Part M, Chapter 23A:
Systematic Descriptions: Hematitida and Donovaniconida

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INTRODUCTION

“... it seems to be a reasonable assumption that the general lack of fossilized coleoid specimens is the result of their low preservation potential, and that there was, in fact, a comparatively wide systematic diversity of coleoids living in marine environments during the Late Paleozoic.” (Mapes & others, 2010, p. 126–127).

This well formulated statement nicely summarizes the picture we presently have about Paleozoic coleoids. With one exception (Hematites), most of the 17 Paleozoic genera are monotypic and based on a single or no more than a handful of specimens. Large fossil gaps and poor preservation additionally complicate the work, although Konservat–Lagerstätten such as the Mazon Creek Lagerstätte (USA, Illinois) or the Bear Gulch Limestones (USA, Montana) have yielded remarkably well-preserved soft parts. The current geographic distribution of the Paleozoic fauna clearly reflects the persistent activities of Larisa Doguzhaeva and Royal Mapes (Ural mountains, USA), the main authorities working close to the evolutionary transition from ectocochleate bactritoids to their endocochleate successors.

Apart from taphonomical problems, researchers are mainly faced with the question of which shell characters delimit coleoids from bactritoids (Klug & others, 2019). Doguzhaeva and Mapes (2014, p. 32) stated: “Paleozoic coleoid recognition is also complicated by the mosaic combination of the ancestral (ectocochleate) and innova-
tive (endocochleate) traits.” Earlier reports on Paleozoic coleoids (e.g. Shimansky, 1954; Flower & Gordon, 1959; Jeletzky 1966; Mapes 1979) have mostly been identified either as bactritoids or aulacoceratids, a practice that indicates that Paleozoic coleoids appear morphologically transitional between bactritoids and aulacoceratids. The presence of a secondary guard-like envelope (rostrum) around the primary shell is certainly a coleoid key feature that delimits bactritoid and other ectocochleates from endocochleate coleoids (Fuchs, 2012). Flower (1945), based on the presence of a rostrum, would have been credited with being the first to correctly identify a Paleozoic coleoid if the stratigraphic age and systematic affiliations of his specimen (Eobelennites) were not dubious (Doyle, Donovan, & Nixon, 1994). It was thus Rosenkrantz (1946), who recognized, based on rostra and disarticulated arm hooks, the first Paleozoic coleoid from the Permian of Greenland. The described remains belong to various aulacoceratid (see Mariotti, Pignatti, & Riegraf, 2021, Treatise Online, Part M, Chapter 23B) and phragmoteuthid coleoids (see Fuchs & Donovan, 2018, Treatise Online, Part M, Chapter 23C).

The first Carboniferous coleoid shell remains (Hematites, Paleoconus) were described by Flower and Gordon (1959) from the lower Carboniferous (Serpukhovian) of North America. Slightly younger specimens with the oldest known ink sacs and arm hooks suggest that the three key coleoid characters (rostral layers, ink sac,
arm hooks) developed rapidly during a short period of time (Mapes, Weller, & Doguzhaeva, 2010); however, the real sequence of these innovations remains obscure (Fig. 1). Septa consisting of lamello-fibrillar nacre (Spirula nacre, nacre type II) represent a fourth convincing argument that reliably points to coleoid affinities (Fuchs, 2006; Fuchs & others, 2012). Such a texture is first evident in upper Carboniferous donovani-conids (Doguzhaeva, Mapes, & Mutvei, 2003). Whether a lamellar-prismatic septal texture, as observed in upper Carboniferous Shimanskya and other lower Carboniferous bactritoid-like forms with uncertain systematic affinities (see Mutvei, Mapes, & Doguzhaeva, 2012), represents the ancestral character state or an aberrant feature of an extinct lineage depends on the unknown septal texture of hematitids, the first unambiguous crown coleoids (Fig. 2).

So-called orthoceratid-like coleoids (Carboniferous Tuborthoceratida Mutvei & Mapes, 2019 and Colororthoceratida Mutvei & Mapes, 2018) are typified by a chitin-rich, lamellar-prismatic (non-nacreous) conotheca and lamellar-prismatic septa. Owing to the lack of unambiguous coleoid characters (rostrum, ink, arm hooks, lamello-fibrillar septa), both orders are preliminary considered as presumed coleoids until the phylogenetic significance of lamellar-prismatic septa is better understood.

Because records of supposed Devonian coleoids have commonly been rejected, earliest unambiguous coleoids are represented by the two orders Hematitida Doguzhaeva, Mapes, and Mutvei, 2002a and Donovaniconida Doguzhaeva, Mapes, and Mutvei, 2007. Both groups are characterized by a rostrum, comparatively low chambers, and a tubular final chamber. The main differences between the Hematitida and Donovaniconida concern the length of the final chamber (Doguzhaeva, Mapes, & Mutvei, 2010). In Hematitida, the final chamber is presumably short, whereas in Donovaniconida it is long, similar to those of aulacoceratids. In contrast to Hematitida, Donovaniconida appear very heterogeneous. Owing to slightly deviating morphologies or inappropriate preservation, classification of some genera have been taken with reservation (e.g., Rhiphaeoteuthis, Belemnitomimus, Flowerites, Mutveiconites). Both Hematitida and Donovaniconida are currently known from the early to late Carboniferous.

Apart from genera assignable to either hematitids or donovaniconoids, classification of the majority of additional named and unnamed specimens (e.g., Jeletzkya, Allison’s soft part coleoid) from Upper Paleozoic deposits is still uncertain (e.g. Johnson & Richardson, 1968; Dawson, 1978; Allison, 1987; Kostak & others, 2002). Late Permian genera Palaeobelemnopsis, Prographularia, and Permotheuthis are classified as Aulacoceratida (see Mariotti, Pignatti, & Riegraf, 2021, Treatise Online, Part M, Chapter 23B) and Phragmoteuthida (see Fuchs & Donovan, 2018, Treatise Online, Part M, Chapter 23C).

Carboniferous genera play a role in the debate on the age of coleoid crown groups. Johnson and Richardson (1968) identified Jeletzkya as the first teuthid. This assignment has been rejected by Gordon (1971) and Doyle, Donovan, and Nixon (1994) as the morphology of the arm hooks exposed Jeletzkya as a belemnoid (see Fuchs & Hoffmann, 2017, Treatise Online, Part M, Chapter 10). Because of the lack of tabular nacre in the conotheca, Shimanskya has been classi-
fied as an early representative of the Spirulida (e.g. Doguzhaeva, Mapes, & Mutvei, 1999; 2010; Nishigushi & Mapes, 2008), whereas Pohlsepia has been ascribed to Cirrata based on a sac-like body outline (Kluessendorf & Doyle, 2000; Doguzhaeva, Mapes, & Mutvei, 2010; Nishigushi & Mapes, 2008). Such an early appearance of different coleoid crown group representatives has been criticized by Kröger, Vinther, and Fuchs (2011), Fuchs (2019), Tanner and others (2017), and Fuchs, 2020, Treatise Online, Part M, Chapter 23G. The latter genera are therefore provisionally accommodated as Paleozoic coleoids incertae sedis.

**Order HEMATITIDA**

Doguzhaeva, Mapes, & Mutvei, 2002a

[Hematitida Doguzhaeva, Mapes, & Mutvei, 2002a, p. 304]

Coleoids with a short, aragonitic-organic, solid rostrum, strongly ridged, with more than two furrows in variable position;
phragmocone ortho- to longiconic; final chamber tubular, short, equals 1.5 to 2 chamber length; cross-section circular to oval; chamber length variable through ontogeny; sutures straight to slightly adventrally inclined with or without a broad ventral lobe; siphuncle submarginal to marginal (neck lobe absent or present); septum concavity shallow to deep; septal ultrastructure unknown; septal necks ortho- to hemichoanitic, short; connecting rings thin; conotheca multilayered (?) without a nacreous layer; earliest chambers regularly truncated; hooks unknown; ink sac unknown. *Carboniferous, Mississippian (lower Serpukhovian): USA (Utah, Arkansas).

Family HEMATITIDAE
Gustomesov, 1976

[Hematitidae GUSTOMESOV, 1976, p. 72]

Hematites Flower & Gordon, 1959, p. 817 [*H. barbara; OD] [=Bacrttriminus Flower & Gordon, 1959]. Phragmocone longiconic (phragmocone angle about 15°), circular to faintly (laterally) compressed, regularly truncated; chamber length variable through ontogeny; sutures slightly adventrally inclined with more or less pronounced broad ventral saddle; siphuncle marginal (neck lobe present, V-shaped); septum concavity shallow; septal necks short; protoconch spherical, comparatively large; first septum with septal foramen; protoconch enveloped by juvenile rostrum (primordial rostrum)?; adult rostrum conical, apex acute or blunt in truncated specimens, rostrum surface finely ridged, furrows present, their spacing and number variable, often asymmetrically situated, generally concentrated on ventral side. *Carboniferous, Mississippian (lower Serpukhovian): USA (Utah, Arkansas).—Fig. 3, 2a–b. *P. bakeri, Fayetteville Shale, lower Serpukhovian, Arkansas, USA; a, holotype, USNM120021, showing rostrum in lateral view, scale bar, 10 mm; b, longitudinally sectioned specimen with truncated apical part of the shell (siphuncle to the left), scale bar, 1 mm; (new; photo, Royal Mapes).

Order DONOVANICONIDA
Doguzhaeva, Maps, & Mutvei, 2007

[Donovaniconida DOGUZHAEVA, MAPES, & MUTVEI, 2007, p. 138]

Phragmocone small to medium-sized; ortho- to breviconic (phragmocone angle 10°–30°); post-alveolar part of rostrum long, solid or short, investment-like; conotheca three-layered, with nacreous layer; final chamber long, tubular, aperture dorsally slightly projected; chamber length short (chamber length to diameter 0.15–0.20); sutures variable; length of mural parts variable; septa lamello-fibrillar; siphuncle ventromarginal; septal necks retrochoanitic; connecting rings thin, organic; arm hooks present; radula present; ink sac present, arm hooks present. *Carboniferous, Pennsylvanian (upper Moscovian–lower Kasimovian): USA.

Family DONOVANICONIDAE
Doguzhaeva, Maps & Mutvei, 2002b

[nom. corr. DOGUZHAEVA, MAPES, & MUTVEI, 2003, p. 70, pro Donovaniconusidae DOGUZHAEVA, MAPES, & MUTVEI, 2002b, p. 35]

Donovaniconus Doguzhaeva, Maps, & Mutvei, 2002b, p. 35 [*D. oklahomensis; M]. Phragmocone ortho- to breviconic (phragmocone angle 20°–30°); final chamber tubular with dorsal lobe-like projection; chamber length moderate to short; sutures nearly straight, not inclined; siphuncle marginal; septal necks cyrtochoanitic; conotheca three-layered, with nacreous layer; no evidence of a rostrum; arm hooks unknown. *Carboniferous, Pennsylvanian (upper Moscovian–lower Kasimovian): Oklahoma (USA).—Fig. 4, I. *D. oklahomensis, Wewoka Formation, upper Moscovian, USA.
Fig. 3. Hematitidae (p 4).
(Oklahoma), holotype, OUZC4074, showing the final chamber (fch), apertural parts of the phragmocone (ph), and ink sac (is) in lateral view, scale bar, 10 mm (Doguzhaeva, Mapes, & Mutvei, 2002b, fig. 4).

**Saundersites** Doguzhaeva, Mapes, & Mutvei, 2007, p. 138 [*S. illinoisiensis*; M]. Phragmocone longito orthoconic (phragmocone angle 12°–15°); final chamber tubular, with short, proostracum-like projection; rostrum investment-like, confined to one-third of apical phragmocone; radula formula C.L1:L2:M:MP1:MP2; arms seemingly short; arm base present, base length moderate (base length to total hook length 0.55–0.65), shaft length moderate (shaft length to total hook length 0.55–0.65), strongly to very strongly inclined (shaft angle 15°–25°); uncinis height moderate (uncinis height to total hook height 0.55–0.65); uncinis moderately curved (uncinis angle 85°–90°) general hook morphology very close to co-occurring *Jeleztya* Carboniferous, Pennsylvania (Missoulian); USA (Illinois).—Fig. 4.2a–c. *S. illinoisiensis*, Francis Creek Shale, upper Moscovian, USA (Illinois), holotype, FMNH PE32521; a, overview; scale bar, 10 mm (Doguzhaeva, Mapes, & Mutvei, 2007, fig. 6.1A); ac, arm crown fch; final chamber; ca, cephalic area; ph, phragmocone; ro, rostrum; b, schematic reconstruction of radula; C, central; L, lateral; M, middle; MP, marginal plate (Nixon, 2015, *Treatise Online*, Part M, Chapter 12, fig. 16b); c, schematic reconstruction of one arm hook (new).

**Family GORDONICONIDAE** Mapes, Weller, & Doguzhaeva, 2010


**Gordoniconus** Mapes, Weller, & Doguzhaeva, 2010, p. 165 [*G. bear gulchensis*; M]. Phragmocone longito orthoconic (phragmocone angle 10°–20°); final chamber tubular, long, as long as the phragmocone, aperture constricted; chambers moderate in length (chamber length to diameter 0.2–0.3); rostrum covering about one-third of apical phragmocone, post-alveolar part solid, moderately slender (Slenderness Index 0.15–0.20); rostrum apex pointed; arms very short (arm length to mantle length 0.1), evidence of modified tentacles absent; arm hooks present, shape indistinct; presence of ink sac questionable. Carboniferous, Mississippian (upper Sperkhovian); USA (Montana).—Fig. 4.3. *G. bear gulchensis*, Bear Gulch Limestone, upper Sperkhovian, Montana, USA, holotype, AMNH43263, scale bar, 10 mm; ac, arm crown; bch, final chamber; ph, phragmocone; ro, rostrum; rs, rostrum solidum (new; photo, Christian Klug).

**Family OKLACONIDAE** Doguzhaeva & Mapes, 2017

[Oklaconidae Doguzhaeva & Mapes, 2017, p. 164]

**Oklaconus** Doguzhaeva & Mapes, 2017, p. 164 [*O. okmulgeensis*; M]. Smooth compressed orthocone with apical angle ~15°; proostracum-like structure on narrowly dorsal and small marginal siphuncle on broadly rounded ventral side, respectively; subequally long body chamber and phragmocone, chamber length short (chamber length to diameter ~0.15); suture line with broad lateral lobe; connecting rings thin; septal necks long holocoonitc ventrally and short cyrtocoanitic dorsally; rostrum thin, sheath-like; ink sac present. Carboniferous, Pennsylvania (Moscovian); USA (Oklahoma).

**ORDER UNCERTAIN**

**Family RIPHAEOTEUTHIDAE**

Doguzhaeva, 2002

[Riphaeoteuthidae Doguzhaeva 2002, p. 15]

**Riphaeotheticus** Doguzhaeva 2002, p. 16 [*R. margaritae*; M]. Phragmocone brevicone (phragmocone angle ~30°); final chamber unknown; chamber length short (chamber length to diameter 0.10–0.15); septal necks short cyrtocoanitic; rostrum unknown. Carboniferous, Pennsylvania (upper Gzhelian); Kazakhstan (southern Ural Mountains).—Fig. 5.1a–b. *R. margaritae*, Gzhelian, Kazakhstan, holotype, PR13871/361; a, phragmocone in ventral view; b, phragmocone in lateral view; scale bar, 10 mm (Doguzhaeva, 2002, pl. 13,1–2).

**Belemnitonimus** Shimansky 1954, pl. 7 [B. palaeozicus; M]. Phragmocone brevicone (phragmocone angle ~30°), chamber length short (chamber length to diameter ~0.1); siphuncle marginal; rostrum unknown. Permian (Cisuralian, Aesclbian); Kazakhstan (southern Ural Mountains).—Fig. 5.2. *B. palaeozicus*, Aesclbian, Kazakhstan, specimen PR13871/362, longitudinally sectioned phragmocone (siphuncle to the right). (Doguzhaeva, 2002, pl. 13,5; scale not indicated).

**Family FLOWERITIDAE** Mapes & others, 2010

[Floweritidae Mapes, Doguzhaeva, Mutvei, & Parin, 2010, p. 133]

**Flowericonus** Mapes & Doguzhaeva, 2017, p. 146 [*F. bellevenensis* Mapes & others, 2010, p. 133; M] [= Flowerites Mapes & others, 2010, p. 133]. Phragmocone small-sized, orthoconic; final chamber short; chamber length short; septa transverse; sutures straight; siphuncle marginal; septal necks probably cyrtocoanitic; rostrum unknown; ink sac present. Carboniferous, Pennsylvania (lower Kasimovian); USA (Nebraska).—Fig. 5.3. *F. bellevenensis*, Denis Formation, lower Kasimovian, Nebraska, USA, unregistered specimen (USNM) showing remains of the phragmocone posterior to the ink sac; scale bar, 10 mm (new; photo, Royal Mapes).
Family MUTVEICONIDAE
Doguzhaeva, 2002

*Mutveiconites* Doguzhaeva, 2002, p. 17 [*M. mirandus*; M]. Phragmocone longiconic; final chamber tubular, long; chamber length long; septa transverse; siphuncle marginal; septal necks retrochoanitic, short; protoconch hemispherical, protoconch wall discontinuous; rostrum investment-like, post-alveolar part very short, dome-like thickened (at least in juveniles). *Carboniferous, Pennsylvanian (Gzhelian)*: Kazakhstan (southern Ural Mountains), USA.——Fig. 5, 4a–b. *M. milleri* Doguzhaeva, Mapes, & Dunca, 2006, p. 59 Graham Formation, Gzhelian, Texas, USA, holotype, OUZC5205; a, juvenile specimen inside the long tubular final chamber of an adult specimen, scale bar, 1 mm; b, close-up of the earliest chambers showing the hemispherical protoconch covered by a dome-like rostrum, scale bar, 0.1 mm. (Doguzhaeva, Mapes, & Dunca, 2006, Fig. 1A–B).

Family SHIMANSKYIDAE
Doguzhaeva, Mapes, & Mutvei, 1999

*Shimanskya* Doguzhaeva, Mapes, & Mutvei, 1999, p. 55 [*Bactrites postremus* Miller, 1930, p. 389–390; OD]. Phragmocone longiconic; phragmocone angle 3°–6°; chamber length to diameter 0.75–0.95; sutures simple; mural parts as long as the chamber length; septa transverse, comprised of prismatic lamellae; siphuncle marginal; septal necks orthochoanitic; thin wrinkle layer intercalated between inner and outer shell layer; nacreous layer absent; outer layer possibly corresponds to a sheath-like rostrum; dorsal attachment scar unknown; protoconch unknown. *Carboniferous, Pennsylvanian (Gzhelian)*: USA (Texas).——Fig. 6, 1–2. *S. postremus* (Miller), Graham Formation, Gzhelian, Texas, USA; 1a–c, specimen SU143924 in lateral (a), dorsal (b), and ventral (c) views, scale bar, 1 mm; 2a–b, specimen SU143925 showing a single chamber in ventral (a), and dorsal (b) views; scale bar, 1 mm (Mapes, 1979, pl. 21, pl. 35).
Fig. 5. Rhiphaoteuthidae, Floweritidae, Mutveiconidae (p. 6–7).
Hematitida and Donovaniconida

**ORDER & FAMILY UNCERTAIN**

Glochinomorpha Gordon, 1971, p. 35 [*G. stifeli; M*]. Phragmocone and rostrum unknown; leaf-like structure preserved in association with the hooks; hook base length moderate (base length to total hook length 0.50–0.60), shaft length moderate (shaft length to total hook length 0.70–0.80), moderately inclined (shaft angle 55°–65°), uncinus height low (uncinus height to total hook height 0.20–0.30), uncinus moderately curved (uncinus angle 90°–100°). Lower Permian (Kungurian): USA (Utah). —— Fig. 7, 1. *G. stifeli*, schematic hook reconstruction (new).

Jeletzkya Johnson & Richardson, 1968, p. 526 [*J. douglassae; M*]. Phragmocone unknown; arms short, equal in length, equipped with hooks; arm base length moderate (base length to total hook length 0.55–0.65), shaft length moderate (shaft length to total hook length 0.55–0.65), strongly to very strongly inclined (shaft angle 15°–25°), uncinus height moderate (uncinus height to total hook height 0.55–0.65), uncinus moderately curved (uncinus angle 85°–95°), general hook morphology very close to co-occurring Saundersites. Carboniferous, Pennsylvanian (upper Moscovian): USA (Illinois). —— Fig. 7, 2. *J. douglassae*, Francis Creek Shale, upper Moscovian, schematic hook reconstruction (new).

Nebraskaconus Mapes & Doguzhava, 2017, p. 148 [*N. whitei; M*]. Phragmocone breviconic; rostrum absent; septa closely spaced, mural part of septum about one-half the cameral length; arm hooks unknown; ink sac present. Carboniferous, Pennsylvanian (upper Kasimovian): USA (Nebraska).
**Pohlsepia** Kluessendorf & Doyle, 2000, p. 920

[*P. mazonensis*; M]. Phragmocone and rostrum unknown; mantle sac-like, ten arms, two of which appear to be elongated, tentacle-like; (?l) fins lobate. *Carboniferous, Upper Pennsylvanian (upper Moscovian*): USA (Illinois).——Fig. 8, 1. *P. mazonensis*, Carbonbide Formation, Moscovian, Illinois, USA, holotype, FMNH PE51527, scale bar, 10 mm (Kluessendorf & Doyle, 2000, Fig. 1A–B).

**Starkites** Mapes & Doguzhaeva, 2017, p. 149 [*S. compressus*; M]. Phragmocone breviconic; body chamber, rostrum, and pro-ostracum absent; septa closely spaced; arm hooks unknown; ink sac present. *Carboniferous, Upper Pennsylvanian (upper Kazimovian*): USA (Nebraska).

**Stenoconites** Gordon, 1966, p. 33 [*S. idahoensis*; M]. Rostrum small-sized, straight, compressed, elliptical in cross sections with prominent dorsolateral ridges, venter rounded, dorsum slightly flatter and narrower than venter; dorsolateral ridges defined by smooth sulcus on either side, smaller sulci may be present locally; surface of rostrum ornamented by fine, slightly irregular, longitudinal ramifying threads, more pronounced on venter; post-alveolar part of rostrum comparatively short; phragmocone circular in cross section; alveolar angle 6°–7°; ratio chamber length: chamber diameter ~0.3–0.4; siphuncle submarginal; septal necks achoanitic; septa horizontal; cameral deposits may be present. *Middle Permian (Kungurian–Guadalupian)–Upper Permian*: USA (Idaho), ?South China (Hubei and Zhejiang).——Fig. 8, 2a–2b. *S. idahoensis*, Phosphoria Formation, Guadalupian, Idaho, USA; a, holotype, USNM146473, showing rostrum in lateral view, scale bar, 10 mm (Gordon, 1966, fig. 2a); b, schematic longitudinal section; m, matrix; r, rostrum; s, septum; s, siphuncle. (Gordon, 1966, fig. 3).

**REFERENCES**


