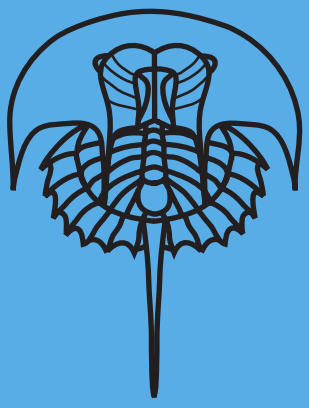

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PART M, COLEOIDEA, CHAPTER 23E: SYSTEMATIC DESCRIPTIONS: DIPLOBELIDA

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INTRODUCTION

The Diplobelida is a small and comparatively rare group of belemnoid-like coleoids that has been supposed to play a central role in the origin of the Decabrachia (Naef, 1922; Meyer, 1993; Hewitt & Jagt, 1999; Haas, 2003; Fuchs, 2012; Fuchs, Keupp, & Wiese, 2012; Fuchs & others, 2013). The order is mainly characterized by an advanced degree of shell reduction (Kröger, Vinther, & Fuchs, 2011), which is expressed by the absence of a bullet-like solid rostrum (rostrum solidum or rostrum proper) and the possession of a pro-ostracum that is distinctly narrower than in the Belemnitida. Its isolated position among belemnoid coleoids is also expressed by an unusual protoconch architecture that appears to be different from the belemnoid and decabrachian condition (Fuchs, Keupp, & Wiese, 2012; Fuchs, 2019). While Jeletzky (1966, 1981) and Doyle, Donovan, & Nixon (1994) assumed that the Diplobelida represented an offshoot of the Belemnitida without any descendants, the significant reduction of the pro-ostracum width led Fuchs and others (2013) to regard diplobelids to be transitional between Belemnitida and Cretaceous Groenlandibelidae. The Cretaceous genus *Longibelus* Fuchs & others, 2013, exhibits a mosaic of diplobelid and groenlandibelid characters and, therefore, plays an important role linking both groups. Moreover, workers derived the Sepiida from breviconic diplobelids such as *Conoteuthis* Orbigny, 1842, or *Vectibelus* Jeletzky, 1981, owing to the presence of distinctly inclined septa (Meyer, 1993; Hewitt & Jagt, 1999; Fuchs, Keupp, & Wiese, 2012). Although unknown in most diplobelid genera, in situ arm hooks recorded in putative diplobelids *Chondroteuthis* Bode, 1933 (Hoffmann, Fuchs, & Weinkauf, 2016) and *Clarkeiteuthis* Fuchs, Donovan, & Keupp, 2013, as well as isolated hooks in Cretaceous sediments without belemnitid rostra suggest that diplobelid arms were likewise equipped with hooks (Fuchs, Reich, & Wiese, 2004; see *Treatise Online* 91, Chapter 10). Fossilized soft parts are virtually absent in unambiguous diplobelids, except for medio-dorsal, soft-tissue attachment scars on the inner surface of each chamber.

Apart from two questionable Early Jurassic genera with a narrow pro-ostracum and without a solid rostrum (Fig. 1), the first unambiguous diplobelids appeared during the Late Jurassic (Kimmeridgian–Tithonian). Although their origin is still obscured, it is reasonable to search the diplobelid root among early belemnitid subgroups with a less developed rostrum (e.g., Coeloteuthididae). The group diversified during the Early Cretaceous but had already declined by the end of the same period. Only a single genus (*Conoteuthis*) occurred during the Late Cretaceous.

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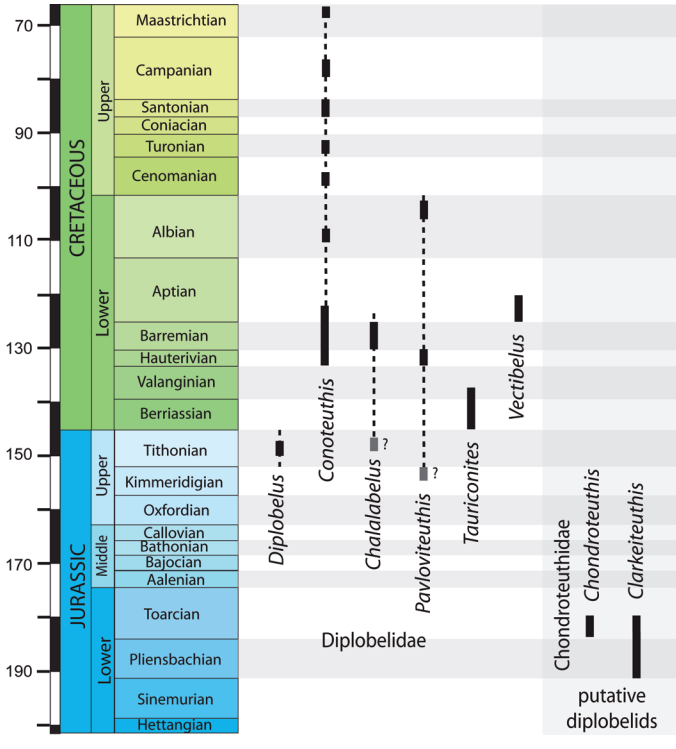

FIG. 1. Stratigraphical occurrences of diplobelid taxa.

ORDER DIPLOBELIDA Jeletzky, 1965

[*nom. transl.* DRUSHCHITS, KABANOV, & NERODENKO, 1984, p. 13, *ex* suborder Diplobelina JELETZKY, 1965, p. 76] [=Diplobeloidea MÜLLER, 1981, p. 335; Diplobeloidei STAROBOGATOV, 1983, p. 7]

Phragmocones ortho- to breviconic, Cretaceous forms adventrally incurved (cyrtoconic); chamber length usually short; solid rostrum solidum unknown; sheath thin and short, lamellar, aragonitic, adapically thickened, medio-dorsally with or without keel; pro-ostracum narrow, only one-eighth of the phragmocone circumference, length uncertain; dorsal sutures characteristically with a distinct saddle; ventral sutures simple with a weak lobe; septa either weakly or distinctly inclined; dorsal parts of the septal necks retrochoanitic; siphuncle mostly submarginal, rarely marginal; mural flaps unknown; medio-dorsal attachment scars narrow and stripe-like, occupying the entire chamber length; studies on the conothecal ultrastructure still missing; internal organization of the spherical protoconch poorly known; caecum absent; arm hooks possibly present. ?*Lower Jurassic (Sinemurian–lower Toarcian), Upper Jurassic (Tithonian)–Upper Cretaceous (Maastrichtian).*

Family DIPLOBELIDAE Naef, 1926

[Diplobelidae NAEF, 1926, p. 4, *nom. correct. pro* Diploconidae NAEF, 1922, p. 278, *nom. dub.*]

Diagnosis as for the order.

Diplobelus NAEF, 1926, p. 4 [**Diploconus belemnitoides* ZITTEL, 1868, p. 552; OD] [=*Diploconus* ZITTEL, 1868, p. 552, *nom. nud.*]. Phragmocone slightly cyrtoconic, apical angle 20°–30°; pro-ostracum narrow, rodlike; ratio of chamber length to diameter ranges from 0.15 to 0.20; keel absent; dorsal sutures with distinct saddles; ventral sutures straight; septa transverse or weakly inclined; siphuncle submarginal; medio-dorsal attach-

ment scars narrow, stripe-like, and as long as the chamber; post-alveolar sheath slightly elongated, dorsally thickened. *Upper Jurassic (Tithonian):* Czech Republic.——Fig. 2,*1a–c. *D. belemnitoides* (Zittel), Tithonian, Stramberg, Czech Republic, holotype, BSPG AS II 329; *a,* lateral view, ×3; *b,* close-up view of medio-dorsal saddles and stripe-like attachment scars, ×7; *c,* close-up view of dorsolateral, forward-projecting growth lines indicating rodlike pro-ostracum, ×7 (new).

Conoteuthis Orbigny, 1842, p. 376 [**C. dupinianus;* OD]. Phragmocone cyrtoconic, apical angle 30°–40°; ratio of chamber length to diameter ranges from 0.15 to 0.2; medio-dorsal keel pronounced, involving conotheca and sheath; pro-ostracum anteriorly acute; dorsal sutures with distinct saddles; ventral sutures straight; septa weakly inclined; siphuncle submarginal; protoconch spherical, adventrally inclined; post-alveolar sheath very short, adapically thickened on its dorsal side, adorally paper thin. *Lower Cretaceous (Hauterivian)–Upper Cretaceous (upper Maastrichtian):* UK, France, southern India, Japan, Greenland.——Fig. 2,*2a–c. *C. dupinianus,* Aptian, Isle of Wight, UK, BMNH C.58037; *a,* medio-dorsal saddles and keel, ×5; *b,* oblique septa in lateral view, ×5; *c,* straight sutures in ventral view, ×5 (new).——Fig. 2,*2d–f, C. hayakawai* Fuchs & Niko, Turonian, Hokkaido, Japan; *d,* overview of holotype, NSM PM23442, ×2.5 (Fuchs & Niko, 2010, fig. 3,*1*); *e–f,* specimen, BSPG MB-710, longitudinal section, ×6; *f,* close-up view of spherical protoconch, ×20 (Fuchs, Keupp, & Wiese, 2012, fig. 4C–D).

Chalalabelus Jeletzky, 1981, p. 141 [**Conoteuthis renniei* Spath, 1939, p. 1; OD]. Phragmocone cyrtoconic, apical angle 45°–50°; ratio of chamber length to diameter ranges from 0.15 to 0.2; medio-dorsal keel present; post-alveolar sheath elongated, dorsally thickened and blunt. *?Upper Jurassic (Tithonian), Lower Cretaceous (Barremian–Aptian):* Mozambique, UK, ?Russia.——Fig. 3,*1a–c. *C. aff. renniei* (Spath), Barremian, UK, BMNH C58036; *a,* frontal view, ×4; *b,* apertural, ×4; *c,* breviconic cast of the alveola, ×4 (new).

Pavloviteuthis Shimansky, 1957, p. 43 [**P. kabanovi;* OD]. Phragmocone orthoconic, weakly adventrally incurved, apical angle 25°; ratio of chamber length to diameter ranges from 0.15 to 0.2; medio-dorsal keel indistinct; dorsal sutures with distinct saddles; ventral sutures slightly lobate; septa weakly inclined; siphuncle marginal; post-alveolar sheath short. *?Upper Jurassic (upper Kimmeridgian), Lower Cretaceous (Hauterivian–upper Albian):* Russia, UK, ?Germany.——Fig. 3,*2a–c. *P. kabanovi,* Hauterivian, Volga region, Russia, holotype, PIN888/10; dorsal (*a*), lateral (*b*), and ventral (*c*) views, ×5 (new).——Fig. 3,*2d. P. cantiana* (Spath), Albian, Gault Formation, Folkstone, UK, holotype, BMNH C.37844, lateral view, ×1.3 (new).

Tauriconites Kabanov in Drushtchits, Kabanov, & Nerodenko, 1984, p. 13 [**T. nikolai;* OD]. Phragmocone orthoconic, weakly adventrally incurved, apical angle 15°–30°; pro-ostracum unknown; septa weakly inclined; siphuncle submarginal; septal necks of protoconch spherical, adventrally inclined; post-alveolar sheath very short, dorsally thickened and blunt. *Lower Cretaceous (Berriasian–lower Valanginian):* Russia (Crimea).——Fig. 3,*3. *T. nikolai,* PIN 2578/240, Berriasian, Letneya, Crimea (adapted from Drushtchits, Kabanov, & Nerodenko, 1984, fig. 2a).

Vectibelus Jeletzky, 1981, p. 135 [**Conoteuthis vectensis* Spath, 1939, p. 3; OD]. Phragmocone cyrtoconic, apical angle 45°–50°; chamber length short; medio-dorsal keel present; dorsal sutures with distinct saddles; ventral sutures slightly lobate; septa strongly oblique; siphuncle submarginal; sheath apex dorsally incurved (spinelike) and thickened; hooks unknown. *Lower Cretaceous (lower Aptian):* UK (Isle of Wight).——Fig. 3,*4a–c. *V. vectensis* (Spath), lost holotype, BMNH C.48619; dorsal (*a*), lateral (*b*), and ventral (*c*) views, ×3 (Jeletzky, 1981, pl. 24,*1J–L*).

PUTATIVE DIPLOBELIDA

Family CHONDROTEUTHIDAE Jeletzky, 1965

[*nom. correct.* herein, *pro* Chondroteuthididae Jeletzky, 1965, p. 76]

Phragmocones ortho- to breviconic; chamber length variable; rostrum unknown; sheath short and thin, aragonitic, medio-dorsally without keel; pro-ostracum narrow, only one-eighth of the phragmocone circumference, length up to twice as long as phragmocone; dorsal sutures with a faint saddle; ventral sutures simple with a weak lobe; septa straight; siphuncle submarginal; medio-dorsal attachment scars narrow, stripe-like, occupying the entire chamber length; conothecal ultrastructure unknown; protoconch morphology unknown; arm hooks present, bi- or uniserial. *Lower Jurassic (Sinemurian–lower Toarcian).*

Chondroteuthis Bode, 1933, p. 55 [**C. wunnenbergi;* OD]. Phragmocone orthoconic, apical angle 15°–16°; ratio of chamber length to diameter ranges from 0.15 to 0.2; pro-ostracum narrow, anteriorly straight to weakly rounded, almost twice as long as the phragmocone; keel absent; dorsal sutures with faint saddle; ventral sutures lobate; siphuncle submarginal; sheath thin covering only the most apical part of the phragmocone; ratio of arm length to mantle length 0.45:0.5; microhooks uniserial, with four different, spurless types; possibly one pair of mega-hooks present; arms

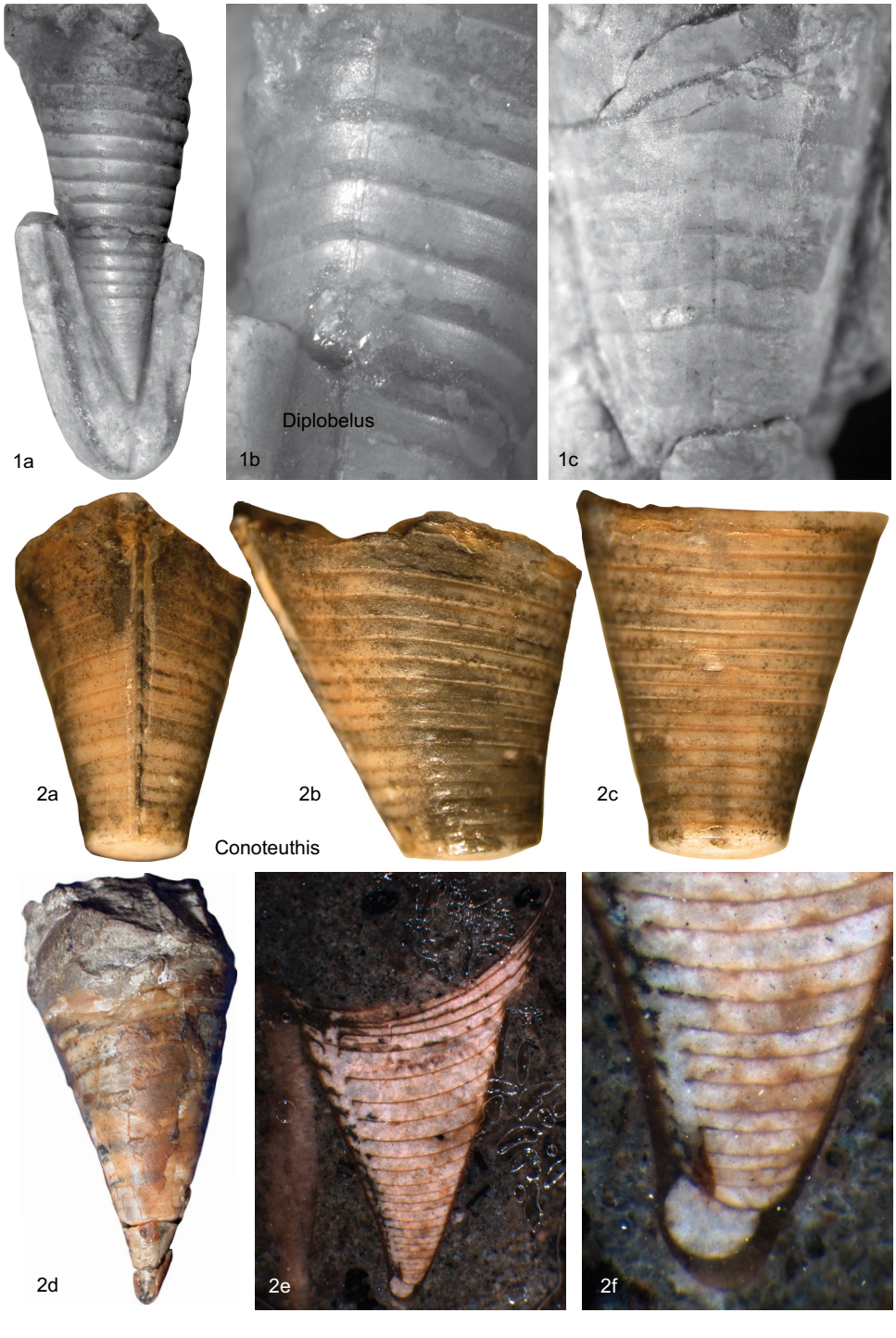

FIG. 2. Family Diplobelidae (p. 2–3).

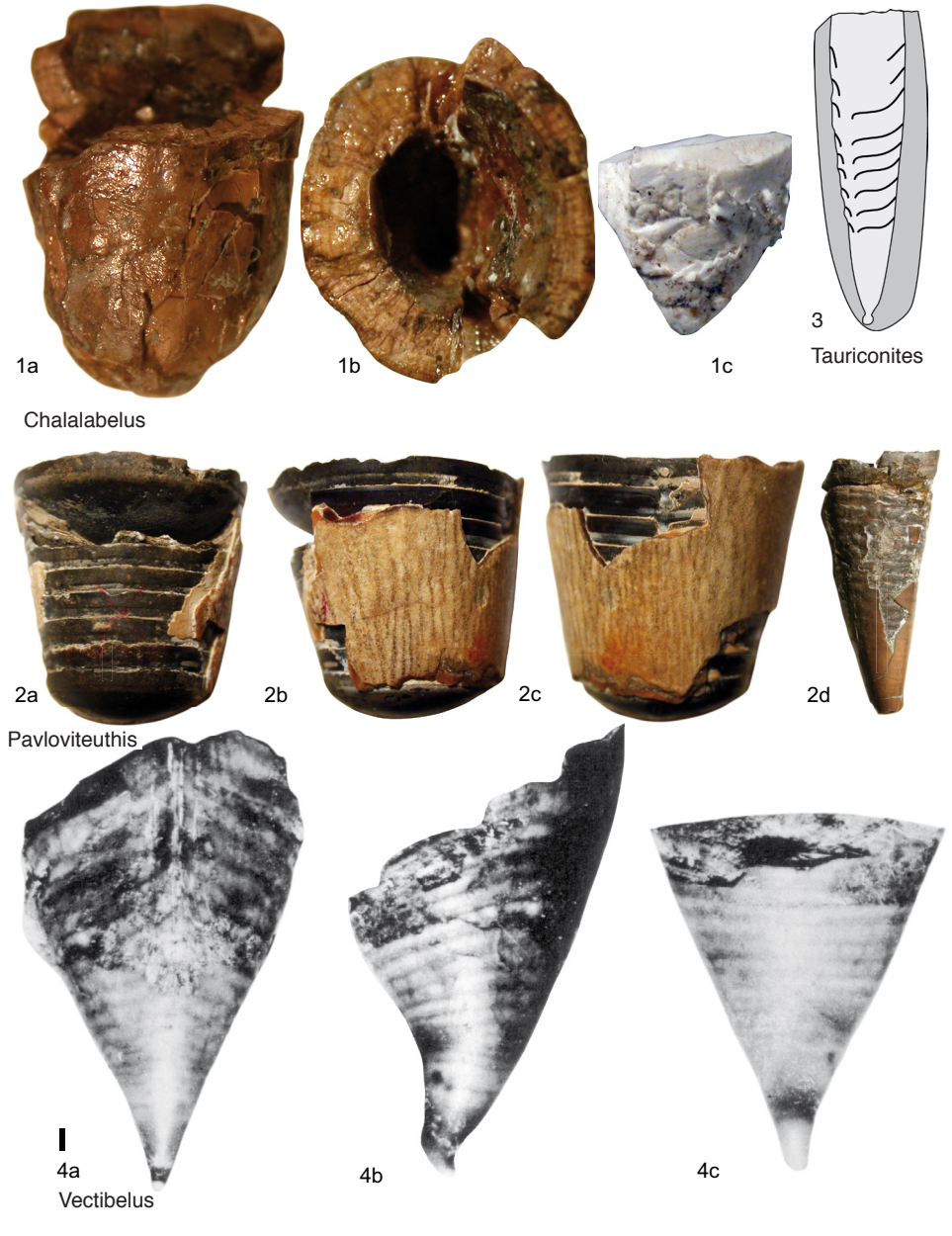

FIG. 3. Family Diplobelidae (p. 3).

differentiated. *Lower Jurassic (lower Toarcian):* Germany, Luxembourg, ?UK.——FIG. 4*a–d.* **C. wunnenbergi;* lower Toarcian, Germany; *a,* holotype, Technische Universität Clausthal-Zellerfeld, ventral view, ×0.5; *b,* specimen, collection Engeser, Berlin, lateral view, ×1; *c,* specimen, BSPG MB746, dorsal view showing pro-ostracum, ×1; *d,* specimen, Bundesanstalt für Geowissenschaften und Rohstoffe, Hanover, Germany, with focus on hook-bearing arm crown, ×2 (new).

Clarkeiteuthis FUCHS, DONOVAN, & KEUPP, 2013, p. 246 [**Onychoteuthis conocauda* QUENSTEDT, 1849

FIG. 4. Family Chondroteuthidae (p. 3–5).

in 1845–1849, p. 529; OD] [=*Phragmoteuthis* MOJSISOVICS, 1882, p. 302, *partim*]. Phragmocone breviconic; pro-ostracum comparatively long and narrow, anteriorly rounded, almost twice as long as the phragmocone; 10 comparatively short arms; ratio of arm length to mantle length ranges from 0.3 to 0.4; hooks biserial, hook shaft perpendicular to hook base, hook pairs appear to articulated like pincers. *Lower Jurassic (Sinemurian–Toarcian):* UK, southern Germany.——FIG. 5*a–g.* **C. conocauda* (QUENSTEDT), lower Toarcian, southern Germany; *a,* complete specimen, coll. UMH, ventral view, ×0.5 (new); *b,* specimen, Banz monastery collection, ventral view showing phragmocone and pro-ostracum, ×0.75 (new); *c,* specimen, Museum Hauff, with focus on hook-bearing arms, ×1 (new); *d–e,* reconstruction of shell, lateral (*d*) and ventral (e) views (new); *f–g,* reconstruction of the hook, lateral (*f*) and frontal (*g*) views (new).

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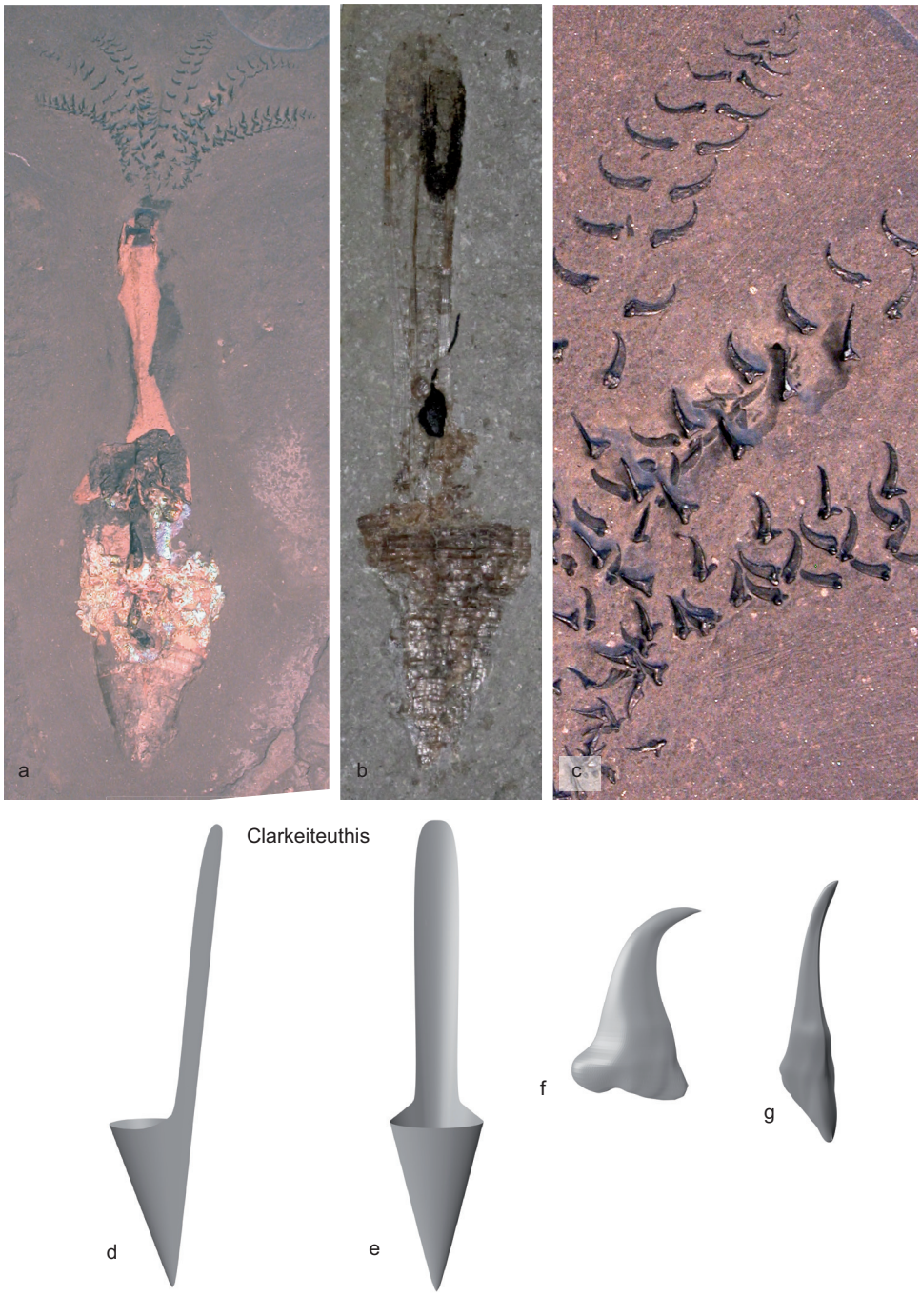

FIG. 5. Family Chondroteuthidae (p. 5–6).

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