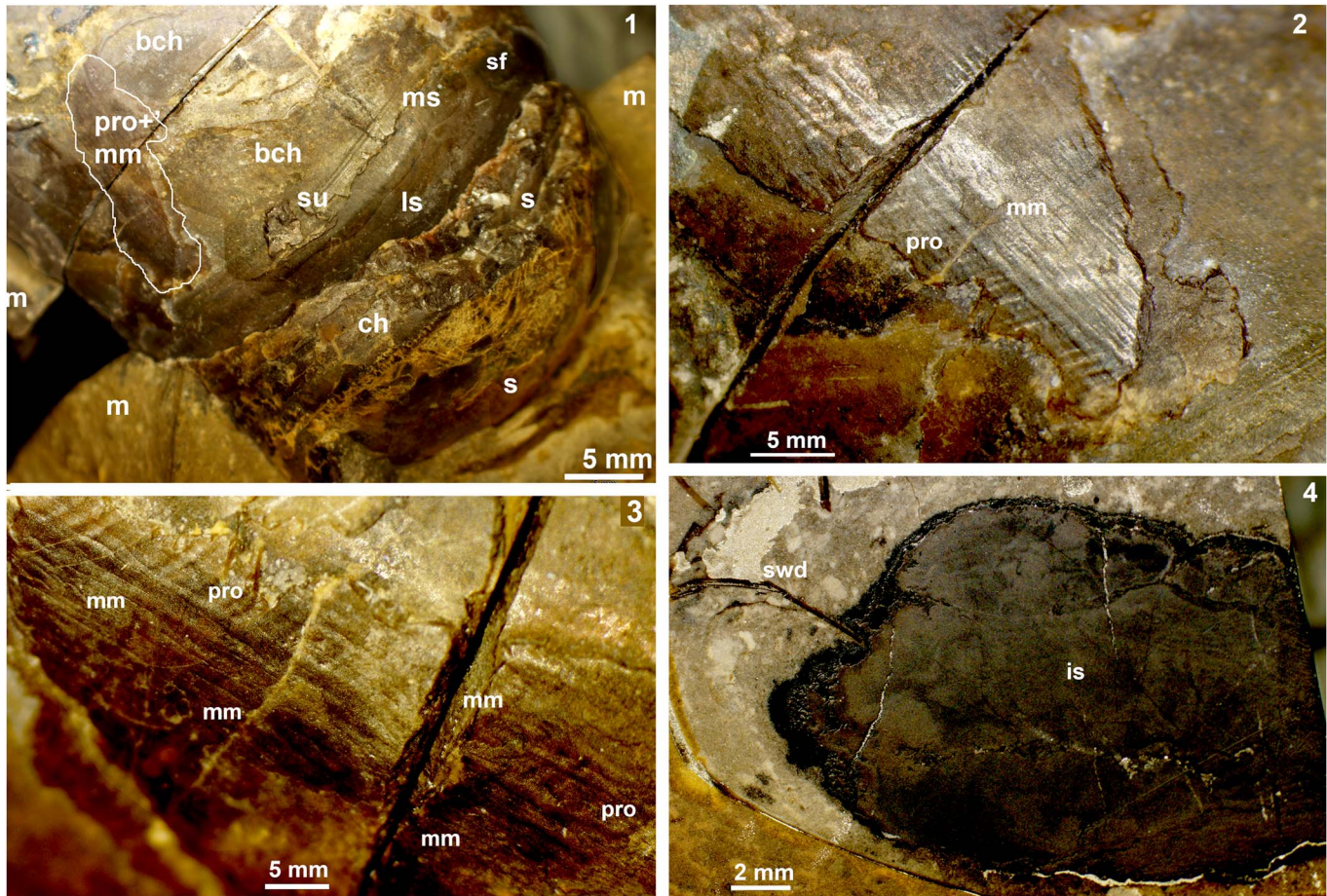


**Fig. 2.** *Oklaconus okmulgeensis* n. gen. n. sp., AMNH 82600, Moscovian, Oklahoma: (1, 2) two views of the deep septum showing a broad lateral lobe; (3) proostracum-like structure positioned in front of the broad mural ring of the last septum; (4) ovoid cross section of the body chamber; (5) ventromarginal septal foramen; (6) narrow convex proostracum-like structure repeating a narrowed shape of the dorsal side of the conch (view from the last septum); (7) proostracum-like structure partially exposed beneath the shell wall and sheath-like rostrum on the narrow dorsal side of the conch. bch = body chamber; D = dorsal side of conch; mm = muscular mantle; msr = mural septal ring; pro = proostracum-like structure; s = septum; sf = septal foramen; sw = shell wall; V = ventral side of conch.

containing an ink sac, a short portion of a fractured phragmocone (Figs. 1.2, 3.4, 6), and a dense sheet of a supposed muscular mantle upon the outer conch surface (Figs. 2.3–2.7, 3.2–3.3, 4). During preparation of the specimens at the outcrop, the concretion, together with the conch, was longitudinally fractured. The conch was split into a part and a counterpart (Fig. 1.1, 1.3). Further study of the specimen at the laboratory showed that the counterpart (Fig. 1.3) with the exposed ‘hollow’ body chamber and last chamber of the phragmocone bears a dense sheet of a potential muscular mantle squeezed between the conch and the matrix of the concretion (Fig. 4.1–4.4). The main

part of the conch (Fig. 1.1) was cut approximately perpendicular to its axis along the bottom portion of the body chamber and the body chamber was then cut longitudinally to search for an ink sac (Fig. 1.2). The counterpart of the conch (Fig. 1.3) was hand-ground on the ventral side for study of the siphuncle, shell wall, and sheath-like rostrum (Fig. 5).

Gross shell morphology was initially studied under Nikon, Wild Photomakroskop M 400, and Olympus SZX10 light microscopes (see Figs. 1, 2, 3). Because the studied conch was fractured into two parts, the shell wall, the sheath-like rostrum, and the proostracum-like structure were partially split and



**Fig. 3.** *Oklaconus okmulgeensis* n. gen. n. sp., AMNH 82600, Moscovian, Oklahoma: (1) position of well-preserved fragment of proostracum-like structure and muscular mantle shown on Figures 2.2 and 3 (detail of 1.1); (2) proostracum-like structure with a central concentric pattern surrounded by longitudinally folded muscular mantle; (3) proostracum-like structure and muscular mantle shown in (2), positioned with an angle of  $\sim 180^\circ$  to show that the dorsal side of the proostracum-like structure is covered by folds of the muscular mantle; (4) ink sac surrounded by shell-wall debris partially fractured by compaction of body chamber. bch = body chamber; ch = chamber of the phragmocone; is = ink sac; ls = last septum; m = matrix; mm = muscular mantle; ms = mural part of septum; pro = proostracum-like structure; pro + mm = proostracum-like structure plus muscular mantle; s = septum; sf = septal foramen; su = suture.

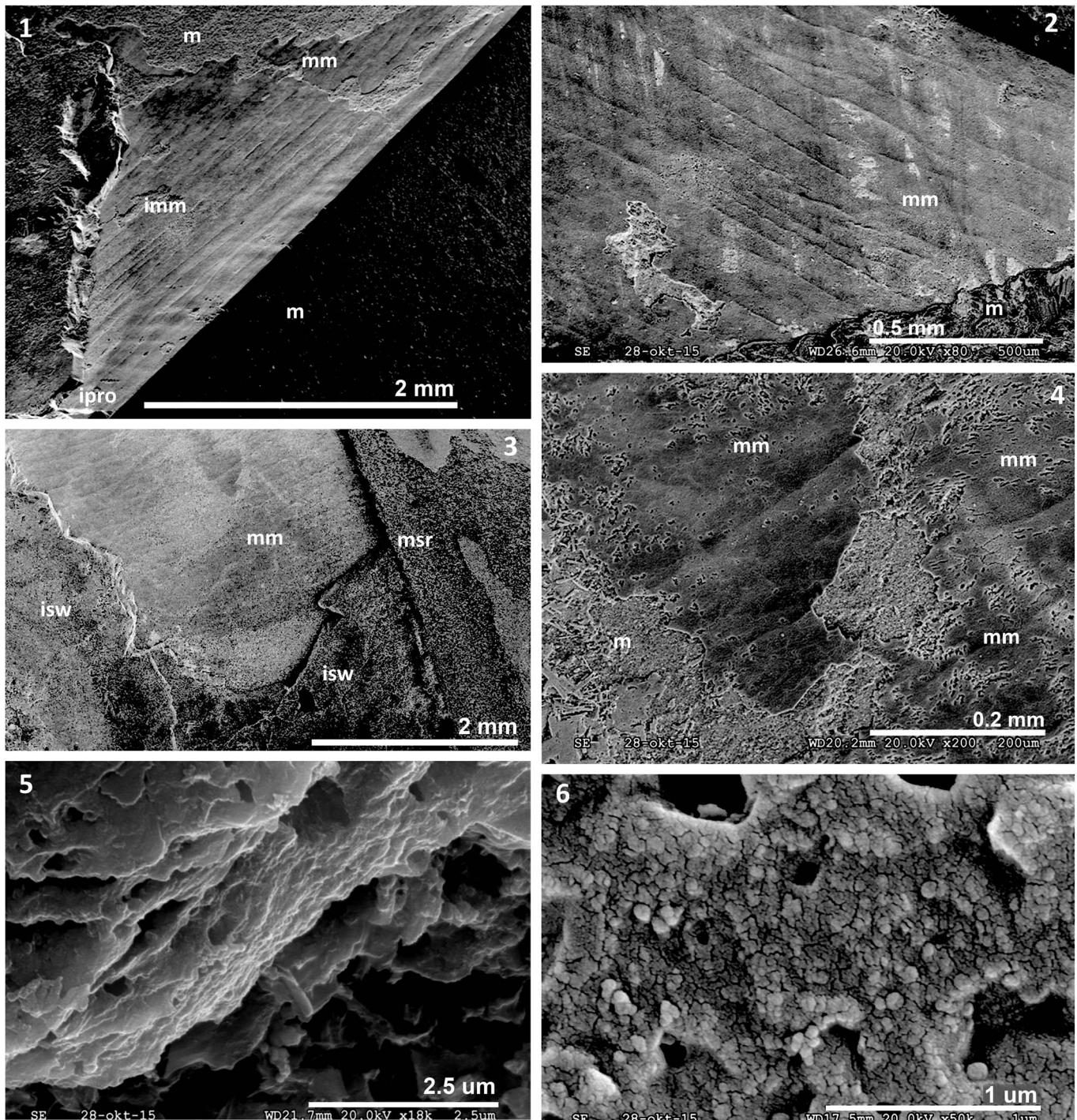
exposed, which enabled observation of these structures on the dorsal side of the conch (Figs. 2.6–2.7, 3.1–3.3). The specimen was then examined using scanning electron microscopy (SEM). It was etched with a 1–3% solution of acidic acid for 6–10 sec and coated with gold for further ultrastructural analyses of shell wall, sheath-like rostrum, siphuncle, ink sac, and mantle (see Figs. 4, 5, 6). Stronger etching chemicals could have been used to better expose the shell wall and sheath-like rostrum ultrastructures, but these were not applied to avoid destruction of nonbiomineralized structures.

*Repositories and institutional abbreviations.*—AMNH, American Museum of Natural History, New York City, USA; SUI, University of Iowa, Paleontological Collection, Iowa City, Iowa, USA; UNSM, University of Nebraska State Museum, Lincoln, Nebraska, USA.

### Ink sac and muscular mantle associated with the analyzed conch

*Ink sac.*—A large black ‘body’ situated deep in the body chamber (Figs. 1.2, 3.4) is here shown to be an ink sac; the

three-dimensional shape of this black ‘body’—if it is flask-like with a rounded posterior reservoir and a tubular, broad gradually narrowing forward duct, like that of well-shaped ink sacs of the Carboniferous age (see Doguzhaeva et al., 2004a, fig. 4A–B; Mapes et al., 2010a, fig. 2A–C)—is unknown. The ‘pockets’ in the black ‘body’ around the chips of the fractured shell wall reveal the elastic wall of this structure (Fig. 3.4). The ink sac wall is fibrous and multilayered; three layers are distinguished due to different orientations of fibers in each layer (Fig. 6.1, 6.4). Like the ink sac of *Donovaniconus* (see Doguzhaeva et al., 2003, figs. 14, 15), the black ‘body’ is subdivided into compartments by internal partitions (Fig. 6.2). The compartments are filled with a structureless material that, when evaluated under high magnification, shows that this is a massive aggregate of globular, 0.1–0.4  $\mu\text{m}$  diameter, microparticles consisting of smaller particles (Fig. 6.2–6.4). A similar microglobular ultrastructure was observed in the dried ink extracted from the ink sacs of the Recent squid *Loligo* Schneider, 1784 (Doguzhaeva et al., 2004a, fig. 2A–B), as well as in fossil ink of the Jurassic *Loligosepia* Quenstedt, 1839 and *Teudopsis* Deslongchamps, 1835 (Doguzhaeva et al., 2004a, fig. 1C, E, F), the Late Triassic *Phragmoteuthis* von Mojsisovics, 1882 (Doguzhaeva et al., 2007c,

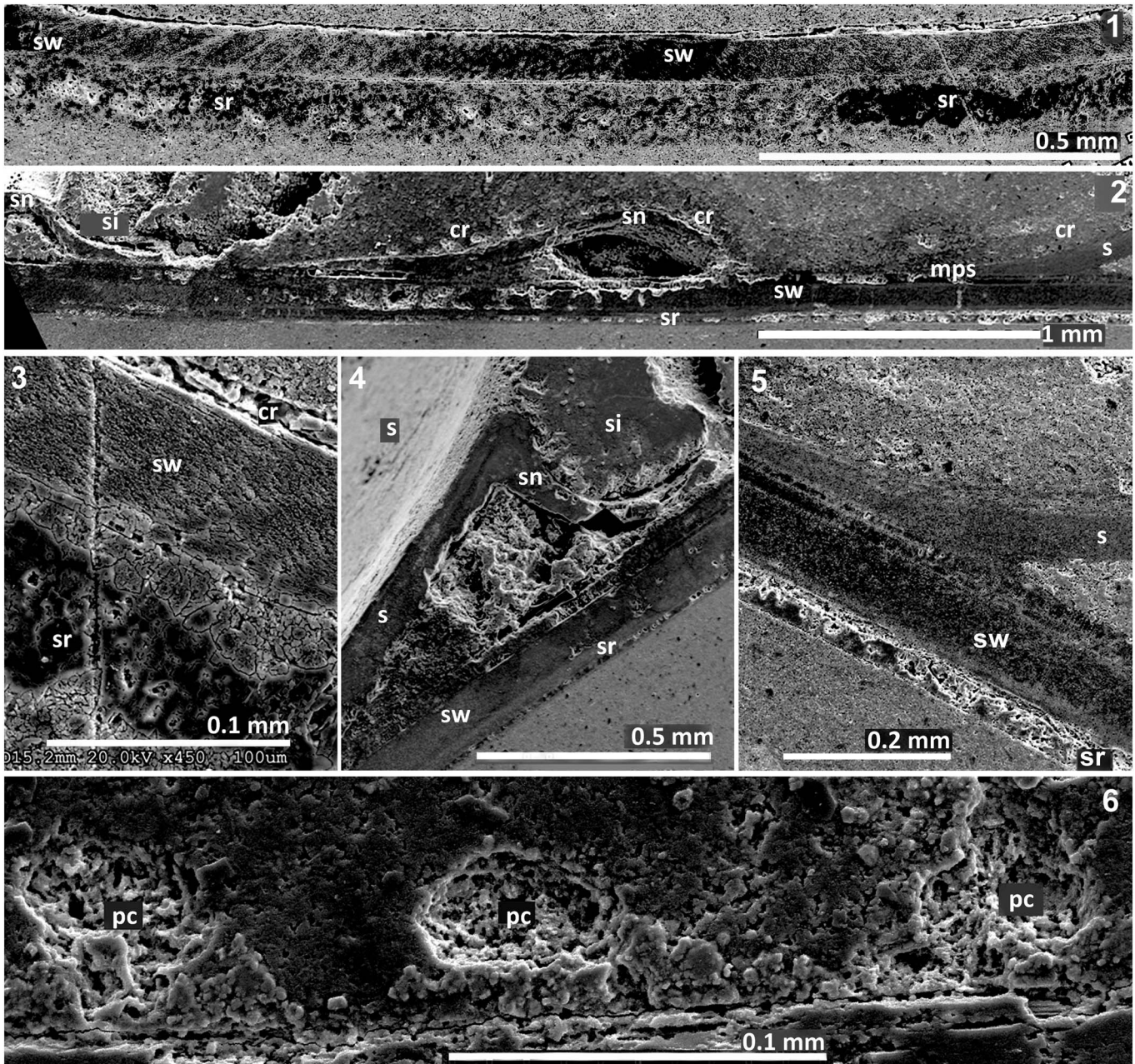


**Fig. 4.** *Oklaconus okmulgeensis* n. gen. n. sp., AMNH 82600, Moscovian, Oklahoma, muscular mantle on the external surface of the body chamber, with an imprint left by removed proostracum-like structure (SEM): (1) the exposed inner surface of the muscular mantle (top left) compressed between the body chamber wall (left) and the matrix of the concretion (bottom right); the imprint of a proostracum-like structure is seen on the inner surface of the muscular mantle (adoral conch direction = top/right corner); (2) crisscross pattern on the internal surface of the muscular mantle; (3) inner surface of the muscular mantle exposed where the shell wall is fractured and removed; fine longitudinal folds of the mantle are evident; (4) crisscross pattern on the inner surface of the muscular mantle; (5) microlaminated ultrastructure of the muscular mantle; (6) microglobular ultrastructure of the muscular mantle. imm = inner surface of muscular mantle; ipro = imprint of proostracum-like structure; isw = inner shell wall surface; m = matrix; mm = muscular mantle; msr = mural septal ring.

fig. 6E), and the Early Cretaceous gladius-bearing *Nesisoteuthis* Doguzhaeva, 2005 (Doguzhaeva, 2005, fig. 3).

Thus, the revealed structural and ultrastructural similarities between the black 'body' in this Wewoka orthocone and the earlier-described fossil ink sacs with well-preserved

flask-like shapes in Carboniferous coleoids (Doguzhaeva et al., 2002c; 2002d, fig. 4; 2003, fig. 4; 2004a, fig. 1) support its interpretation as an ink sac. The nonbiomineralized wall of the large ink sac within the body chamber of the studied specimen suggests this container was flexible and



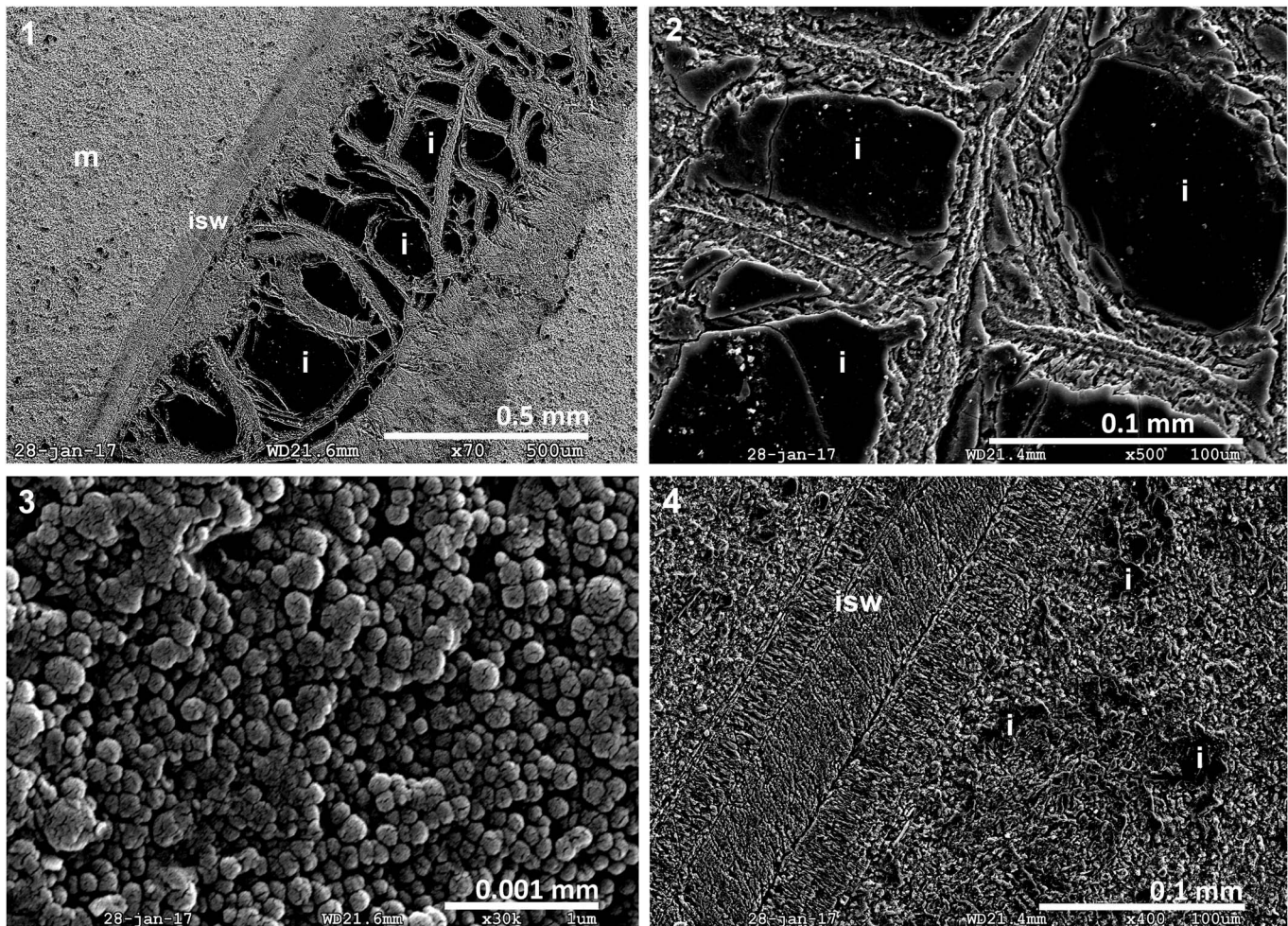
**Fig. 5.** *Oklaconus okmulgeensis* n. gen. n. sp., AMNH 82600, Moscovian, Oklahoma (SEM): (1) approximately equally thick shell wall (top) and sheath-like rostrum (bottom) in the middle part of the body chamber; (2) narrow ventral siphuncle with long mural parts of septa and holochoanitic ventral portion of septal neck; (3) equally thick shell wall and loosely mineralized, supposedly organic rich sheath-like rostrum; (4) adoral surface and longitudinal section of last septum, spherical portion of siphuncle, proportionally thick shell wall, and thin sheath-like rostrum; (5) long mural part of septum, shell wall, and sheath-like rostrum in the penultimate chamber of the phragmocone where the sheath-like rostrum is proportionally thinner; (6) porous structure of connecting ring showing regularly spaced pore channels. cr=connecting ring; mps=mural part of septum; pc=pore channel of connecting ring; s=septum; si=siphuncle; sn=septal neck; sr=sheath-like rostrum; sw=shell wall.

capable of expansion to accommodate changes of the amount of stored ink.

**Mantle.**—In the ‘hollow’ body chamber and ‘hollow’ last chamber of the phragmocone (Fig. 1.3), a dense sheet-like structure is seen in places where the shell wall was fractured and removed (Fig. 4.1–4.4). This structure is preserved between the conch and the matrix of the concretion. It bears a crisscross pattern and fine longitudinal folds that are

imprinted on the mold of the body chamber (Figs. 2.3, 2.7, 3.1–3.3; for comparison, see Doguzhaeva et al., 2002d, pls. 1–5). The dense sheet-like structure with a crisscross pattern and longitudinal folds has a globular-lamellar ultrastructure (Fig. 4.5–4.6).

Imprints of the mantle with a crisscross pattern and fine longitudinal folds were also observed on the external surface of the phragmocone in some Jurassic belemnites (Doguzhaeva et al., 2002d, pl. 1, figs. 1, 2, pl. 2, figs. 1, 2; 2014, fig. 9A–D).



**Fig. 6.** *Oklaconus okmulgeensis* n. gen. n. sp., AMNH 82600, Moscovian, Oklahoma, ink sac wall, ink structures, and ultrastructures (SEM): (1) cross section of the ink sac from the body chamber; (2) compartment structure of ink sac and complex ultrastructure of the partitions between compartments; (3) microglobular ultrastructure of ink material; (4) three-layered ink sac wall ultrastructure. i = fossilized ink; isw = ink sac wall; m = matrix.

Microglobular aggregates similar to those of the ink are typical for fossilized nonbiomineralized materials, and the microlamination (which is missing in the ink) is typical for originally microlaminated materials like the chitin of arm hooks, gladii (Doguzhaeva and Mutvei, 2006, pl. 1, figs. A–F; Doguzhaeva et al., 2007c, figs. 5D, 6A, B), mandibles, buccal muscles, and muscular mantle (Doguzhaeva et al., 2004b, figs. 2A, B, 5C, 6A, B; 2007a, fig. 6.9A, B, 6.10A, B, 6.11A–D; 2007b, fig. 11.2, 11.3A–C, 11.4A–F, 11.5A–F, 11.6A–C, 11.7A–F, 11.8A–F; 2007c, fig. 6C–F). Previously, soft tissues preserved due to postmortem microgranular replacement were recorded in the late Carboniferous coleoid *Saundersites illinoisensis* Doguzhaeva, Mapes, and Mutvei, 2007a from the Mazon Creek Lagerstätte in which the cephalic remains also include a radula and arm hooks (Doguzhaeva et al., 2007a, fig. 6.2, 6.5, 6.9B). The dried mantle of the Recent squid *Loligo* and *Nautilus* Linnaeus, 1758, as well as the mantle of the Late Triassic ceratitid *Austratrachyceras* Krystyn, 1978 from Austrian Alps, also show microglobular ultrastructures (Doguzhaeva et al., 2007b, fig. 11.4A–F, 11.7A–D).

The crisscross pattern, fine longitudinal folding, and globular-lamellar ultrastructure of the dense sheet-like structure

between the conch and the matrix of the concretion show muscular mantle preservation in the studied specimen. Along the dorsal side of the conch (as opposed to the side with a siphuncle), the mantle bears an imprint of proostracum-like structure marked with concentric, convex forward, growth lines typical for its central part (for comparison, see Doguzhaeva et al., 2010a, fig. 7).

### Systematic paleontology

Subclass Coleoidea Bather, 1888

Order Donovaniconida Doguzhaeva, Mapes, and Mutvei, 2007a

*Diagnosis.*—Straight smooth conch with long body chamber and phragmocone, thin sheath-like rostrum, short proostracum-like structure, small, ventral siphuncle. Apical angle ~12–30°. Estimated conch length ~200 mm or less. Chambers short, length ~0.15–0.2 of dorsoventral diameter. Septa deep, with long mural parts ~0.3–0.7 of chamber length. Suture lines straight or with broad lateral lobe. Septal necks long holochoanitic ventrally, short cyrtchoanitic dorsally. Connecting rings thin. Ink sac large. Arm hooks present. Radula with seven teeth and two

marginal plates on each side. Sheet-like muscular mantle on top of conch. Shell wall with or without nacreous layer.

*Occurrence.*—Early Carboniferous (late Namurian, late Chesterian, Serpukhovian) to late Carboniferous (Moscovian; early Stephanian).

*Remarks.*—The diagnosis is emended from that by Doguzhaeva et al. (2007a). A proostracum-like structure, one of the attributes of the order Donovaniconida, can be assumed for the Carboniferous members of the order Aulacocerida as well, although it is so far known only in a single Late Triassic aulacocerid, namely *Austrateuthis* Jeletzky and Zapfe, 1967 (Jeletzky and Zapfe, 1967, pl. 1). A long body chamber, another character of the order Donovaniconida, could be shared with the order Aulacocerida, even though a body chamber has only been described from two juvenile specimens of the late Carboniferous aulacoceratids *Mutveiconites mirandus* Doguzhaeva, 2002a and *M. milleri* Doguzhaeva, Mapes, and Dunca, 2006b (Doguzhaeva, 2002b, pl. 17, figs. 1, 2; Doguzhaeva et al., 2006b, pl. 1, fig. A). A sheath-like rostrum distinguishes the order Donovaniconida from the Aulacocerida. Unlike the short proostracum-like structures in the orders Donovaniconida and Aulacocerida, large, broad, long, and trilobate proostraca associated with short terminal chambers of the phragmocones are developed in the order Phragmoteuthida Jeletzky in Sweet, 1964 (Middle Triassic–Early Jurassic). In *Phragmoteuthis*, the proostracum has three longitudinal fields (a median field and lateral wings) with concentric ornamentation, like that of a single field in the proostracum-like structures of the Donovaniconida and the Aulacocerida (compare Doguzhaeva and Summesberger, 2012, fig. 1; Doguzhaeva et al., 2003, fig. 2; Jeletzky and Zapfe, 1967, fig. 2).

Family Oklaconidae new family

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*Diagnosis.*—Orthocone compressed, smooth, with flattened lateral, narrowed crest-like dorsal, and broadly rounded ventral sides. Apical angle  $\sim 15^\circ$ . Estimated conch length  $\sim 200$  mm. Proportionally long body chamber and phragmocone. Dorsoventral diameter maximum width ratio  $\sim 1.4:1$ . Septa deep. Suture line with broad lateral lobe. Mural parts of septa long,  $\sim 0.3$ – $0.7$  of chamber length. Chambers in phragmocone short,  $\sim 0.15$  of dorsoventral diameter. Ventral siphuncle small. Septal necks long holochaoanitic ventrally, short cyrthochoanitic dorsally. Connecting rings thin. Shell wall microlaminated with strongly oblique growth lines. Rostrum thin, sheath-like. Proostracum-like structure short, strongly convex. Ink sac present. Muscular mantle over conch surface.

*Occurrence.*—Upper Carboniferous (Moscovian).

*Remarks.*—Three families—Donovaniconidae Doguzhaeva, Mapes, and Mutvei, 2002b, Gordoniconidae Mapes, Weller, and Doguzhaeva, 2010b, and Rhiphaeoteuthidae Doguzhaeva, 2002a—have been referred to the order Donovaniconida. The Donovaniconidae is typified by *Donovaniconus* having a long

body chamber, a thin sheath-like rostrum, a short proostracum-like structure, a breviconic phragmocone with short chambers and a moderately large apical angle ( $20$ – $30^\circ$ ), a small ventral siphuncle, a nacreous layer in the shell wall, and an ink sac (Doguzhaeva et al., 2002b, 2003). *Saundersites* Doguzhaeva, Mapes, and Mutvei, 2007a is provisionally referred to this family because of a long body chamber, a proostracum-like structure, and a thin sheath-like rostrum. Additionally, this genus is known to have arm hooks, a coleoid-type radula, and an ink sac (Doguzhaeva et al., 2007a). The family Gordoniconidae is typified by *Gordoniconus* Mapes, Weller, and Doguzhaeva, 2010b having a longiconic body chamber of approximately equal length with a breviconic phragmocone with an apical angle of  $15^\circ$ , a long, pointed, weakly mineralized rostrum that covers one-third of the closely septate phragmocone, between six and seven chambers per phragmocone length of the corresponding phragmocone width, arm hooks, and ink sac (Mapes et al., 2010b). The Rhiphaeoteuthidae has been provisionally referred to the order Donovaniconida although a body chamber and a sheath-like rostrum have not yet been demonstrated in the late Carboniferous *Rhiphaeoteuthis* Doguzhaeva, 2002a. It has a breviconic phragmocone with a smooth surface, short,  $\sim 0.15$  of conch diameter, chambers of the phragmocone; long mural parts of septa about chamber length; shell wall and septa thin, about equal in thickness, and a small marginal ventral siphuncle; sutures with shallow ventral and lateral lobes; septal necks short, cyrthochoanitic dorsally and long holochaoanitic ventrally; an ovoid conch section with a narrow dorsal side and inclined apical septa and straight adoral ones (Doguzhaeva, 2002a, pl. 13, figs. 1–4). The morphology of *Oklaconus* n. gen. does not fit within the diagnoses of the three families currently assigned to the order, and therefore a new family is erected to accommodate the genus.

Genus *Oklaconus* new genus

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*Type species.*—*Oklaconus okmulgeensis* new species, by monotypy.

*Diagnosis.*—As for the type species by monotypy.

*Etymology.*—Named for the state of Oklahoma, USA where the holotype of *Oklaconus okmulgeensis* n. sp. (type species) was collected.

*Occurrence.*—The middle transgressive-regressive cycle of the Wewoka Formation, upper Carboniferous (Moscovian), Oklahoma, USA.

*Remarks.*—Diagnosis is based on an adult specimen. *Oklaconus* is assigned to the coleoid cephalopods on the basis of an ink sac within the body chamber, a sheath-like rostrum, and a muscular mantle situated on top of the conch surface.

*Oklaconus* n. gen. is similar to the co-occurring *Donovaniconus* (see above) from which it differs by having a smaller apical angle ( $15^\circ$ ), oval conch in cross section with flattened lateral, narrowed crest-like dorsal and broadly rounded ventral sides, a suture line with a deep broad lateral lobe, and microlaminated



shell wall with strongly oblique growth lines. Whereas, the latter genus has a larger apical angle (20–30°), rounded conch in cross section, straight sutures, and a shell wall with a nacreous layer. Both genera are assigned to the order Donovaniconida on the basis of having a long body chamber, a proostracum-like structure, a thin sheath-like rostrum, and an orthoconic phragmocone with short chambers and a small ventral siphuncle.

*Oklaconus okmulgeensis* new species

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Figures 1–6

**Holotype.**—AMNH 82600, upper Carboniferous (Moscovian), Wewoka Formation, middle transgressive-regressive cycle, Okmulgee community, Oklahoma, USA.

**Diagnosis.**—Smooth compressed orthocone with apical angle ~15°; proostracum-like structure on narrowed dorsal and small marginal siphuncle on broadly rounded ventral side, respectively; subequally long body chamber and phragmocone, short, ~0.15 of dorsoventral diameter, chambers; suture line with broad lateral lobe; connecting rings thin; septal necks long holochoanitic ventrally and short cyrthochoanitic dorsally; rostrum thin sheath-like; ink sac present.

**Occurrence.**—The type locality is a brown to gray marine shale exposed at the base of several hills and in ravines on the western side of the Deep Fork River Bridge on Oklahoma Highway 56, ~4.8 km west of the community of Okmulgee, Oklahoma (for details see Mapes 1979, locality P-6, p. 9–10; Doguzhaeva et al., 2003, p. 64). This marine shale is upper Carboniferous (Moscovian) in age and occurs in the middle transgressive-regressive cycle of the Wewoka Formation.

**Description.**—Holotype ~85 mm long, partially preserved smooth orthocone. Apical angle ~15°. Conch incomplete, comprising ~65 mm long body chamber and 20 mm long fractured phragmocone retaining last three chambers and short, crushed posterior portion. Conch compressed; cross section dorsally narrow, somewhat crest-like, ventrally broadly rounded producing egg-like shape. Dorsoventral diameter and maximum width (measured at bottom of body chamber) ~18.2 mm and 14.9 mm, respectively. Proostracum-like structure narrow, ~0.15 of circumference length near last septum, crest-like, with fine concentric, convex forward, growth lines. Sheath-like rostrum approximately as thick as shell wall in middle part of body chamber but proportionally thinner posteriorly. Suture line with broad deep lateral lobe. Septa deep. Mural parts of septa ~0.3–0.5 of chamber length. Septal foramen small, oval, situated near base of septum. Siphuncle small, ventral. Septal necks long holochoanitic ventrally, short, cyrthochoanitic dorsally. Connecting rings thin porous. Shell wall microlaminated with strongly oblique growth lines. Muscular mantle on top of conch surface, with crisscross pattern and fine longitudinal folds. Ink sac large.

**Etymology.**—From the name of the community of Okmulgee, located 4.8 km east of the site where the described coleoid was found.

**Remarks.**—The description is based on an adult orthocone comprising a short adapertural part of the phragmocone with a small marginal siphuncle and a long body chamber with a proostracum-like structure, a sheath-like rostrum, an ink sac, and a muscular mantle preserved on top of the conch. The muscular mantle is a dense sheet-like structure, with a crisscross pattern and a globular-lamellar ultrastructure. The bulk of the phragmocone is not preserved; protoconch and apical chambers of the phragmocone are unknown.

## Discussion

**Records of ink sacs of Carboniferous coleoids.**—The Stark Shale (Pennsylvanian, Kasimovian) in Nebraska yielded the first five reported specimens of coleoid ink sacs (SUI 62497, UNSM 16562B) (Doguzhaeva et al., 2002c). They have a flask-like shape as in living coleoids (Doguzhaeva et al., 2004a, fig. 1A–C; Mapes et al., 2010a, fig. 2A–C). The ink material from these well-shaped ink sacs differs in color and texture relative to the black shale matrix. Under SEM, the fossilized ink is a massive aggregate of variably sized spheres (~0.5–3.0 μm), each of which is a globular mass of smaller particles (Doguzhaeva et al., 2004a, fig. 1A–C).

The Wewoka Formation in Oklahoma has now yielded two coleoid genera with ink sacs preserved within the body chambers—*Donovaniconus* (Doguzhaeva et al., 2002b, fig. 4; Doguzhaeva et al., 2003, fig. 4) and *Oklaconus* n. gen., herein (Figs. 1.2, 3.4, 6). In these specimens, large cone-shaped ink sacs are only partially exposed and do not exhibit a typical flask-like shape. They are black, filled with microglobular material formed by aggregates of microbial-sized particles. In these specimens, the ink sac has a compartmented structure, a three-layered wall ultrastructure, internal partitions, and microglobular ultrastructure of the solidified ink (Fig. 6).

The late Carboniferous (Moscovian) Mazon Creek Lagerstätte in Illinois yielded a specimen of *Saundersites illinoisiensis* showing the ink dispersed on the surface of the mantle coating the body chamber, associated with the cephalic remains, the arm hooks, and a radula exposing a previously unknown structure with two marginal plates on each side (Doguzhaeva et al., 2007a, fig. 6.1–6.10). The ink is a black mass of tiny, globular granules, 0.1–0.4 μm in diameter; each granule consists of smaller particles. This mass is ultrastructurally different from the matrix, but is identical to the dried ink extracted from the ink sacs in living squids and Late Triassic and Jurassic coleoids.

The early Carboniferous (Serpukhovian) Bear Gulch Limestone Lagerstätte in Montana yielded four specimens of *Gordoniconus* showing the ink sacs in the body chambers. As in *Donovaniconus*, the ink sac of *Gordoniconus* is compartmentalized, and the ink substance is an agglomerate of microglobules each of which consists of smaller particles (Mapes et al., 2010b, figs. 3.2, 4.1–4.3).

Thus, there are 12 recently recorded Carboniferous specimens with ink sacs or dispersed solidified ink preserved. Ink sacs are considered a marker of the coleoid affiliation of these specimens.

For ink to be sufficiently solid to resist compaction, the ink must have solidified after the demise of the animal, but prior to postmortem compaction and crushing. The rapid solidification

can be explained as a result of a chemical reaction in a slightly acid or neutral (as opposed to alkaline) bottom water medium (Fox, 1966) causing melanin (the main ink component providing the black color) to precipitate into a solid phase while still in the coleoid body. In an alkaline environment, melanin would be dispersed colloiddally (Fox, 1966). To preserve the ink, the burial environment must have also been anoxic or strongly dysoxic, which is the case for the Bear Gulch Limestone in Montana, the Wewoka Formation in Oklahoma, and the Stark Shale in Nebraska. By contrast, the Illinois occurrence is thought to have been a shallow-water deposit in a delta, however, rapid concretion formation acted as an oxygen shield, which preserved the ink in the coleoids.

*Recent knowledge on the early to late Carboniferous shelled coleoids.*—The first recognized Carboniferous coleoids—*Hematites*, *Paleoconus*, and *Bactritimimus*—were distinguished by the presence of a well-developed rostrum covering a breviconic phragmocone (Flower and Gordon, 1959). An ultrastructural approach for recognition of Carboniferous coleoids was introduced at the end of the twentieth century. This method is based on the evolutionary stability of shell ultrastructure in cephalopods (for more information, see Doguzhaeva, 1994, 1996, 2002a, 2008, 2012; Doguzhaeva et al., 1996, 1999, 2002a, 2006b, 2010a, 2017). Ultrastructural methods were used to help recognize the late Carboniferous coleoid *Shimanskya* Doguzhaeva, Mapes, and Mutvei, 1999 in which the shell wall, as in extant *Spirula* Lamarck, 1799 and the Early Cretaceous spirulid *Adygeya* Doguzhaeva, 1996, lacks a nacreous layer (Doguzhaeva et al., 1999). *Shimanskya* shell-wall type was also identified in several taxa that were earlier described as bactritoids (Mapes, 1979). The taxa '*Bactrites*' *quadri-lineatus* Mapes, 1979, '*Ctenobactrites*' *lesliensis* Mapes, 1979, and '*Rugobactrites*' *jacksboroensis* Mapes, 1979 from North America are now considered to be coleoids (Mutvei et al., 2012). Based on shell-wall ultrastructure, '*Bactrites*' *carbonarius* Smith, 1903 is referred to Coleoidea as well (Doguzhaeva and Mapes, 2017). Using ultrastructural examination of the concretion matrix in front of conch apertures, the arm hooks were revealed and defined as a coleoid affiliation of *Saundersites* from the Mazon Creek Lagerstätte in Illinois (Doguzhaeva et al., 2007a) and *Gordoniconus* from Bear Gulch Bes in Montana (Mapes et al., 2010a). This approach also helped identify the arm hooks, a *Saundersites*-type radula, and the cartilaginous capsule of an unnamed coleoid from Eudora Shale, Oklahoma preserved without any traces of a mineralized conch (Doguzhaeva et al., 2010b).

Therefore, we now know that Carboniferous coleoids possessed the following innovative structures: (1) a rostrum with a free postalveolar portion (*Hematites*, *Gordoniconus*, *Saundersites*), (2) a primordial rostrum (*Mutveiconites* Doguzhaeva, 2002a), (3) a thin sheath-like rostrum (*Donovaniconus*, *Oklaconus* n. gen.), (4) loss of the body chamber (*Hematites*), (5) a shell wall without nacre (*Shimanskya*, '*Bactrites*' *quadri-lineatus*, *B. carbonarius*, '*Ctenobactrites*' *lesliensis*, '*Rugobactrites*' *jacksboroensis*, *Oklaconus* n. gen.), (6) a proostracum-like structure (*Donovaniconus*, *Saundersites*, *Gordoniconus*, *Oklaconus* n. gen.), (7) an ink sac (*Gordoniconus*, *Saundersites*, *Donovaniconus*, *Flowerites* Mapes et al., 2010a, *Oklaconus* n.

gen.), (8) arm hooks (*Gordoniconus*; *Saundersites*; unnamed coleoid from Eudora Shale, Oklahoma, Doguzhaeva et al., 2010b), (9) lamellar-fibrillar nacre in the septa (*Shimanskya*, *Donovaniconus*), (10) a radula with two marginal plates on each side, which is atypical for nautiloids (*Saundersites*; unnamed coleoid from Eudora Shale, Oklahoma, Doguzhaeva et al., 2010b), and (11) a muscular mantle on the conch surface (assumed in all; observed in *Saundersites* and *Oklaconus* n. gen.). These novelties, together with morphological structures derived from the ancestral bactritoid stock (i.e., a spherical protoconch, a straight phragmocone, a small ventral siphuncle, thin nonbiomineralized connecting rings, a long body chamber, a nacreous layer in the shell wall, and columnar nacre in the septa) provide the diverse morphological combinations considered to be high-level taxonomic traits. These diverse combinations of both ancestral and innovative structures show that Carboniferous coleoids possessed high morphological plasticity with a capacity for being altered (Doguzhaeva et al., 2010a). Novelty appeared in Carboniferous coleoids at an early evolutionary stage in one taxon, but the 'old' traits existed for a long time after the novelty appeared in other taxa. An example of this phenomenon is the lack of a body chamber in the early Carboniferous *Hematites* (Doguzhaeva et al., 2002a). *Hematites* and *Gordoniconus* are the earliest recorded Carboniferous coleoids (dated 318–333 Ma), however, *Gordoniconus* has a long body chamber (Mapes et al., 2010b). Many of the younger coleoids, e.g., the late Carboniferous *Oklaconus* n. gen. and *Donovaniconus* in the Donovaniconida, and juvenile *Mutveiconites* in the Aulacocerida, have body chambers (Doguzhaeva, 2002a; Doguzhaeva et al., 2002d, 2003, 2006b; herein). In *Hematites*, loss of the body chamber did not lead to formation of a proostracum or proostracum-like structure. This illustrates forms at an early stage of coleoid evolution that lacked skeletal protection in the form of a body chamber, yet did not have dorsal support for the body in the shape of a proostracum (Doguzhaeva, 2012).

Another character of the Carboniferous stage of coleoid evolution is the independent appearance of new morphological traits and their further convergent evolution. This is exemplified by rostrum development. The early Carboniferous *Hematites* has a comparatively massive rostrum with a unique ultrastructure (Flower and Gordon, 1959; Doguzhaeva et al., 2002a), whereas the early to late Carboniferous donovaniconids *Gordoniconus*, *Saundersites*, *Donovaniconus*, and *Oklaconus* n. gen. have thin sheath-like rostra, and the late Carboniferous aulacocerid *Mutveiconites* has a primordial rostrum continuing as a sheath-like rostrum along the phragmocone (Doguzhaeva, 2002a; Doguzhaeva et al., 2006b). These observations suggest that the long-term (~60 Myr) Carboniferous evolution of coleoid cephalopods included many experimental attempts before a comparatively stable coleoid model, similar to that of modern gladius-bearing taxa, appeared in the Early Triassic (Olenekian) (Brayard et al., 2017). Kröger et al. (2011), in our opinion, erroneously suggested that the orders Hematitida and Donovaniconida could represent the evolutionary lineage that gave rise to Middle–Late Triassic phragmoteuthids and Permian–Cretaceous belemnites. Fuchs et al. (2013, fig. 12) also erroneously assumed that the Carboniferous Donovaniconida and the Middle Triassic–Early Jurassic Phragmoteuthida gave rise to all of the Mesozoic coleoids. It is worth noting in this context

that the different shell morphologies of the Hematitida and Donovaniconida, discussed briefly above, illustrate principle differences between these two orders that do not allow combining them into a single evolutionary lineage. As is shown above, in hematitids, a pronounced rostrum is associated with the loss of the body chamber and a proostracum-like structure, whereas in donovaniconids, there is a long body chamber, a proostracum-like structure, and a sheath-like rostrum. These two different morphological combinations of conch traits support the hypothesis that there are two very different evolutionary strategies involved in the evolutionary histories of the Hematitida and Donovaniconida. The assumption that belemnoids and modern coleoids originated from the order Donovaniconida via the order Phragmoteuthida (Kröger et al., 2011; Fuchs et al., 2013) in our opinion erroneously postulates that the proostracum-like structure of the donovaniconids gave rise to the broad three-part proostracum of the phragmoteuthids by means of elimination of the ventrolateral wall of the body chamber in donovaniconids. This still popular, but doubtful, hypothesis on formation of the proostracum by means of elimination of the ventrolateral wall of the body chamber in precursors (see Naef, 1922) has not yet been supported by the available data on the early–late Carboniferous orthocone cephalopods. Moreover, recent examinations of the ultrastructure of proostraca in different belemnoids and fossil gladii suggests that proostracum (Doguzhaeva, 2012; Doguzhaeva and Summesberger, 2012; Doguzhaeva et al., 2006a, 2007c) as well as gladii (Gordon, 1971; Doguzhaeva and Mutvei, 2006; Doguzhaeva and Mapes, 2015) can hardly have been derived from a conch wall. Ultrastructural and chemical examinations of the well-preserved proostraca in Late Triassic (Carnian) *Phragmoteuthis* and *Lunzoteuthis* Doguzhaeva, Summesberger, and Mutvei, 2006c from the Austrian Alps (Doguzhaeva et al., 2006c, 2007c; Doguzhaeva and Summesberger, 2012), Early Jurassic (Sinemurian) *Nannobelus* Pavlow, 1914 from Belgium (Doguzhaeva, 2012), and Middle Jurassic *Belemnoteuthis* from England (Doguzhaeva et al., 2006a) favor the interpretation of proostracum as a novelty of the skeleton in coleoids rather than as a dorsal projection of the phragmocone wall. Additionally, the small Late Triassic coleoid *Lunzoteuthis*, which coexisted with *Phragmoteuthis* in the northern Tethys, has an innovative proostracum structure by lateral fields with thin converging striations that are absent in *Phragmoteuthis* (compare Doguzhaeva et al., 2006c, fig. 1A–C; Doguzhaeva and Summesberger, 2012, figs. 1, 2A–B). The *Lunzoteuthis* proostracum type seems to have further evolved in the Early Jurassic belemnitids, in which lateral fields show overlapping, longitudinal, forward tapering, chevron-like bends that supposedly provided proper fixation of the mantle to the proostracum, which could have allowed for increased maneuverability in belemnites (Doguzhaeva, 2012, figs. 1A–D, 2A–D, 3A–F). The ancestor/descendent evolutionary relationship between donovaniconids and phragmoteuthids suggested by Kröger et al. (2011) and Fuchs et al. (2013) is not supported by currently available data on the early Carboniferous–Late Triassic coleoids (Doguzhaeva et al., 2006a, c, 2007c, 2010a; Doguzhaeva, 2012; Doguzhaeva and Mapes, 2015; Brayard et al., 2017).

## Conclusions

- (1) Recognition of high biodiversity among the Carboniferous coleoid cephalopods is reinforced by the bacritoid-like coleoid *Oklaconus okmulgeensis* n. gen. n. sp. in Oklaconidae n. fam. described herein.
- (2) Records of the late Carboniferous coleoids having an ink sac is expanded by the described *Oklaconus okmulgeensis* n. gen. n. sp.
- (3) A muscular mantle in *Oklaconus okmulgeensis* n. gen. n. sp. is reported; it is fossilized as a dense sheet-like structure between the conch and the matrix of the concretion and is distinguished by a crisscross pattern, fine longitudinal folds, and globular-lamellar ultrastructure.
- (4) Thinning of a weakly mineralized external portion of the shell wall in the adapical direction observed in *Oklaconus okmulgeensis* n. gen. n. sp. supports the interpretation that this skeletal part acted as a sheath-like rostrum rather than as an outer shell wall layer.
- (5) Different shell morphologies of members of the orders Hematitida and Donovaniconida refute their consideration as a single evolutionary lineage.
- (6) Carboniferous evolutionary development in shelled coleoid cephalopods was perhaps principally driven by the capacity for variation among bacritoid-like coleoids, as can be seen by the diverse combinations of ‘bacritoid’ and ‘coleoid’ structures (orders Hematitida, Donovaniconida, Aulacocerida, Spirulida).
- (7) Recent knowledge of the ultrastructural differences between the shell wall and proostracum or gladius, as well as an Early Triassic record of a slender gladius similar to that of extant squids, refute the hypothesis that extant gladius-bearing coleoids evolved from Donovaniconida via Phragmoteuthida.

## Acknowledgments

This study was supported by the Royal Swedish Academy of Sciences and personally by Professors S. Bengtson, E. Friis, and V. Vajda, Department of Palaeobiology of the Swedish Museum of Natural History, in 2013–2016. We are grateful to C. Klug (Palaeontological Institute and Museum, University of Zurich, Zurich, Switzerland), D. Fuchs (Freie Universität, Berlin, Germany), B. Hunda (Department of Invertebrate Paleontology, Cincinnati Museum Center, Cincinnati, Ohio, USA), P. Weaver (North Carolina Museum of Natural Sciences, Raleigh, North Carolina, USA), and M. Yacobucci (Department of Geology, Bowling Green State University, Bowling Green, Ohio, USA), all of whom reviewed the manuscript.

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Accepted 13 July 2017