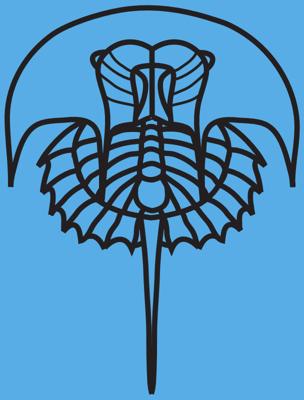

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PART M, VERSION, CHAPTER 23F
SYSTEMATIC DESCRIPTIONS: DECABRACHIA

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INTRODUCTION

Extant Decabrachia is a highly variable group of coleoids, which is nevertheless well typified by its key character, the modification of the fourth ventrolateral arm pair into retractile tentacles (e.g., Naef, 1922; Engeser, 1990; Young & Vecchione, 1996; Haas, 2003). Decabrachian shells can either retain a more or less calcified phragmocone (Spirulida, Sepiida), can be developed as a chitinous gladius (Oegopsida, Myopsida, a few sepiids, Sepiolida, Idiosepiidae), or can entirely be lost (Sepiadariidae).

In more than 200 years of intensive research, a remarkable number of names has been accumulated for the crown group of the ten-armed cephalopods (see Donovan & Fuchs, 2012). Decapoda Leach, 1817 was in use for a long time but had to be discontinued because the name was preoccupied by the ten-armed crustaceans (Boettger, 1952, Hoffmann, 2015). A comparison of most recent classifications shows that only two names have prevailed up to the present, Decabrachia Haeckel, 1866 and Decapodiformes Young, Vecchione, & Donovan 1998. Originally, and in the sense of most present authorities, both groupings include the same recent orders, namely the Spirulida, Sepiida, Oegopsida, Myopsida, and Sepiolida. The main difference refers to the inclusion or exclusion of likewise ten-armed belemnoids. In his famous phylogenetic tree, Haeckel (1866) included the Belemnitida within his Decabrachia (belemnoid rootstock theory), while Young, Vecchione, and Donovan (1998) excluded this extinct group from their 'Decapodiformes'. The intentional exclusion of belemnoid coleoids is rooted in a concept introduced by Haas (1997), who distinguished between sucker-bearing neocoleoids and hook-bearing paleocoleoids (belemnoids). However, paleontological support for this sister-group relationship has been considered to be weak (e.g., Boletzky, 1992; Fuchs, Boletzky, & Tischlinger, 2010, Fuchs, Hoffmann, & Klug, 2021). Since most recent approaches have found support for the phylogenetic origin of the decabrachian crown group within a belemnoid subgroup (Fuchs & others, 2013, 2015; Fuchs, 2019a; Sutton, Perales-Raya, & Gilbert, 2015; Klug & others, 2016; Tanner & others, 2017; Hoffmann & others, 2022), the more neutral term Decabrachia *sensu* Haeckel (1866) is herein preferred, which is in accordance with the terminologies used by Haas (1997) or Doyle, Donovan, and Nixon, 1994.

In contrast to the relatively consistent higher-level system of the Octobrachia (see Fuchs, 2020), the supraordinal system of recent Decabrachia is highly controversial. The debate mainly focuses on the question whether the groupings Sepioidea *sensu* Naef, 1916 (Camerophora *sensu* Khromov, 1990; originally including Sepiida, Spirulida, and Sepiolida) and/or Teuthoidea *sensu* Naef, 1916 (Incamerophora *sensu* Khromov, 1990; including the Myopsida and Oegopsida) represent natural units. With only a few exceptions (e.g., Berthold & Engeser, 1987; Haas, 1997, 2003), most

Fuchs, Dirk. 2023. Part M, Coleoidea. Chapter 23F: Systematic descriptions: Decabrachia. Treatise Online 171: 1–41, 16 fig.

morphology-based classifications followed this distinction between primary phragmocone- and gladius-bearing decabrachians (e.g., Naef, 1916, 1921, 1921–1923; Voss, 1964; Jeletzky, 1966; Fioroni, 1981; Nesis, 1987; Clarke, 1988). Many modern molecular studies, however, have found no support for the monophyly of either the Sepioidea or the Teuthoidea (e.g., Carlini, Reece, & Graves, 2000; Lindgren, Giribet, & Nishiguchi, 2004; Bonnaud, Pichon, & Boucher-Rodoni, 2005; Strugnell & others, 2005; Strugnell & Nishiguchi, 2007; Lindgren, 2010; Tanner & others, 2017; Uribe & Zardoya, 2017; Anderson & Lindgren, 2021). The validity of the Sepioidea and/or the Teuthoidea particularly involves the real position of loliginids and spirulids. Both groups appear to be morphologically and genetically transitional between Sepioidea and Oegopsida (Young, Vecchione, & Donovan, 1998, p. 410; Lindgren, Giribet, & Nishiguchi, 2004, p. 472; Strugnell & others, 2005, p. 438; Strugnell & Nishiguchi, 2007, p. 408; Strugnell, Lindgren, & Allcock, 2009, p. 244; Lindgren & others, 2012; Anderson & Lindgren, 2021).

By the end of the twentieth century, the systematics of fossil Decabrachia was impacted by the exclusion of Mesozoic gladius-bearing coleoids (fossil teuthids). Their reassignment to the Octobrachia by Bandel and Leich (1986) and Engeser (1988) was originally based mainly on the general lack of a fifth arm pair, but recently the reassignment received further support from the presence of more soft part features. Additional arguments against decabrachian affinities of Mesozoic gladius-bearing coleoids are discussed by Fuchs (2016) and Donovan and Fuchs (2016).

Thanks to numerous new Late Cretaceous and Cenozoic discoveries, we can, on the other hand, register remarkable progress in understanding the evolutionary level of early Spirulida and Sepiida (e.g., Meyer, 1993; Weaver, Dockerty, & Ciampaglio, 2010, Fuchs & others, 2012, 2013; Košťák & others, 2013, 2017, 2021; Košťák, Jagt, & Schlögl, 2018). Despite this paleontological progress, we are still far from resolving the unstable relationships within the Decabrachia (compare Haas, 2003; Kröger, Vinther, & Fuchs, 2011; Fuchs & others, 2013).

Fossil crown decabrachians are represented by the orders Spirulida, Sepiida, Sepiolida, Oegopsida, and Myopsida (see Fig. 1). The extinct orders Belemnitida and Diplobelida are considered separately in an article in preparation and Fuchs (2019b). Thirty-one fossil genera of crown decabrachians are arranged in nine extinct and two extant families (five spirulid families, two sepiid, four of uncertain affinities). The recent family Spirulidae is currently monotypic, whereas the Sepiidae also include the extinct genera *Archaeosepia* and *Notosepia*. Fossil cuttlebones assigned to *Sepia* appeared during the Miocene, while the first planispiral shells of *Spirula* were found in Pleistocene deposits. The Eocene remains of *Belosepiella* are assumed to represent the only sepiolid remains. Loliginidae and oegopsid Onychoteuthidae are finally represented by unnamed fossils.

The fossil record of the Decabrachia is clearly dominated by Cenozoic forms. They are most abundant in localities in the Paris and Vienna basin as well as the London Clay. Their oldest unambiguous members belong to Late Cretaceous groenlandibelid spirulids and belosaepiid sepiids. Significantly older taxa originally ascribed to decabrachian subgroups are currently under discussion, as explored herein.

Ideas about the phylogenetic origin of the Decabrachia are surprisingly very rare. Naef (1922) had integrated all known belemnoids within the Decabrachia (his Decapoda) by that time and assumed—according to his phylogenetic scheme (p. 303)—the crown-group to be paraphyletic. He therefore followed the view of Voltz (1830, p. 23), who first introduced the idea of a belemnoid root stock. In contrast to Naef (1922), Jeletzky (1966) and several subsequent workers such as Doyle, Donovan,

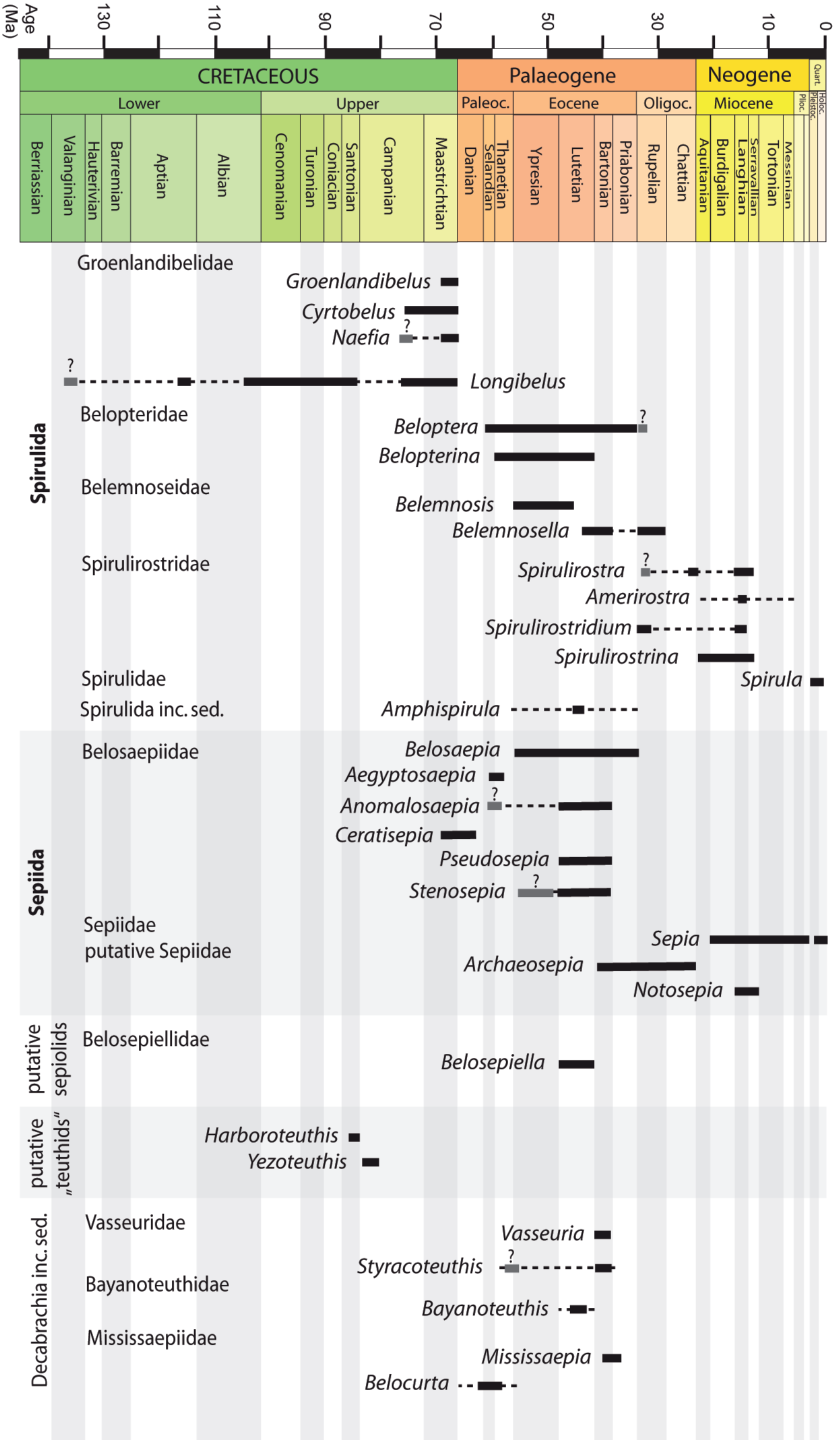

FIG. 1. Stratigraphic distribution of Decabrachia (*sensu stricto*).

and Nixon (1994), Young, Vecchione, and Donovan (1998), and Haas (2002) excluded belemnoids. Jeletzky (1966), Donovan (1977), and Doyle, Donovan, and Nixon (1994) considered Phragmoteuthida to be the direct ancestors of Decabrachia (and Octobrachia) (see Fuchs & Donovan, 2018; Clarke & Hart, 2018). More recent works have been influenced by the introduction of Late Carboniferous *Shimanskya,* which was determined to be a spirulid by Doguzhaeva, Mapes, and Mutvei (1999). Fuchs (2006) for the time being accepted the existence of Carboniferous decabrachians and excluded belemnoids as potential precursors. The assumption of Late Carboniferous spirulids implies that Decabrachia diverged from Early Carboniferous bactritoid-like coleoids through retention of protoconch characteristics (e.g., Jeletzky, 1966, p. 82). Later, Fuchs and others (2012, 2013) and Fuchs (2019a) questioned this presumed homology and rejected a Paleozoic origin of the Decabrachia. In doing so, Fuchs (2019a) agreed with Meyer (1993) and Hewitt and Jagt (1999), who stated a close phylogenetic relationship between diplobelid belemnoids and crown group decabrachians.

A Triassic origin of the Decabrachia within a phragmoteuthid subgroup, as Jeletzky (1966), Donovan (1977) and Doyle, Donovan, and Nixon (1994) suggested, is therefore conceivable only provided that Belemnitida and Diplobelida are regarded as stem decabrachians (Sutton, Perales-Raya, & Gilbert, 2015; Klug & others, 2016; Hoffmann & others, 2022). According to a hypothesis of Arkhipkin, Bizikov, and Fuchs (2012), teuthid squids evolved directly from true belemnites. If spirulids and sepiids derived from diplobelids (Sepioidea concept), while myopsids and oegopsids (Teuthida concept) evolved from belemnitids, the crown group would be, as Naef (1922) assumed, paraphyletic.

To conclude, the majority of recent phylogenetic studies support a Mesozoic origin of crown decabrachians within diplobelid and/or belemnitid belemnoids and, thus, the extended Decabrachia concept, similar to the proposal of Haeckel (1866) and Naef (1922). Alternative ideas on a palaeozoic origin still bear a large set of phylogenetic conflicts (e.g., Fuchs, 2021). As a result of this, the orders Belemnitida and Diplobelida are here arranged within the superorder Decabrachia. (Their systematic information can be found in other Treatise Online Part M chapters, as identified below).

Superorder DECABRACHIA Haeckel, 1866

[*nom. transl.* Doyle, Donovan, & Nixon, 1994, p. 6, *ex* order Decabrachia Haeckel, 1866, pl. 6] [=Decapoda Leach, 1817, p. 137; =Decacera Blainville, 1825, p. 366; =Decolenae Haeckel, 1896, p. 593; =Decembrachiata Winckworth, 1932, p. 248; =Decabrachia Boettger, 1952, p. 290; =Decapodiformes Young, Vecchione, & Donovan, 1998, p. 405; =Decabrachiomorpha Haas, 2002, p. 341]

Coleoids with five arm pairs; shell calcareous phragmocone; chamber length variable; conotheca with or without layer of tabular nacre; mediodorsal attachment scar narrow stripe-like or wide rectangular; proostracum present, one quarter or less of its phragmocone circumference; guard-like sheath aragonitic; rostrum proper where present calcitic; protoconch complex variable. [Diagnosis *sensu lato.*] *Lower Triassic* (*Olenekian*)*–Holocene.*

Order BELEMNITIDA Haeckel, 1866

See Fuchs & others, *Treatise Online,* Part M, Chapter 23D, Systematic Descriptions: Belemnitida.

Order DIPLOBELIDA Jeletzky, 1965

See Fuchs, 2019b, *Treatise Online,* Part M, Chapter 23E, Systematic Descriptions: Diplobelida.

CROWN DECABRACHIA

Coleoids with five arm pairs, arm pair 4 (ventrolateral) modified into retractile tentacles; shell a calcareous phragmocone, chitinous gladius, or lost; phragmocone-bearing forms: chamber length variable;

conotheca without layer of tabular nacre; mediodorsal attachment scar rectangular, shorter than chamber length; siphuncle submarginal; proostracum where present narrow, rodlike, one-sixteenth of its phragmocone circumference; guard-like sheath aragonitic; ?rostrum proper absent. [Diagnosis *sensu stricto.*] *?Lower Cretaceous* (*?Valanginian, Aptian*), *Upper Cretaceous* (*Campanian*)*–Holocene.*

SPIRULIDA

Introduction

The extant Ram's Horn squid *Spirula* represents—similar to the genus *Nautilus*—the last survivor of a formerly very diverse group of cephalopods, the Spirulida. The small-sized spirulids are characterized mainly by the retention of a calcareous phragmocone, which underwent—unlike the sepiid cuttlebone—comparatively little evolutionary transformations. The planispiral *Spirula* shell is therefore an essential source for comparative analyses between fossil and Recent morphologies of the Cephalopoda (e.g., APPELLÖF, 1893; NAEF, 1922; BANDEL & BOLETZKY, 1979; FUCHS, 2019a, HOFFMANN & others, 2021). Stranded shells of this mesopelagic cephalopod can be collected worldwide from subtropical beaches.

Detailed studies of fossil spirulid shells began during the first half of the nineteenth century with the works about the Eocene of France and the UK (BLAINVILLE, 1825; SOWERBY, 1829; FERRUSSAC & D'ORBIGNY, 1835–1848). In the following years, the number of Cenozoic taxa recorded from central Europe continuously increased. The first fossil spirulids outside Europe were found by MEYER and ALDRICH (1886) from the Eocene of North America. Maastrichtian deposits in Chile and Greenland yielded the first Cretaceous spirulids (WETZEL, 1930; BIRKELUND, 1956). The last comprehensive revision of fossil Spirulida was done by NAEF (1922). Most recent works consider systematically, stratigraphically, and/or biogeographically restricted aspects of the Spirulida (e.g., JELETZKY, 1969; WEAVER, DOCKERTY, & CIAMPAGLIO, 2010; FUCHS & others, 2012; 2013; FUCHS & LUKENEDER, 2014; FUCHS & KOŠŤÁK, 2015).

The evolutionary trend of the spirulid lineage is defined by the reduction of the proostracum and a gradually increased shell coiling. The first undoubted spirulids appeared during the Late Cretaceous (late Campanian) with the family Groenlandibelidae (JELETZKY, 1966; FUCHS & others, 2012; 2013; FUCHS, 2019a; FUCHS & others, 2020). These early forms possessed an orthoconic phragmocone with a conspicuously narrow, rodlike proostracum and a thin sheath enveloping the phragmocone. Other key characters, by which groenlandibelid phragmocones can be delimited from belemnoids, are the absence of tabular nacre in the conotheca, a siphuncle that enters the lumen of the protoconch, and the presence of rectangular mediodorsal attachment scars. FUCHS and others (2013) suggested that groenlandibelids derived from the Diplobelida via Aptian–Maastrichtian *Longibelus,* because it portrays a mosaic of characters intermediate between diplobelid belemnoids and the Groenlandibelidae. Evidence of a significantly reduced layer of nacre in the conotheca of *Longibelus* particularly challenges the assumed existence of Carboniferous spirulids that seemingly lacked a nacreous layer (DOGUZHAEVA, MAPES, & MUTVEI, 1999, 2010, MUTVEI, MAPES, & DOGUZHAEVA, 2012). The idea of Carboniferous spirulids is also rooted in the fact that recent *Spirula* possess a so-called caecum, the initial segment of the siphuncular tube (NAEF, 1922; JELETZKY, 1966, p. 82; FUCHS, 2019a). As in bactritoids and ammonoids, the caecum represents the blind end of the siphuncle that enters the lumen of the protoconch. It therefore seems obvious that spirulids inherited their caecum directly from their ectocochleate ancestors, particularly in the light of a fundamentally different protoconch architecture in belemnoids. However, HEWITT and JAGT (1999), FUCHS and others (2012, 2013), and FUCHS (2019a) argued for a convergent evolution of the caecum, owing to significant differences between the spirulid and the bactritoid/ammonoid type of protoconch.

Apart from the endogastric shell coiling that involves only the ontogenetically youngest chambers, Cenozoic spirulids are generally typified by the total loss of a proostracum (please note that a proostracum as Naef (1922) indicated in his figures could not be confirmed) and by the development of a thickened, lamellar sheath. The thickening of the sheath is, by contrast to the regular lamination of the belemnitid rostrum proper, irregular and therefore remarkably variable, forming a complex arrangement of apical, lateral, and ventral outgrows (expansions, projections) or swellings. The post-alveolar part of the sheath can be spine- or club-like elongated (see Fig. 3). Lateral outgrows can be bulge- or wing-like. The ventral side is keel- or callus-like or significantly reduced (medioventral depression of Jeletzky, 1966). In taxa with a distinct medioventral depression, the dorsal sheath appears to be elongated, which led many authors to misinterpret this dorsal projection as a proostracum. In *Spirula,* remains of the sheath are commonly known as the outer plate, the outer reticulated shell layer that forms the so-called ventral ridge. Except for unpaired attachment scars on the mediodorsal inner surface of each chamber, we have no information on the soft tissue organization of fossil Spirulida.

In contrast to the vertical orientation observed in Recent *Spirula,* proostracum-bearing groenlandibelids as well as their Cenozoic descendants most probably achieved a horizontal swimming position (Monks & Wells, 2000). The bulk of Cenozoic spirulids have been recorded from shallow water deposits (northwestern Atlantic Ocean, the Pre-Mediterranean Sea—Paratethys, and the Gulf of Mexico region. Since a post-mortem drift of these solid shells is unlikely, Cenozoic spirulids probably roamed neritic waters indicating that the migration of *Spirula* to oceanic waters occurred comparatively late in the evolution of the Spirulida (Hoffmann & others, 2021).

Altogether, fossil spirulids are organized into five families (Groenlandibelidae, Belopteridae, Belemnoseidae, Spirulirostridae, and Spirulidae) and 14 genera. Their stratigraphic occurrences are illustrated in Fig. 1.

Order SPIRULIDA Haeckel, 1866

[*nom. transl.* Pompeckj, 1912, p. 296, *ex* suborder Spirulida Haeckel, 1866, pl. 6, *non* Spirularia Rafinesque, 1815, p. 140] [=Spiruloidea Pompeckj, 1912, p. 296; =Spiruloidea Stolley, 1919, p. 58; =Spiruliformes Starobogatov, 1983; =Spirulina Nesis, 1982]

Phragmocone ortho- to longiconic, slightly cyrtoconic, or gyroconic with an apical angle of 13°–20°; chamber length variable; coiling endogastric; dorsal sutures straight or with weak lobe; ventral sutures with weak lobes; septa not or only slightly inclined, composed of lamello-fibrillar nacre, mural flap present; ventral septal necks retrochoanitic, dorsal septal necks variable; siphuncle submarginal or marginal; mediodorsal attachment scars rectangular; conotheca generally without layer of tabular nacre (earliest forms possibly with significantly reduced layer of nacre); sheath thin, investment-like, uni- or multilamellar in Cenozoic forms with complex swellings and projections; rostrum proper absent; proostracum narrow or absent; protoconch subspherical with caecum and prosipho. *Upper Cretaceous* (*Campanian*)*–Holocene.*

Family GROENLANDIBELIDAE Jeletzky, 1966

[Groenlandibelidae Jeletzky, 1966, p. 90]

Phragmocones ortho- to longiconic or slightly cyrtoconic with an apical angle of 13–20°; ratio chamber length-to-diameter 0·20–0·50; dorsal sutures straight or with weak lobe; ventral sutures with weak lobes; septa not or only slightly inclined, mural flap present; ventral septal necks retrochoanitic, dorsal septal necks variable; siphuncle submarginal; mediodorsal attachment scars rectangular; conotheca without or a significantly reduced layer of tabular nacre; sheath thin, investment-like, apically cone-like thickened, unilamellar; rostrum proper absent; proostracum width narrow, rodlike, less than one-sixteenth of the phragmocone circumference, proostracum length-to-phragmocone length ratio unknown; protoconch subspherical with caecum and prosipho. *Upper Cretaceous* (*Campanian–Maastrichtian*): Greenland, Chile, Canada.

Groenlandibelus Jeletzky, 1966, p. 90 [**Belemnoteuthis rosenkrantzi* Birkelund, 1956; M]. Phragmocone longiconic with an apical angle of 13°–14°; ratio chamber length-to-diameter 0.40–0.46; suture lines almost straight; septa not inclined; siphuncle submarginal; conothecal ultrastructure still unknown; sheath apically thickened and high-conically elongated, adorally thin, investment-like; proostracum very narrow, rodlike, less than one-sixteenth of the phragmocone circumference; protoconch subspherical. *Upper Cretaceous* (*upper Maastrichtian*): Greenland.——Fig. 2,*1a–b*. **Gr. rosenkrantzi* (Birkelund), holotype, MMK 7758, upper Maastrichtian, Agatdalen valley, western Greenland; phragmocone in lateral (*a*) and dorsal (*b*) views; scale bar 10 mm (Fuchs & others, 2012, fig. 1A).

Cyrtobelus Fuchs, Keupp, Trask, & Tanabe, 2012, p. 289 [**C. birkelundae;* OD]. Phragmocone slightly cyrtoconic with an apical angle of 17°–20°; ratio chamber length-to-diameter 0.27–0.33; sutures lines with weakly developed ventral and dorsal lobes; septa slightly inclined; siphuncle submarginal; dorsal attachments scars rectangular; conotheca without tabular nacre; sheath thin and investment-like, adapically on top of the protoconch bulge-like thickened; proostracum very narrow, rodlike; protoconch spherical with long caecum and short prosipho, protoconch conotheca continues into adult stages without interruption. *Upper Cretaceous* (*upper Campanian–upper Maastrichtian*): Canada, Greenland.——Fig. 2,*2a–b*. **C. birkelundae,* cast of paratype, MMK 13001, upper Maastrichtian, Agatdalen valley, western Greenland; phragmocone in lateral (*a*) and dorsal (*b*) views; scale bar 10 mm (new).

Naefia Wetzel, 1930, p. 92 [**N. neogaeia;* M]. Phragmocone orthoconic with an apical angle of 13-19°; ratio chamber length-to-diameter 0.26–0.37; suture lines almost straight; septa not inclined; ventral part of septal necks short retrochoanitic, dorsal parts still unknown; siphuncle submarginal; dorsal attachment scars located apertural, short and rectangular; tabular nacre in the conotheca unknown; sheath thin investment-like; proostracum very narrow, rodlike, less than one-sixteenth of the phragmocone circumference; protoconch poorly known (?spirulid-like with caecum). *Upper Cretaceous* (*?Campanian–Maastrichtian*): Chile, ?Antarctica, USA (?California).——Fig. 2,*3a–b*. **N. neogaiea,* Q/3509, upper Maastrichtian, Quiriquina Formation, Chile; phragmocone in lateral (*a*) and dorsal (*b*) views; scale bar 1 mm (new).

PUTATIVE GROENLANDIBELIDAE

Longibelus Fuchs, Iba, Ifrim, Nishimura, Kennedy, Keupp, Stinnesbeck, & Tanabe. 2013, p. 1090 [**Naefia matsumotoi* Hirano, Obata, & Ukishima, 1991; OD] [=*Naefia* Wetzel, 1930, p. 92 (type, *N. neogaeia,* M, *partim*]. Phragmocone longiconic with an apical angle of 10–13°; ratio chamber length-to-diameter 0.37–0.50; dorsal sutures lines almost straight; ventral sutures with distinct ventral lobe; septa not inclined; mural flap short; dorsal part of septal necks achoanitic or prochoanitic; siphuncle marginal; dorsal attachments scars narrow stripe-like; conotheca with a very thin nacreous layer, restricted to the ventral side; sheath thin and investment-like with a dorsal bipartite keel; rostrum proper absent; proostracum width encompass one-eighth of the phragmocone circumference; protoconch still unknown. *Lower Cretaceous* (*?Valanginian, upper Aptian*)*–Upper Cretaceous* (*upper Maastrichtian*): Russia, South Africa, southern India, Japan, Chile, Mexico, USA (Alaska), ?Hungary.——Fig. 2,*4a–c*. **L. matsumotoi* (Hirano, Obata, & Ukishima), BSPG MB-723, Santonian, Harborogawa Formation, Hokkaido, Japan; *a*, phragmocone in lateral view, scale bar 10 mm; *b,* three chambers in dorsal view; *c,* reconstruction of the proostracum (dotted line: proostracum width in Groenlandibelidae *sensu stricto*); (a–c, new).

Family BELOPTERIDAE Fischer,1887

[Belopteridae Fischer, 1887, p. 358, *non* Belopteridae Owen, 1856, p. 4] [=Belopteridae Naef, 1921, p. 536; =Belopterinae Avnimelich, 1958, p. 64, *partim;* =Belemnosisidae Avnimelich, 1958, p. 63, *partim;* =Belopteriidae Doyle, Donovan, & Nixon, 1994, p. 6]

Phragmocone slightly cyrtoconic, curvature affects only the first two to four chambers, chamber length variable; septa not inclined; ventral suture distinctly lobate; neck lobe distinct; siphuncle marginal; proostracum absent; conotheca without tabular nacre; sheath with complex extensions, medioventral depression absent, post-alveolar part long, club-like, thickened, and oriented towards the venter, adorally investment-like with ventral ridge. *Palaeocene* (*Selandian*)*–Eocene* (*Priabonian*): Europe.

Beloptera Blainville, 1825, p. 622 [**B. belemnoidea* M] [=*Belopterella* Naef, 1921, p. 536 (type, *Belopterella cylindrica* Koenen, 1885, M]. Chamber length-to-diameter ratio <0.2, except earliest (post-embryonic–juvenile) chambers; post-alveolar sheath oriented towards venter, length of club variable, lateral extensions well developed, winglike, oriented towards venter, ventral ridge moderately developed. *Paleocene* (*Selandian*)*–Eocene* (*?lower Oligocene*):

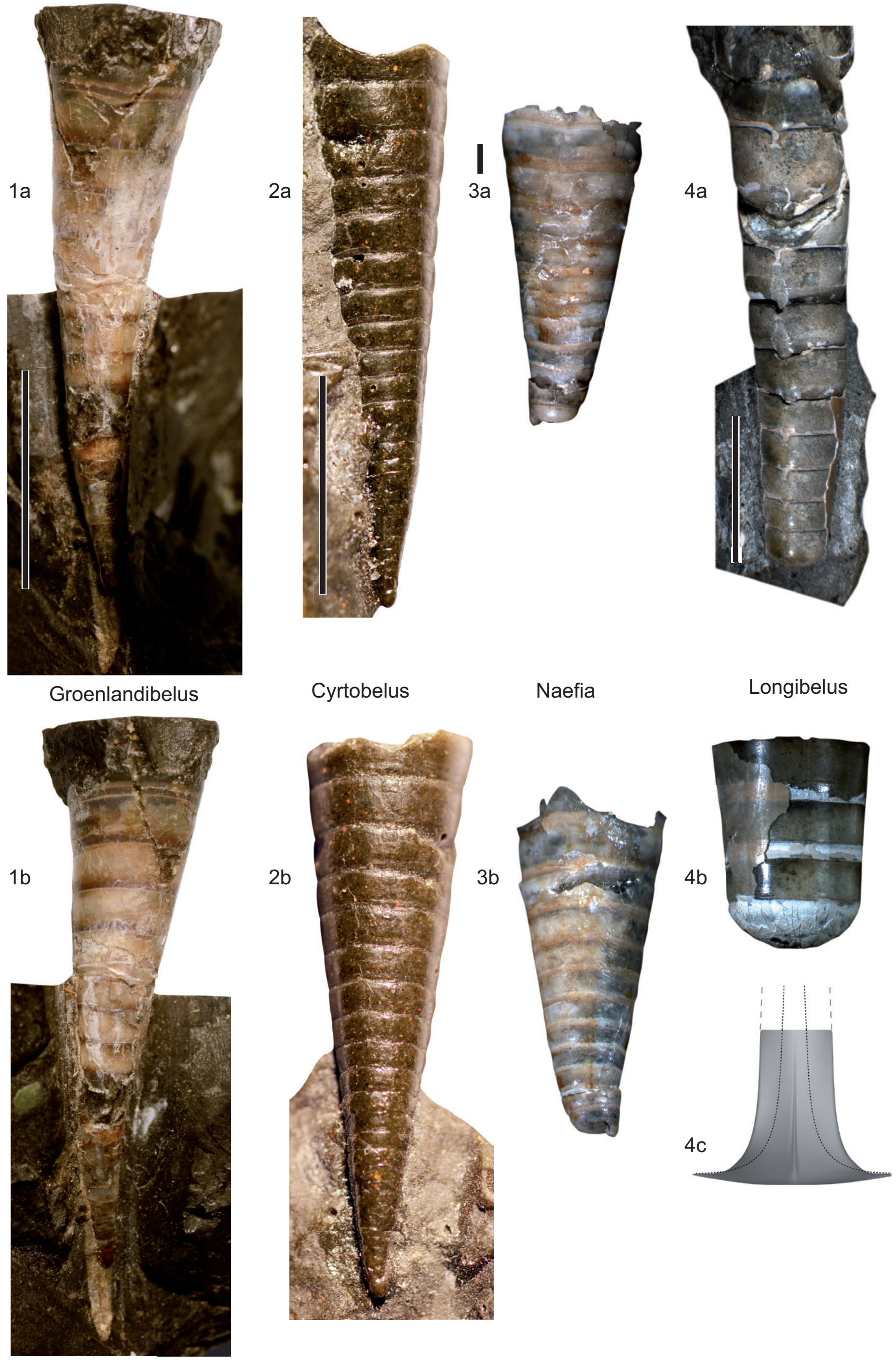

FIG. 2. Groenlandibelidae (p. 7).

France, Belgium, UK (England), northern Germany, Denmark, Ukraine, ?Italy.——Fig. 3,*1a–e. B. curta,* Cossmann, 1896, MNHN J03303, upper Eocene (Bartonian), France; *a,* sheath in ventral view; *b,* reconstruction in ventral view; *c,* sheath in lateral view, scale bar 10 mm; *d,* reconstruction in lateral view; *e,* reconstruction of cross-section (*a–e,* new).

Belopterina Munier-Chalmas, 1872, p. 531 [**Beloptera levesquei* d'Orbigny, 1845, p. 307; OD] [=*Belopteridium* Naef, 1922, p. 54 (type, *B. puerilis*, M)]. Chamber length-to-diameter ratio <0.2; sheath without or poorly developed lateral extensions, apical thickening short or long, ventral ridge pronounced. *Paleocene* (*Thanetian*)*–Eocene* (*Lutetian*): Belgium, Austria, France, UK (England).——Fig. 3,*2a–e.* **B. levesquei* (d'Orbigny), MNHN R05666, lower Eocene (Ypresian), France; *a,* sheath in ventral view; *b,* reconstruction in ventral view; *c,* sheath in lateral view, scale bar 10 mm; *d,* reconstruction in lateral view; *e,* reconstruction of cross-section.——Fig. 3,*3f–i. B. fabrezanensis* Doncieux, 1908, lower Eocene, France; *f,* sheath in ventral view; *g,* reconstruction in ventral view; *h,* sheath in lateral view, scale bar 10 mm; *i,* reconstruction in lateral view; (*a–d,* new).

Family BELEMNOSEIDAE
Wiltshire, 1869

[*nom. corr.* Jeletzky, 1966, p. 106, *pro* Belemnosidae Wiltshire, 1869, p. 33] [=Belemnosidae Naef, 1921, p. 536; =Belemnosisidae Avnimelich, 1958, p. 63, *partim*].

Phragmocone slightly cyrtoconic; curvature of apical part of phragmocone weak; chamber length short to moderate; septa not inclined; conotheca without tabular nacre; proostracum absent; conotheca without tabular nacre; sheath investment-like without prominent swellings or extensions; post-alveolar part shortest among spirulids, either obtusely rounded or extended into short spine; laterally without extensions; medioventral depression distinct; outer surface of sheath granulated or rugose. *Eocene* (*Ypresian*)*–Oligocene:* Europe, southeastern USA.

Belemnosis Edwards, 1849, p. 38 [**Beloptera anomala* Sowerby, 1829, M] [=*Beloptera* Blainville, 1825, p. 622 (type, *B. belemnoidea;* M]. Chamber length short; post-alveolar sheath bulbous, obtusely rounded, ventrally largely reduced; laterally developed as diverging bulges. *Eocene* (*Ypresian–Lutetian*): UK (England), France.——Fig. 4,*1a–e.* **B. anomala* (Sowerby), BMNH C43823, lower Eocene (Ypresian), London Clay, Highgate, UK; *a,* sheath in ventral view; *b,* reconstruction in ventral view; *c,* sheath in lateral view, scale bar 10 mm; *d,* reconstruction in lateral view; *e,* reconstruction of cross-section; scale bar 10 mm (*a–e,* new).

Belemnosella Naef, 1922, p. 48 [**Belemnosis americana* Meyer & Aldrich, 1886, M] [=*Advena* Palmer, 1937 (*non Advena* Gude, 1913), =*Anevda* Palmer, 1940; =*Spirulirostrella* Naef, 1921, p. 536 (type, *Spirulirostra szainochae* Wojchik, 1903, OD)]. Ratio chamber length-to-diameter 0.2–0.25; post-alveolar sheath slightly extended into a spine-like projection, ventral sheath adapically callus-like, adorally reduced forming a medioventral depression. *Eocene* (*upper Lutetian–lower Bartonian*)*–Oligocene* (*Rupelian*): southeastern USA, Poland.——Fig. 4,*2a–d.* **B. americana* (Meyer & Aldrich), holotype, USNM 638750, middle Eocene (Bartonian), USA; *a,* sheath in ventral view; *b,* reconstruction in ventral view; *c,* sheath in lateral view, scale bar 10 mm; *d,* reconstruction in lateral view (*a–d,* new).

Family SPIRULIROSTRIDAE
Naef, 1921

[Spirulirostridae Naef, 1921, p. 536] [includes Spirulirostrinidae Naef, 1921, p. 536]

Phragmocone distinctly cyrtoconic to gyroconic; curvature of the apical part of phragmocone involves half turn; chamber length long; septa not inclined; proostracum absent; conotheca without tabular nacre; sheath with prominent swellings and extensions, post-alveolar part comparatively long, either rounded, nipple- or spine-shaped, laterally extended flange-like, ventrally with callus-like capitulum medioventral depression distinct; outer surface of the sheath granulated or rugose; protoconch located either inside or outside ventral callus. *Oligocene–Miocene:* New Zealand, Australia, Japan, Mexico, Europe.

Spirulirostra d'Orbigny, 1842, p. 362 [**S. bellardiana,* M]. Post-alveolar sheath extended into a comparatively long, dorsally directed spine; capitulum well developed, enveloping the protoconch. *Oligocene* (*Chattian*)*–Miocene* (*Langhian*): New Zealand, Australia, Japan, northern Germany, Italy, ?Austria, (?lower Oligocene of Hungary).——Fig. 5,*1a–d. Sp. hoernesi* Koenen, 1865, BSPG MC-183-3, Miocene (Langhian), northern Germany; *a,* ventral view; *b,* reconstruction; *c,* lateral view; *d,* reconstruction; *a–d,* scale bar 10 mm (new).

Amerirostra Jeletzky, 1969, p. 27 [**Spirulirostra americana* Berry, 1922; M] [=*Spirulirostra* d'Orbigny, 1842, p. 362 (type *Sp. Bellardiana* d'Orbigny, 1842, OD)]. Post-alveolar sheath extended into a comparatively long, dorsally directed spine; capitulum strongly granulated, but sparsely pronounced, not enveloping the protoconch as in *Spirulirostra. Miocene:* Mexico.——Fig. 5,*2a–d.* **A. americana* (Berry), lectotype, USNM 644841a,

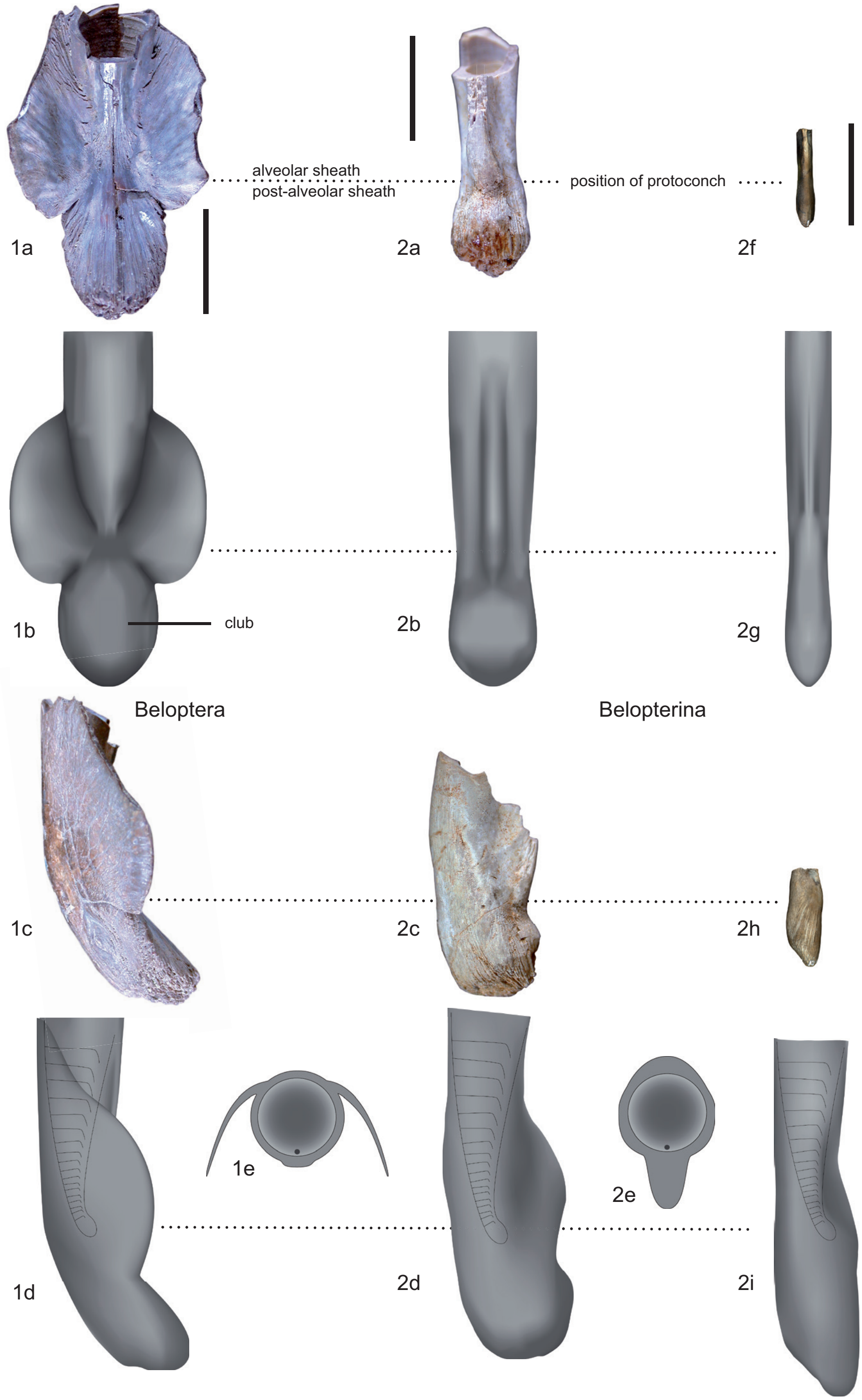

Fig. 3. Belopteridae (p. 7–9).

Miocene, Vera Cruz, Mexico; *a,* ventral view; *b,* reconstruction; *c,* lateral view; *d,* reconstruction; *a–d,* scale bar 10 mm (new).

Spirulirostridium Naef, 1922, p. 61 [**S. obtusum* Naef, 1922; M]. Post-alveolar sheath comparatively short, obtusely or nipple-like extended, ventral callus well developed, enveloping the protoconch. *Lower Oligocene* (*Rupelian*)*–Miocene* (*Langhian*): Austria, Czech Republic, Malta.——Fig. 5,*3a–d. S.* (*unknown species*), RGM 516.883, middle Miocene, Zebbug, Malta; *a,* ventral view; *b,* reconstruction; *c,* lateral view; *d,* reconstruction; *a–d,* scale bar 10 mm (new).

Spirulirostrina Canavari, 1892, p. 65 [**Sp. lovisatoi*; M] [=*Nipponirostra* Obata, Ogawa, & Oishi, 2004, p. 118 (type, *N. jeletzkyi*, M)]. Curvature of the phragmocone tighter than in other spirulirostrids; septa not distinctly inclined; sheath generally thin, post-alveolar part spine-like extended, wing-like extensions located ventrally, ventral callus weakly developed. *Miocene* (*Langhian*): Italy, Japan, ?Belgium.——Fig. 5,*4a–c.* **Sp. lovisatoi,* SMNS 9185, Miocene, Sardina, Italy; *a,* reconstruction in ventral view; *b,* specimen in lateral view; *c,* reconstruction in lateral view; *a–c,* scale bar 10 mm (new).

Family Spirulidae Owen, 1836

[Spirulidae Owen, 1836, p. 519] [=Lituitae Gray, 1847, p. 206]

Spirula Lamarck, 1799, p. 80 [**Nautilus spirula* Linnaeus, 1758, p. 710; M] [=*Lituina* Link, 1806, p. 84 (type, *Nautilus spirula* Linnaeus, 1758, p. 710, M); =*Spirularius* Dumeril, 1806, p. 157 (new name for *Spirula* Lamarck)]. Phragmocones gyrconic, planispiral; curvature tight; ratio dorsal chamber length-to-diameter 0.50–0.60; dorsal sutures straight, ventral sutures with distinct lobe; septa not inclined; mural flap present, septal necks holochoanitic, reaching inner surface of preceding septal neck; connecting rings lining entire inner surface of preceding septal neck; siphuncle marginal; mediodorsal attachment scars rectangular; conotheca (inner plate) unilayered, without layer of tabular nacre; sheath (outer plate) thin, investment-like, unilayered (forming a ventral ridge along early ontogenetic chambers), absent around final chamber; rostrum proper absent; proostracum absent; protoconch subspherical with caecum and prosipho. *Pleistocene–Holocene:* Worldwide, tropical seas and oceans.——Fig. 6,*1a–b.* **S. spirula* (Linnaeus), Holocene (extant), Mozambique; *a,* left lateral view; *b,* median section; scale bar 10 mm (new; photo by René Hoffmann).

SPIRULIDA *INCERTAE SEDIS*

Amphispirula Fuchs & Košťák, 2015, p. 93 [**A. herspica;* M)]. Phragmocone gyroconic with a continuous curvature; ratio chamber length-to-diameter 0.18–0.26; septa distinctly inclined; sutures without lobes or saddles; proostracum absent; sheath unknown, probably investment-like. *Eocene:* Czech

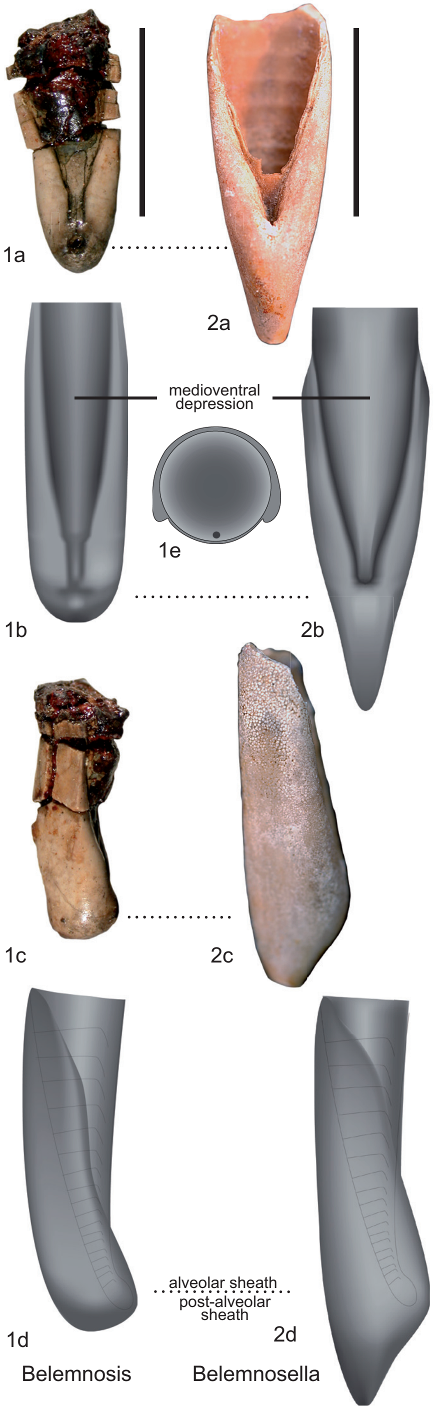

Fig. 4. Belemnoseidae (p. 9).

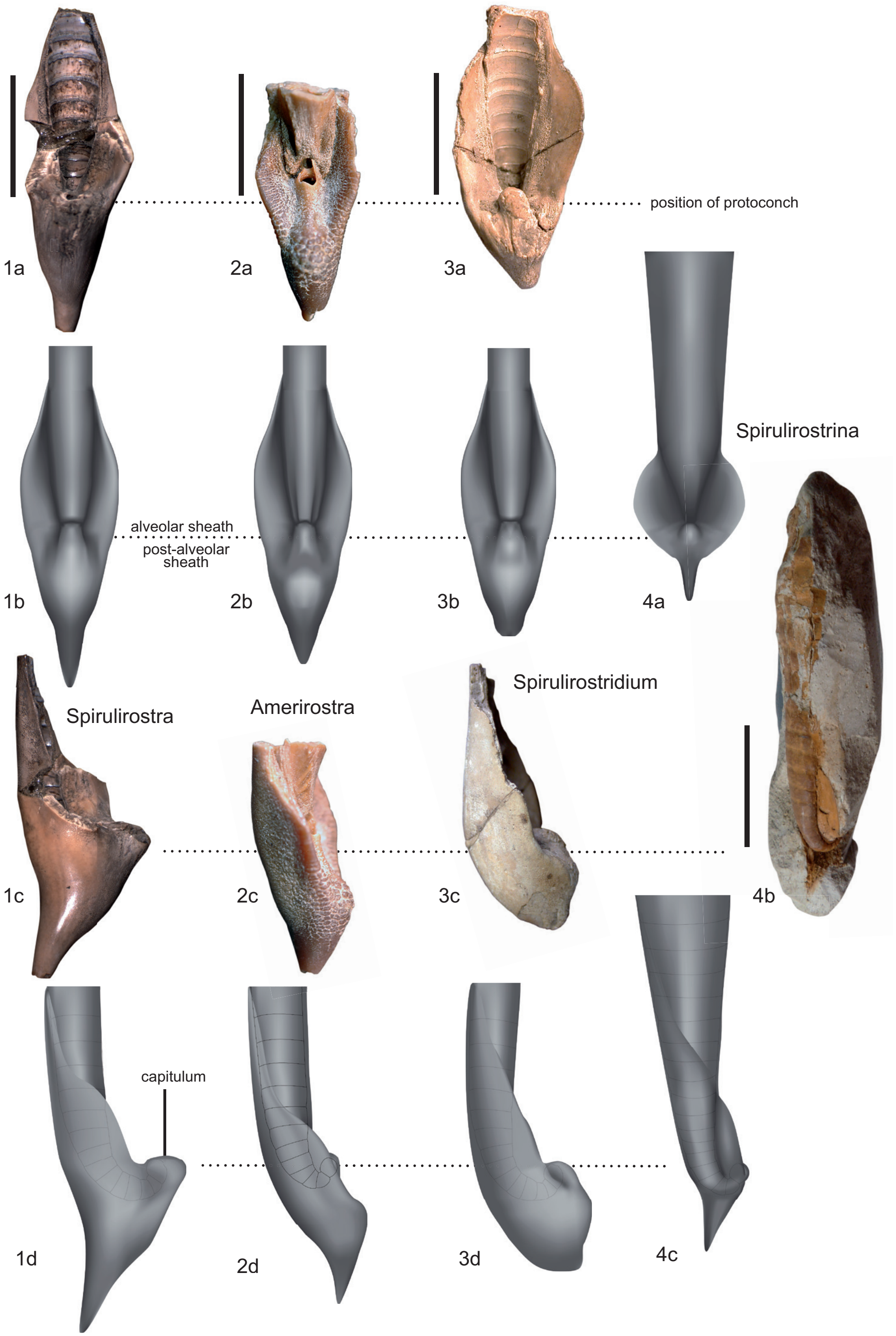

Fig. 5. Spirulirostridae (p. 9–11).

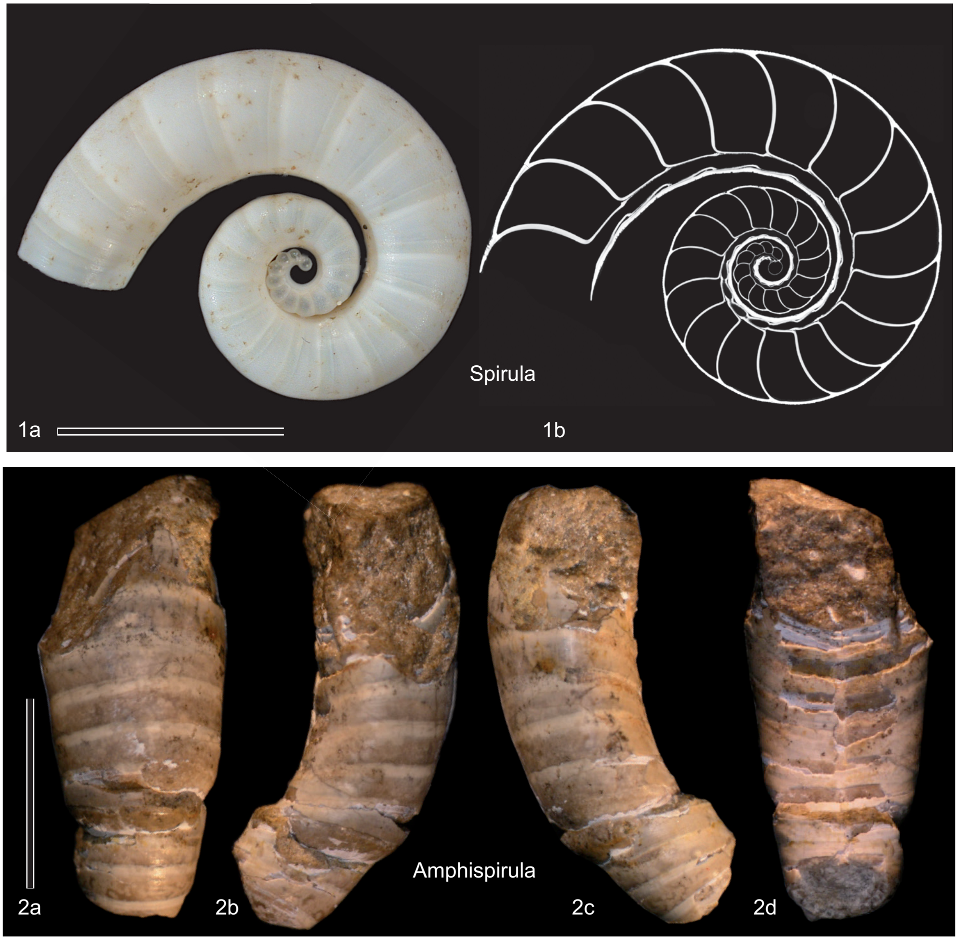

Fig. 6. Spirulidae, Spirulida *incertae sedis* (p. 11–13).

Republic.——Fig. 6,*2a–d*. **A. herspica,* holotype, GE 30 226, Eocene, Heršpice, Brno region, Czech Republic; dorsal (*a*), right lateral (*b*), left lateral (*c*), and ventral (*d*) views; scale bar 10 mm (Fuchs & Košťák, 2015, fig. 3A–D).

SEPIIDA

Introduction

Sepiida is a nectobenthic group of dorsoventrally flattened decabrachians with high species diversity, remarkable cognitive abilities, and high ecological and economical importance. Its key innovation is, besides several soft part features (e.g. dorsoventrally flattened mantle, arm pair 4 flattened), certainly the fundamental reorganization of the calcareous shell, which is commonly called a cuttlebone. Fossil sepiids are therefore well defined and rarely confused with other coleoid groups, although soft tissues are unknown—apart from evidence of muscle attachment sites and ink (Košťák, Jagt, & Schlögl, 2018). Despite its peculiarity, the homology with the cephalopod phragmocone had already been recognized by the pioneers of systematic zoology (e.g., Linnaeus, 1758; Lamarck, 1799; Voltz, 183, p. 23; d'Orbigny, 1845, p. 137). The alternative interpretations suggesting that the narrow interspaces between the lamellae are not equivalent to true chambers did not achieve general acceptance (e.g., pseudochambers theory of Seilacher & Chinzei, 1993, p. 366).

In general, the cuttlebone consists of a tough dorsal shield underlain by a soft buoyancy tank. In detail, the cuttlebone is a composite of highly complex substructures, each of which has its equivalent in the typical cephalopod phragmocone. Appellöf (1893) is widely acknowledged to have established the modern standard description of this sophisticated buoyancy device, although earlier workers already used a very similar terminology (e.g. Riefstahl, 1886). Denton and Gilbin-Brown (1959, 1961a, 1961b, 1961c, 1964) provided the fundamentals of our current knowledge about the mechanical properties and the detailed physiology and functional morphology of the cuttlebone. Some extant cuttlebones are strong enough to withstand hydrostatic pressures in water depths down to 600 m (Birchhall & Thomas, 1983; Ward & Boletzky, 1984; Sherrard, 2000). The deepest depth of a *Sepia* species recorded by Reid (2016) is nearly 1000 m. We are still at the beginning of understanding the morphological and physiological adaptations to such enormous diving depths (Ward & others, 2022). Essential insights into the early shell formation of *Sepia officinalis* were given by Naef (1928), Spiess (1972), Bandel and Boletzky (1979), and more recently by Pabic and others (2016, 2019). Age determination approaches based on cuttlebones were conducted, for example, by Bettencourt and Guerra (2001) and Nabhitabhata & others (2022). Ultrastructural (SEM) investigations started with Barskov (1973), Bandel and Boletzky (1979), and Dauphin (1981). Authors such as Adam and Rees (1966), Khromov (1987), LU (1998), Bonnaud, Lu, and Boucher-Rodoni (2006), and Neige (2006) discussed the systematic-taxonomic value of the cuttlebone. Spatial patterns of disparity, diversity, and body sizes were reconstructed based on cuttlebones (Neige, 2003, 2021). Molecular phylogenetic relationships among sepiids were analyzed by Bonnaud, Lu, and Boucher-Rodoni (2006) and Yoshida, Tsuneki, and Furuya (2006). The geochemistry and the use of the cuttlebone for water temperature reconstructions were investigated by Bettencourt and Guerra (1999) and Rexfort and Mutterlose (2006, 2009), while Gutowska and others (2010) (Gutowska, Pörtner, & Melzner, 2008) studied abiotic effects on the calcification process. The latest physico- and biochemical characterization of the cuttlebone came from Florek and others (2009), Pabic and others 2017, and Liu and others (2021).

Today, workers subdivide the modern cuttlebone into the dorsal shield, the ventral chamber complex, the fork, and the apical spine. In addition, one distinguishes between the inner and outer cone (e.g., Lu, 1998). As a result of the enormous evolutionary transformations, this morphological subdivision is only, in part, applicable for the shells of the stem group of the Sepiidae, the Belosaepiidae, which is well known from the Cenozoic fossil record.

Dorsal Shield

It is widely accepted that the dorsal shield evolved through gradual reduction of the ventral parts of an originally cyrto-breviconic shell. Haas (2003) recapitulated the growth modalities of the sepiid phragmocone and regarded the modern cuttlebone as a result of exponential growth of a cyrtoconic (endogastrically enrolled) phragmocone, which possesses a radius that is logarithmically growing. This eccentric mode of growth caused the compression and later reduction of the ventral shell wall. As Haas explained, "The biological advantage of this is to move the centre of buoyancy to the mid-point of the animal and thus to enable a greater maneuverability on short distance. (Haas, 2003, p. 121)."

Compared to the modern cuttlebone, the dorsal shield of the less specialized belosaepiids is more convex (transversally as well as longitudinally), because the underlying phragmocone is still conical, particularly in early ontogenetic stages (see Fig. 7). In addition, the posterior shield of belosaepiids can be characteristically thickened, forming a callus-like shoulder (capitulum).

In both fossil and extant forms, the dorsal shield is composed of the granulated sheath (outer plate, guard), the intermediate, irregularly mineralized (and therefore mainly organic) periostracum, and a thin, inner prismatic shell layer to which the septa insert. The latter two layers structurally belong to the primary shell wall (conotheca), whereas the laminated sheath represents a secondary shell formation that is a secretion product of the dorsal (secondary) shell sac epithelium (e.g., Riefstahl, 1886; Barskov, 1973; Bandel & Boletzky, 1979; Fuchs, 2006, 2012). A layer of nacre is absent in the primary shell wall.

Occasionally, one can find a subdivision of the dorsal shield in a median field and lateral wings (cone fields) as it is commonly in use in gladius-bearing coleoids (e.g., Bizikov, 2008; Košťák & others, 2016). Such a subdivision is hardly determinable in belosaepiids.

Dissolution of the calcified components of the cuttlebone exposes a chitinous gladius-like structure (Hunt & Nixon, 1981). Authors such as Khromov (1987) and Bizikov (2008) therefore regarded the dorsal shield as a modified pro-ostracum. However, Sepiida lack any evidence of a true pro-ostracum (Naef, 1922; Barskov, 1973, p. 290; Haas, 2003, p. 119; Fuchs & Iba, 2015), which is widely accepted to represent the anteriorly projecting dorsal remains of the terminal chamber. The morphological series *Ceratisepia–Belosaepia–Sepia* markedly demonstrates that the shell reduction affected the entire ventral shell wall rather than only the ventral side of the terminal chamber (homologization of the dorsal shield and the dorsal pro-ostracum would afford an anterior shift of the septal attachments onto the anterior pro-ostracum rim and this is regarded as unlikely). As a result of phragmocone-related transformations, the sepiid cuttlebone moved from an originally posterior to a dorsal position, which allowed the dorsal shield to look like a pro-ostracum. Young, Vecchione, and Donovan (1998, p. 407) compared the dorsal shield with a secondary pro-ostracum.

Intracameral Muscle Attachment Scars

Mediodorsal attachment scars on the inner surface of the conotheca suggest that belosaepiids—unlike modern sepiids—conserved (at least as juveniles) a visceral sac-conotheca connection typical for phragmocone-bearing coleoids (Fuchs & others, 2013).

Ventral Chamber Complex

The gradual migration of the chamber complex from a posterior to a dorsal position, in which the centers of buoyancy and gravity are vertically aligned, represents the most remarkable modification of the sepiid cuttlebone. The modern cuttlebone thus differs significantly from those of belosaepiids and particularly of other cephalopods.

In contrast to most other phragmocone-bearing coleoids, the early sepiid lineage is characterized by a laterally depressed phragmocone, i.e., the dorsoventral diameter exceeds the lateral diameter. This is already observable in Maastrichtian–Danian belosaepiid *Ceratisepia* (see Fig. 8) and accompanied by gradually inclined septa (Meyer, 1993). In belosaepiids, the inclination of septa relative to the longitudinal axis of the phragmocone can be considered as moderate compared to the vertical position in other phragmocone-bearing coleoids and the nearly horizontal orientation in later cuttlebones. A similar evolutionary tendency involves the phragmocone curvature, which is gradually decreasing. As a combined result of decreasing shell curvature and increasing septal inclination, the sepiid phragmocone became flatter during evolution. In juvenile *Belosaepia,* the dorsoventral diameter of the phragmocone is still larger than the lateral diameter.

More differences between Belosaepiidae and Sepiidae concern the septal complex:

1) Belosaepiid septa were originally concave, unlike the straight or even convex septa in the members of the Sepiidae.

2) Septa are significantly less crowded in belosaepiids than in sepiids.

3) Septum supporting pillars (intracameral walls, columns, undular plates, vertical walls, trabeculae in other terminologies) throughout the entire chamber are still absent in belosaepiids and first evolved in the Sepiidae. Mutvei (1971) and Bandel and Boletzky (1979, p. 316, 349) postulated that intracameral pillars are equivalents of the pillars in the siphuncular tube (specifically the connecting rings) of other cephalopods. Barskov (1973), Bandel and Boletzky (1979, p. 316), and Tanabe, Fukuda, and Ohtsuka (1985) recognized that, in contrast to belosaepiids, the septa of modern cuttlebones are unique in being comprised of two structurally different components. The latter authors distinguished between the upper "chamber floor," in which lamello-fibrillar ultrastructure indicates the septum proper, and the lower, semi-prismatic "chamber roof," which has been interpreted as a thin, dorsal (upper) continuation of the pillars. Ideas about the morphogenetic development of this unusual septal architecture are still in flux.

Authors such as Fuchs (2006, p. 36), and Doguzhaeva and Mutvei (2012, p. 16) correlated the sepiid septa with those of other phragmocone-bearing cephalopods, whereas authors such as Bandel and Boletzky (1979, p. 316), Khromov and others (1998), and Bizikov (2008) regarded the sepiid septa as equivalents of only the septal necks.

In Sepiidae, the posterior, striated part of the chamber complex is also known as the siphuncular surface (siphuncular zone, striated zone in other terminologies), because it is the site where the siphuncular epithelium regulates the liquid exchange in the chambers (see Denton & Gilbin-Brown, 1961a, 1961b, 1961c). It is noticeably flat in contrast to the tubular siphuncle in other cephalopods, and also in contrast to belosaepiids, in which the siphuncle forms a wide conical alveola (see Fig. 8). The early belosaepiid genus *Ceratisepia* impressively demonstrates the evolutionary development of the siphuncular complex in the Sepiida (see Meyer, 1993). The diameter of the initially tubular siphuncle continuously increased until the ventral portion of the septal necks became separated from the rest of the septum proper (approximately at septum 10–12). In Recent *Sepia,* the septal foramen is still closed in septa 1–2 but opens immediately after the formation of the third septum (Pabic & others, 2016). Altogether, the evolutionary trend of the sepiid siphuncular complex is dominated by the dislocation from the interior of the phragmocone to its exterior.

Fork

In modern Sepiidae, the fork (furca in older terminologies) embraces the siphuncular surface. Such a coherent structure did not exist in belosaepiids. In cross sections, the fork is laminated. The lamello-fibrillar ultrastructure (*Spirula* nacre, nacre type 2) of each lamina reveals that the fork derived from the septa (see Adam & Rees, 1966, p. 134). The anteriorly directed limbs of the fork can therefore be seen as laterally crowded and as reverted remains of the septa (Gabellamellen in Riefstahl, 1886, p. 212; Gabelsepten in Naef, 1922; Bandel & Boletzky, 1979: p. 340).

The reversal point of the U- or V-shaped fork in modern sepiids is known as the inner cone. The latter is reminiscent of the ventral side of the siphuncular conus (Haas, 2003, p. 121). In belosaepiids, the equivalent structure is rarely preserved and therefore poorly known. It has variously been named ventral deck, ventral plate, or furcal process (Latin). The ventral deck is slightly curved (*Ceratisepia*) to planar (*Belosaepia*) and its inner surface bears the ventral mural parts of the septa (see Fig. 7,*1d*); it thus corresponds to the vestiges of the ventral conotheca. Pillar-like structures between each septum have only been reported in this part of densely spaced septal remains (Meyer, 1993; Haas, 2003; Yancey, Garvie, & Wicksten, 2010).

Apical Spine

Irrespective of its relative size, which is usually larger in belosaepiids than in modern sepiids, the lamellar texture of the apical spine (thorn, prong) is very similar (see Fig. 7,*1c*). Although the spine's ultrastructure appears relatively uniform (e.g., Barskov, 1973; Bandel & Boletzky, 1979; Dauphin, 1981; 1984; 1985), its phylogenetic interpretations are contradictory. Whether the sepiid spine represents a homologue of the belemnite rostrum proper (e.g., Naef, 1922; Dauphin, 1984) or not (e.g., Mutvei, 1964; Jeletzky, 1966; Doyle, Donovan, & Nixon, 1994; Haas, 2003) it is still subject to intensive discussions (see Fuchs, 2012). Newest evidence of calcitic components in the spine (and sheath) of belosaepiids by Yancey and Garvie (2011) and Košťák and others (2013) may support the idea of homology.

Ventral Process

Belosaepiidae, by contrast to Sepiidae, possessed a well-developed and heavily mineralized ventral process (also termed the corona or ventral lip). It represents backward bending parts of the ventral shell wall (Fig. 7,*1c–e*). Seen in ventral view, the ventral process can be short, collar-like, or long, forming a more-or-less flat, flabelliform plate. Its base is mostly in contact with the apical spine; more distal parts can be free. According to Naef (1922), the ventral process represents the attachment site of the ventral mantle. It further corresponds to the posterior parts of the outer cone of modern cuttlebones (e.g., Bizikov, 2008).

Origin of Sepiida

Ideas on the hypothetical ancestry of the Sepiida have a long and changeable history. In pre-Darwinian times, the pioneers of coleoid research regarded either Eocene *Belosaepia* (Blainville 1825, p. 622; Voltz, 1830, p. 23) or Late Jurassic *Trachyteuthis* (Rüppell, 1829; Münster, 1837; Ferussac & Orbigny, 1835–1848; Meyer, 1846; Quenstedt, 1849) as the earliest sepiids. The assumption of a *Sepia-Trachyteuthis* relationship is based on a superficially similar shell outline and a similar dorsal granulation. It is presently clear that *Trachyteuthis,* as well as its closest Cretaceous relatives *Glyphiteuthis* and *Actinosepia,* possessed an unmineralized gladius without any evidence of a chambered part (Fuchs, 2016). Apart from the lack of a true cuttlebone, the overall soft part morphology clearly indicates placement of trachyteuthids in the stem lineage of octopods rather than in the Decabrachia (Bandel & Leich, 1986; Haas, 2002; Donovan, Doguzhaeva, & Mutvei, 2003; Bizikov, 2004; Fuchs, Engeser, & Keupp, 2007; Fuchs & Larson, 2011; Sutton, Perales-Raya, & Gulbert, 2015; Fuchs & Iba, 2015; Fuchs, 2016; Fuchs & Donovan, 2016; Fuchs & others, 2019; Fuchs, 2020).

Naef (1922, p. 94) postulated a morphological series leading from *Sepia–Belosepia* via spirulirostrid and belemnoseid spirulids back to belemnites. He thought that their guard-like posterior sheath represents a modification of a belemnite rostrum. Naef further assumed Late Jurassic *Diplobelus,* a member of the belemnoid order Diplobelida (Fuchs, 2019b), to be a potential ancestor of the Spirulida/Sepiida clade.

Jeletzky (1966, p. 62, 66, 70) argued for sepiid roots within Late Cretaceous Groenlandibelidae. In contrast to Naef (1922), he rejected a homology between the belemnite rostrum proper and the variously shaped sheaths of spirulids and sepiids.

Maastrichtian and Danian records of *Ceratisepia* by Meyer (1993) and Hewitt and Jagt (1999) can be considered a breakthrough. The presence of distinctly inclined septa combined with a widely opened siphuncle in a slightly enrolled breviconic phragmocone is diagnostic for the Sepiida and therefore seminal for understanding the evolutionary transformations leading to a typical cuttlebone (Haas, 2003). A sepiid origin via Eocene spirulids, as Naef (1922) assumed, therefore appears stratigraphically and morphologically implausible. Both Meyer (1993) and Hewitt and

Jagt (1999), nevertheless, accentuated the remarkable similarity of *Ceratisepia* with likewise cyrto-breviconic phragmocones that are furnished with slightly oblique septa typical of the diplobelid genus *Conoteuthis,* which appeared during the later part of the Early Cretaceous and became extinct after the Late Cretaceous Maastrichtian. Many authors, such as Engeser and Bandel (1988), Doyle, Donovan, and Nixon (1994), Haas (1997, 2003), Young, Vecchione, and Donovan (1998), and Doguzhaeva (2000) rejected belemnitid or diplobelid affinities, mostly owing to differences in the construction of the protoconch. This argument in turn has been criticized by Hewitt and Jagt (1999), Yancey, Garvie, and Wicksten (2010), and Fuchs, Keupp, and Wiese (2012). Fuchs (2019a) noted that the diplobelid protoconch is structurally closer to sepiids (and spirulids) than to belemnitids. This view, as well as additional mutualities between diplobelid and groenlandibelid phragmocones (Fuchs, & others, 2013), supports a common origin of Sepiida and Spirulida (the Sepioidea concept). On the basis of distinctly inclined septa as well as an unusual swelling of the posterior sheath, Fuchs, Keupp, and Wiese (2012) proposed the Aptian diplobelid *Vectibelus* to be an ideal forerunner of the Sepiida.

Origin of Sepiidae

The divergence of the Sepiidae from the Belosaepiidae is widely accepted (e.g., Young, Vecchione, & Donovan, 1998; Haas 2003; Fuchs, 2006; Košťák, & others, 2013; Goolaerts & others, 2022). The modern type of cuttlebone has probably occurred since the Late Eocene (Lörenthey, 1899; Szörenyi, 1934; Wagner, 1938; Fornasiero & Vicariotto, 1995). This type of Eocene cuttlebone was ascribed to the genus *Archeosepia,* although a generic distinction between *Archeosepia* and *Sepia* is only approximate. The dispersion of pillars in the chambers and the development of the fork are therefore decisive characters. Both characters—pillar-bearing chambers and a fork, are proven from middle Miocene cuttlebones (Schloenbach, 1868; Baluk, 1984; Fuchs & Lukeneder, 2014; Košťák & others, 2017). Middle Eocene (Lutetian) statoliths from the Paris Basin identified as *Sepia* sp. by Neige, Lapierre, and Merle (2016) concur with a Late Eocene divergence, although these statoliths may belong to the genus *Belosaepia* with its abundant shell remains co-occurring in the same deposits.

Systematic Problems

The Eocene Belosepiellidae with its sole genus *Belosepiella* was for a long time considered to represent another group of the Sepiida until Haas (1997, 2003) observed characteristics of sepiolid shell remains. Since this enigmatic type of shell is indeed hardly congruent with sepiid ground patterns, Belosepiellidae is herein tentatively dealt with as a stem-group of the Sepiolida.

Recently, Yancey and Garvie (2011) excluded the Eocene genus *Anomalosaepia* from the Belosaepiidae and erected a new family, the Anomalosaepiidae Yancey and Garvie, 2011, based on the presence of an outermost calcitic shell layer. Because the overall morphology of the phragmocone as well as the post-alveolar sheath is very close to *Belosaepia,* and because small amounts of calcite have also been detected in the dorsal shield of *Aegyptosaepia* (Košťák & others, 2013) and *Sepia officinalis* (Jasso-Gastinel & others, 2009), and because the diagenetic loss of the same layer in other belosaepiids cannot be excluded, the genus *Anomalosaepia* is provisionally retained within the Belosaepiidae.

Belocurta (Paleocene) and *Mississaepia* (Eocene), both rare and morphologically enigmatic genera with a cyrtoconic phragmocone, have been ascribed to Sepiida on the basis of inclined septa (Meyer, 1993; Doguzhaeva, Weaver, & Ciampaglio, 2014). Significant dorsal and lateral swellings are however atypical for sepiids, but instead resemble the sheaths of Cenozoic spirulids. *Belocurta* and *Mississaepia* are therefore preliminarily classified as Decabrachia *incerta sedis*. The Carboniferous genus *Pohlsaepia* Kluessendorf & Doyle, 2000, identified as a Palaeozoic coleoid of uncertain order and family (see Fuchs, 2021), has nothing to do with cuttlebone-bearing sepiids.

General Preservation of Fossil Cuttlebones

In the Belosaepiidae, the post-alveolar thickened guard-like sheath as well as the spine and the ventral process are heavily calcified and more solid than the thinner anterior shield-like part. The large majority of belosaepiid records are therefore missing anterior parts. Apart from mineralogical and ultrastructural alternations, the posterior shell remains additionally suffered strong erosion, which resulted in a huge variety of different shapes. As a result, diagnostic characters, such as the original length of the spine, the shape of the shoulder, or the lateral and posterior extension of the ventral process are determinable only in well-preserved specimens. Systematic-taxonomic valuable (hence, scarcely weathered) specimens are present, e.g., when the primary shell wall (conotheca) covers the inner surface of the sheath. Although septa are regularly missing, even in scarcely weathered specimens, the stubs of the septa as well as mediodorsal soft tissue attachment scars between the stubs may indicate the presence of the very thin, whitish conotheca.

Records of belosaepiid phragmocones either *in situ* with their guards (Edwards, 1849; Meyer, 1993; Fuchs, 2006; Yancey, Garvie, & Wicksten, 2010) or isolated (Weaver, Ciampaglio, & Chandler, 2007) are indispensable for our morphological understanding, but are unfortunately very rare.

Fossil cuttlebones assigned to the Sepiidae are often known by vague imprints in the sediment, but also through preserved shell material (see Fig.10,*4b*). In such cases, the dorsal shield and the apical spine were also more likely to be preserved than the chambered part. However, some Miocene fossil records have yielded insights into the high organization level of the septal complex (e.g., Fuchs & Lukeneder, 2014, Košťák & others, 2017).

All in all, fossil sepiids are organized into two families (Belosaepiidae and Sepiidae) and nine genera. Belosaepiidae appeared during the Maastrichtian and disappeared by the end of the Priabonian (see Fig. 1). The extant family Sepiidae is certainly established since the Miocene.

Order SEPIIDA Gray, 1849

[*nom. correct.* Zittel, 1895, p. 445, suborder *pro* Sepiophora Gray, 1849, p. 96; *nom. transl.* Pompeckj, 1912, p. 296, *ex* suborder Sepioidea Zittel, 1895, p. 445; *nom. correct.* Jeletzky, 1965, p. 76, *pro* order Sepioidea Zittel, 1895, p. 445]

Phragmocone cyrto-breviconic to strongly flattened, laterally compressed; degree of coiling ontogenetically decreasing; ventral shell wall compressed to distinctly reduced; septa distinctly inclined to nearly parallel with the dorsal shell wall, inclination increasing during ontogeny, lamellofibrillar in ultrastructure; septal distance (chamber length) dorsally wide to very dense, ventrally dense; septal necks holochoanitic to rectified; pillars restricted to the siphuncular complex or present throughout the entire chamber; siphuncle wide, with a trend towards ventral opening, either conus-shaped inside the phragmocone or planar outside the phragmocone; mediodorsal attachment scars present in early forms and absent in later forms; conotheca without tabular nacre; sheath dorsally well developed, ornamented, shield-like, ventrally reduced or bent backwards forming a ventral process, post-alveolar sheath guard-like thickened, apically with nipple- or spine-like extension; true proostracum absent; protoconch hemispherical or bowl-shaped; existence of caecum and prosipho assumed. *Upper Cretaceous* (*Maastrichtian*)*–Holocene.*

Family BELOSAEPIIDAE Dixon, 1850

[*nom. correct.* Fischer, 1887, p. 357, *pro* Belosepiadae Dixon, 1850, p. 190; *nom. correct.* Palmer, 1937, p. 505, *pro* Belosepiidae Fischer, 1887, p. 357] [=subfamily Belosepiinae Naef, 1921, p. 536; =Anomalosaepiidae Yancey & Garvie, 2011, p. 912]

Dorsal shield strongly convex; phragmocone cyrto-breviconic, septal distance comparatively wide, dorsally significantly wider than ventrally; septa distinctly inclined, septal surface weakly concave; septal necks holochoanitic, weakly deviated from septum proper; siphuncle very wide, conus-shaped; pillars restricted to the siphuncular complex; fork absent; mediodorsal attachment scars present; ventral process distinct, variable in size, shape, ornamentation, and length of posterior free margin; ventral deck slightly curved or planar; dorsal sheath coarsely granulated, reticulated, or labyrinthic, posteriorly thickened forming a callus-like shoulder (crest); postalveolar sheath with adorsally directed, robust apical spine, base of the spine in contact with base of the shoulder, forming a connective fissure; protoconch hemispherical, evidence of caecum and prosipho weak. *Upper Cretaceous* (*Maastrichtian*)–*Eocene* (*Priabonian*).

Belosaepia Voltz, 1830, p. 23 [**Beloptera sepioidea* Blainville, 1825; OD]. [=*Beloptera* Blainville, 1825, p. 622, *partim*; =*Belosepia* Deshayes, 1835, p. 756 (*nom. null.*)]. Phragmocone of belosaepiid type; mediodorsal attachment scars short; posterior shell remains large- to medium sized, ventral process large, lateral diameter wider than dorsal shield, radially grooved, anterior base in contact with spine, posterior free margin, not in contact with spine, serrated, adventrally curved; ventral deck planar; dorsal shield anteriorly planar; shoulder pronounced, in lateral view angled, in dorsal view V-shaped to keel-like; apical spine medium- to large-sized, adorsally directed, profile straight to dorsally curved, cross section oval to spindle-shaped, often with sharp, dorsal keel, apex variable. *Eocene* (*Ypresian–Priabonian*): France, Belgium, Netherlands, UK, ?Hungary, Ukraine, Turkey, Egypt, Nigeria, India, USA. [A large number of species have been assigned to *Belosaepia.* However, most of them must be regarded as synonyms because important factors such as taphonomic artifacts, ontogenetic differences, and intraspecific variability were often neglected, particularly by authors dealing with specimens from the Eocene of France, Belgium, and UK].——Fig. 7,*1a–f.* **B. sepioidea* (Blainville), Lutetian, Bracklesham, UK; *a–b,* complete cuttlebone in lateral (*a*) and dorsal (*b*) views, BMNH c.46818; *c,* median section of the postalveolar sheath, BMNH c.3054; *d,* ventral view, BMNH c.82884; *e,* specimen frontal view, MNHN-F-A69280; *f,* internal (silicon) cast showing earliest chambers; scale bars 10 mm (new).

Aegyptosaepia Košťák, Jagt, Speijer, Stassen, & Steurbaut , 2013, p. 4 [**Ae. lugeri;* M]. Phragmocone characteristics poorly known, generally of belosaepiid type; posterior shell remains small-sized; anterior shell unknown; ventral process short, collar-like; ventral deck slightly curved; shoulder rounded; apical spine well developed, adorsally directed, almost vertical, with sharp dorsal keel, cross section triangular. *Paleocene* (*upper Selandian–lower Thanetian*): Egypt.——Fig. 7,*2a–b.* **Ae. lugeri*, lateral (*a*) and frontal (*b*) views, holotype, IGP-BDA 09/01, upper Selandian/lower Thanetian boundary, Western Desert, Egypt, scale bars 10 mm (Košťák & others, 2013, Fig. 8A1–5)

Anomalosaepia Weaver & Ciampaglio, 2003, p. 1103 [**A. alleni;* OD] [=*non Anomalosepia* Khromov, 1987]. Phragmocone characteristics poorly known, generally of belosaepiid type; posterior shell remains small-sized; ventral process well developed, radially grooved, margins serrated, adorsally recurved, free part short; ventral deck unknown; shoulder evenly rounded, U-shaped in dorsal view; apical spine moderately developed, adorsally directed, profile triangular, cross section spindle-shaped, apex blunt. ?*Paleocene* (*Selandian–Thanetian*), *Eocene* (*Lutetian–Bartonian*): USA, ?Egypt.——Fig.7, *3a–c. A. jeletzkyi* (Allen, 1968), PRI 27553, middle Eocene, Cook Mountain Formation, Louisiana, USA; lateral (*a*), ventral (*b*). and dorsal (*c*) views, scale bars 10 mm (Weaver & Ciampaglio, 2003, fig. 1,*13–15*).

Ceratisepia Meyer, 1989, p. 30 [**C. elongata,* p. 32; M]. Phragmocone generally belosaepiid-like, but stronger curved; mediodorsal attachment scars stripe-like occupying entire chamber length; ventral deck distinctly curved; ventral process short; sheath thin, with weak granulation, longitudinally and transversally convex, barely shield-like, shoulder absent; apex bulbous; spine absent. *Upper Cretaceous* (*Maastrichtian*)–*Palaeocene* (*Danian*): Netherlands, France.——Fig. 8,*a–d.* **C. elongata,* Danian, Vigny, France; *a,* specimen MNHN XIVb131, phragmocone in lateral view showing moderately inclined septa; *b,* specimen MNHN XIVb133 showing a septum in apertural view (chamber 7–9); *c,* specimen MNHN XIVb134 showing a septum (chamber 10–12) in apertural view; *d,* specimen MNHN XIVb132 showing earliest part of siphuncular conus formed by holochoanitic septal necks (septa broken off); scale bars 10 mm (new).

Pseudosepia Naef, 1923 in 1921–1923, p. 794 [**Sepia vera* Deshayes, 1866; p. 613; M]. Phragmocone characteristics poorly known, generally of belosaepiid type; posterior shell remains small-sized; anterior shell parts unknown; posterior shield without distinct shoulder; ventral process indistinct; ventral deck unknown; apical spine short, hooked, adorsally directed. *Middle Eocene* (*Lutetian–Bartonian*): France, ?USA. [The limited set of characters of this monotypic and very rare genus might alternatively point to juvenile features of *Belosaepia*].——Fig. 9,*1a–c.* **P. vera* (Deshayes),

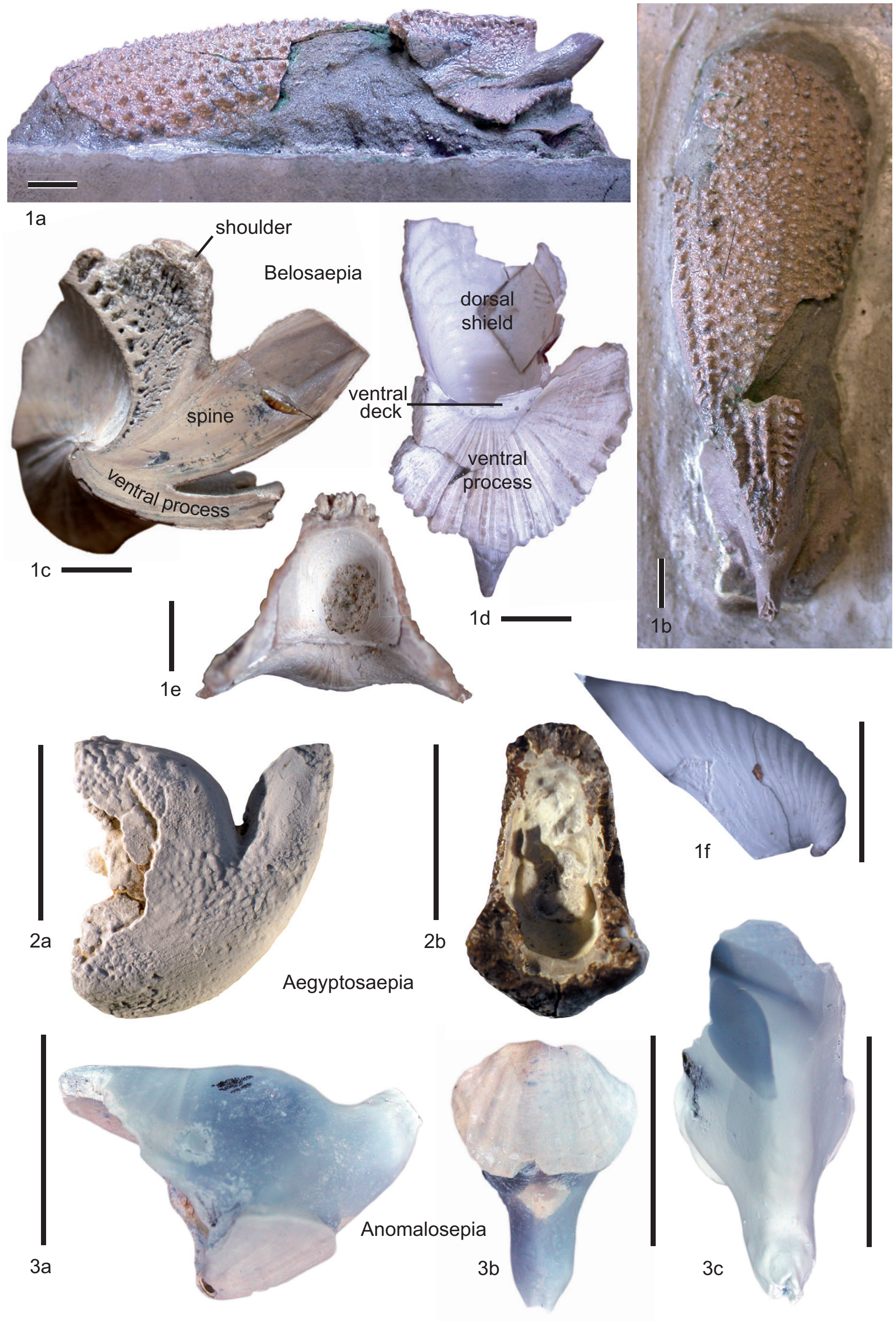

Fig. 7. Belosaepiidae (p. 20).

Fig. 8. Belosaepiidae (p. 20).

Lutetian, Parnes, France; lateral (*a*), ventral (*b*), and dorsal (*c*) views, scale bar, 10 mm (Cossmann & Pizarro, 1910–1913, pl. 60, fig.1,1).

Stenosepia Vincent, 1900, p. 20 [**Beloptera compressa* Blainville, 1827, p. 110; M] [=*Beloptera* Deshayes, 1835; =*Sepia* Linnaeus, 1758; =Belosaepia Voltz, 1830; =*Belosepia* Deshayes, 1835]. Phragmocone characteristics poorly known, generally of belosaepiid type; posterior shell remains large sized, significantly compressed; anterior shell unknown; post-alveolar sheath distinctly elongated; shoulder rounded; in dorsal view narrow, V-shaped, keel-like; ventral process elongated, oval, lateral diameter wider than dorsal shield, radially grooved, fused with spine over its almost entire length, posterior margin weakly serrated, adorsally recurved; ventral deck unknown; apical spine relatively small, adorsally directed, apex blunt.

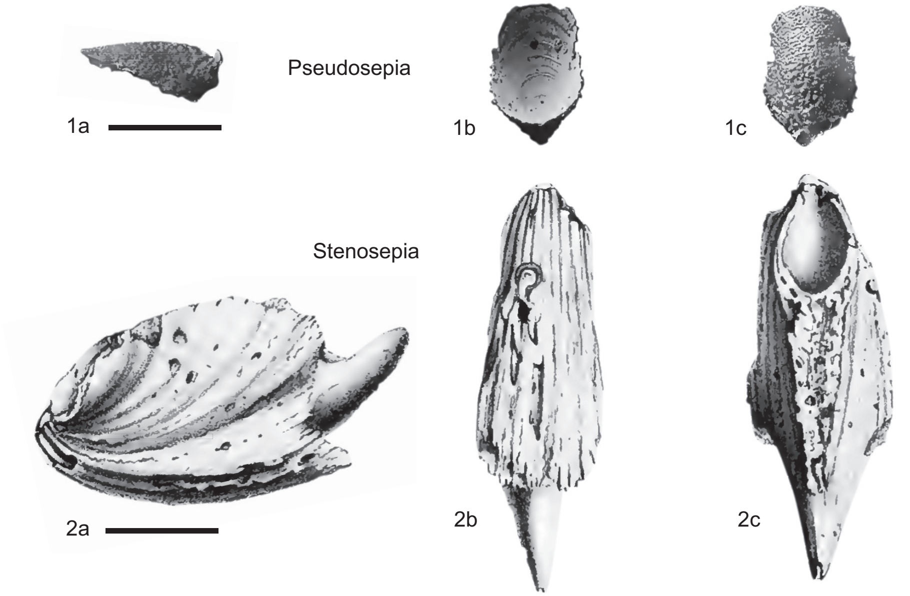

FIG. 9. Belosaepiidae (p. 20–23).

Eocene (?*Ypresian, Lutetian–Bartonian*): France, Belgium.——FIG. 9,*2a–c*. **S. compressa* (BLAINVILLE), Lutetian, Valmondois, France; lateral (*a*), ventral (*b*), and dorsal (*c*) views, scale bar 10 mm (Deshayes, 1835, pl. 101,*1–3*).

Family SEPIIDAE Leach, 1817

[D'ORBIGNY, 1840, p. 30, *pro* Sepiidea LEACH, 1817, p. 138; *nom. correct.* FISCHER, 1887, p. 355, *pro* Sepidae D'ORBIGNY, 1840]

Shell of modern cuttlebone type; shape variable ranging from oval to rhomboidal; dorsal shield weakly convex, posteriorly winglike forming outer conus; phragmocone strongly depressed; septal distance dense; septa nearly parallel with the dorsal shell wall, composed of a dorsal lamello-organic (medially agglutinated with aragonite crystals, laterally purely organic) and a ventral prismatic layer; septal surface adorally convex; dorsal parts of septal necks rectified, achoanitic, lateral and ventral parts of septal necks separated and modified into U- to V-shaped fork; pillars present throughout each chamber; siphuncular complex planar; mediodorsal attachment scars absent; ventral process and ventral deck rudimentary; dorsal sheath finely granulated, posterior part without shoulder; apical spine weakly developed or reduced; protoconch plate- or bowl-shaped, caecum and prosipho absent. [Species of the living *Hemisepius* group may have secondarily lost most the calcified features]. *Eocene–Holocene.*

Sepia LINNAEUS, 1758, p. 658 [**Sepia officinalis* LINNAEUS, 1758; p. 658] [=*Saepia* MÜLLER, 1775, p. 13, *nom. van*.]. Cuttlebone of modern type, outline elliptical to subrhomboidal or lanceolate; dorsal shield well calcified, granulation variable; inner conus conical or flared backwards; fork with long limbs, sometimes ridgelike; outer conus bowl-shaped, posterior margin directed to the venter; apical spine present or absent. *Miocene* (*Burdiglian*)*–Holocene:* Mediterranean Sea (Italy, Malta, Spain, Turkey), Paratethys (Hungary, Austria, Poland, Slovakia, Slovenia), Atlantic Ocean (France, Denmark), Indian Ocean (western India), western Pacific Ocean (Australia).——FIG. 10,*1a*. *S. vindobonensis* SCHLOENBACH, 1868, holotype, GBA collection, Langhian, Baden near Vienna, Austria; ventral view, scale bar 10 mm (SCHLOENBACH, 1868, pl. 7,*20*).——FIG. 10,*1b*. *S. juliebarborae* KOŠŤÁK & others, 2016, paratype, SNM Z 24851, Serravallian, Bratislava, Slovakia, scale bar 10 mm.

Fig. 10. Sepiidae, Putative Sepiidae (p. 23–25).

PUTATIVE SEPIIDAE

Archaeosepia Szörényi, 1934, p. 186 [**A. naefi;* SD Jaworski, 1936, p. 100] [=*Hungarosepia* Doyle, Donovan, & Nixon, 1994, p. 12]. Dorsal shield with pronounced, rip-like growth increments, outline oval, granulation coarse, differentiation between median field and lateral fields possible; chambered part unknown; presence of fork unclear; apical spine indistinct. *Eocene* (*Bartonian–Priabonian*)–*Oligocene* (*Rupelian–Chattian*): Mediterranean Sea (Italy, Hungary), Paratethys (Hungary). [Generic status preliminarily since a differentiation with *Sepia* is indistinct.]——Fig. 10,*2a. A. monticulimajoris* Fornasiero & Vicariotto, 1995, dorsal view, holotype, MGPD 27817, Onte Valley, northern Italy, upper Eocene, scale bar 10 mm (Fornasiero & Vicariotto, 1995, Fig. 5b).——Fig. 10,*2b. A. harmati* Szörenyi, 1934, dorsal view, IGP A898, Rupelian, Budapest, Hungary, scale bar 10 mm.

Notosepia Chapman, 1915, p. 357 [**N. cliftonensis;* M]. Dorsal shield convex; posterior shell remains massive, belosaepiid-like; ventral process short, grooved; ventral deck absent; fork present; shoulder indistinct; apical spine slender, adapically directed, apex pointed. *Middle Miocene* (*Langhian–Serravalian*): southeastern Australia.——Fig. 11,*a–d.* **N. cliftonensis,* Langhian–Serravalian, Victoria, Australia; *a–c,* holotype, VM P12610, lateral (*a*), ventral (*b*), and dorsal (*c*) views; scale bar 10 mm (Chapman, 1915, pl. 7,*16–17*, pl. 8,*22*); *d,* ventral view of syntype VM P324157, scale bar 10 mm. (new).

SEPIOLIDA

Introduction

The Sepiolida is a small-sized group of decabrachiate coleoids with a rounded body. The shell of these benthic or pelagic animals is either an unmineralized gladius-like structure or is absent. Where present, the shell vestige does not reach the posterior mantle, i.e., it does not equal the mantle length as in most other gladius- or phragmocone-bearing coleoids. Recent Sepiolida includes only the family Sepiolidae Leach, 1817 (e.g., Doyle, Donovan, & Nixon, 1994; Boletzky, 1999; Reid & Jereb in Reid, Jereb, & Roper, 2005). Some authors additionally included the families Sepiadariidae Fischer, 1882 in Fischer, 1880–1887 (e.g., Grimpe, 1921, 1922; Fioroni, 1981; Allcock, Lindgren, & Strugnell, 2014) and/or Idiosepiidae Appellöf, 1898 (e.g., Clarke, 1988; Sweeney & Roper, 1998). The systematic position of the latter two

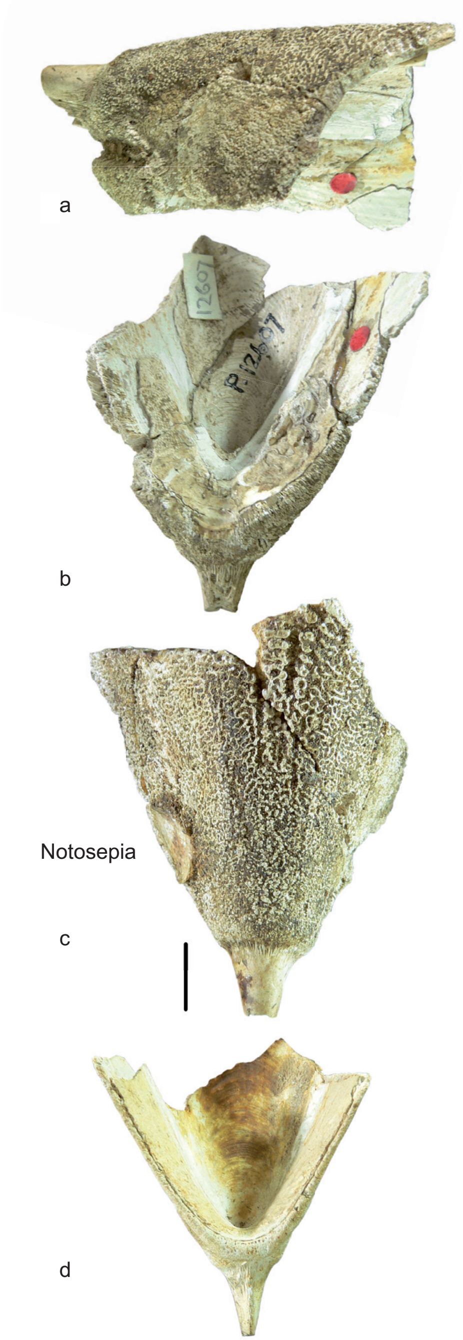

Fig. 11. Putative Sepiidae (p. 25).

families is obscured and still subject to controversial discusions (see Allcock, Lindgren, & Strugnell, 2014, p. 29). Concerning phylogenetical relationships of the Sepiolidae, also morphological and molecular data did not yield a clear resolution. The crucial question is whether the Sepiolida (either with or without the Idiosepiidae and Sepiadariidae) is phylogenetically closer to the sepioid (e.g., Vecchione & Young, 2004; Strugnell, Lindgren, & Allcock, 2009; Allcock, Cook, & Strugnell, 2011;) or to the teuthoid clade (e.g., Bonnaud, Pichon, & Boucher-Rodoni, 2005; Strugnell & others, 2005; Lindgren, 2010; Lindgren & others, 2012; Strugnell & others, 2017; Tanner & others, 2017; Uribe & Zardoya, 2017). The answer to this question is essential for understanding the evolutionary history of the Decabrachia. Phylogenetic certainty could specifically decide whether the sepiolid shell rudiment is morphogenetically derived from a mineralized shell or from an organic gladius. A gladius evolved two to four times (Young, Vecchione & Donovan, 1998, p. 409; Fuchs & Iba, 2015; Fuchs, 2016), depending on the proposed phylogeny. To better know the sister-group relationships of the Sepiolida would strongly facilitate the search for ancestral sepiolids, which are virtually absent from the fossil record.

So far, only Haas (1997, 2003) suspected the Eocene genus *Belosepiella* to be a stem-lineage representative of the Sepiolida. *Belosepiella* has been erected on the basis of a rare and peculiar shell which is fundamentally different from what is known about guard-like sheaths of contemporary sepiids and spirulids. The putative sepiolid shell rudiment is calcareous and consists of an elongated cap-like structure with a conical depression (gap) on the convex surface (Fig.12). The posterior apex of the cap is covered by a rostrum-like layer, which is extended in a spine-like manner.

The systematic history of *Belosepiella* is accordingly very inconsistent. Leriche (1906), Abel (1916), Bülow-Trummer (1920, p. 239), and Strausz (1974) assumed that the conical depression corresponds to an empty alveola and that the *Dentalium*-like shell of *Vasseuria* perfectly fits into this structure. However, Naef (1922, p. 60) recognized that the *Vasseuria* remains themselves represent a guard-like sheath. Naef (1922) and Roger (1952) put *Belosepiella* along with spirulid coleoids, a relationship that Curry (1955) clearly rejected, because the hypothetical *Belosepiella* phragmocone must have been straight rather than ventrally enrolled. Haas (1997, 2003, fig. 17–19) recognized similarities with a sepiid cuttlebone (e.g., ventral deck and process) and reconstructed a new scenario in which the irregularly mineralized shell of *Belosepiella* is transitional between a sepiid cuttlebone and a demineralized sepiolid gladius.

Although morphological support for the hypothesis of Haas (1997, 2003) is very fragile, the monogeneric family Belosepiellidae is preliminarily regarded as a putative member of the Sepiolida until new data can verify this placement.

Order SEPIOLIDA Leach, 1817

[*nom. corr.* Keferstein, 1866 in 1862–1866, p. 1443, *pro* family Sepiolidea Leach, 1817, p. 137; *nom. transl.* Grimpe, 1921, p. 298, *ex* family Sepiolidae Leach, 1817, p. 137; *nom. correct.* Fioroni, 1981, p. 181, *pro* Sepioloidea Grimpe, 1921, p. 298; *nom. correct.* Clarke, 1988, p. 334, *pro* Sepiolioidea Fioroni, 1981, p. 181] [=Sepiolaemorphae Grimpe, 1922, p. 42; =Sepioloidea Starobogatov, 1983, p. 7].

Shell thin, rudimentary gladius-like structure or absent, located in the anterior mantle; pro-ostracal anterior portion narrow, rodlike, either long or short, never reaching posterior shell margin, posterior portion Y-shaped with posterolateral projections.

PUTATIVE SEPIOLIDS

Family BELOSEPIELLIDAE Naef, 1921

[Belosepiellidae, Naef, 1921, p. 536]

Belosepiella Alessandri, 1905, p. 147 [**B. cossmanni;* SD Curry, 1955, p. 116] [=*partim Vasseuria* Munier-Chalmas, 1880]. Posterior shell remains mineralized, small-sized, capulus-shaped with conical depression on convex side (empty alveola?); apex nose-shaped, located close to posterior margin, covered by spine-like extension, which can easily be lost; anterior shell portion unknown (?organic); phragmocone probably absent. *Middle Eocene* (*Lutetian*): France, UK (England), Hungary.——Fig. 12,*a–d*. **B. cossmani; a–b,* BMNH C46559, Lutetian, Liancourt, France; *a,* ventral view; *b,* dorsal view, scale bar, 10 mm; *c,* lateral view, MNHN FB56208, Lutetian, Oise, France, scale bar 10 mm (new); *d,* drawing of longitudinal section (adapted from Haas, 2003, Fig. 18).

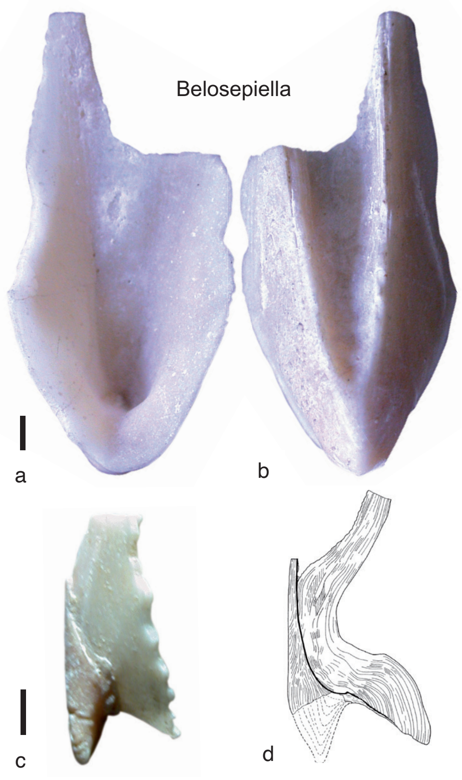

Fig. 12. Belosaepiidae (p. 26–27).

MYOPSIDA AND OEGOPSIDA

Introduction

Myopsida and Oegopsida are streamlined, fast-swimming squids of highest importance in marine food chains. Both groups bear a gladius in their dorsal mantle and were therefore traditionally united as Chondrophora (e.g., Keferstein, 1866 in 1862–1866) or more frequently as Teuthoidea (e.g. Naef, 1921; Jeletzky, 1966; Nesis, 1982; Clarke, 1988, Sweeney & Roper, 1998). The shared presence of a branchial canal and an interstellate connective support a sister-group relationship between the neritic myopsids and the oceanic oegopsids (Young & Vecchione, 1996). However, as already outlined earlier, the monophyly of the Teuthoidea Naef, 1916 is not beyond doubt because characters such as the possession of benthic, yolk-rich eggs, beak without angle point, or cornea-bearing eyes also suggests myopsid squids may derive from the sepioid lineage (e.g., Berthold & Engeser, 1987; Haas, 2003). Furthermore, molecular studies provided evidence of a closer phylogenetic relationship between myopsids and sepioids (e.g., Lindgren, Giribet, & Nishiguchi, 2004; Strugnell & others, 2005; Strugnell & Nishiguchi, 2007; Anderson & Lindgren, 2021). The inclusion of myopsids in the Sepioidea topology proposes an independent development of the teuthoid gladius. The formation of a chitinous gladius, which is widely accepted to be equivalent to a decalcified proostracum-bearing phragmocone, apparently occurred multiple times in the evolution of the Coleoidea (see Fuchs & Iba, 2015; Fuchs, 2016). The correlation between convergent traits and lifestyle in coleoids were impressively demonstrated by Lindgren and others (2012). It has also been shown that characters such as the cornea or the branchial canal might be habitat-related adaptations. Although most of the shared features of a clade consisting of sepioids and myopsids may be plesiomorphic within the Decabrachia, there is currently no general agreement concerning the monophyly of the Teuthoidea.

The term “fossil teuthids” frequently appears in the literature of the nineteenth and twentieth century. The reassignment of these Mesozoic gladius-bearing coleoids from the decabrachian to the octobrachian clade has no influence on neontological understanding (see Fuchs, 2020); however, it resolves many homology problems that arose from fossil soft part morphologies. For instance, the presence of uniserial circular suckers, ventromarginal mantle-gladius contact, the absence of sucker rings (and arm hooks), or the absence of mantle- and funnel-locking cartilages, would hardly be explainable if Mesozoic gladius-bearing coleoids were classified as ancestral teuthids (see DONOVAN & FUCHS, 2016, FUCHS, 2016). The systematic reassignment impacts the fossil record of teuthid decabrachians in a way that only a very few fossils can reliably be identified as myopsid and oegopsid remains. Currently, paleontological knowledge can contribute neither pros nor cons for the Teuthoidea concept.

Why are true oegopsids and myopsids so rare in the fossil record? This question arises particularly in the light of abundant and high-fidelity preserved (squid-like) octobrachians in Mesozoic *Konservat–Lagerstaetten* such as the Toarcian Posidonian shales of Central Europe, the Tithonian limestones of southern Germany, or the Cenomanian-Santonian limestones of Lebanon. In decay experiments, CLEMENTS and others (2017) observed that ammonitelic squids are more subject to decomposition than non-ammonitelic octopods. A taphonomical bias might be one explanation for the absence of Mesozoic teuthids. Alternatively, Mesozoic teuthids were adapted to other habitats, such as deeper waters. Ancestral character states observed in spirulids and sepiids by the end of the Cretaceous alternatively suggest that both myopsids and oegopsids may have first evolved during the Cenozoic (KRÖGER, VINTER, & FUCHS, 2011; FUCHS & others, 2012, 2013, FUCHS, 2019a). In this time period, typical *Konservat–Lagerstaetten* that provide the preservation potential of at least chitinous structures are unfortunately unknown.

In the following section, we consider fossil structures that were previously discussed as teuthoid remains.

Shell Remains. HAAS (1997, 2003) assumed the enigmatic Eocene genus *Vasseuria* to be a stem-lineage representative of the Myopsida. Before, Vasseuridae had variously been classified either as the last survivors of the belemnites or an aberrant offshoot of the Spirulida. This new idea of HAAS (1997, 2003) is mainly based on the retention of—by contrast to spirulids and sepiids—a straight phragmocone and a forward-projecting pro-ostracum. The shared presence of a bowl-shaped protoconch led him to place *Vasseuria* (and therefore the Myopsida) closer to the sepiid lineage than to the spirulid branch that is typified by an egg-shaped protoconch. Since his argument creates stratigraphic as well as phylogenetic problems, and since affiliations with oegopsid squids cannot properly be excluded, the entire family Vasseuridae (including *Vasseuria* and *Styracoteuthis*) is considered as Decabrachia *incertae sedis*.

KRETZOI (1942) and several later authors (e.g., JELETZKY, 1966; DOYLE, DONOVAN, & NIXON, 1994) determined the shell remains of *Necroteuthis* from the Oligocene of Hungary to be a teuthoid gladius, whereas other workers assumed a mineralized dorsal shield of a sepiid cuttlebone (e.g., RIEGRAF, JANSSEN, & SCHMITT-RIEGRAF, 1998). Most recent studies suggest a non-mineralized gladius morphologically intermediate between the Loligosepiina and Vampyromorpha (KOŠŤÁK, & others, 2021; FUCHS, 2020).

Non-mineralized, spatulate-shaped fossils have repeatedly been interpreted as a teuthid gladius (ENGESER & PHILLIPS, 1988). The Early Permian genus *Glochinomorpha* GORDON, 1971 is based on belemnoid hooks associated with leaf-like structures (ENGESER & PHILLIPPS, 1986; DOYLE, DONOVAN, & NIXON, 1994; FUCHS, 2021).

Two Triassic gladiuses (*Germanoteuthis* and *Reitneriteuthis*) are here classified as octobrachian gladius owing to their similarity to Jurassic examples (FUCHS, 2020). Teuthid affinities of the Triassic genus *Idahoteuthis* DOGUZHAEVA & others, 2018 are rejected owing to associated belemnoid arm hooks.

Statoliths. CLARKE and FITCH (1975, 1979) recognized myopsids and oegopsids among the first fossil statoliths. Their samples came from the Cenozoic successions of

North America (ten myopsid species, middle Eocene–lower Pleistocene; five oegopsid species, upper Pliocene–lower Pleistocene). Since these statoliths were isolated without any further body remains, Clarke and Fitch introduced a parataxonomy based on statoliths (similar to the parataxonomy based on belemnoid arm hooks). Clarke, Maddock, and Steurbaut (1980) found the first statoliths from Europe. These samples recovered from the lower Miocene (Burdigalian) were identified as *Loligo* sp. Neige, Lapierre, and Merle (2016) distinguished between sepiid, myopsid, and oegopsid statoliths from the Eocene of France. Lehmann (2010) recently reemphasized that statoliths can easily be confused with otoliths and suggested that fish remains commonly identified as *Neobythinarum* (e.g., from the Eocene of France) might represent cephalopod statoliths.

From Lower (Hettangian–Toarcian), Middle (upper Bathonian–upper Callovian) and Upper Jurassic deposits from the UK, Clarke, and Maddock (1988) as well as Hart and others (2009, 2010, 2015) isolated huge amounts of statoliths possessing an unusual morphology, which has given rise to a controversial discussion about their systematic affinities. Clarke and Maddock (1988) assumed teuthid affinities, whereas Fuchs (2006), and Clarke and Hart (2018) did not want to exclude the option that these uniform statoliths may belong to belemnoteuthid belemnites. Engeser (1990, p. 156) reemphasized that these Jurassic statoliths should not be excluded per se from being categorized as ammonoid cephalopods.

Since a fossil (para)genus that is based on statoliths has not yet been introduced, please refer to Clarke and Hart, 2018 for more morphological information about fossil statoliths.

Beaks.Tanabe, Hikida, and Iba (2006) erected the genus *Yezoteuthis* from the Late Cretaceous (Campanian) of northern Japan on the basis of the existence of two upper beaks. After a phylogenetic comparison with extant forms, the fossil beaks grouped with oegopsid teuthids. Furthermore, the Santonian genus *Harboroteuthis* based on a lower beak has been classified as a member of the Teuthida. Herein, we preliminarily follow the original classification, but it is worthwhile to note—particularly in the light of poor knowledge about belemnoid beaks—that we are still far from being able to reconstruct ancestral character states of beaks.

Arm hooks. Pre-Cenozoic arm hooks, commonly attributed to belemnoid coleoids, strikingly differ from those of various oegopsid families (Fuchs & Hoffmann, 2017). The oegopsid type of arm hook is mainly characterized by an aperture, which is known to represent a reminiscence of the decabrachian sucker rings (Engeser & Clarke, 1988; Fuchs, Hoffmann, & Klug, 2021. Harzhauser (1999), who recorded cephalopod arm hooks from the middle Miocene of Austria, explained their assignment to onychoteuthid oegopsids, although the lack of an aperture is quite atypical.

In summary, the existence of oegopsid and myopsid squids is reliably evidenced by Cenozoic statoliths. Their coexistence with primitive spirulids and sepiids during the Late Cretaceous needs further confirmation.

Order MYOPSIDA d'Orbigny, 1842 in Ferussac & d'Orbigny, 1835–1848

[*nom. correct.* Keferstein, 1866 in 1862–1866, p. 1441, *pro* Myopsidés d'Orbigny, 1842 in Ferussac & d'Orbigny, 1835–1848, p. xxxvii; *nom. transl.* Chun, 1910, contents page, *ex* superfamily Myopsidae d'Orbigny, 1842 in Ferussac & d'Orbigny, 1835–1848, p. xxxvii, *non* Myopsida *sensu* Chun, 1910] [=Loliginida *sensu* Khromov, 1990 and Haas, 2002]

Order OEGOPSIDA d'Orbigny, 1842 in Ferussac & d'Orbigny, 1839–1848

[*nom. correct.* Keferstein, 1866 in 1801–1866, p. 1442, *pro* Oigopsidés d'Orbigny, 1842 in Ferussac & d'Orbigny, 1839–1848, p. xxxvii; *nom. transl.* Chun, 1910, p. 3, *ex* Oigopsidae d'Orbigny, 1842 in Ferussac & d'Orbigny, 1839–1848, p. xxxvii]

SUPPOSED 'TEUTHIDS'

Harboroteuthis Tanabe, Misaki & Ubukata, 2015, p. 34 [**H. poseidon;* M]. Beak large sized; upper beak

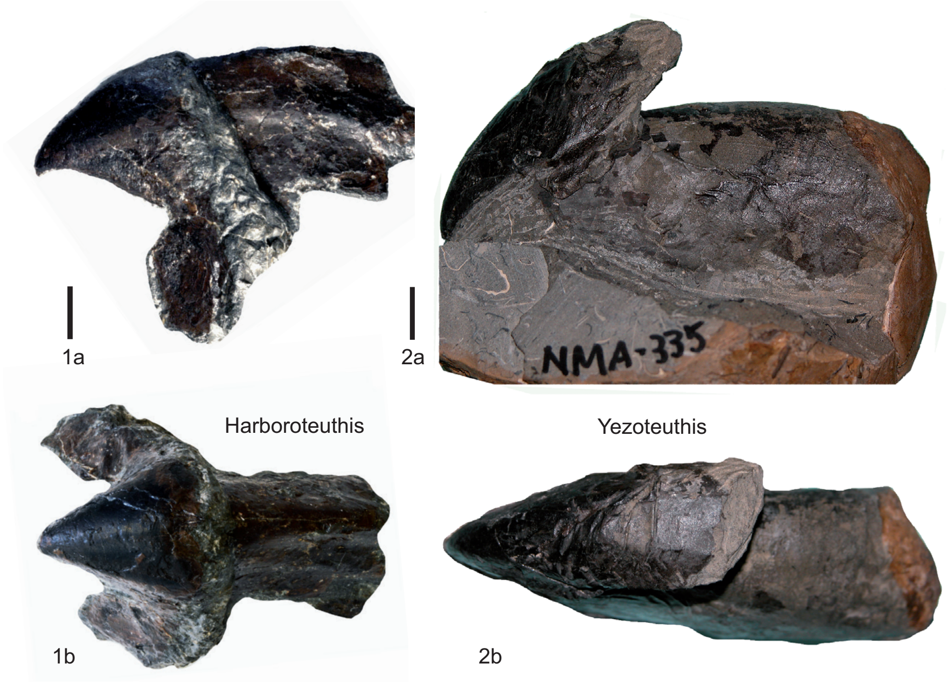

Fig. 13. Supposed 'Theuthids' (p. 29–30).

unknown; lower beak with long rostrum, sharply pointed; hood relatively narrow, weakly convex, notch weakly developed; wing short, shoulder dorsally convex; crest anteriorly weakly curved; lateral wall comparatively long, parallelogram-shaped, with broad fold. *Upper Cretaceous* (upper *Santonian*): northern Japan.——Fig. 13,*1a–b*. **H. poseidon,* holotype, KMNH IvP 902,002, upper Santonian, Harborogawa Formation, Harboro region, northern Japan; *1a,* left lateral view, *1b,* dorsal view; scale bar 10 mm (Tanabe, Misaki, & Ubukata, 2015, Fig. 7).

Yezoteuthis Tanabe, Hikida, & Iba, 2006, p. 142 [**Y. giganteus;* M]. Beak large sized; lower beak unknown; upper beak with rostrum long, sharply pointed; hood posteriorly extended, gently convex; wing concave inward at mid-lateral margin, ventral margin posteriorly weakly expanded; shoulder ventrally gently arched; lateral wall margin concave; crest gently convex; outer lamella smooth on dorsal side; inner lamella sculptured by equally spaced, very fine concentric growth lines with fine radial striations on ventrolateral side. *Upper Cretaceous* (*lower Campanian*): northern Japan.——Fig. 13, *2a–b,* **Y. giganteus,* holotype, NMA-335, Campanian, Osousyunai Formation, Nakagawa region, northern Japan; *2a,* left lateral view; *2b,* dorsal view; scale bar, 10 mm (Tanabe, Hikida, & Iba, 2006, fig. 1.4–1.6).

DECABRACHIA *incertae sedis*

Family VASSEURIDAE Naef, 1921

[*nom. correct.* Doyle, Donovan, & Nixon, 1994, p. 6, *pro* Vasseuriidae, Naef, 1921, p. 534] [=Neobelemnitidae Pavlow in Schwetzow, 1913, p. 44, *partim*]

Phragmocone orthoconic with moderate chamber length and unusually curved septa; sutures in early stages symmetrical; in later stages asymmetrical with wide ventral lobes and lateral saddles, dorsal suture straight; septa distinctly inclined; pro-ostracum probably present; conotheca without tabular nacre; post-alveolar sheath belemnoid-like in being long and conical.

Vasseuria Munier-Chalmas, 1880, p. 183 [**V. occidentalis;* M]. Phragmocone orthoconic with an apical angle of 14–15°; ratio chamber length-to-diameter ~0.2–0.3; cross sections oval; dorsoventrally flattened; septal necks retrochoanitic; siphuncle marginal; mediodorsal attachment scars rectangular; sheath investment-like; post-alveolar part long, conical, apically pointed; outer surface with longitudinal furrows and ridges, alveolar part rugose; pro-ostracum present; protoconch cup-like; caecum and prosipho unknown. *Eocene* (*Barto-*

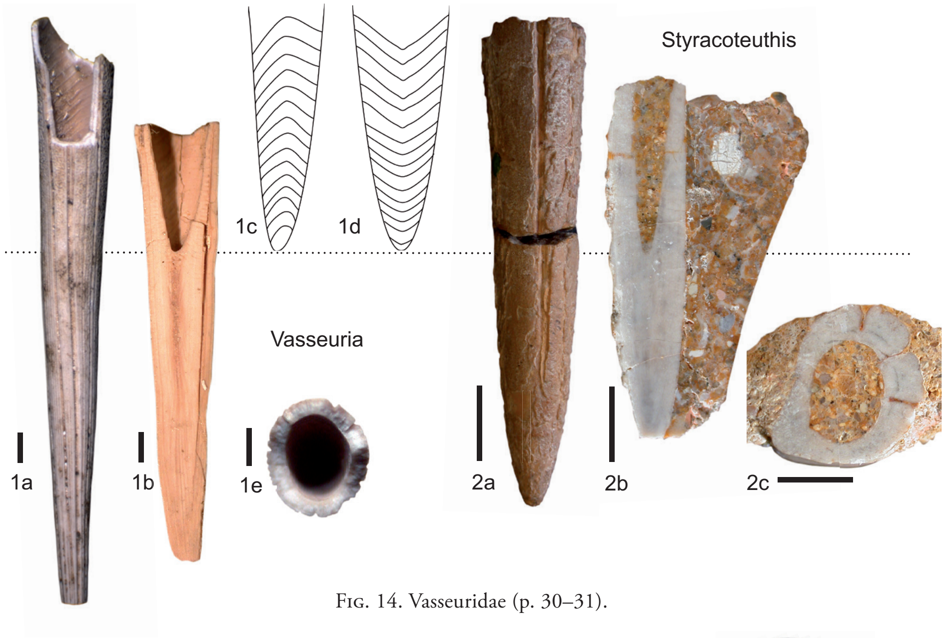

FIG. 14. Vasseuridae (p. 30–31).

nian): France, UK (England), Italy, ?Hungary.——FIG. 14,*1a–e*. **V. occidentalis*, BMNH C46546 (Eocene (Bartonian), France; *a,* sheath in lateral view; *b,* longitudinal section, *c,* drawing of lateral phragmocone with unusual suture lines; *d,* drawing of ventral phragmocone; *e,* transversal fracture of alveolar part; scale bars 10 mm (new)

Styracoteuthis CRICK, 1905, p. 275 [**S. orientalis;* M]. Phragmocone orthoconic with an apical angle of 11–12°; chambers comparatively low; sheath thick; post-alveolar part long, conical, pointed; outer surface typified by two dorsolateral and one mediodorsal deep, longitudinal grooves; proostracum possibly present; protoconch probably cuplike; caecum and prosipho unknown. ?*Palaeocene–Eocene:* Israel, Oman, Pakistan.——FIG. 14, *2a–c*. **S. orientalis,* holotype, BMNH c.8010, lower Eocene, Oman; *a,* sheath in dorsal view*; b,* longitudinal section (Ru Smith collection); *2c,* transversal section of alveolar part; scale bars 10 mm (new).

Family BAYANOTEUTHIDAE
Naef, 1922

[*nom. transl.* JELETZKY, 1966, p. 6, *ex* subfamily Bayanoteuthinae, NAEF, 1922, p. 259] [=Neobelemnitidae PAVLOW in SCHWETZOW, 1913, p. 44, *partim*]

Bayanoteuthis MUNIER-CHALMAS, 1872, p. 530 [**Belemnites rugifer* SCHLOENBACH, 1868, OD (M)] [=*Belemnites* LAMARCK, 1801]. Sheath thick, post-alveolar part very long, with radial-concentrical growth rings, outer surface with dorso- (or ventro-)

FIG. 15. Bayanoteuthidae (p. 31).

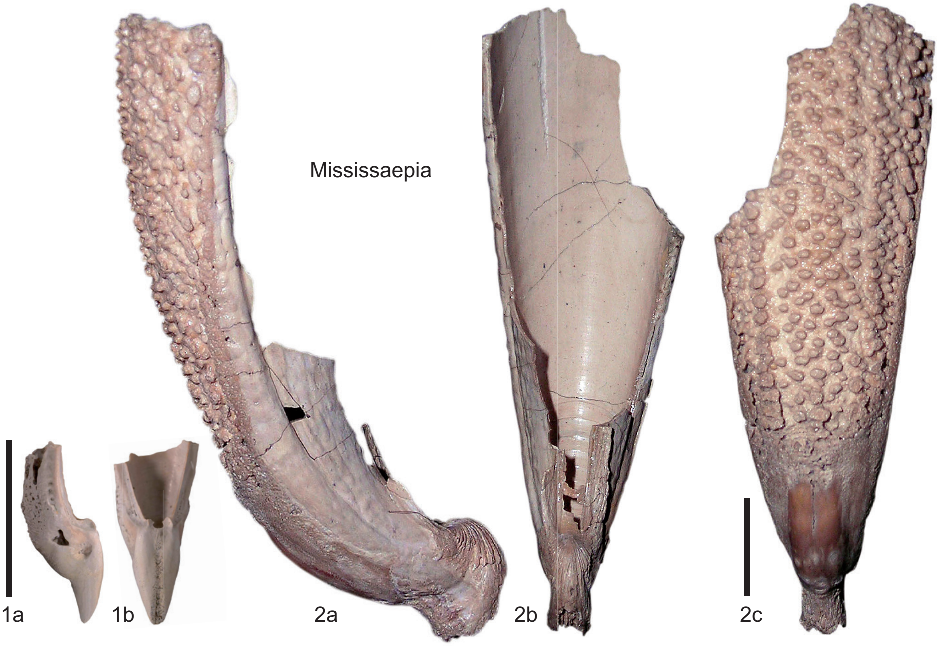

Fig. 16. Mississaepiidae (p. 32).

lateral furrows and faint longitudinal striation; apex unknown; phragmocone longiconic, elliptical in cross section, apical angle low. *Middle Eocene:* northern Italy, ?France, ?Australia.——Fig. 15, *a–d.* **B. rugifer* (Schloenbach), MNHN R07487, middle Eocene, northern Italy; *a,* sheath in lateral view, scale bar 10 mm; *b,* close-up of alveolar part, scale bar 10 mm; *c,* transversal section of alveolar part; *d,* transversal section of post-alveolar part (new).

Family MISSISSAEPIIDAE Doguzhaeva, Weaver, & Ciampaglio, 2014

[Mississaepiidae Doguzhaeva, Weaver, & Ciampaglio, 2014, p. 153]

Mississaepia Weaver, Dockerty, & Ciampaglio, 2010, p. 58 [**M. mississippiensis;* M]. Phragmocone cyrtoconic, curvature involves chambers 2–10, cross sections circular, chamber length variable, particularly in earliest stages; early septa distinctly inclined, later perpendicular to phragmocone axis, septa weakly mineralized; ventral suture simple, dorsal suture with wide, indistinct saddle; siphuncle submarginal; pro-ostracum unknown; conotheca without tabular nacre; sheath well developed with complex swellings and extensions, post-alveolar part long, ventrally spinelike, dorsally callus-like thickened; anterior alveolar part investment-like with bipartite ventral ridge, laterally and dorsal surfaces extensively rugose, dorsolateral sides with rudimental flange giving dorsal sheath shield-like appearance. *Eocene* (*Bartonian–Prianbonian*): USA.——Fig. 16,*1–2.* **M. mississippiensis,* Bartonian-Prianbonian boundary, Moodys Branch Formation, Mississippi, USA; *1a–b,* MGS 1945, lateral (*a*) and ventral (*b*) views; scale bar 8 mm (Doguzhaeva, Weaver, & Chiampaglio, 2014, fig. 1); *2a–c,* paratype, MGS 1941; lateral (*a*), ventral (*b*), and dorsal (*c*) views, scale bar 10 mm (Weaver, Dockery, & Ciampaglio, 2010, pl. 1,G–H).

FAMILY UNKNOWN

Belocurta Avnimelech, 1958, p. 61 [**B. yahavensis;* OD]. Phragmocone cyrtoconic, cross section laterally compressed; septa oblique (?); post-alveolar part of the sheath short, apically obtuse, dorsally thickened; ventral process present (?). *Palaeocene:* Israel, Belgium.

REJECTED MYOPSIDA

Idahoteuthis Doguzhaeva & others, 2018, p. 347 [**I. parisiana;* OD]. *Lower Triassic:* USA (Idaho).

REJECTED TEUTHIDA

Glochinomorpha Gordon, 1971, p. C35 [**G. stifeli;* p. C36; OD]. *Permian* (*Kungurian*): USA (Utah).

For detailed systematic information on *Glochinomorpha,* see Fuchs, 2021.

ABBREVIATIONS FOR MUSEUM REPOSITORIES

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

BSPG: Bayerische Staatssammlung für Paläontologie und Geologie, München, Munich, Germany

GBA: Geologische Bundesanstalt Wien, Germany

GE: The Moravian Museum, Brno, Czech Republic

IGP: Institute of Geology and Palaeontology, Charles University, Prague, Czeck Republic

KMNH: Kitakyushu Museum of Natural History and Human History, Kitakyushu, Japan

MGPD: Paleontological Museum, University Padova, Italy

MMK: Statens Naturhistoriske Museum, Copenhagen, Denmark

MNHNL: Musée National d´Histoire Naturelle de Luxembourg, Luxembourg

NMA: Nakagawa Museum of Natural History, Nakagawa, Japan

PRI: Paleontological Research Institution, Ithaca, New York, USA

RGM: Naturalis, National Museum of Natural History, Leiden, The Netherlands

SMNS: Staatliches Museum für Naturkunde Stuttgart, Germany

SNM Z: Slovak National Museum, Bratislava, Slovakia

USNM: US National Museum of Natural History, Washington, DC, USA

VM: Museums Victoria, Melbourne, Australia

Q: Geological department of the University of Concepcion, Chile

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