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PART M, CHAPTER 23B: SYSTEMATIC DESCRIPTIONS: AULACOCERATIDA

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INTRODUCTION

The order Aulacoceratida Stolley, 1919 is a group of rostrum-bearing orthoconic coleoids, which was established as distinct from true belemnites starting with Bather in Blake (1892). Schwetzov (1913), Abel (1916), Stolley (1919), Naef (1921b), and Jeletzky (1966) recognized its independence from the Belemnitida Zittel, 1895. Later, the order was further circumscribed, and various taxa were reassigned to other belemnoid orders (Belemnitida, Hematitida Doguzhaeva, Mapes, & Mutvei, 2002, and Phragmoteuthida Mojsisovics, 1882) (Engeser, 1990).

The Aulacoceratida comprise 15 genera, belonging to three families grouped into two superfamilies (Aulacoceratoidea Mojsisovics, 1882 and Xiphoteuthidoidea Bather in Blake, 1892), and in addition two genera *incertae sedis*. They are mainly characterized by a long and tubular (i.e., ventrally closed) body chamber (see Donovan & Riegraf, 2016, *Treatise Online,* Part M, Chapter 21) and an aragonitic and massive rostrum (e.g., Jeletzky, 1966). The tubular body chamber may possess a small dorsal lip projection, as in *Dictyoconites* Mojsisovics, 1902 (Bandel, 1985). The rostrum, for which the term telum has also been used (Jeletzky, 1966), is formed of superposed alternating lamellae (*laminae obscurae* and *laminae pellucidae*) (e.g., Müller-Stoll, 1936; Dauphin & Cuif, 1980; Doyle, 1990). The rostrum is primarily comprised of aragonite and organic substance (Dauphin & Cuif, 1980); the *laminae obscurae* of the rostrum are primarily more organic-rich than the intervening predominantly calcareous *laminae pellucidae* (Fig. 1). The structure of the rostrum is coarser than in the Belemnitida; it differs in the two superfamilies of the Aulacoceratida. In the Aulacoceratoidea the lamellae are corrugated, strongly and deeply folded (Fig. 2a) (Doyle & Shakides, 2004), suggesting intense radial folding (Keupp, 2012) of the rostrum-secreting epithelium. In the Xiphoteuthidoidea the lamellae of the rostrum are concentric and not corrugated (Fig. 2b). The surface of the rostrum is accordingly either smooth (in the Xiphoteuthidoidea) or with longitudinal ribs and grooves, striae, granules, and pits (in the Aulacoceratoidea). The key character delimiting the three aulacoceratid families, is the appearance of the surface of the rostrum, which can be either strongly ribbed (Aulacoceratidae Mojsisovics, 1882), striated (Dictyoconitidae Gustomesov, 1978), or smooth (Xiphoteuthididae Bather in Blake, 1892). Surficial patterns of fine, branching marks, interpreted as vascular imprints (Bülow, 1915), have been recorded in *Aulacoceras* Hauer, 1860 and *Buelowiteuthis* Jeletzky, 1965. Additional diagnostic characters of the order are narrow alveolar angles (4°–12°) and long chambers (with a few exceptions, e.g., *Breviatractites* Mariotti & Pignatti, 1992, *Metabelemnites* Flower, 1944); adult septal necks are generally prochoanitic (Jeletzky, 1966). The alveolus is the conical cavity in the rostrum containing the phragmocone, and its angle

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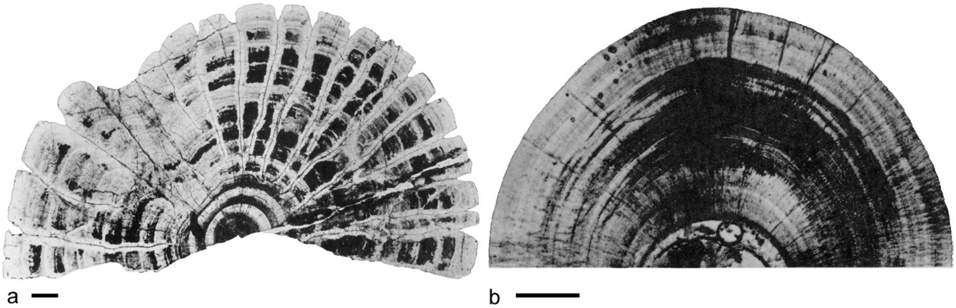

FIG. 1. Growth patterns of the rostrum in the Aulacoceratida as seen in thin section; *a,* corrugated growth and well-marked radial sectors in the cross section of the *rostrum solidum* of *Aulacoceras* sp., lower Norian, Alakır Çayı, Turkey (Dauphin & Cuif, 1980, pl. 9,*1*); *b,* concentric growth in the *rostrum cavum* of *Crassiatractites* sp., lower Norian, Alakır Çayı, Turkey (Dauphin & Cuif, 1980, pl. 1,*3*). Scale bars, 10 mm.

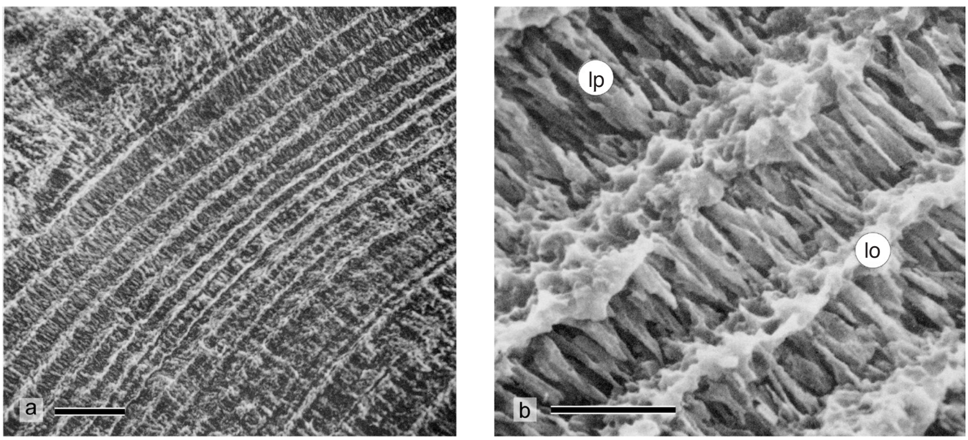

FIG. 2. SEM micrographs of *Crassiatractites* sp., lower Norian, Alakır Çayı, Turkey; *a,* cross section of *rostrum solidum* showing the concentric alternating lamellae, scale bar, 100 µm (Dauphin & Cuif, 1980, pl. 1,*4*); *b,* detail of the alternating *laminae pellucidae* (*lp*) and *laminae obscurae* (*lo*), scale bar, 10 µm (Dauphin & Cuif, 1980, pl. 1,*6*).

is known as the alveolar angle. Following MÜLLER-STOLL (1936), the post-alveolar part of the rostrum is called the *rostrum solidum*, the alveolar part the *rostrum cavum*. Rostra may be constricted at the *rostrum solidum–rostrum cavum* transition, having a waist, as in *Atractites* GÜMBEL, 1861 (Fig. 3). In cross section, the rostra are circular, compressed (laterally flattened), or depressed (dorsoventrally flattened). According to the total length of the preserved rostrum, the following descriptive size categories are distinguished: very small (<30 mm), small (30–60 mm), medium (61–100 mm), large (101–150 mm), and very large (>150 mm).

As regards early ontogeny, the Aulacoceratida do not appear to differ significantly from the Belemnitida (JELETZKY, 1966; BANDEL, 1985). Two ontogenetic stages can be recognized in aulacoceratid rostra, the primordial rostrum and the rostrum (FUCHS, 2006); and the occurrence of an epirostrum (MÜLLER-STOLL, 1936), as developed in the Belemnitina ZITTEL, 1895, has never been reported in the Aulacoceratida.

Undisputed aulacoceratids with soft parts, beaks, and arm hooks are unknown (JELETZKY, 1966; ENGESER & CLARKE, 1988). In *Treatise Online*, Part M, Chapter 10: Arm armature in belemnoid coleoids, FUCHS and HOFFMANN (2017) considered aulacoceratids

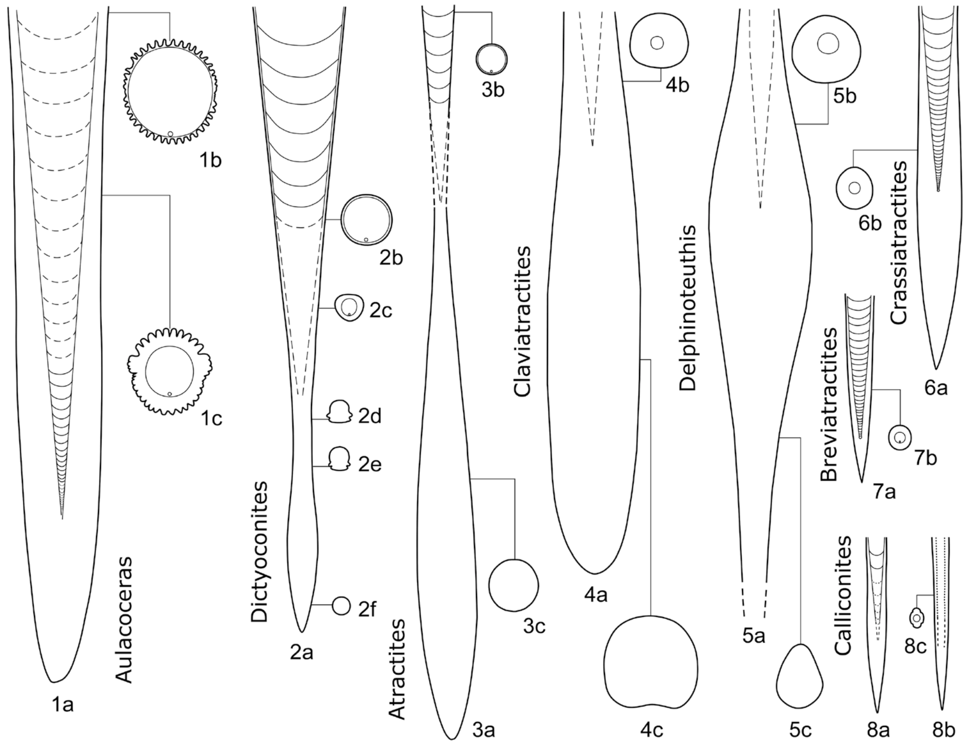

FIG. 3. Schematic profiles, outlines, longitudinal sections, and cross sections of rostra in different aulacoceratid genera. *1, Aulacoceras timorense* (WANNER, 1911); *a,* longitudinal section; *b–c,* cross sections of *rostrum cavum. 2, Dictyoconites doylei* RIEGRAF IN RIEGRAF, JANSSEN, & SCHMITT-RIEGRAF, 1998; *a,* reconstructed longitudinal section of rostrum; *b–f,* cross sections of phragmocone and rostrum. *3, Atractites alpinus* GÜMBEL, 1861; *a,* reconstructed longitudinal section of rostrum; *b,* cross section of *rostrum cavum; c,* cross section of *rostrum solidum. 4, Claviatractites claviger* (BÜLOW, 1915); *a,* longitudinal section of rostrum; *b,* cross section of *rostrum cavum; c,* cross section of *rostrum solidum. 5, Delphinoteuthis aenigmatica* MARIOTTI & PIGNATTI, 1994; *a,* longitudinal section of rostrum; *b,* cross section of *rostrum cavum; c,* cross section of *rostrum solidum. 6, Crassiatractites tenuirostris* (HAUER, 1887); *a,* longitudinal section of rostrum; *b,* cross section of *rostrum cavum. 7, Breviatractites pusillus* (HAUER, 1887); *a,* longitudinal section of rostrum; *b,* cross section of *rostrum cavum. 8, Calliconites dieneri* GEMMELLARO, 1904; *a,* longitudinal section of rostrum; *b,* lateral view of rostrum showing the paired grooves; *c,* cross section of rostrum (new).

as hook-bearing, in contrast to authors such as ENGESER (1990) and DOYLE, DONOVAN, and NIXON (1994). Aulacoceratids are commonly regarded as primitive coleoids, owing to their stratigraphic range and the absence of a proostracum (JELETZKY, 1966). The lack of the latter precludes the development of a free muscular mantle and may have prevented powerful jet swimming in contrast to later coleoids (FUCHS & others, 2016).

The first undisputed Aulacoceratida are from the Upper Permian. The order became widespread from the Lower Triassic (Olenekian) to the upper Lower Jurassic (Toarcian) (Fig. 4). Pre-Permian records, by contrast, are controversial. JELETZKY (1966), ENGESER (1990), and DOYLE (1990) hypothesized that the Aulacoceratida originated during the Upper Devonian. However, all putative Devonian–Carboniferous aulacoceratids are now widely accepted either as belonging to the coleoid order Hematitida (*Hematites* FLOWER & GORDON, 1959, *Bactritimimus* FLOWER & GORDON, 1959, and *Palaeoconus* FLOWER & GORDON, 1959) or considered Coleoidea *incertae sedis* (*Jeletzkya douglassae* JOHNSON & RICHARDSON, 1968; *Mutveiconites* DOGUZHAEVA, 2002) or

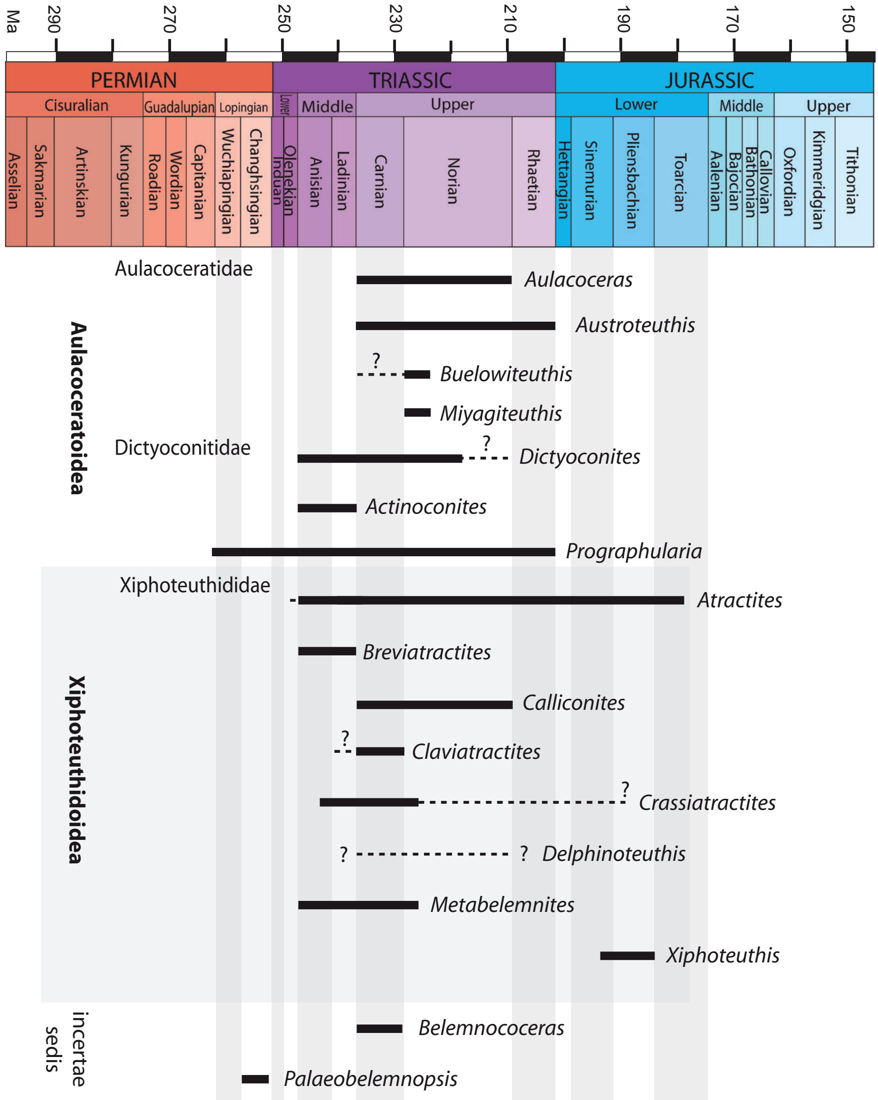

FIG. 4. Stratigraphic distribution of aulacoceratid genera, families, and superfamilies (new).

non-cephalopods (e.g., *Protoaulacoceras longirostris* BANDEL, REITNER, & STÜRMER, 1983) (DOYLE, DONOVAN, & NIXON, 1994; RIEGRAF, JANSSEN, & SCHMITT-RIEGRAF, 1998). There is still uncertainty in the supra-generic assignment of the Permian genus *Palaeobelemnopsis* CHEN IN CHEN & SUN, 1982 and the Triassic genus *Belemnoceras* POPOV, 1964, which are here provisionally regarded as Aulacoceratida *incertae sedis*.

All considered, the order Aulacoceratida is here circumscribed in a more restricted sense than any other previous proposals (e.g., JELETZKY, 1966; DOYLE, 1990; MARIOTTI & PIGNATTI, 1992, 1994, 1996, 1999). In consequence, the Aulacoceratida has become a comparatively well-defined group that originated during the Permian, possibly from the Hematitida, dominated with 15 genera among the coleoids of the Triassic, and became extinct at the end of the Lower Jurassic (Fig. 4).

No consensus has so far been reached concerning the origin as well as the descendants of the Aulacoceratida (e.g., Abel, 1916; Stolley, 1919; Erben, 1964; Jeletzky, 1966; Doyle, Donovan, & Nixon, 1994; Kröger, Vinther, & Fuchs, 2011; Keupp & Fuchs, 2014). The order Aulacoceratida has been treated as a monophyletic group (e.g., Jeletzky, 1966; Engeser & Bandel, 1988; Engeser, 1990; Fuchs, 2006), but the lack of unambiguous autapomorphies and its relation with the Belemnitida, possibly via the Phragmoteuthida (see *Treatise Online*, Part M, Chapter 23C), led others to consider it as a paraphyletic group (Haas, 1989; Doyle, Donovan, & Nixon, 1994; Pignatti & Mariotti, 1996; Keupp & Fuchs, 2014).

Insofar as is known, all aulacoceratids were nektonic but possibly less effective swimmers than later coleoids (Fuchs & others, 2016). They are found typically in moderately deep to deep-marine deposits, being notably rare or absent in shallow-marine settings. Accumulations of oriented aulacoceratid rostra, such as the so-called belemnite battlefields, have been rarely recorded (Miller, 1961). Whereas the known distribution of some genera appears to be rather restricted, more than half of the genera were cosmopolitan in distribution (Doyle, 1990). Generally, they are found in small numbers in Permian to Lower Jurassic cephalopod assemblages, attaining greater abundance only locally, particularly in the Upper Triassic and Lower Jurassic.

Due to their mineralogy and structure, aulacoceratid shells are often crushed, recrystallized, or dissolved during diagenesis and some rostra show regeneration after injuries (Keupp, 2012; Keupp & Fuchs, 2014; see also Keupp, Hoffmann, & Fuchs, 2020, *Treatise Online*, Part M, Chapter 20: Pathology of fossil and extant coleoid shells). Many nominal species are based on inner molds of phragmocones lacking diagnostic characters and fragmentary rostra, and cannot be assigned to any genus with certainty.

Because of their sparse fossil record and the lack of preserved soft parts, our knowledge of the Aulacoceratida and their evolution is still incomplete, and the classification used herein should be viewed as a provisional attempt. Their suprageneric systematics is based on detailed studies on the structure and surface characters of the rostrum, notably those of Dauphin and Cuif (1980), Dauphin (1983), and Bandel (1985). The generic classification of the Aulacoceratida also takes into account other characters of the rostrum and the phragmocone, as already outlined by Steinmann (1910), Bülow (1915), Diener (1917), Naef (1922), Müller-Stoll (1936), Jeletzky (1966), Gustomesov (1976), Engeser (1990), Doyle (1990), Doyle, Donovan, and Nixon (1994), Riegraf (1995), Riegraf, Janssen, and Schmitt-Riegraf (1998), and Mariotti and Pignatti (1992, 1994, 1996, 1999).

Order AULACOCERATIDA Stolley, 1919

[*nom. correct.* Doyle, Donovan, & Nixon, 1994, p. 6, *pro* suborder Aulacoceratidae Stolley, 1919, p. 57] [=Protobelemnoidea Erben, 1964, p. 496; Aulacocerida Jeletzky, 1965, p. 73; Aulacoceratiformes Stolley, 1919, *nom. correct.* Starobogatov, 1983, p. 7; Palaecoleoidea Haas, 1997, p. 64, *partim;* Palaeocoleoidea Haas, 2002, p. 341, *partim*]

Coleoidea possessing long, tubular, and ventrally closed body chamber (living chamber), i.e., true pro-ostracum absent; peristome simple, sinuous, with short to very short, arched dorsal crest and similar, faint ventral crest; crests of peristome separated by shallow, rounded embayments centered on ventrolateral quadrants of phragmocone; *rostrum solidum* (i.e., the post-alveolar part of the rostrum) generally well developed, multilayered, formed of corrugated or concentric layers (lamellae), comprised of aragonite and organic substance; the organic-rich layers (*laminae obscurae*) of the rostrum generally thicker than intervening predominantly calcareous layers (*laminae pellucidae*); rostrum coarser and more loosely constructed than in Belemnitida, lacking epirostrum; surface of the rostrum either smooth or with longitudinal ribs and grooves, striae, granules, and pits; conotheca consisting of three layers, shows growth lines, and may possess longitudinal riblets; phragmocone longiconic, with horizontal or slightly inclined septa and narrow alveolar angle (4°–12°); chambers of the phragmocone generally longer than in Belemnitida (height/diameter ratio from ~0.4 to 0.7); siphuncle thin-walled, marginal or submarginal, ventral; immature to adult septal necks are retrochoanitic to essentially achoanitic, more markedly retrochoanitic in ventral side; septal necks may be prochoanitic in first septum; protoconch spherical or subspherical, sealed by convex closing membrane, preceding closely spaced first septum; caecum and prosiphon apparently absent; occurrence of arm hooks uncertain. *Upper Permian (Wuchiapingian)–Lower Jurassic (Toarcian).*

Superfamily AULACOCERATOIDEA Mojsisovics, 1882

[*nom. transl.* PIGNATTI & MARIOTTI, 1996, p. 42, *ex* Aulacoceratinae MOJSISOVICS, 1882, p. 295]

Adult rostrum with distinctive pattern of corrugated and folded laminae; distinctive ribs and grooves present on rostrum surface; conotheca with longitudinal riblets. *Upper Permian (Wuchiapingian)–Upper Triassic (Rhaetian).*

Family AULACOCERATIDAE Mojsisovics, 1882

[*nom. transl.* BATHER in BLAKE, 1892, table 4, facing p. 288, *ex* Aulacoceratinae MOJSISOVICS, 1882, p. 295] [=Protobelemnitidae PAVLOW in SCHWETZOV, 1913, p. 43, *partim;* Aulacoceratidae NAEF, 1921b, p. 46, *partim*]

Rostrum longitudinally striated, ribbed and grooved, formed of thick lamellae with corrugated, feathered, or septate appearance in cross section, retaining rib-and-groove pattern of conothecal surface throughout growth, cross sections showing intersecting radial lamellae and corrugated concentric lamellae, rostrum traversed by radial lines connecting axis with longitudinal grooves on surface; transversely striated radial splitting surfaces, more marked underlying lateral grooves of rostrum; surface of conotheca longitudinally striated with riblets. *Upper Triassic (Carnian–Rhaetian).*

Aulacoceras HAUER, 1860, p. 115 [*A. *sulcatum;* SD TATE, 1868, p. 9] [=*Asteroconites* TELLER, 1885, p. 360 (type, *A. radiolaris*, M)]. Rostrum large to very large, up to 25 cm long, slender conical, gradually tapering toward an elongated apex, surface with strong, tightly crowded, rounded longitudinal ridges with deep interspaces; ridges at first rounded, separated by small shallow interspaces, gradually becoming more acute during ontogeny, with deeper and broader interspaces; ridges bear faint longitudinal striae without transverse striation; ventrolateral grooves well marked, broad, deep; dorsolateral grooves present; ventral groove deepens anteriorly; convex ventral and dorsal growth lines on anterior rostrum; apical half of rostrum with impressions interpreted as linked to blood vessels; apex elongated and more or less smooth; alveolus penetrating two-thirds or more of the length of rostrum; chamber length to diameter ratio 0.5–0.7; alveolar angle 7°–12°. *Upper Triassic (Carnian–Norian):* Austria, Slovenia, Sicily, Cyprus, Turkey, Tibet, Indonesia (Timor, Rote Island), Canada (British Columbia), USA (Oregon, California).——FIG. 5,*1a–i. A. timorense* WANNER, 1911, Norian, Timor; *a,* MPUR NS20 1514, left lateral view (new); *b–f,* GPIBo Bülow collection; *b,* right lateral view; *c,* dorsal view; *d,* cross section at uppermost alveolar region of the same specimen; *e,* right lateral view of a different specimen; *f,* cross section at uppermost alveolar region of *e; asterisks (d* and *f)* indicate the dorsolateral grooves (Bülow, 1915, pl. 57(1),*1a–c, 2a–b*). Scale bars, 10 mm.

Austroteuthis JELETZKY & ZAPFE, 1967, p. 83 [*A. *kuehni;* OD] [=*Pachysceptron* HAAS, 1909, p. 158, *nom. nud.*]. Rostrum large, cylindro-conical with paired mediodorsal grooves, a mediodorsal ridge, and a single medioventral longitudinal groove; cross section with indistinct feathered arrangement of wavering, fairly coarse radial fibers; lacks regular *Aulacoceras*-like folding and septate appearance of the concentric lamellae; surface of conotheca longitudinally ribbed and with transversal growth lines, devoid of dorsolateral ridges; conotheca with fine, dense longitudinal ribbing; septa with weak lateral and midventral lobes; alveolar angle ~12°; chamber length to diameter ratio ~0.5; alveolus penetrates up to half rostrum; dorsal parts of septal necks achoanitic in the middle growth stages. [*Austroteuthis* differs from *Aulacoceras, Buelowiteuthis,* and *Dictyoconites* in lacking the strong dorsolateral longitudinal ribs on the surface of the conotheca and the corresponding lateral or dorsolateral grooves on the surface of the rostrum, and by the presence of a single medioventral and a double-mediodorsal longitudinal groove. It thus combines characters of the Aulacoceratoidea and the Xiphoteuthidoidea. In spite of its weakly striated rostrum, it is placed in the Aulacoceratidae because of its longitudinally ribbed conotheca, following Jelezky and Zapfe (1967).] *Upper Triassic (Carnian–Rhaetian):* Austria.——Fig. 5,*2a–c*. **A. kuehni,* holotype, middle–upper Rhaetian, Zlambach Formation, Austria, NHMW 708/1967; ventral (*a*), dorsal (*b*), and left lateral (*c*) views; scale bar, 10 mm (Jelezky & Zapfe, 1967, pl. 2,*1a–c*).

Buelowiteuthis Jeletzky, 1965, p. 73 [**Dictyoconites planus* Bülow, 1915, p. 50; OD]. Rostrum large-sized, extremely slender, daggerlike, strongly depressed dorsoventrally; rostrum surface covered with subparallel, regular-spaced longitudinal ribs and grooves; lateral longitudinal depressions and ridges much thinner, higher, and more sharply delimited than in *Dictyoconites;* ridges with sharp edges, not rounded; alveolar angle 8°–12°. *Upper Triassic (?Carnian–lower Norian):* Canada (British Columbia), ?Austria, ?Himalaya, Timor.——Fig. 5,*3a–i*. **B. plana* (Bülow); *a–b,* lower Norian, Pardonet beds, northeastern British Columbia, Canada, GSC 21,164; *a,* ventral view of segment of alveolar part of rostrum; *b,* close-up of the alveolar part of the same specimen (Jeletzky, 1966, pl. 18,*1a–b*); *c–i,* Carnian–Norian, Timor; *c,* lateral view; *d,* ventral view; *e,* dorsal view; *f,* cross section of upper alveolar part; *g,* cross section of lower alveolar part (Bülow, 1915, pl. 60(4),*4a–e*); *h,* ventral view; *i,* cross section near the apex of phragmocone, scale bars, 10 mm (Bülow, 1915, pl. 60(4), *5a–b*).

Miyagiteuthis Niko & Ehiro, 2018, p. 1 [**Dictyoconites nipponicus* Shimizu & Mabuti, 1941, p. 923; OD]. Rostrum large, compressed, cylindro-conical, gradually tapering toward elongated apex, surface with tightly crowded, rounded longitudinal ridges, dorsally with deeper and broader interspaces than ventrally; dorsolateral grooves well marked, broad, deep; alveolus strongly depressed, penetrating less than two-thirds of length of rostrum; chamber length to diameter ratio ~0.6; alveolar angle ~10°. *Upper Triassic (lower Norian):* Japan.——Fig. 5,*4a–e*. **M. nipponica* (Shimizu & Mabuti), lower Norian, Chonomori Formation, Honshu, Japan; *a,* lectotype, longitudinal section of rostrum, IGPS 49600-1; *b,* paralectotype, longitudinal section of rostrum, IGPS 49600-2; *c–d,* paralectotype, IGPS 49600-41, cross section of rostrum cavum (*c*) and cross section of rostrum in the apical region (*d*); *e,* paralectotype, cross section of rostrum cavum showing strongly depressed phragmocone and marginal siphuncle, IGPS 49600-47 (Niko & Ehiro, 2018, fig. 2,*1–2.2,* 2,*5,10,9*). Scale bars, *a–d,* 10 mm; *e,* 5 mm.

Family DICTYOCONITIDAE Gustomesov, 1978

[Dictyoconitidae Gustomesov, 1978, p. 11] [=Protobelemnitidae Pavlow in Schwetzov, 1913, p. 43, *partim;* =Aulacoceratidae Naef, 1921a, p. 534, *partim*]

Rostrum slender and elongated, more or less hastate in outline and profile, compressed in its alveolar part and generally flattened dorsoventrally (depressed) in much of its postalveolar part; rostrum surface either with longitudinal striae, riblets, and impressions interpreted as linked to blood vessels, or smooth, except for its anterior part; dorsal and ventral parts distinctly separated by broad system of dorsal and ventrolateral grooves (lateral groove zone), provided with a longitudinal ridge (asymptotic ridge), which may subdivide the rostrum into two almost symmetrical halves with similar arched dorsal and ventral halves; dorsal half generally equal to or smaller than the ventral one; phragmocone not as deeply penetrating as in Aulacoceratidae; dorsal part of septal necks prochoanitic in the second septum, retrochoanitic in later septa. *Upper Permian (Wuchiapingian)–Upper Triassic (Rhaetian).*

Dictyoconites Mojsisovics, 1902, p. 182 [**D. doylei* Riegraf in Riegraf, Janssen, & Schmitt-Riegraf, 1998, p. 141; *nom. nov. pro Orthoceras reticulatum* Hauer, 1847, p. 258, *non* Phillips, 1836, p. 238, SD Diener, 1915, p. 24, SD Bülow-Trummer, 1920; =*Aulacoceras haueri* Mojsisovics, 1871, invalid (nominal species originally not included) =‘*Dictyoconites striati’* Mojsisovics, 1902, p. 185]. Rostrum hastate, medium- to large-sized, narrow-waisted, more or less dorsoventrally depressed at waist, and compressed to subcircular toward the apex; well-marked ventrolateral grooves characterized by a proper sculpture, dorsolateral grooves with narrow slits directed to median part of the rostrum in apical portion, shifting gradually to flanks toward the alveolar part; ventrolateral grooves shallow, broad, and smooth, or bearing fine longitudinal striation; lateral ridge of grooves narrow, ranging from high and acute to low and rounded in transverse section, may disappear completely in adult specimens; lateral groove zone limited by the ventral section at one side, and the longitudinal ridge on the other, may be narrowed due to expansion of dorsal and ventral portions; rostrum surface strongly striated with numerous longitudinal riblets to fine striae and with impressions interpreted as linked to blood vessels, forming an irregular pattern; sculpture less marked in anterior direction; phragmocone circular in cross section; alveolar angle ~12°; conotheca consisting of three layers, with external one bearing up to 60 or more fine longitudinal riblets, inner one very finely longitudinally striated; dorsal side of conotheca with convex-forward growth lines, crossed by fine longitudinal striation, forming reticulate pattern.

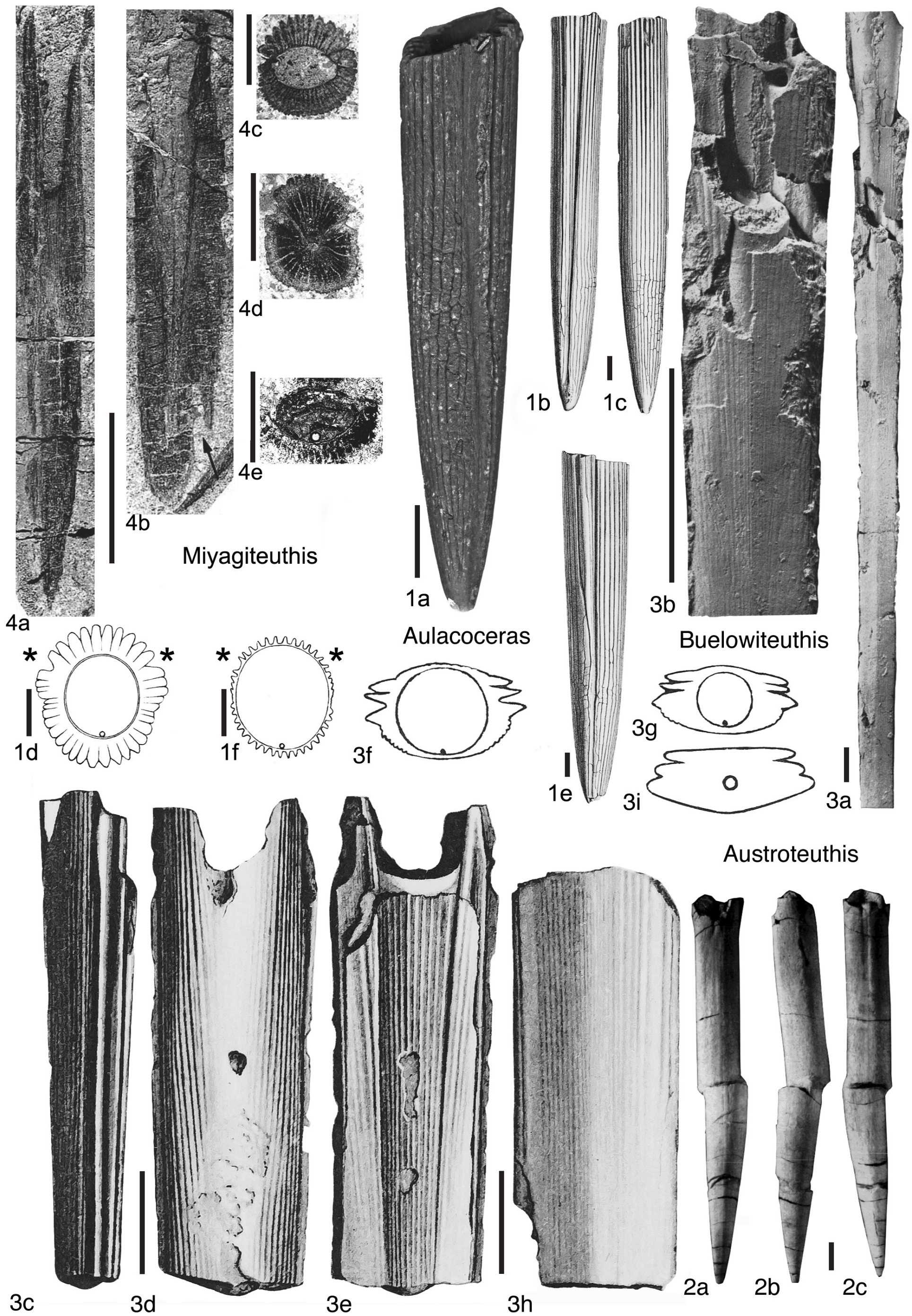

FIG. 5. Aulacoceratidae (p. 6–7)

[*Dictyoconites* differs from *Aulacoceras* in possessing a narrow waist and a pair of well-marked, deep ventral grooves, whereas in *Aulacoceras* the ventral groove is not sharply delimited from the ventral half of the rostrum. The dorsal grooves are much deeper than in *Aulacoceras*. It differs from *Prographularia* chiefly in possessing a stronger dorsoventral depression and more prominent lateral ribs and grooves; the transverse section of the rostrum of *Prographularia* is more rounded, and the ventral side more convex than in *Dictyoconites. Dictyoconites* differs from *Buelowiteuthis* in possessing a hastate rostrum and lacking the characteristic pinnate striae. Doubtful records of *Dictyoconites* from the Permian of Greenland (FISCHER, 1947) and Montana, USA (GORDON, 1966) do not appear to belong in the Aulacoceratida.] *Lower Triassic (upper Olenekian)–Upper Triassic (lower Norian):* Italy (Sicily), Southern Alps, Austria, Romania (Dobrogea), Cyprus, Himalaya, Canada (British Columbia), Mexico (Sonora).——FIG. 6,*1a–d*. **D. doylei* RIEGRAF in RIEGRAF, JANSSEN, & SCHMITT-RIEGRAF, 1998, lower Carnian, Hallstatt Formation, Austria (Styria); *a,* dorsal view; *b,* detail of rostrum surface pattern; *c,* cross section close to the end of phragmocone; *d,* cross section near the waist of the rostrum solidum; scale bars, 10 mm (Mojsisovics, 1902, pl. 14,*4*).

Actinoconites STEINMANN, 1910, p. 115 [**Aulacoceras acus* HAUER, 1892, p. 252; SD RIEGRAF, 1995, p. 19; =‘*Dictyoconites laeves*’ of MOJSISOVICS, 1902, p. 190]. Differs from *Dictyoconites* in possessing weakly sculptured, medium-sized rostrum, with dorsal and ventral grooves and fine striation confined to anterior part of rostrum. *Middle Triassic (Anisian–Ladinian):* Bosnia-Hercegovina (Dinaric Alps).——FIG. 6,*2a–f*. **A. acus* (HAUER), holotype, upper Anisian–lower Ladinian, Han Bulog, Bosnia-Hercegovina; dorsal (*a*), lateral (*b*), and ventral (*c*) views; *d–f,* cross sections of the alveolar region (*d*); near the waist of the rostrum solidum (*e*); and of the rostrum solidum in the apical region (*f*); (Hauer, 1892, pl. 1,*1a–f*). Scale bars, 10 mm.

Prographularia FRECH, 1890, p. 90 [**P. triadica;* M]. Rostrum small- to medium-sized, slender, slightly hastate, subrounded in cross section, with characteristic folding of concentric lamellae resulting in radially septate-like structure in cross section; characteristic splitting surfaces present, strongest of these occur beneath the dorsolateral longitudinal depressions; dorsolateral, longitudinal grooves extending full length of the rostrum, angular in cross section except near apical and alveolar ends, with fine longitudinal riblets all over rostrum surface, resembling those of *Dictyoconites* and *Buelowiteuthis*. *Permian, Lopingian (Wuchiapingian)–Upper Triassic (Rhaetian):* Austria, Greenland, USA (Montana), Canada (British Columbia), Japan, New Zealand.——FIG. 6,*3a–g*. **P. triadica*, middle-upper Rhaetian, Zlambach Formation, Austria; *a–f,* holotype; *a–b*, dorsal, ventral views; *c–d,* enlarged cross sections of rostrum; *e–f,* cross sections of rostrum (*a–f,* Frech, 1890, pl. 21,*17*); *g,* thin section of cross section of rostrum solidum (Dauphin & Cuif, 1980, pl. 4,*3a*). Scale bars, 1 mm.

Superfamily XIPHOTEUTHIDOIDEA Bather in Blake, 1892

[*nom. transl.* PIGNATTI & MARIOTTI, 1996, p. 42, *ex* Xiphoteuthidae BATHER in BLAKE, 1892, table 4, opposite p. 288]

Rostrum with distinctive pattern of concentric growth lines and laminae; rostrum surface devoid of ribs and deep grooves; conotheca lacking longitudinal riblets. *?Lower Triassic (?Olenekian), Middle Triassic (Anisian)–Lower Jurassic (Toarcian)*.

Family XIPHOTEUTHIDIDAE Bather in Blake, 1892

[Xiphoteuthidae BATHER in BLAKE, 1892, table 4, opposite p. 288; *nom. correct.* JELETZKY, 1966, p. 26, *pro* Xiphoteuthidae NAEF, 1921a, p. 534] [=Protobelemnitidae PAVLOW in SCHWETZOV, 1913, p. 43, *partim;* =Aulacoceratidae NAEF, 1921b, p. 46, *partim;* =Xiphoteuthidae NAEF, 1921b, p. 47; =Chitinoteuthididae MÜLLER-STOLL, 1936, *nom. correct.* JELETZKY, 1965, p. 73, *pro* Chitinoteuthidae MÜLLER-STOLL, 1936, p. 199; =Atractitidae JELETZKY, 1965, p. 73, *nom. nud.*]

Rostrum shape variable, slender conical, cylindrical, fusiform or hastate, generally medium-sized to very large, lacking longitudinal grooves, ribs, corrugated concentric growth lines, paired radial lamellae, and splitting surfaces of the Aulacoceratoidea; rostrum comprised of aragonitic and organic layers, typically recrystallized or dissolved; concentric growth lines and radial prismatic structure of rostrum resemble those in Belemnitida, except for their greater coarseness and the considerably thicker *laminae obscurae;* size larger and typically more massive than in Aulacoceratoidea; surface smooth or with weak striae, granules, and pits; rostrum constricted adorally (narrow-waisted) or unconstricted; one or two, generally weak longitudinal grooves on each flank; a median longitudinal depression may occur on the alveolar part; alveolar angle 5°–12°. *Lower?/Middle Triassic (?Olenekian/Anisian)–Lower Jurassic (Toarcian):* chiefly in Alpine Tethyan domain during the Triassic, worldwide during the Early Jurassic.

Atractites Gümbel, 1861, p. 475 [**A. alpinus;* OD; =*Orthoceras liasicus* Gümbel, 1861, p. 475] [=*Orthoceratites* Gesner, 1758, p. 42 (included in a work suppressed under the plenary powers for nomenclatural purposes, ICZN Opinion 230, 1954, p. 233), *non Orthoceratites* Lamarck, 1799, p. 81; =*Mesosceptron* Fucini, 1915, p. 5 (type, *M. neumayeri* Di Stefano in Fucini,1915, p. 5, SD Pignatti & others, 2019); *non Atractilites* Link, 1807, p. 9 (type, *A. belemniticus,* M)]. Rostrum large- to very large-sized, fusiform, hastate to extremely hastate, with circular to elliptical compressed cross section, extremely narrow-waisted near protoconch expanding strongly in middle of its long fusiform postalveolar region; one faint lateral longitudinal groove present on each flank; surface of rostrum smooth or covered by minute and wavering, longitudinal and subtransverse striae; their intersection may result in reticulate, pitted, or granulated pattern; alveolar angle 5°–12°; chamber length to diameter ratio 0.5–0.75, increasing in adult chambers. [Alleged post-Toarcian records are based on isolated belemnite phragmocones with relatively long chambers and small alveolar angle.] ?*Lower/Middle Triassic (?Olenekian/Anisian)–Lower Jurassic (middle Toarcian):* Germany, Austria, Switzerland, Italy, Morocco, Spain (Betic Chain), France, Hungary, Greece, Turkey, Russia (Caucasus), Iran, Nepal, Tibet, Vietnam, Indonesia (Timor, Sula, Moluccas [Seram]), Japan, New Zealand, Canada (Alberta), USA (Nevada, California), Mexico (Sonora), Chile, Peru, Greenland, ?Norway (Svalbard). [Distribution was mainly confined to the Alpine Tethyan domain area during the Triassic; essentially worldwide in the Lower Jurassic.]——Fig. 6,*4a–b*. **A. alpinus,* syntype, Hettangian–?lower Sinemurian, Salzburg, Austria, BSM 1929 XI 548; *a*, outline; *b,* profile; scale bars, 10 mm (new).

Breviatractites Mariotti & Pignatti, 1992, p. 130 [**Atractites pusillus* Hauer, 1887, p. 10; OD]. Rostrum very small- to small-sized, narrow conical to cylindro-conical, circular in cross section, adorally unconstricted; profile similar to outline, symmetrical; flanks of rostrum becoming parallel at rostrum half-length; rostrum surface smooth or irregularly granulated, possibly corrugated with "wrinkles"; phragmocone circular in cross section, penetrating about three-fourths of the rostrum; alveolar angle ~9°; chamber length to diameter ratio ~0.4. *Middle Triassic (Anisian–Ladinian):* Bosnia-Hercegovina and Montenegro (Dinaric Alps), Austria, Germany, Romania (Dobrogea).——Fig. 6,*5a–b*. **B. pusillus* (Hauer), lectotype, upper Anisian–lower Ladinian, Han Bulog, Bosnia-Hercegovina; *a,* dorsal view; *b,* cross section of rostrum cavum; scale bar, 10 mm (Hauer, 1887, pl. 1,*13a–b*).

Calliconites Gemmellaro, 1904, p. 310 [**C. dieneri;* OD]. Rostrum medium-sized, fusiform in outline, compressed, with ventrolateral and dorsolateral longitudinal grooves, elliptical in cross section; surface of well-preserved rostra smooth or finely granulated; phragmocone penetrating one-third to one-half rostrum. [*Calliconites* differs from *Atractites* in the presence of a dorsolateral and a ventrolateral groove on each flank, strong lateral compression, oval cross section, lack of an extremely narrow waist at the base of the alveolus, and much smaller size; it differs from *Metabelemnites* in the much longer, fusiform postalveolar part of its rostrum, its more compressed rostrum, and the much more incised paired lateral grooves.] *Upper Triassic (Carnian–Norian):* Sicily, Timor, Mexico (Sonora), USA (California, Nevada), Canada (?British Columbia).——Fig. 6,*6a–c*. **C. dieneri,* lectotype, upper Carnian–Norian, Sicily; *a–b,* dorsal, lateral views; *c,* cross section of rostrum solidum; scale bar, 10 mm (Gemmellaro, 1904, pl. 30,*23–24,26*).

Claviatractites Mariotti & Pignatti, 1996, p. 45 [**Atractites claviger* Bülow, 1915, p. 67; OD]. Rostrum very large-sized, fusiform to clavate, stout, thick, narrow-waisted; outline fusiform; profile asymmetrically fusiform, more convex ventrally; cross section of alveolar part circular to subcircular; one wide ventral groove, starting near end of the alveolar part of rostrum and extending throughout its length; lateral flanks flattened; cross section of rostrum at mid-length subquadrate, at distal end of rostrum pyriform to ovate; phragmocone slightly compressed, excentric, penetrating about one-third of the rostrum; alveolar angle 9°; chamber length to diameter ratio 0.6. ?*Middle Triassic (Ladinian)–Upper Triassic (Carnian):* Timor, ?Japan.——Fig. 6,*7a–b*. **C. claviger* (Bülow), lectotype, Carnian, Timor, GPIBo Bülow collection 29b; *a–b,* dorsal, ventral views; scale bar, 10 mm (new).

Crassiatractites Mariotti & Pignatti, 1992, p. 127 [**Atractites crassirostris* Hauer, 1887, p. 7; OD]. Rostrum large-sized, robust, thick-waisted, cylindrical to markedly hastate, distally expanding in its middle portion; outline symmetrical, cylindrical to subhastate; profile similar, but asymmetrical; cross section of rostrum circular to subcircular, rarely compressed and subelliptical; apex moderately acute to acute; rostrum surface apparently smooth, granulated or shagreen-like without grooves; maximum thickness of rostrum approximately at level of protoconch; alveolus circular to subcircular in cross section, penetrating one-third to one-half of the rostrum; alveolar angle 9°–12°; chamber length to diameter ratio 0.45–0.65. [*Crassiatractites* differs from *Atractites* in its thick waist, more penetrating phragmocone, lack of grooves and weak lateral compression; it differs from *Breviatractites* in the presence of a distinct, thick waist, its less penetrating phragmocone, and its cylindrical-hastate rostrum.] *Middle Triassic (upper Anisian–lower Ladinian)–Upper Triassic (lower Norian); ?Lower Jurassic (?Pliensbachian):* Dinaric Alps (Bosnia-Hercegovina, Montenegro, Albania), ?Austria, Romania (Dobrogea), Turkey, Oman, Afghanistan, Timor, ?USA (Nevada).——Fig. 6,*8a*. **C. crassirostris* (Hauer), lectotype, upper Anisian–lower Ladinian, Han Bulog, Bosnia-

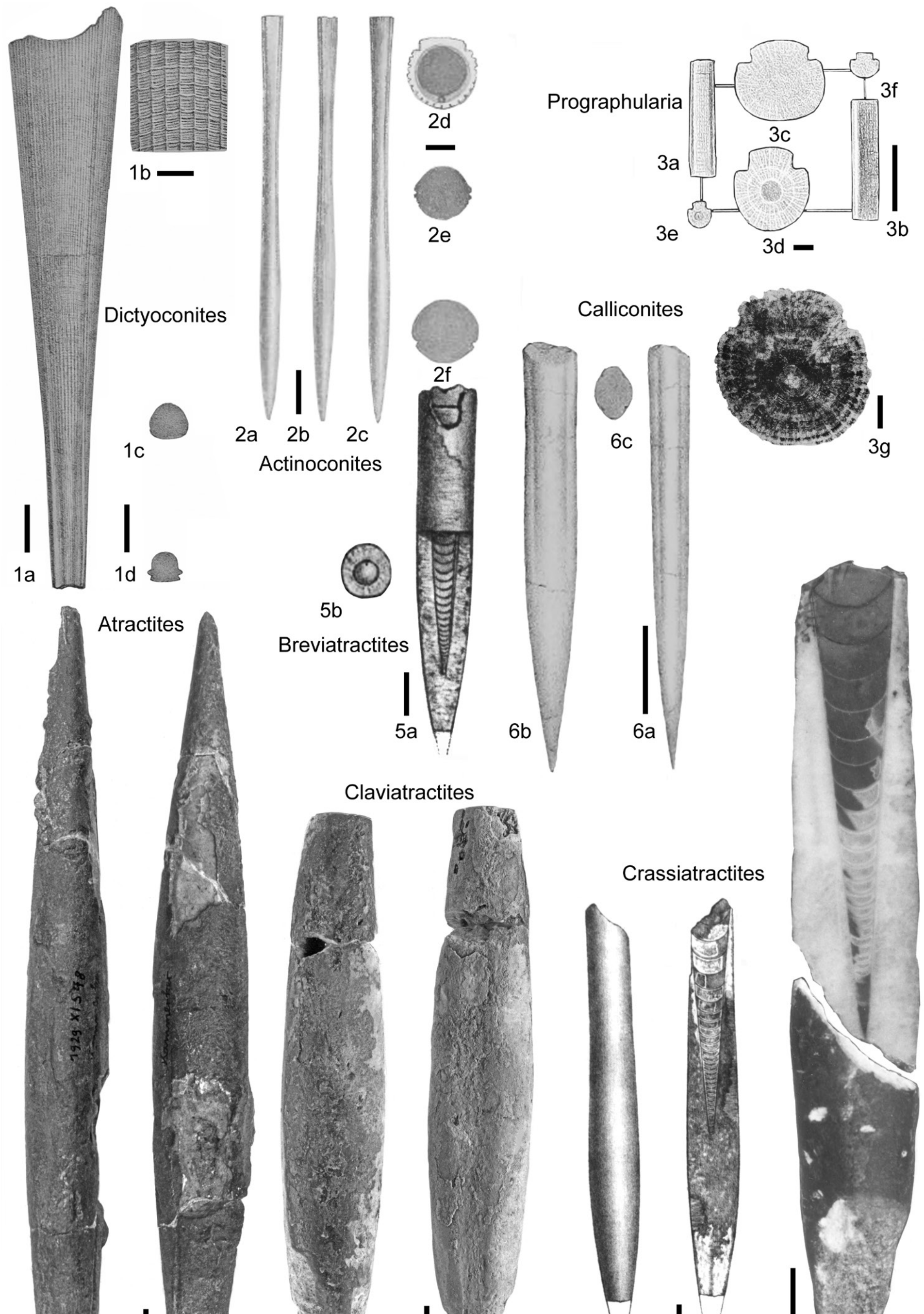

FIG. 6. Dictyoconitidae and Xiphoteuthididae (p. 7–12)

Hercegovina, NHMW 8108, partially sectioned rostrum, scale bar, 10 mm (new).——FIG. 6,*8b–c*. *C. tenuirostris* (HAUER, 1887), holotype, upper Anisian–lower Ladinian, Han Bulog, Bosnia-Hercegovina; *b,* longitudinal section of rostrum; *c,* external view of rostrum; scale bars, 10 mm (Hauer, 1887, pl. 1,*1a–b*). [The doubtful record of the genus from the Lower Jurassic refers to the uncertain generic attribution of *Aulacoceras wittei* MOJSISOVICS, 1871 from the Northern Alps (Austria).]

Delphinoteuthis MARIOTTI & PIGNATTI, 1994, p. 160 [**D. aenigmatica;* OD]. Rostrum very large-sized, narrow-waisted, fusiform, distinctly expanding in its middle portion; outline fusiform, symmetrical; profile asymmetrical, fusiform with almost straight dorsum and convex venter; cross section of rostrum circular in proximal alveolar portion, distally subquadrate approximately at its maximum diameter, pyriform to ovate at its distal end; one faint shallow groove on each flank of rostrum; rostrum surface smooth; phragmocone penetrating about one-third of rostrum; alveolar angle ~10°; longitudinal section of the rostrum with sheathlike laminae, diverging radially outward, starting from an ideal central line. [The description is based on a single specimen, for which the exact stratigraphic level and geographical provenance are unknown. *Delphinoteuthis* differs from *Claviatractites* by its asymmetrical profile and its pyriform cross section at the distal end; it differs from *Atractites* by its profile and the alveolus penetrating deeper into the rostrum.] ?*Triassic (*?*Carnian,* ?*Norian):* Alps, Europe.——FIG. 7,*1a–d*. **D. aenigmatica,* holotype, ?Alpine Triassic, MPUR 4900; *a,* dorsal view of rostrum; *b,* longitudinal section of rostrum; *c,* lateral view of rostrum; *d,* cross section of rostrum solidum at the transverse fracture about one-third of way adorally from the broken-off apical end, showing narrow ventral and broad dorsal sides; scale bar, 10 mm (new).

Metabelemnites FLOWER, 1944, p. 764 [**Atractites philippii* HYATT & SMITH, 1905, p. 205; OD]. Rostrum small- to large-sized, conical, compressed, adorally unconstricted, with mucronate apex, markedly displaced dorsally; phragmocone deeply penetrating, ending close to apex of the rostrum; one faint longitudinal ventrolateral groove on each flank; rostrum smooth except for wavy, subtransverse vascular imprints, ramifying in places; alveolar angle 12°; chamber length to diameter ratio 0.3; septal necks very short, not exceeding one-twentieth of the length of the corresponding chamber. *Middle Triassic (Anisian)–Upper Triassic (Carnian–lower Norian):* Western Cordillera Belt of North America (California, Oregon, and British Columbia), Russia (Caucasus).——FIG. 7,*2a–c*. **M. philippii* (HYATT & SMITH), lower Norian, Pardonet beds, northeast British Columbia, Canada, GSC 21,165; *a–b,* ventral, right lateral views; *c,* cross section; scale bar, 10 mm (Jeletzky, 1966, pl. 18,*4a,d–e*).

Xiphoteuthis HUXLEY, 1864, p. 18 [**Orthocera elongata* DE LA BECHE, 1829, p. 28; M], *non Ommatostrephes* (*Xiphoteuthis*) OWEN, 1881, p. 144 (type, *O.* (*X.*) *ensifer*, M)] [=*Xiphoteuthis* HUXLEY in DAY, 1863, p. 291, *nom. nud.;* =*Chitinoteuthis* MÜLLER-STOLL, 1936, p. 199 (*Chitinoteuthis* MÜLLER in FRENTZEN, 1934, p. 47, *nom. nud.*, *Chitinoteuthis* MÜLLER in BESSLER, 1935, p. 83, *nom. nud.*) (type, *C. decidua;* OD, =*Belemnites macroconus* KURR, 1845, p. 235, =*Orthoceratites liasinus* FRAAS, 1847, p. 218).] Rostrum large-sized, very slender, cylindrical or slightly hastate, adorally constricted, often not preserved; may bear fine longitudinal striation; alveolar angle 4°–8°; chamber length to diameter ratio 0.39–0.84 increasing in adult chambers. [The holotype of *Orthocera elongata* is spurious (MÜLLER-STOLL, 1936), constructed from at least two specimens or more (PHILLIPS, 1980); the specimens generally referred to the genus *Chitinoteuthis* have highly compressed decalcified rostra with a thin film of pyrite and coaly tissue and aragonite dissolution remains.] *Lower Jurassic (upper Sinemurian–Pliensbachian):* UK (England, Dorset), France, southwest Germany, Italy (Sicily).——FIG. 7,*3*. **X. elongata* (DE LA BECHE), lectotype, Pliensbachian, Dorset, UK, BMNH 39852; artificially joined fragments of different rostra, scale bar, 10 mm (new).

AULACOCERATIDA INCERTAE SEDIS

Family UNCERTAIN

Belemnococeras POPOV, 1964, p. 72 [**B. darkense;* OD] [=*Belemnococeras* POPOV in SACHS, 1961, p. 431 (*B. darkense* POPOV in SACHS, OD, *nom. nud.*)]. Rostrum small-sized, moderately elongated, with radial prismatic structure and distinct wavy concentric growth lines; one deep longitudinal dorsolateral groove on each flank, extending throughout rostrum length; rostrum cross section pyriform, with narrower dorsal and expanded ventral part; phragmocone penetrates about one-third of rostrum; alveolus slightly eccentric, shifted ventrally; rostrum surface granulated, with radial prisms forming polygonal pattern. [The rostrum of *Belemnococeras* resembles that of *Metabelemnites,* but its microstructure, as illustrated by DAGYS and NALNIAEVA (1987), appears to be different.] *Upper Triassic (Carnian):* Russia, northeastern Siberia (Kharaulakh Mountains, Yakutia, Kotel'ny Island, New Siberian Islands, Magadan Oblast), Arctic Canada (Axel Heiberg Island).——FIG. 7,*4a–c*. **B. darkense*, upper Carnian, Yakutia, Siberia, Russia, CSGM 88-73; *a–b,* lateral, dorsal views; *c,* cross section of rostrum at the anterior end; scale bar, 10 mm (new; photo by O. Dzyuba).

Family PALAEOBELEMNOPSEIDAE Chen in Chen & Sun, 1982

[*nom. correct.* PIGNATTI & MARIOTTI, 1996, p. 35 *pro* Palaeobelemnopsidae CHEN in CHEN & SUN, 1982, p. 185]

Palaeobelemnopsis CHEN in CHEN & SUN, 1982, p. 185 [**P. sinensis;* OD]. Rostrum very small-sized, fusiform to hastate, slightly compressed in

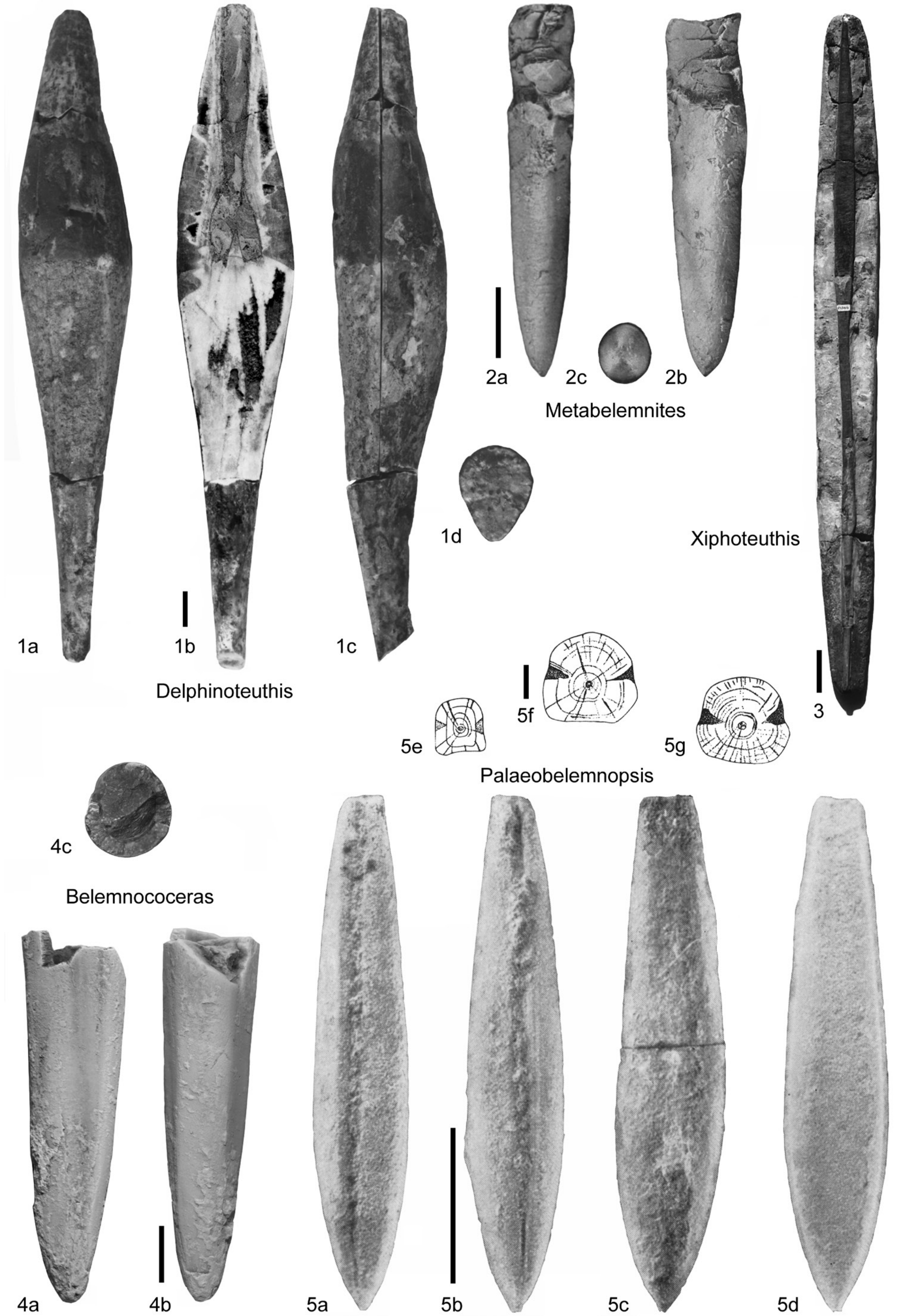

FIG. 7. Xiphoteuthidae, Palaeobelemnopseidae, and Uncertain (p. 12–14).

anterior part, with two deep longitudinal dorsolateral grooves and a shallow ventral groove. *Upper Permian (Changhsingian):* China (Hubei, Hunan, Zhejiang).——FIG. 7,*5a–g*. **P. sinensis,* Changhsingian, Dalong Formation, Hubei province, China, NIGP 67838; *a–d*, holotype, lateral right (*a*), lateral left (*b*), ventral (*c*), dorsal (*d*) views of rostrum, scale bar, 10 mm; *e–g,* paratype, NIGP 67839, cross sections of rostrum solidum (Chen & Sun, 1982, fig. 3, pl. 1,*1–4*). Scale bar, 1 mm.

NOMINA DUBIA

Ausseites FLOWER, 1944, p. 760 [**Aulacoceras ausseeanum* MOJSISOVICS, 1871, p. 50; OD]. Based on a type species established on a syntype of fragmentary, heterogeneous phragmocones from the Alpine Upper Triassic, these phragmocones are circular or compressed in cross section, with long chambers and straight or oblique sutures, and in part bear a thin rostrum cavum that is smooth as in the Xiphoteuthididae. Lacking both the early rostrum cavum and the rostrum solidum, the syntypes cannot be definitely assigned to any of the genera of the Aulacoceratida with smooth rostrum; moreover, a syntype shows oblique sutures and an alveolar angle of at least 18° that are unknown in the Aulacoceratida. [This genus has been established on a type species that its author considered as a "collective or conventional name for a group of phragmocones" ("Sammel- oder Verlegenheitsnamen"; MOJSISOVICS, 1902, p. 193) and later used as a taxonomic bucket or as a collective name (MARIOTTI & PIGNATTI, 1999) for Triassic and Lower Jurassic coleoid phragmocone fragments of uncertain taxonomic affinity.]

Choanoteuthis FISCHER, 1951, p. 385 [**C. mulleri;* OD]. Based on a type species established on a single fragment of phragmocone consisting of three complete chambers within a rostrum cavum from the Norian of Nevada (USA). Rostrum probably large; rostrum surface smooth; alveolar angle of ~11.5°; chamber length to diameter ratio 0.40–0.45; septal necks prochoanitic. [This unsatisfactorily characterized genus is referred to the Aulacoceratida because of its alveolar angle and its chamber length, and to the Xiphoteuthididae because of its smooth rostrum. It has been synonymized with *Atractites* by JELETZKY (1966), but it seems to lack the typical narrow waist of the latter and instead has a much more deeply penetrating phragmocone, as in *Crassiatractites*. Lacking any further details on the rostrum solidum, this genus remains too poorly characterized to be used with any certainty.]

TAXA FORMERLY REFERRED TO AULACOCERATIDA

Family PROTOAULACOCERATIDAE Bandel, Reitner, & Stürmer, 1983

[Family Protoaulacoceratidae BANDEL, REITNER, & STÜRMER, 1983, p. 399]

Protoaulacoceras BANDEL, REITNER, & STÜRMER, 1983, p. 399. [**P. longirostris;* OD]. *Lower Devonian*, Hunsrückschiefer, Eifel, Germany. [The holotype of *Protaulacoceras* has been reassessed as a fish remain (ENGESER, 1990).]

ABBREVIATIONS OF MUSEUM REPOSITORIES

BMNH: The Natural History Museum [formerly British Museum (Natural History)] London, UK

BSM: Bayerische Staatssammlung für Paläontologie und historische Geologie, München (Munich), Germany

CSGM: Central Siberian Geological Museum, Novosibirsk, Russia

GPIBo: Steinmann-Institut für Geologie, Mineralogie und Paläontologie, Rheinische Friedrich-Wilhelms-Universität, Bonn, Germany

GSC: Geological Survey of Canada, Ottawa, Ontario, Canada

IGPS: Institute of Geology and Paleontology, Faculty of Science, Tohoku University Museum, Sendai, Japan.

MPUR: Museo di Paleontologia del Dipartimento di Scienze della Terra dell'Università degli Studi "La Sapienza," [now part of Museo Universitario di Scienze della Terra] Rome, Italy

NHMW: Naturhistorisches Museum, Vienna, Austria

NIGP: Nanjing Institute of Geology and Palaeontology, Nanjing, China

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