TREATISE
ONLINE
Number 138

Part M, Chapter 23G:
Systematic Descriptions: Octobrachia

Dirk Fuchs

2020

KU PALEONTOLOGICAL INSTITUTE
The University of Kansas
Lawrence, Kansas, USA
ISSN 2153-4012
paleo.ku.edu/treatiseonline

PART M, CHAPTER 23G: SYSTEMATIC DESCRIPTIONS: OCTOBRACHIA

Dirk Fuchs

[SNSB-Bayerische Staatssammlung für Paläontologie und Geologie, Richard-Wagner-Str. 10, 80333 Munich, Germany, drig.fuchs@gmail.com]

INTRODUCTION

As the name Octobrachia indicates, the key character that unites this group of phragmocone-less coleoids is the presence of four arm pairs. The only exception represents the modern deep sea squid *Vampyroteuthis* Chun, 1903, which is typified by an additional pair of filamentous arms. The position of this arm pair within the arm crown as well as embryonic development suggest that true octobrachians (Cirrata Grimpe, 1916; Incirrata Grimpe, 1916) are lacking the dorsolateral (II) arm pair (Boletzky, 1978–1979; 1999; Young & Vecchione, 1996). Ten arms combined with the possession of a well-developed gladius (as well as molecular genetic data) induced some authors to link *Vampyroteuthis* with decabrachians (e.g., Jeletzky, 1966; Fioroni, 1981), but systematists now generally accept *Vampyroteuthis* as a phylogenetic relic that belongs to the octobrachiate branch.

Despite a general systematic-phylogenetic agreement, the nomenclatural history of the Octobrachia is surprisingly inconsistent in the literature. Leach (1817, p. 137) distinguished between the orders Octopoda and Decapoda. His Octopoda included only octopods without fins and cirri along their arms. Keferstein (1866, p. 1420) and Haeckel (1866, p. 116) first delimited octopods with fins and cirri (Cirroteuthidae) from fin- and cirri-less octopod families (Eledoniden, Phylonexiden). While the former author kept Leach's Octopoda/Decapoda concept, the latter used the names Octobrachien and Decabrachien for the same grouping. Increasing knowledge about mesopelagic cirrate octopods during the second half of the 19th century provoked Grimpe (1916, p. 353) to subdivide the order Octopoda into the finned Cirrata and the finless Incirrata. The large majority of subsequent workers followed this more than 100-years-old concept, although alternative names for the same groupings have been proposed (e.g., Naef, 1922; Jeletzky, 1966; Starobogatov, 1983; Young, 1989; Engeser, 1990). After Grimpe (1916), controversial discussions focused only on the position and rank of the Vamyromorpha with its only living representative *Vampyroteuthis* (e.g., Pickford, 1939; Boletzky, 1978–1979; Fioroni, 1981). Since its closer relationship with the octobrachiate lineage has been established, various names have been proposed for the monophylum uniting the Octopoda and the Vampyromorpha. Berthold and Engeser (1987) proposed Octopodiformes, Engeser and Bandel (1988) Vampyromorphoidea, Doyle, Donovan, and Nixon (1994) Octobrachia, Boletzky (1992) Vampyropoda, and Haas (2002) Octobrachiomorpha. A comparison of the most recent coleoid literature shows that only the names Octobrachia, Vampyropoda, and Octopodiformes have found wide acceptance. The present classification prefers the superorder Octobrachia in order to accommodate the second coleoid superorder Decabrachia (see Hoffmann, 2015). It therefore follows the concept of

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FIORONI (1981) except that Vampyromorpha is included within the Octobrachia rather than Decabrachia. It is hence identical to the system proposed by DOYLE, DONOVAN, and NIXON (1994); SALVINI-PLAWEN and STEINER (1996); and SWEENEY and ROPER (1998) and differs only slightly from that of YOUNG, VECCHIONE, and DONOVAN (1998), who have applied the name Octopodiformes instead of Octobrachia.

Until 1986, the fossil record of the Octobrachia comprised only four specimens of the Upper Cretaceous incirrate *Palaeoctopus* WOODWARD, 1896b and a few Cenozoic argonaut egg cases. Owing to some resemblance with modern gladii, the highly diverse group of Mesozoic gladius-bearing coleoids were classified as Teuthoidea (fossil teuthids; e.g., NAEF, 1922; JELETZKY, 1966; DONOVAN, 1977; TEICHERT, 1988; RIEGRAF, JANSSEN, & SCHMITT-RIEGRAF, 1998; see also FUCHS, 2016, *Treatise Online*, Part M, Chapter 9B on fossil gladii and DONOVAN & FUCHS, 2016, *Treatise Online*, Chapter 13 on fossilized soft tissues). After BANDEL and LEICH (1986) postulated closer affinities to vampyromorphs rather than to teuthids, the fossil record of Octobrachia must suddenly be considered as rich (see ENGESER, 1988). Subsequent focus on extraordinarily well-preserved soft tissues known from Konservat-Lagerstätten such as the Lower Jurassic (Toarcian) Posidonia Shales of Central Europe (FUCHS, KEUPP, & SCHWEIGERT, 2013); the Middle Jurassic (Callovian) of Christian Malford, UK and La Voulte-sur-Rhône, France (FUCHS, 2014; KRUTA & others, 2016); the Upper Jurassic (Kimmeridgian–Tithonian) Solnhofen and Nusplingen Plattenkalks of Germany (HAAS, 2002; FUCHS, KEUPP, & ENGESER, 2003; FUCHS, 2006a; FUCHS, KLINGHAMMER, & KEUPP, 2007; KLUG & others, 2005, 2015); and the Upper Cretaceous (Cenomanian–Santonian) Plattenkalks of Lebanon (FUCHS, 2006b; FUCHS & LARSON, 2011a, 2011b; JATTIOT & others, 2015) have confirmed octobrachiate affiliations (also see DONOVAN & FUCHS, 2016, *Treatise Online*, Part M, Chapter 13).

The systematic rearrangement of the three fossil suborders Prototeuthina, Loligosepiina, and Teudopseina (NAEF's Mesoteuthoidea) had no influence on the ordinal system of the Octobrachia. BANDEL and LEICH (1986) and shortly later ENGESER (1988) considered the new octobrachians as vampyromorphs. Since the octopod gladius vestiges (fin supports), particularly the unpaired gladius rudiment of cirrate octopods, has been recognized as derivatives of a teudopseid gladius, the Teudopseina have been seen as the stem group of the Octopoda (HAAS, 2002; BIZIKOV, 2004; FUCHS, 2009; FUCHS & SCHWEIGERT, 2018; FUCHS & others, 2019). Owing to similarities in body and gladius shapes, loligosepiid forms remained linked with Vampyromorpha (e.g., CLARKE, 1988; DOYLE, DONOVAN, & NIXON, 1994; FISCHER & RIOU, 2002; STRUGNELL & others, 2006; FUCHS, 2006c; FUCHS & WEIS, 2008). In contrast to Loligosepiina and Teudopseina, the systematic position of the Prototeuthina represented by the Plesioteuthidae have not yet received general consensus (compare DOYLE, DONOVAN, & NIXON, 1994; YOUNG, VECCHIONE, & DONOVAN, 1998; VECCHIONE & others, 1999; HAAS, 2002; STRUGNELL & others, 2006; FUCHS, KLINGHAMMER, & KEUPP, 2007; FUCHS & LARSON, 2011a). For reasons comprehensively outlined in *Treatise Online*, Part M, Chapter 9B (FUCHS, 2016) and Chapter 13 (DONOVAN & FUCHS, 2016), the Prototeuthina (one family, 12 genera) are here treated as a stem group of the Octobrachia.

The system of the Octobrachia is accordingly enriched by 61 fossil gladius- or gladius vestige-bearing genera. They belong to 15 families arranged in 3 extinct and 3 extant suborders. The suborders Loligosepiina (4 families, 9 genera) and Teudopseina (6 families, 24 genera) are respectively placed with the Vampyromorpha and Octopoda. *Palaeocirroteuthis* is thus far the only fossil genus of the extant suborder Cirrata, while the Incirrata is represented by the fossil family Palaeoctopodidae, consisting of at least 2 genera. *Styletoctopus* on the one side, and 5 argonaut genera on the other side are considered as fossil representatives of the extant families Octopodidae and Argonautidae. In addition, one ichnotaxon (*Oichnus*), which consists of a drilling hole, is assigned to the Octopodidae.

The oldest known genus (*Germanoteuthis*) of the Octobrachia (Fig. 1) comes from the Middle Triassic (Ladinian) of the German Muschelkalk and, due to its gladius morphology, is preliminarily classified as a member of the Prototeuthina (Schweigert & Fuchs, 2012). The genus *Pohlsepia* from the Pennsylvanian Mazon Creek Lagerstätte (Illinois, USA) shows the relief and stains of what resembles the sac-like body of an octopod. Based on the lack of a gladius and a well-defined head, as well as the presence of 10 arms and fins, Kluessendorf and Doyle (2000) discussed cirrate affinities. Apart from the fact that interpretations based on vague outlines of structures (e.g., 10 arms) in the single Mazon Creek specimen appear premature, the total absence of any gladius vestige speaks against placement within the Cirrata. One might alternatively assume incirrate affiliations; however, this interpretation is also questionable in the light of well-developed gladius vestiges in Upper Cretaceous incirrates, a fact that Kluessendorf and Doyle (2000) were not aware of (Fuchs, 2009; Fuchs, Bracchi, & Weis, 2009).

In general, the phylogenetic origin of the Octobrachia within a group of ten-armed coleoids is unquestioned (see, e.g., Jeletzky, 1966; Boletzky, 1992). In detail, proposed ideas have concentrated on the Phragmoteuthida (see Fuchs & Donovan, 2018, *Treatise Online*, Part M, Chapter 23C), a Middle Triassic–Lower Jurassic group of phragmocone-bearing belemnoids with a three-lobed pro-ostracum and without a solid rostrum (Jeletzky, 1966, p. 35; Donovan, 1977, p. 43; Doyle, Donovan, & Nixon, 1994, p. 4; Fuchs, 2006d, p. 121; also see Fuchs & Donovan, 2018, *Treatise Online,* Chapter 23C). Owing to the retention of a closed, funnel-like conus, Fuchs (2006a, Fig. 3,*6*–3,*13*) suggested the prototeuthid gladius to be more ancestral than the ventrally opened conus of loligosepiid and teudopseid gladii. This assumption and the subsequent discovery of the Ladinian prototeuthid *Germanoteuthis*, which is only slightly younger than the oldest unambiguous phragmoteuthid *Breviconoteuthis* (Anisian), challenge the classical view. More recently, Schweigert and Fuchs examined the pros and cons of the octobrachian root stock (see Schweigert & Fuchs, 2012). The deep sea vampire squid *Vampyroteuthis* is the only living representative of the order Vampyromorpha. The suborder Loligosepiina has often been referred to as the phylogenetic origin of the Vampyromorpha (e.g., Doyle, Donovan & Nixon, 1994; Fuchs & Weis, 2008; Fuchs & Iba, 2015). *Necroteuthis* from the Oligocene of Hungary supports this view as its gladius exhibits a mosaic of loligosepiid and vampyroteuthid characters. *Necroteuthis* is accordingly seen as the connecting link between the two vampyromorph suborders.

The origin of the Octopoda has been discussed by Haas (2002), Bizikov (2004), Fuchs (2009), Fuchs and Schweigert (2018), and Fuchs and others (2019). Each of the latter authors assumed the octopod root within the Teudopseina, which is why this group is here dealt with as the stem group of the Octopoda (Cirrata plus Incirrata). Middle Jurassic (Callovian) *Proteroctopus* had originally been described as the oldest record of an incirrate octopod. This idea has been doubted by Engeser (1988), Haas (2002), Fuchs (2009), and Fuchs, Bracchi, and Weis (2009). Furthermore, recent CT-scans by Kruta and others (2016) have indeed revealed a well-developed gladius and have therefore confirmed placement outside the Incirrata. Instead, Callovian *Pearceiteuthis* and Kimmeridgian *Patelloctopus* (superfamily Muensterelloidea) may be seen due to their reduced gladius as the teudopseid branch leading to the Cirrata and Incirrata (Fuchs & others, 2019). Upper Cretaceous (Cenomanian) genera *Keuppia*

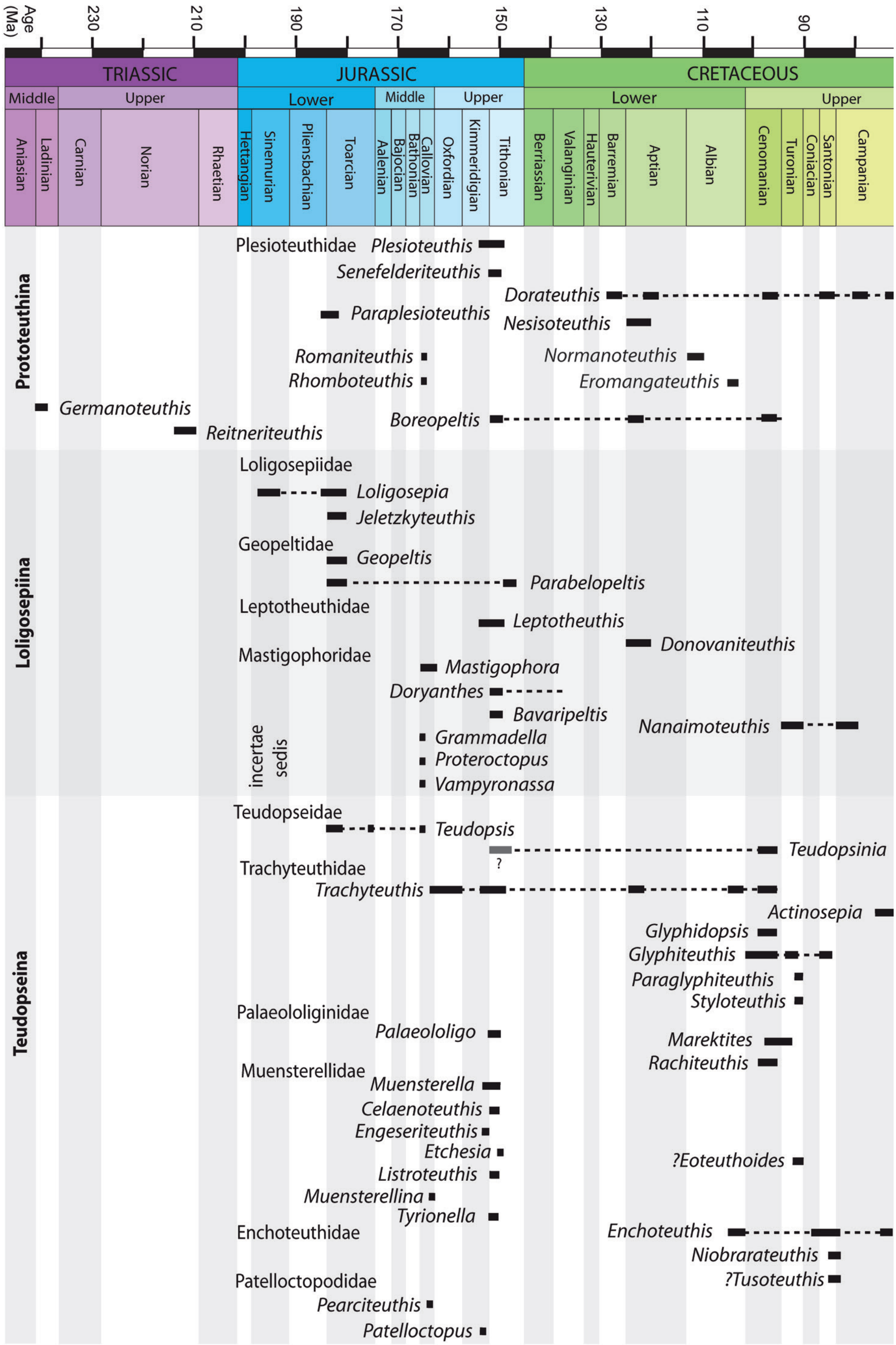


FIG. 1a. Stratigraphic distribution of suborders Prototeuthina, Loligosepiina, and Teudopseina genera, families, and superfamilies (new). Cirrata and Incirata are shown on page 6 in FIG. 1b. *Chart is continued on facing page.*

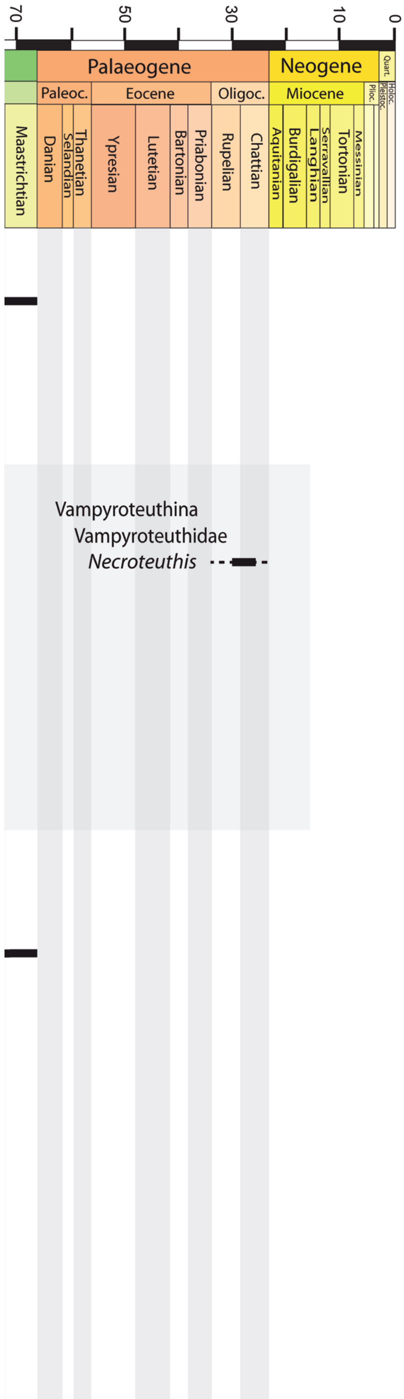


FIG. 1a. *Continued from facing page.*

and *Styletoctopus,* with their bipartite gladius, therefore remain the oldest known members of the incirrate clade (FUCHS, 2009; FUCHS, BRACCHI, & WEIS, 2009).

The system of fossil Octobrachia is dominated by the morphology of the gladius and gladius vestige, which is comprehensively explained in *Treatise Online,* Part M, Chapter 9B (FUCHS, 2016). Size, position, length, and width categories, as used in the diagnoses, are listed in Table 1. A comparative overview of diagnostic gladius parameters (e.g., gladius width, median field width, lateral fields width, and hyperbolar zone length) in Table 2 helps to identify the family level.

Superorder OCTOBRACHIA Haeckel, 1866

[*nom. corr.* BOETTGER, 1952, p. 268, *pro* Octobrachien HAECKEL, 1866, p. 116; *nom. transl.* FIORONI, 1981, p. 225, *ex* order Octobrachia BOETTGER, 1952, p. 268, 290] [=Vampyromorphoidea ENGESER, 1986, p. 27; =Octopodiformes BERTHOLD & ENGESER, 1987, p. 202; =Vampyropoda BOLETZKY, 1992, p. 756; =Octobrachiomorpha HAAS, 2002, p. 341]

Coleoids whose dorsolateral arm pair (homologous to arm pair II in Decabrachia) is either modified into retractile filaments or absent, true tentacles (arm pair IV) absent; shell developed as gladius (gladius length equals mantle length), reduced to unpaired or paired gladius vestiges (vestige length shorter than mantle length), or absent; suckers radially symmetrical, sessile, uniserial, alternating, or biserial; sucker rings absent; cirri biserial or absent; fins, when present, with cartilaginous axial support, position subterminal, shape variable, number either one or two pairs, attachment site dorsal surface of posterior gladius; shape of muscular mantle variable, attachment to gladius ventromarginal; funnel- and mantle-looking cartilages absent (rudimentary in *Vampyroteuthis*).

Suborder PROTOTEUTHINA Naef, 1921

[*nom. correct.* JELETZKY, 1965, p. 75, *pro* Prototeuthoidea NAEF, 1921a, p. 534; *nom. correct.* JELETZKY, 1966, p. 43, *pro* Prototeuthidina JELETZKY, 1965, p. 75]

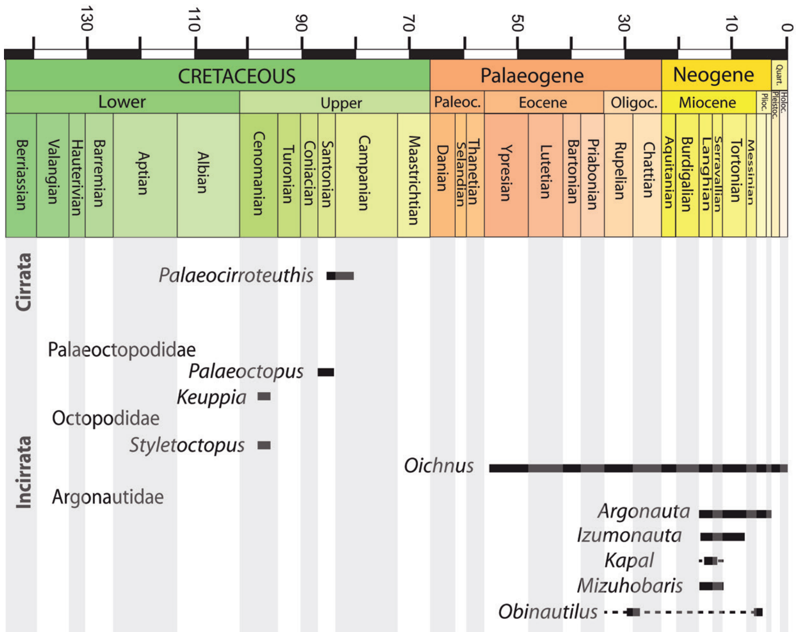


FIG. 1b. Stratigraphic distribution of suborders Cirrata and Incirrata genera, families, and superfamilies (new).

Octobrachiates with torpedo-shaped body; gladius length (=median field length) equals mantle length; gladius with triangular median field and ventrally closed (funnel-like) conus; gladius very slender to moderately wide, maximum gladius width usually coincides with maximum median field width (by contrast to Loligosepiina and Teudopseina); median field slender (compared to most loligosepiids and teudopseids), with median and lateral reinforcements; lateral reinforcements and central median field may be projected; median field area large to very large compared to lateral fields (gladius is median field dominated); hyperbolar zone indistinct or absent, hyperbolar zone length to median field length <0.6; lateral fields very slender to moderately wide. ?*Middle Triassic (Ladinian), Lower Jurassic (upper Pliensbachian)–Upper Cretaceous (Maastrichtian).*

Family PLESIOTEUTHIDAE Naef, 1921

[Plesioteuthidae NAEF, 1921a, p. 534]

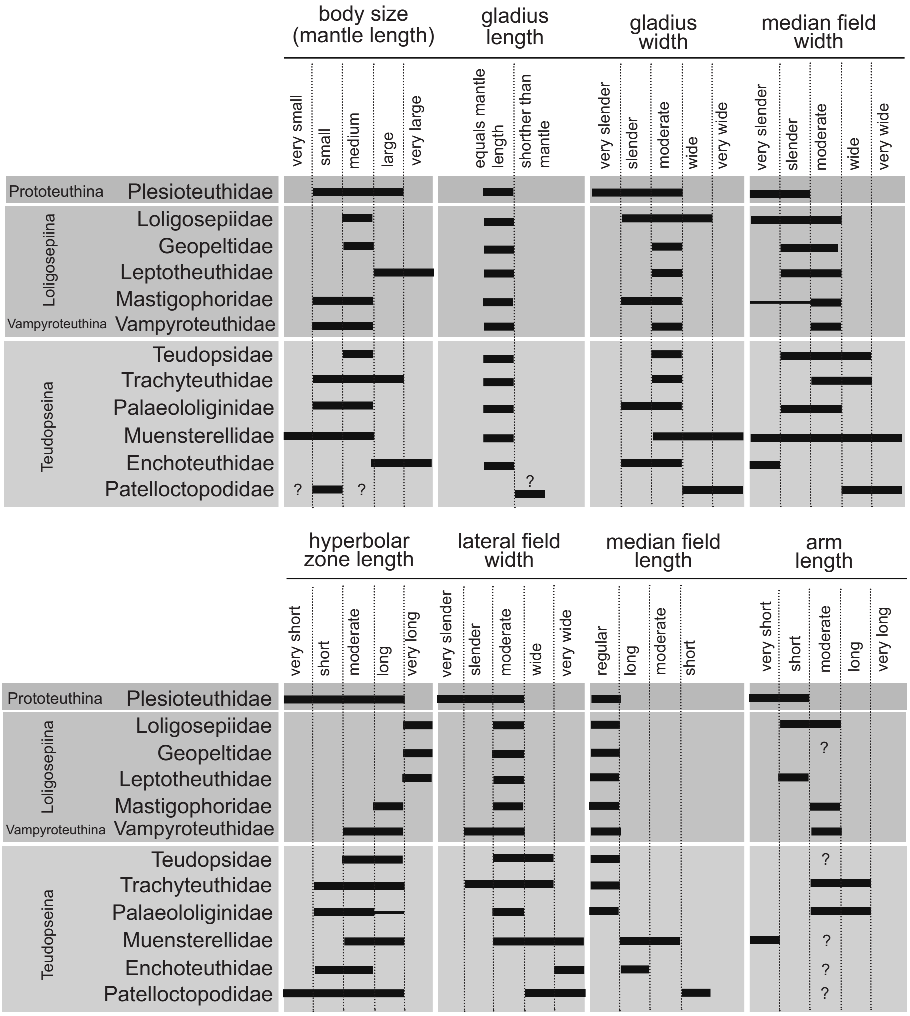
Medium-sized prototeuthids; gladius very slender to moderately wide (gladius $width_{max}$ to gladius length 0.05–0.25), with triangular median field and ventrally closed (funnel-like) conus; median field very slender to slender (median field $width_{hypz}$ to hyperbolar zone length <0.35 = opening angle <20°); median field area large to very large (median field area to gladius area 0.70–1.0); lateral fields very slender to moderately wide; hyperbolar zone very short to long (hyperbolar zone length to median field length <0.6); median and lateral reinforcements present on the median field; vestiges of septa and guard unknown; eight arms equipped with uniserial circular suckers, sucker-rings absent; arm length variable; funnel- and nuchal-locking cartilages absent; fins terminal; fin shape variable. *Lower Jurassic (upper Pliensbachian, lower Toarcian)–Upper Cretaceous (Maastrichtian).*

Plesioteuthis WAGNER, 1859, p. 277 [**Loligo priscus* RÜPPELL, 1829; SD BÜLOW-TRUMMER, 1920]. Medium-sized plesioteuthids; gladius very slender to slender (gladius $width_{max}$ to gladius length 0.05–0.15); median field slender (median field $width_{hypz}$ to hyperbolar zone length 0.25–0.34 = opening angle 12°–19°) with a pronounced unipartite or bipartite median keel in posterior half and lateral

TABLE 1: Size, position, length, and width categories used in the diagnoses of fossil Octobachia.

Character	Character state	Categories	Indices	Correspond-ing character	Character state corresponding character	Remarks
gladius length	as long as mantle	1	gladius length: mantle length			v
	shorter than mantle	<1				
median field length	regular	1	median field length: gla-dius length			ratios of <1 refer only to Muensterelloidea
	long	0.75–0.99				
	moderate	0.74–0.50				
	short	<0.50				
hyperbolar zone length	very long	>0.70	hyperbolar zone length: median field length	free median field length		not meaningful in Muensterelloidea
	long	0.50–0.70				
	moderate	0.30–0.49				
	short	0.10–0.29				
	very short	<0.10				
median field width	very wide >60°	>1.15	median field $width_{hypz}$: hyperbolar zone length	opening angle of median field (inner asymptotes)		
	wide 39–60°	0.70–1.15				
	moderate 20–38°	0.35–0.69				
	slender 12–19°	0.20–0.34				
	very slender <12°	<0.20				
lateral field width	very wide	>2.50	lateral fields $width_{max}$: median field $width_{max}$			corresponds to patella width: median field $width_{max}$ in Muensterelloidea
	wide	2.00–2.50				
	moderate	1.00–2.00				
	slender	0.50–0.99				
	very slender	<0.50				
gladius width	very wide	>0.80	gladius $width_{max}$: gladius length			corresponds to patella width: gladius length in Muensterelloidea
	wide	0.50–0.80				
	moderate	0.20–0.49				
	slender	0.10–0.19				
	very slender	<0.10				
patella shape	wide oval	>1.20	patella width: patella length			only Muensterelloide
	cicular	0.80–1.20				
	long oval	<0.80				
position of patella apex	posterior	>0.60	hyperbolar zone length: patella length			only Muensterelloide
	central	0.40–0.60				
	anterior	<0.40				
free median field length	short	>0.70	patella length: gladius length	patella length	long	only Muensterelloide
	moderate	0.50–0.70			moderate	
	long	<0.50			short	
median field area	very large	>0.80	median field area: gladius $area_{total}$	lateral field area:	very small	
	large	0.60–0.80			small	
	moderate	0.40–0.59			moderate	
	small	0.20–0.39			large	
	very small	<0.20			very large	
body size	very large	>1500 mm				measured as mantle length
	large	401–1500 mm				
	medium	201–400 mm				
	small	50–200 mm				
	very small	<50 mm				
arm length	very long	>1.00	arm length: mantle length			
	long	0.80–1.00				
	moderate	0.40–0.80				
	short	0.20–0.40				
	very short	<9.20				

Table 2: Comparative overview of diagnostic parameters used to identify family level.



keels present along anterior half of median field, keels solid; anterior median field margin weakly convex; median field area very large (median field area to gladius area >0.90); lateral fields slender (lateral fields widthmax to median field widthmax 0.65–0.75); hyperbolar zone very short to short (hyperbolar zone length to median field length 0.05–0.15); arms short to very short (arm length to mantle length about 0.2) and stout; dorsal arm pair elongated; cirri present; two pairs of fins; fins short, lobate. *Upper Jurassic (upper Kimmeridgian–lower Tithonian):* southern Germany, France.——Fig. 2,*1a–d*. **P. prisca* (Rüppell), Tithonian, Solnhofen Formation, vicinity of Eichstätt, Germany; *a,* complete specimen, JME SOS5669.71.4.4, in left lateral view showing mantle, head, buccal mass, and short arm crown (new); *b,* BSPG MC-8, showing mantle and gladius in dorsal view (Fuchs, Klinghammer, & Keupp, 2007, fig. 1D); *c,* gladius reconstruction (new); *d,* detail of (*a*) showing posterior gladius funnel-like conus in lateral view (new). Scale bars, 10 mm.

Boreopeltis Engeser & Reitner, 1985, p. 252 [**B. helgolandiae;* M]. Medium-sized plesioteuthids; gladius slender to moderately wide (gladius width$_{max}$ to gladius length 0.15–0.25) with a broad median line and without pronounced median keel; median field slender (median field width$_{hypz}$ to hyperbolar zone length 0.20–0.30 = opening angle 12°–17°), triangular with lateral plate- or channel-like reinforcements, lateral reinforcements anteriorly projected; median field area large (median field

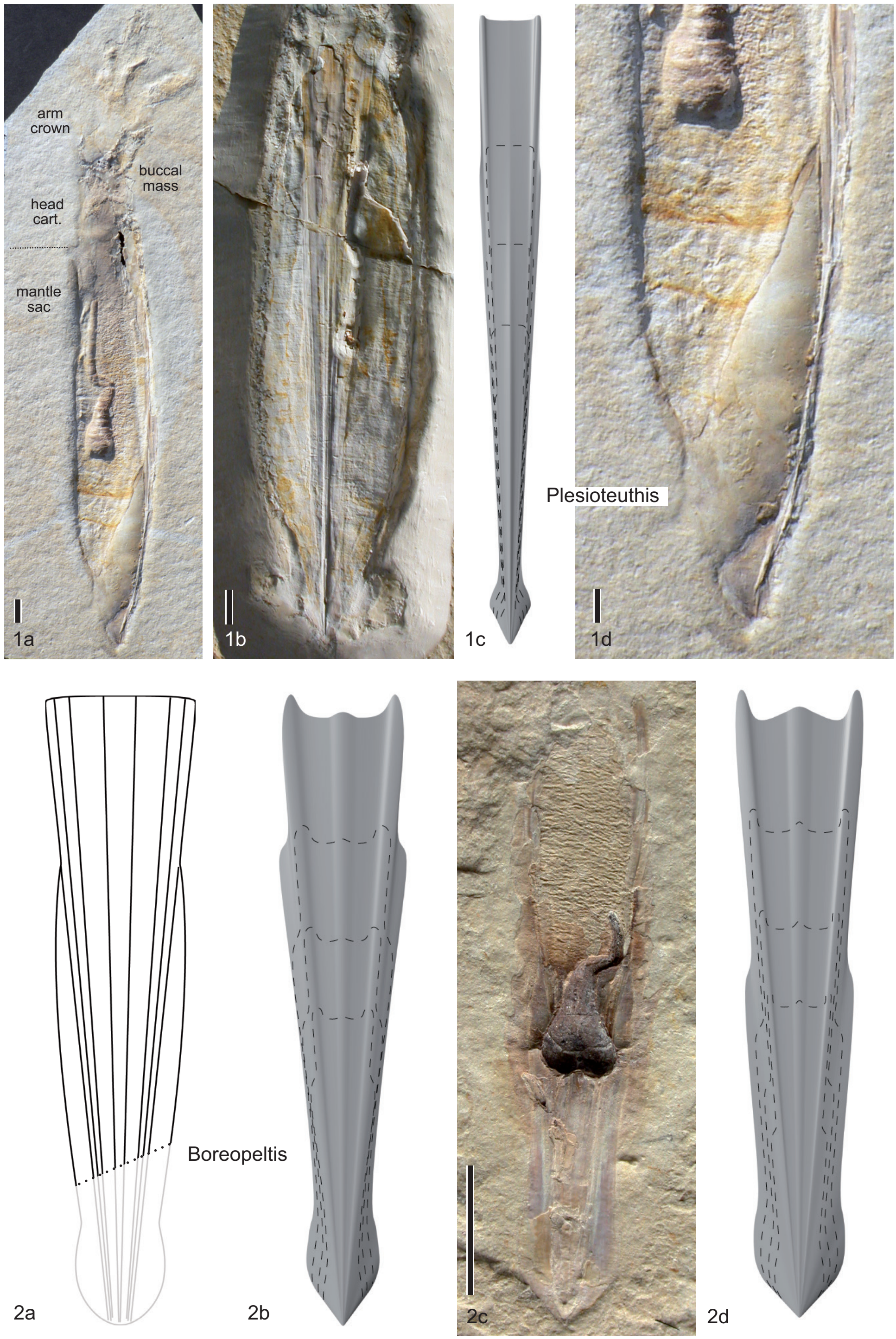


FIG. 2. Plesioteuthidae (p. 6–10).

area to gladius area 0.70–0.80); lateral fields anteriorly narrow, posteriorly wide, forming a pointed conus; lateral fields slender (lateral fields $width_{max}$ to median field $width_{max}$ 0.55–0.80); hyperbolar zones long, difficult to determine (hyperbolar zone length to median field length 0.50–0.70); soft parts unknown. *Upper Jurassic (lower Tithonian)–Upper Cretaceous (upper Cenomanian):* Germany, Lebanon.——FIG. 2*a*. **B. helgolandiae* (ENGESER & REITNER), Aptian, Heligoland, northern Germany, gladius reconstruction (adapted from Engeser & Reitner, 1985, fig. 8).——FIG. 2*b*. *B. sagittata* (NAEF, 1921b), Tithonian, Solnhofen Formation, southern Germany, gladius reconstruction (new).——FIG. 2*c–d*. *B. smithi* FUCHS & LARSON, 2011a, Cenomanian, Hâkel, Lebanon; *c,* holotype, MNHNL CRE11, showing the gladius in dorsal view (Fuchs & Larson, 2011a, Fig. 8,*1–3*); *d,* gladius reconstruction (new). Scale bar in 2c, 10 mm.

Dorateuthis WOODWARD, 1883, p. 4 [**D. syriaca;* M] [=*Maioteuthis* REITNER & ENGESER, 1982, p. 212 (type, *M. morroensis,* OD); =*Neololigosepia* REITNER & ENGESER, 1982, p. 210 (type, *N. stahleckeri,* OD)]. Medium-sized plesioteuthids, gladius slender (gladius $width_{max}$ to gladius length 0.10–0.19) without a median keel; median field very slender (opening angle <12°) with pronounced lateral reinforcements continuous from anterior to posterior extremities; lateral reinforcements and central median field anteriorly projected; median field area very large (median field area to gladius area >0.95); lateral fields and conus poorly known (if present then both very short and very slender); arm length moderate (arm length to mantle length about 0.5); dorsal arm pair elongated; cephalic cartilage without lateral projections, ring shaped in lateral view; fins oar shaped. *Lower Cretaceous (Barremian)–Upper Cretaceous (Maastrichtian):* Lebanon, northern Germany (Cape Verde Islands), the Netherlands.——FIG. 3,*1a–e*. **D. syriaca*, Cenomanian, Hâkel, Lebanon; *a*, complete specimen, BHI 5814, in left lateral view showing mantle, ink sac, head cartilage, buccal mass with lower beak, and arm crown (new; photo taken under UV light); *b*, gladius in dorsal view, BHI 5579 (Fuchs & Larson, 2011a, fig. 4,*10*); *c*, gladius reconstruction (new); *d*, specimen BHI 2132 showing the cephalic cartilage in dorsal view (new; photo taken under UV light); *e*, specimen showing a pair of oar-shaped fins; scale bars, 10 mm (new).

Eromangateuthis FUCHS 2019, p. 1 [**Boreopeltis soniae* WADE, 1993, p. 364; M]. Large-sized plesioteuthids; gladius slender to moderately wide (gladius $width_{max}$ to gladius length 0.15–0.25) with a pronounced solid median keel, which tapers anteriorly; median field very slender to slender (median field $width_{hypz}$ to hyperbolar zone length 0.15-0.25 = opening angle 10°–15°); anterior margin distinctly convex, with lateral plate- or channel-like like reinforcements; median field area very large (median field area to gladius area 0.85–0.95); lateral fields very slender to slender (lateral fields $width_{max}$ to median field $width_{max}$ 0.45–0.55); hyperbolar zones very short to short, difficult to determine (hyperbolar zone length to median field length 0.15–0.25); conus unusually deep, ventrally oriented (not funnel-like), patella shaped; soft parts unknown. *Upper Cretaceous (upper Albian):* Australia.——FIG. 3,*2a–c*. **E. soniae* (WADE), upper Albian, Allaru Formation, Queensland, Australia; *a,* specimen showing the gladius in dorsal view, scale bar, 10 cm (exhibition of the Kronosaurus Korner Museum, Richmond, Australia); *b,* gladius reconstruction (new); *c,* reconstruction of the gladius conus in lateral view (new).

Nesisoteuthis DOGUZHAEVA, 2005, p. 43 [**N. simbirskensis;* M]. Gladius slender (gladius $width_{max}$ to gladius length <0.20); median field slender (opening angle 15°–20°), triangular and with lateral ridge-like reinforcements, median keel absent; lateral fields and conus unknown. *Lower Cretaceous (lower Aptian):* central Russia.——FIG. 3,*3*. **N. simbirskensis,* lower Aptian, middle Volga area, central Russia, gladius reconstruction, anterior and posterior parts are hypothetical (new).

Normanoteuthis BRETON, STRUGNELL, & DONOVAN, 2013, p. 277 [**N. inopinata;* M]. Gladius known only by an unusual funnel-shaped conus; ventral fissure present suggesting a secondary conus; dorsally with a pronounced solid median keel flanked by grooves (opening angle 8°–9°), lateral keels unknown in conus region. *Lower Cretaceous (lower Albian):* France (Normandy).——FIG. 3,*4a–c*. **N. inopinata,* lower Albian, Normandy, France, reconstruction of the conus part; ventral (*a*), dorsal (*b*), and lateral (*c*) views (new).

Paraplesioteuthis NAEF, 1921a, p. 534 [**Geoteuthis sagittata* MÜNSTER, 1843; SD NAEF, 1922, p. 111] [=*Belemnosepia* BUCKLAND & AGASSIZ in BUCKLAND, 1836, p. 39, *nom. nud., partim;* =*Geoteuthis* MÜNSTER, 1843, p. 57, *nom. oblit., partim*]. Gladius medium-sized, slender to moderately wide (gladius $width_{max}$ to gladius length 0.15–0.25) with a bipartite median ridge; median field slender to moderately wide (median field $width_{hypz}$ to hyperbolar zone length 0.25–0.35 = opening angle 14°–20°), triangular and with lateral platelike reinforcements; lateral reinforcements and central median field anteriorly projected; median field area large to very large (median field area to gladius area 0.75–0.85); lateral fields slender (lateral fields $width_{max}$ to median field $width_{max}$ 0.85–0.95); hyperbolar zone moderately long to long (hyperbolar zone length to median field length 0.45–0.55); soft parts poorly known. *Lower Jurassic (upper Pliensbachian–lower Toarcian):* southern Germany, France, Canada (Alberta).——FIG. 4,*1a–b*. **P. sagittata* (MÜNSTER), Posidonia Shale Formation, Toarcian, southern Germany; *a,* gladius in dorsal view, UMH collection (Fuchs, 2006a, pl. 16,*B–C*); *b,* gladius reconstruction; scale bars, 10 mm (new).

Romaniteuthis FISCHER & RIOU, 1982a, p. 302 [**Plesioteuthis gevreyi* ROMAN, 1928; M]. Medium-sized plesioteuthids, torpedo-shaped; gladius very slender to slender (gladius $width_{max}$ to gladius

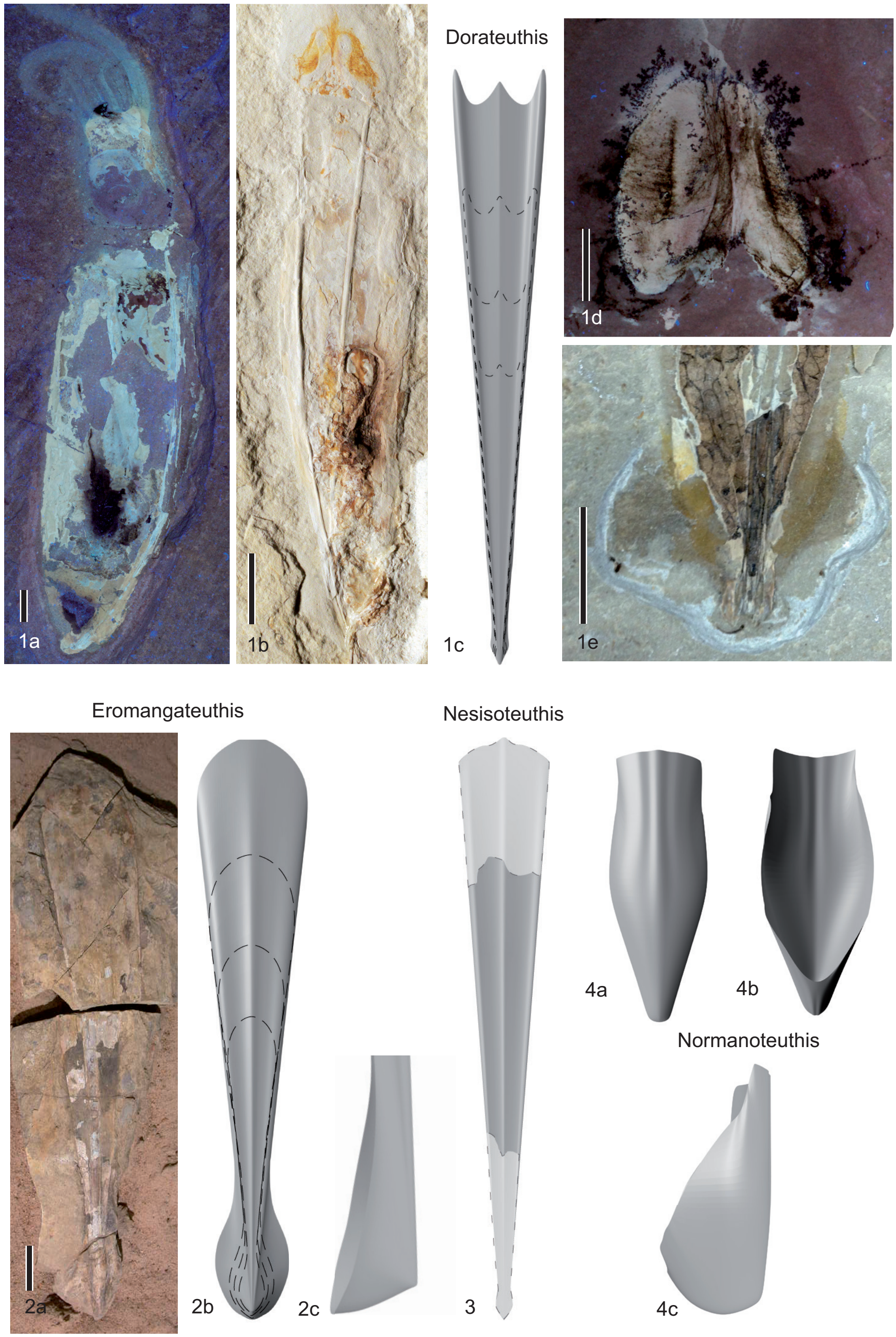


FIG. 3. Plesioteuthidae (p. 10).

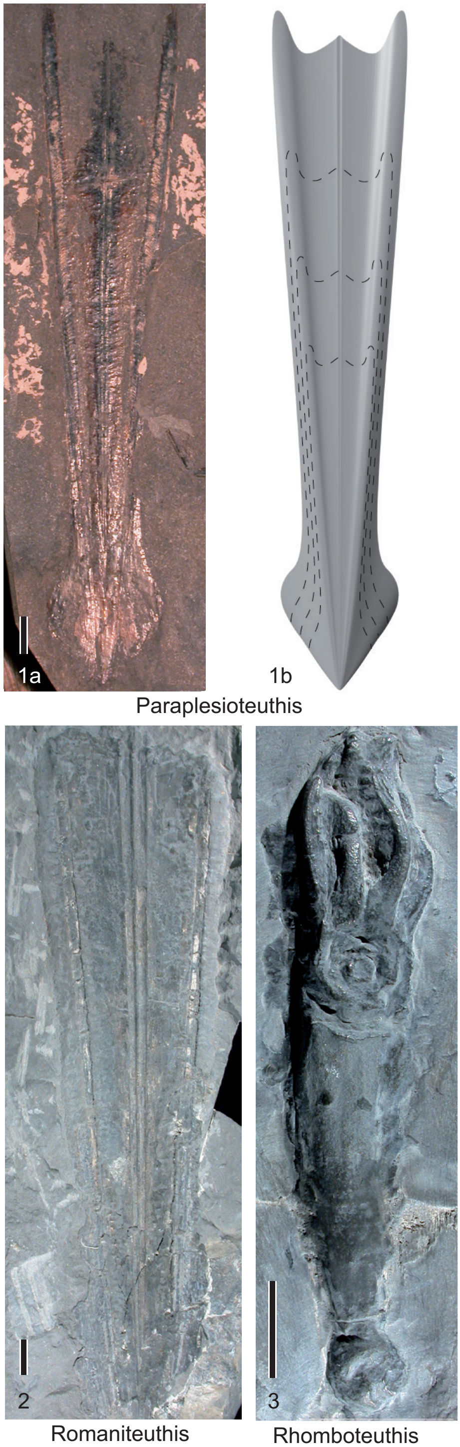


FIG. 4. Plesioteuthidae (p. 10–12).

length 0.05–0.15); median field very slender (median field width$_{hypz}$ tohyperbolar zone length 0.10–0.19 = opening angle <12°); anterior gladius margin poorly known, median field with median keel; median field area large to very large (median field area to gladius area 0.75–0.85); lateral fields slender to moderately wide (lateral fields width$_{max}$ to median field width$_{max}$ 0.95–1.05); hyperbolar zone short (hyperbolar zone length to median field length 0.20–0.29); arm length short (arm length to mantle length ~0.25). *Middle Jurassic (lower Callovian):* France, ?Germany, ?UK.——FIG. 4,*2*. **R. gevreyi* (ROMAN), lower Callovian, La Voulte, France, gladius (?in dorsal view), MNHN, scale bar, 10 mm (Fuchs, 2006a, pl. 17,*A*).

Rhomboteuthis FISCHER & RIOU, 1982a, p. 307 [**R. lehmanni;* OD]. Body small-sized, torpedo-shaped; gladius plesioteuthid-like slender to very slender, otherwise poorly known; arms short (arm length to mantle length ~0.30–0.40); fins lobate. *Middle Jurassic (lower Callovian):* France.——FIG. 4,*3*. **R. lehmanni*, lower Callovian, La Voulte, France, specimen in lateral view, MNHN, scale bar, 10 mm (new).

Senefelderiteuthis ENGESER & KEUPP, 1999, p. 22 [**Acanthoteuthis tricarinata* MÜNSTER, 1846; SD FUCHS & LARSON, 2011a, p. 236; =*Senefelderiteuthis kraussi* ENGESER & KEUPP, 1999, p. 22]. Medium-sized plesioteuthids, gladius very slender to slender (gladius width$_{max}$ to gladius length 0.05–0.15); median field very slender to slender (median field width$_{hypz}$ to hyperbolar zone length 0.15–0.25 = opening angle 9°–14°), pronounced median keel absent except in conus region; anterior median field with broad median reinforcement and well-developed, continuous rounded lateral keels extending from anterior to posterior extremities; median field area large to very large (median field area to gladius area 0.75–0.85); lateral fields moderately wide (lateral fields width$_{max}$ to median field width$_{max}$ 1.00–1.10); hyperbolar zone moderately long (hyperbolar zone length to median field length 0.35–0.45); arms long (arm length to mantle length 0.7–1.0) and slender. *Upper Jurassic (upper Kimmeridgian–lower Tithonian)*: southern Germany.——FIG. 5, *a–d*. **S. tricarinata,* Tithonian, Altmühltal Formation, vicinity of Eichstätt, southern Germany; *a,* specimen with preserved arms crown, BSPG MC-107 (new); *b,* gladius in dorsal view, BHI (Fuchs & others, 2016, fig. 1F); *c,* gladius reconstruction (new); *d,* detail of posterior conus, BSPG MC-128; scale bars, 10 mm (new).

PROTOTEUTHINA *INCERTAE SEDIS*

Germanoteuthis SCHWEIGERT & FUCHS, 2012, p. 22 [**G. donai;* M]. Gladius fragments prototeuthid-like; posterior part of the median field spatulate with distinct median depression; soft parts unknown. *Middle Triassic (lower Ladinian)*:

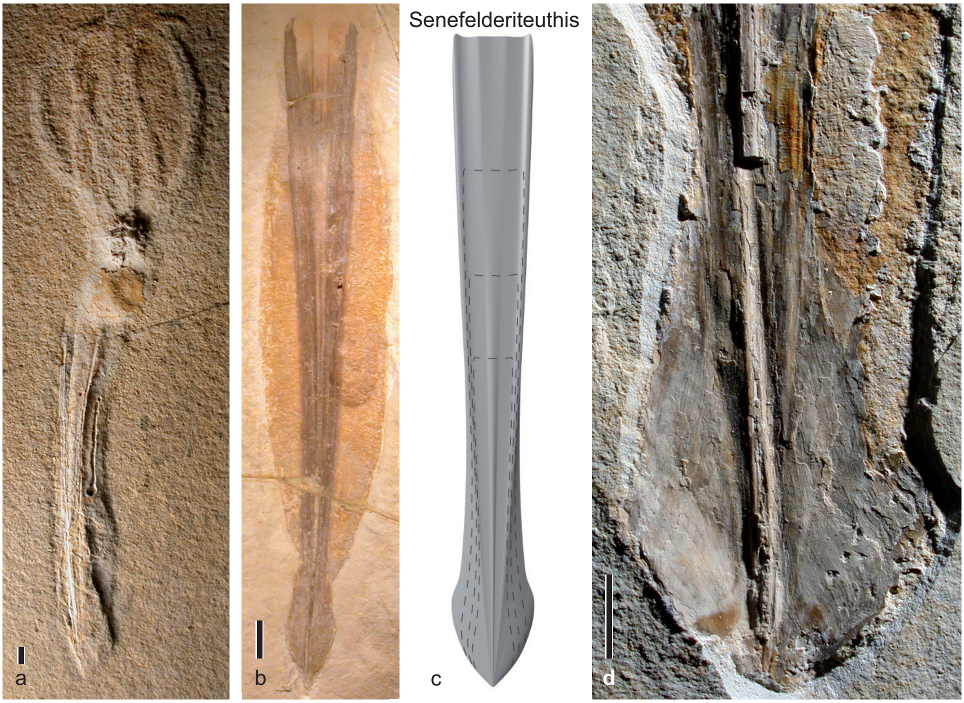


FIG. 5. Plesioteuthidae (p. 12).

Germany.——FIG. 6,*1a–b*. **G. donai,* lower Ladinian, upper Muschelkalk, Illingen near Vaihingen, Germany; *a,* holotype, SMNS 75405, showing the posterior gladius, scale bar, 5 mm (SCHWEIGERT & FUCHS, 2012, fig. 3); *b,* gladius reconstruction, length of the anterior free median field unknown (new).

Reitneriteuthis SCHWEIGERT & FUCHS, 2012, p. 24 [**Loligosepia neidernachensis* REITNER, 1978; M] [=*Loligosepia* QUENSTEDT, 1839, p. 163 (type, *L. aalensis,* SD SCHÜBLER in ZIETEN, 1832 in 1830–1833]. Gladius prototeuthid-like, moderately long (gladius $width_{max}$ to gladius length 0.25–0.35); median field slender (median field $width_{hypz}$ to hyperbolar zone length 0.25–0.34 = opening angle 14°–19°), triangular with lateral reinforcements; lateral reinforcements and central median field anteriorly projected; median field area moderate to large (median field area to gladius area 0.55–0.65); lateral fields moderately wide (lateral fields $width_{max}$ to median field $width_{max}$ 1.25–1.35); hyperbolar zone indistinct, long (hyperbolar zone length to median field length about 0.60); soft parts unknown. *Upper Triassic (upper Norian)*: southern Germany.——FIG. 6,*2a–b*. **R. neidernachensis* (REITNER), upper Norian, Kössen Formation, vicinity of Garmisch-Partenkirchen, southern Germany; *a,* holotype, GPIT 1529/1, showing the gladius (Schweigert & Fuchs, 2012, fig. 6); *b,* gladius reconstruction (new). Scale bar, 10 mm.

Order VAMPYROMORPHA Robson, 1929

[*nom. transl.* PICKFORD, 1939, p. 346, *ex* suborder Vampyromorpha ROBSON, 1929, p. 484; *nom. correct.* DOYLE, DONOVAN, & NIXON, 1994, p. 7, *pro* Vampyromorphida PICKFORD, 1936, p. 77] [=Pseudoctobrachia GUERRA, 1992, p. 17]

Coleoids whose dorsolateral arm pair (homologous to arm pair II in Decabrachia) is either modified into retractile filaments or absent, true tentacles (arm pair IV) absent; gladius well developed; suckers radially symmetrical, sessile, uniserial, sucker rings absent; one or two pairs of fins, cartilaginous axial support unknown, position subterminal, shape variable; funnel- and mantle-looking cartilages absent or rudimentary. *Lower Jurassic (Sinemurian)–Holocene.*

Suborder LOLIGOSEPIINA Jeletzky, 1965

[Loligosepiina JELETZKY, 1965, p. 75] [=Prototeuthoidea NAEF, 1921a, p. 534, *partim*; =Trachyteuthoidea Kretzoi, 1942, p. 134, *partim*; =Loligosepioidei STAROBOGATOV, 1983, p. 7]

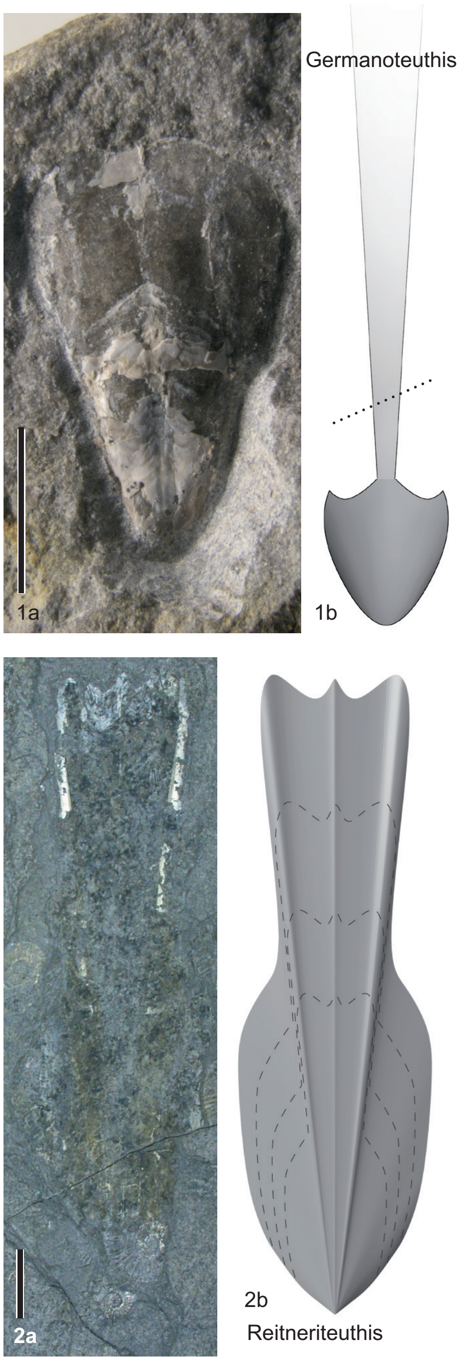


FIG. 6. Prototeuthina *incertae sedis* (p. 12–13).

Small- to large-sized octobrachiates with bullet-shaped body; gladius length (= median field length) equals mantle length; gladius with triangular median field and cup-shaped conus; gladius slender to wide, maximum gladius width always exceeds maximum median field width; median field width very slender to moderately wide without pronounced median reinforcements, anterior median field margin concave, straight or convex; median field area small to large; hyperbolar zone mostly well-arcuated, rarely indistinct, long to very long; lateral fields usually moderately wide. *Lower Jurassic (Sinemurian)–Lower Cretaceous (Aptian).*

Family LOLIGOSEPIIDAE Regteren Altena, 1949

[Loligosepiidae REGTEREN ALTENA, 1949, p. 58] [=Geoteuthidae NAEF, 1921a, p. 534, *partim*; =Belopeltidae NAEF, 1921a, p. 534, *partim*; =Belemnosepiidae NAEF, 1921b, p. 47, *partim*]

Medium-sized loligosepiids; gladius slender to wide (gladius $width_{max}$ to gladius length 0.10–0.60), with deeply concave (V-shaped) hyperbolar zones; median field very slender to moderately wide (median field $width_{hypz}$ to hyperbolar zone length 0.10–0.40 = opening angle 7°–23°), anterior median field margin slightly convex; median field area small to moderate (median field area to gladius area 0.35–0.45); hyperbolar zones very long (hyperbolar zone length to median field length 0.85–0.95); lateral fields moderately wide (lateral fields $width_{max}$ to median field $width_{max}$ 1.30–1.85), anterior limit of lateral fields clearly pointed (spine like); inner and outer asymptotes ridge-like. *Lower Jurassic (lower Sinemurian–lower Toarcian).*

Loligosepia QUENSTEDT, 1839, p. 163 [**Loligo aalensis* SCHÜBLER in ZIETEN, 1832 in 1830–1833; SD REGTEREN ALTENA, 1949, p. 57] [=*Belopeltis* VOLTZ, 1840, p. 31, *nom. oblit., partim*; =*Geoteuthis* MÜNSTER, 1843, p. 68, *partim* (type, *Loligo bollensis* SCHÜBLER in ZIETEN, 1832 in 1830–1833, p. 34)]. Medium-sized loligosepiids, gladius moderately wide to wide (gladius $width_{max}$ to median field length 0.30–0.60); median field slender to moderately wide (median field $width_{hypz}$ to hyperbolar zone length 0.20–0.40 = opening angle 12°–23°); anterior median field margin convex; median field area small to moderate (median field area to gladius area 0.35–0.45); hyperbolar zone very long (hyperbolar zone length to median field length 0.85–0.95); lateral fields moderately wide (lateral fields $width_{max}$ to median field $width_{max}$ 1.35–1.80); arms short to moderate (arm length to mantle length ~0.45). *Lower Jurassic (lower Sinemurian–lower Toarcian)*: Germany, Luxembourg, France, UK, Canada (Alberta).——FIG. 7,*1a–c*. **L. aalensis* (SCHÜBLER in ZIETEN), lower Toarcian, Posidonia Shale Formation, Germany; *a,* original of QUENSTEDT (1849, pl. 32,*1*) specimen showing mantle, ink sack, GPIT Ce 3/33/1 (new); *b,* gladius reconstruction (new); *c,* specimen LWL P60140 showing mantle, ink sac, and arm crown (Fuchs, Keupp, & Schweigert, 2013, fig. 2). Scale bars, 10 mm.

Jeletzkyteuthis DOYLE, 1990, p. 198 [**Loliginites coriaceus* QUENSTEDT, 1849, p. 512; SD REGTEREN ALTENA, 1949, p. 56]. Medium-sized loligosepiids, gladius slender (gladius $width_{max}$ to median field length 0.10–0.19); median field very slender (median field $width_{hypz}$ to hyperbolar zone length 0.10–0.19 = opening angle 7°–11°), anterior median field margin convex; median field area moderate (median field area to gladius area 0.40–0.50); hyperbolar zone narrow (difficult to be seen) and very long (hyperbolar zone length to median field length 0.90–0.95); lateral fields moderately wide (lateral fields $width_{max}$ to median field $width_{max}$ 1.35–1.45). *Lower Jurassic (lower Toarcian)*: southern Germany, Luxembourg, France, Switzerland, UK, Canada (Alberta).——FIG. 7,*2a–c*. **J. coriaceus* (QUENSTEDT), lower Toarcian, Posidonia Shale Formation, Holzmaden, Germany; *a,* paralectotype 1, GPIT, showing the long and slender gladius (new); *b,* gladius reconstruction (new); *c,* paralectotype 2, GPIT, showing growth increments of the posteriormost gladius (new). Scale bar, 10 mm.

Family GEOPELTIDAE Regteren Altena, 1949

[Geopeltidae REGTEREN ALTENA, 1949, p. 56] [=Belopeltidae NAEF, 1921a, p. 535, partim; =Belemnosepiidae NAEF, 1921b, p. 47, partim; =Geopeltididae JELETZKY, 1966, p. 42].

Medium-sized loligosepiids; gladius moderately wide (gladius $width_{max}$ to median field length 0.40–0.49), with distinctly arcuated hyperbolar zones; median field slender to moderately wide (median field $width_{hypz}$ to hyperbolar zone length 0.25–0.45 = opening angle 14°–25°), anterior median field slightly concave or straight; median field area moderate (median field area to gladius area 0.45–0.55); hyperbolar zone very long (hyperbolar zone length to median field length 0.71–0.85); lateral fields moderately wide (lateral fields $width_{max}$ to median field $width_{max}$ 1.00–1.50), anteriorly not pointed; inner asymptotes distinct; outer asymptotes indistinct. *Lower Jurassic (upper Pliensbachian, lower Toarcia–Upper Jurassic (Tithonian).*

Geopeltis REGTEREN ALTENA, 1949, p. 56 [**Belopeltis simplex* VOLTZ, 1840, p. 23; SD REGTEREN ALTENA, 1949, p. 56] [=*Belopeltis* VOLTZ, 1840, p. 21, *nom. oblit., partim; =Geoteuthis* MÜNSTER, 1843, p. 57, *nom. oblit., partim* (type, *Loligo bollensis* SCHÜBLER in ZIETEN, 1832 in 1830–1833, p. 34)]. Medium-sized loligosepiids; gladius moderately wide (gladius $width_{max}$ to median field length 0.40–0.49); median field moderately wide (median field $width_{hypz}$ to hyperbolar zone length 0.35–0.45 = opening angle 20°–25°), anterior median field margin slightly concave; median field area moderate (median field area to gladius area 0.45–0.55); hyperbolar zone very long (hyperbolar zone length to median field length 0.75–0.85), exceeding lateral fields, weakly arcuated; outer asymptotes indistinct; lateral fields moderately wide (lateral fields $width_{max}$ to median field $width_{max}$ 1.35–1.45). *Lower Jurassic (upper Pliensbachian–lower Toarcian):* southern Germany, Canada (Alberta).——FIG. 8,*1a–b*. **G. simplex* (VOLTZ), lower Toarcian, Posidonia Shale Formation, Holzmaden, southern Germany; *a,* original of REITNER & ENGESER (1981, fig. 3) showing the gladius in dorsal view, GPIT collection (new); *b,* gladius reconstruction (new). Scale bar, 10 mm.

Parabelopeltis NAEF, 1921a, p. 534 [**Geoteuthis flexuosa* MÜNSTER, 1843, p. 75; SD NAEF, 1922, p. 128] [=*Geoteuthis* MÜNSTER, 1843, p. 57, *nom. oblit.*, *partim* (type, *Loligo bollensis* SCHÜBLER in ZIETEN, 1832 in 1830–1833, p. 34)]. Medium-sized loligosepiids; gladius moderately wide (gladius $width_{max}$ to median field length 0.40–0.49); median field slender (median field $width_{hypz}$ to hyperbolar zone length 0.25–0.34 = opening angle 14°–19°), anterior median field margin straight; median field area moderate (median field area to gladius area 0.45–0.55); hyperbolar zone very long (hyperbolar zone length to median field length 0.71–0.80), well arcuated, as long as lateral field; outer asymptote indistinct; lateral fields moderately wide (laterals field $width_{max}$ to median field $width_{max}$ 1.10–1.20). *Lower Jurassic (upper Pliensbachian, lower Toarcian)–Upper Jurassic (Tithonian):* Germany, Luxembourg, UK, Switzerland, Russia, Canada (Alberta).——FIG. 8,*2a–b*. **P. flexuosa* (MÜNSTER), lower Toarcian, Posidonia Shale Formation, Dudelange, Luxembourg; *a,* gladius in ventral view, Streitz private collection, Luxembourg (Fuchs & Weis, 2008, fig. 7A); *b,* gladius reconstruction (new). Scale bars, 10 mm.

Family LEPTOTHEUTHIDAE Naef, 1921a

[*nom. correct.* ENGESER, 1988, p. 27 *pro* Leptoteuthidae NAEF, 1921a, p. 534]

Large-sized loligosepiids; gladius moderately wide; median field slender to moderately wide, anteriorly convex, with platelike lateral

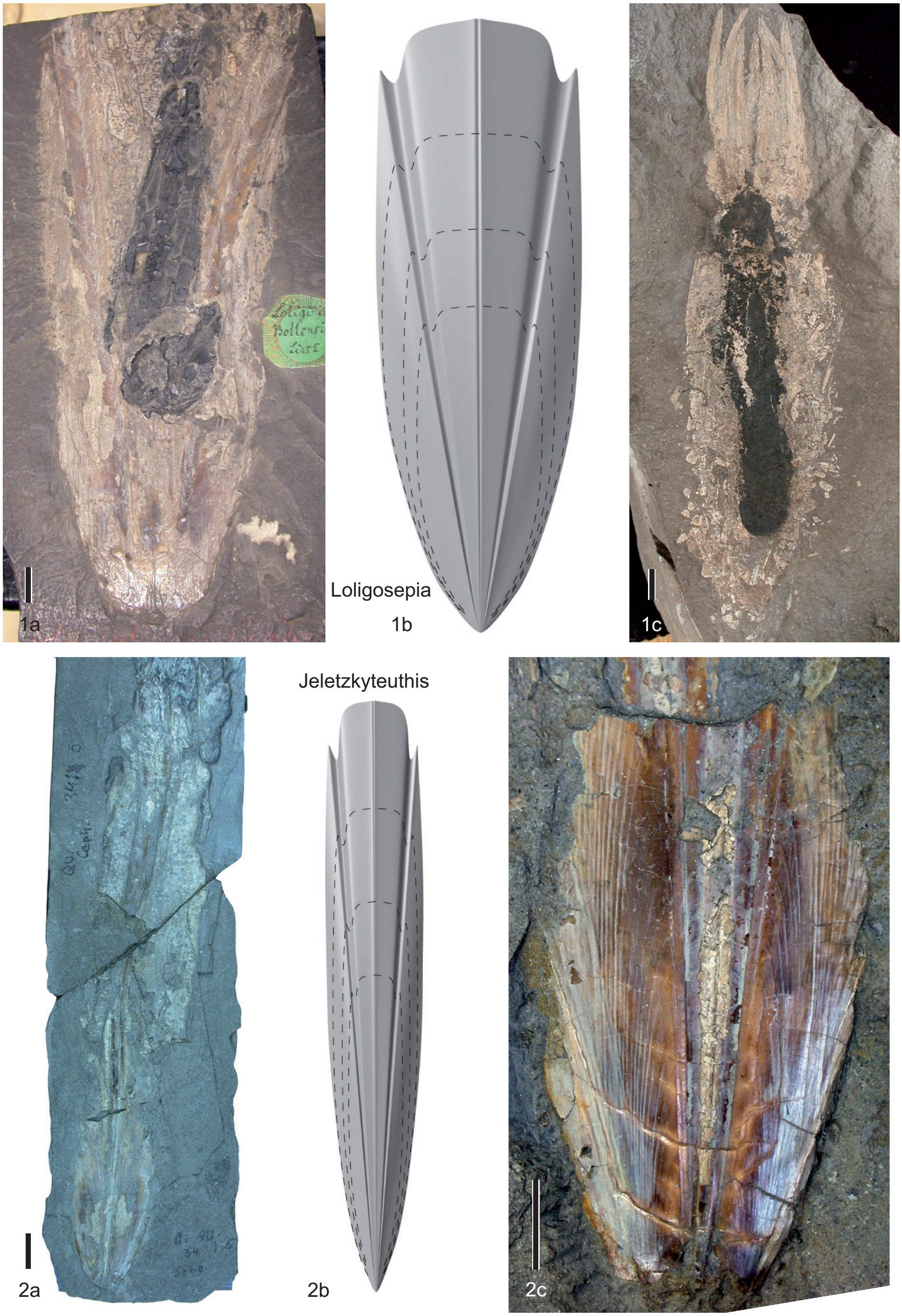


FIG. 7. Loligosepiidae (p. 14–15).

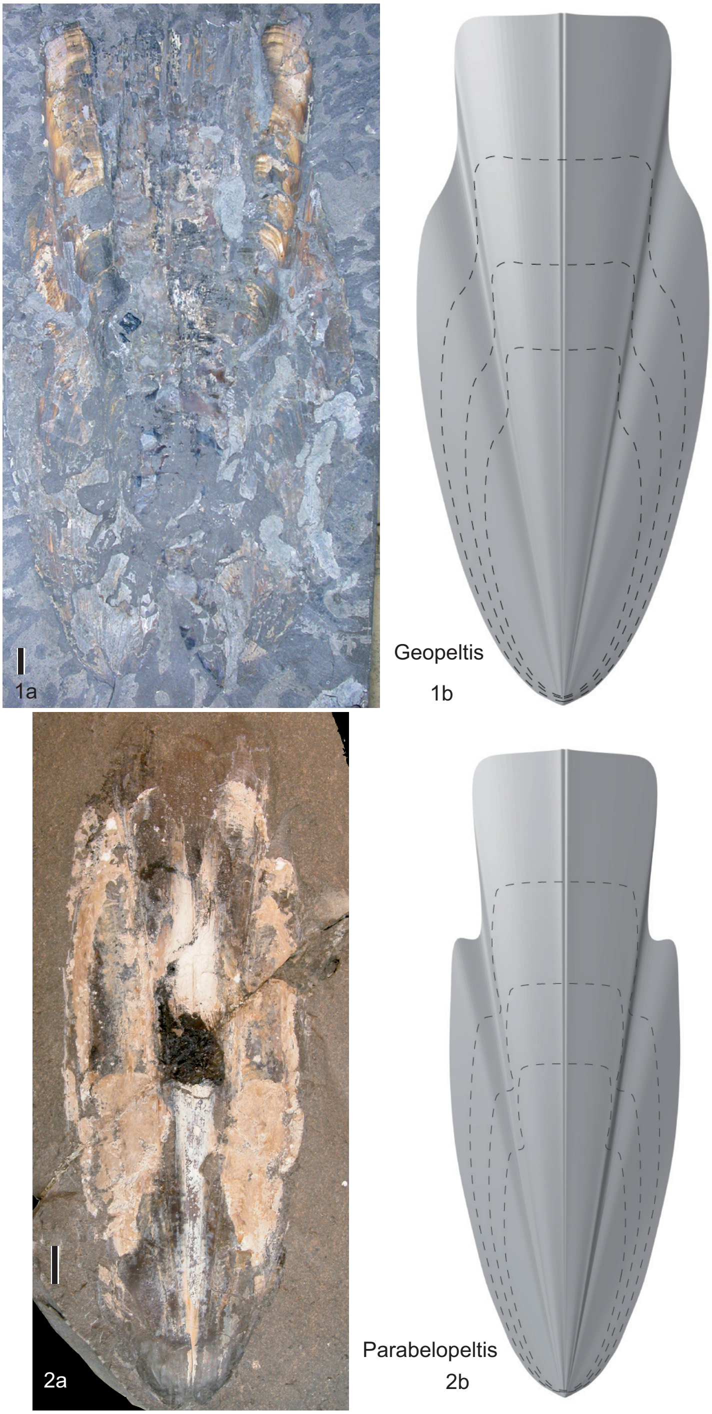


FIG. 8. Geopeltidae (p. 15).

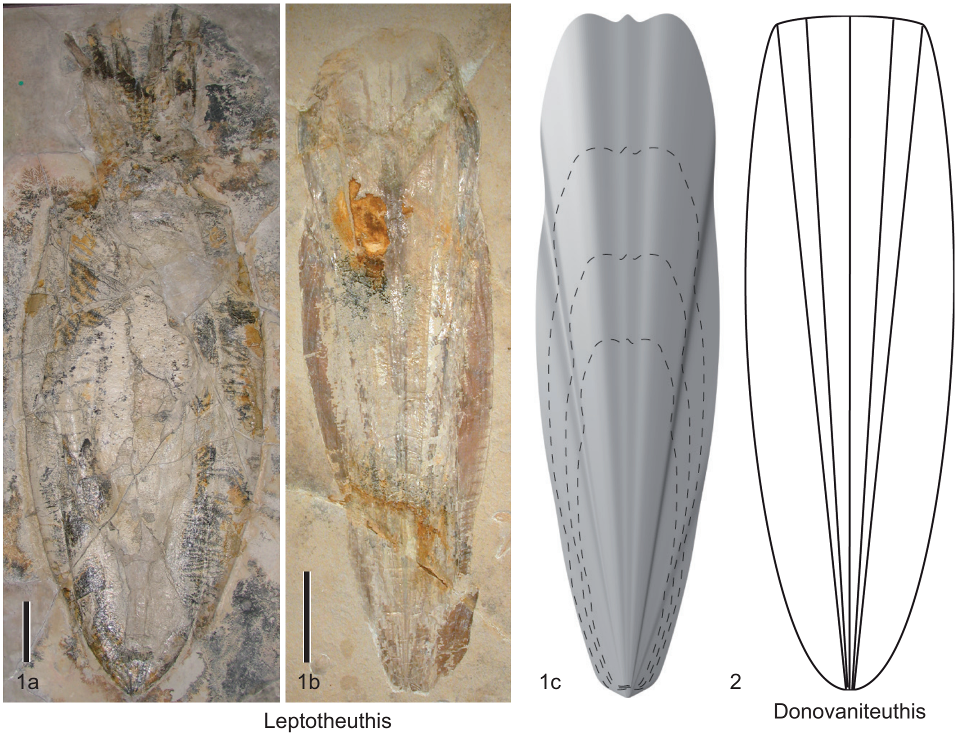


FIG. 9. Leptotheuthidae (p. 18).

reinforcements; median field area large; hyperbolar zone weakly arcuated, indistinct, very long; lateral fields slender to moderately wide. *Upper Jurassic (Tithonian)–Lower Cretaceous (Aptian).*

Leptotheuthis MEYER, 1834, p. 292 [**L. gigas;* M]. Large-sized loligosepiid; gladius moderately wide (gladius width$_{max}$ to median field length 0.25–0.35); median field slender to moderately wide (median field width$_{hypz}$ to hyperbolar zone length 0.30–0.40 = opening angle 17°–23°) with sublateral, platelike lateral reinforcements, central median field with anterior, nose-like projection; median field area large (median field area to gladius area 0.60–0.70); hyperbolar zone weakly arcuated, very long (hyperbolar zone length to median field length 0.71–0.80); lateral fields moderately wide (lateral fields width$_{max}$ to median field width$_{max}$ 1.00–1.10), posteriorly constricted; arms sturdy and short (arm length to mantle length 0.25–0.3). *Upper Jurassic (upper Kimmeridge–lower Tithonian):* southern Germany.——FIG. 9,*1a–c*. **L. gigas,* lower Tithonian, Altmühltal Formation, vicinity of Eichstätt, southern Germany; *a,* overview, JME collection (Fuchs, 2015, fig. 451a); *b,* gladius in dorsal view, Tischlinger collection (Fuchs, 2015, fig. 451b); *c,* gladius reconstruction (new). Scale bars, 10 cm.

Donovaniteuthis ENGESER & KEUPP, 1997, p. 49 [**Mastigophora stuehmeri* ENGESER & REITNER, 1985, p. 248; OD]. Gladius poorly known; median field with platelike lateral reinforcements; lateral fields assumed to be as long as median field; hyperbolar zones unknown. *Lower Cretaceous (lower Aptian):* northern Germany.——FIG. 9,*2*. **D. stuehmeri* (ENGESER & REITNER), lower Aptian, Heligoland, northern Germany, gladius reconstruction (adapted from Engeser & Reitner, 1985, fig. 3).

Family MASTIGOPHORIDAE Engeser & Reitner, 1985

[Mastigophoridae ENGESER & REITNER, 1985, p. 248]

Small- to medium-sized loligosepiids; gladius slender to moderately wide (gladius width$_{max}$ to gladius length 0.15–0.50), with wide and elongated hyperbolar zones; median field very slender to moderately wide (median field width$_{hypz}$ to hyperbolar zone length 0.35–0.50 = opening angle 20°–28°), anterior median field margin concave; median field area moderate to large (median field area to gladius area 0.50–0.70); hyperbolar zone weakly arcuated, transition median field/hyperbolar zone/lateral field smooth, inner and outer asymptotes therefore indistinct, hyperbolar zone long (hyperbolar zone length to median field length >0.50); lateral field distinctly shorter than hyperbolar zone, moderately wide (lateral field $width_{max}$ to median field $width_{max}$ 1.10–1.60); arms short (arm length to mantle length 0.20–0.30). *Middle Jurassic (Callovian)–Upper Jurassic (lower Tithonian), Upper Cretaceous (upper Cenomanian).*

Mastigophora Owen, 1856, p. 1 [**M. brevipinnis;* M]. Medium-sized loligosepiids; gladius moderately wide (gladius $width_{max}$ to median field length 0.25–0.35); median field moderately wide (median field $width_{hypz}$ to hyperbolar zone length 0.35–0.45 = opening angle 20°–25°), anterior median field margin concave; median field area large (median field area to gladius area 0.65–0.75); hyperbolar zone weakly arcuated, long (hyperbolar zone length to median field length 0.55–0.65); lateral fields moderately wide (lateral fields $width_{max}$ to median field $width_{max}$ 1.15–1.25); arms short (arm length to mantle length 0.26); anterior mantle margin collar-like, thickened; fins small, subterminal, nodular. *Middle Jurassic (lower–upper Callovian):* UK, France.——Fig. 10,*1a–c. *M. brevipinnis,* upper Callovian, Oxford Clay, Christian Malford, UK; *a,* overview, NHMUK C34025; *b,* gladius in dorsal view, BMNH C88606; *c,* gladius reconstruction (new). Scale bars, 10 mm.

Doryanthes Münster, 1846, p. 58 [**Ommastrephes munsterii* d'Orbigny, 1845, p. 207; SD Engeser, 1988, p. 17] [=*Geoteuthis* Münster, 1843, p. 57, *nom. oblit. partim;* =*Geoteuthinus* Kretzoi, 1942, p. 125]. Small-sized loligosepiids; gladius moderately wide (gladius $width_{max}$ to median field length 0.40-0.49); median field triangular, moderately wide (median field $width_{hypz}$ to hyperbolar zone length 0.40–0.50 = opening angle 23°–28°), anterior margin concave subdivided into a thin central part and lateral, platelike reinforcements; median field area moderate to large (median field area to gladius area 0.55–0.65); hyperbolar zone weakly arcuated, long (hyperbolar zone length to median field length 0.60–0.70); lateral fields moderately wide (lateral fields $width_{max}$ to median field $width_{max}$ 1.45–1.55); soft parts poorly known. *Upper Jurassic (lower Tithonian):* southern Germany.——Fig. 10,*2a–b*. **D. munsterii* (d'Orbigny), lower Tithonian, Mörnsheim Formation, Germany; *a,* neotype, JME SOS5768, showing gladius in dorsal view (Fuchs, 2006c, fig. 1A); *b,* gladius reconstruction (new). Scale bars, 10 mm.

LOLIGOSEPIINA *INCERTA SEDIS*

Bavaripeltis Engeser & Keupp, 1997, p. 49 [**Mastigophora bavarica* Engeser, 1986, p. 32; M]. Gladius (although poorly known) slender (gladius $width_{max}$ to median field length 0.10–0.19), median field probably triangular, very slender (median field $width_{hypz}$ to hyperbolar zone length <0.20 = opening angle <12°); dimensions of hyperbolar zones and lateral field unknown; conus cup shaped. *Upper Jurassic (lower Tithonian):* southern Germany.——Fig. 10,*3*. **B. bavarica* (Engeser), lower Tithonian, Solnhofen Formation, Solnhofen, southern Germany, holotype, NHMUK C83735, showing gladius in ventral view, scale bar, 10 mm (new).

Suborder VAMPYROMORPHINA Robson, 1929

[*nom. corr.* Jeletzky 1965, p. 76 *pro* suborder Vampyromorpha Robson, 1929, p. 484]

Small to medium-sized vampyromorphs; gladius with triangular median field and cup-shaped conus; gladius moderately wide, maximum gladius width may or may not exceed maximum median field width; median field moderately wide without pronounced longitudinal or diverging reinforcements; anterior median field margin convex; hyperbolar zones indistinct, variable in length; lateral field variable in width; conus part rostrum-like extended (rostral process). *Oligocene–Holocene.*

Family VAMPYROTEUTHIDAE Thiele in Chun, 1915

[Vampyroteuthidae Thiele in Chun, 1915, p. 534]

Small- to medium-sized vampyromorphs; gladius moderately wide (gladius $width_{max}$ to gladius length 0.25–0.45); median field moderately wide (median field $width_{hypz}$ to hyperbolar zone length 0.45–0.55 = opening angle 25°–31°), anterior median field margin convex; hyperbolar zone moderately long to long (hyperbolar zone length to median field length 0.35–60); lateral fields slender to moderately wide (lateral field $width_{max}$ to median field $width_{max}$ 0.5–1.05); conus part posteriorly rostrum-like extended (rostral process); arm pair II modified as retractile filaments; arms with paired cirri alternating

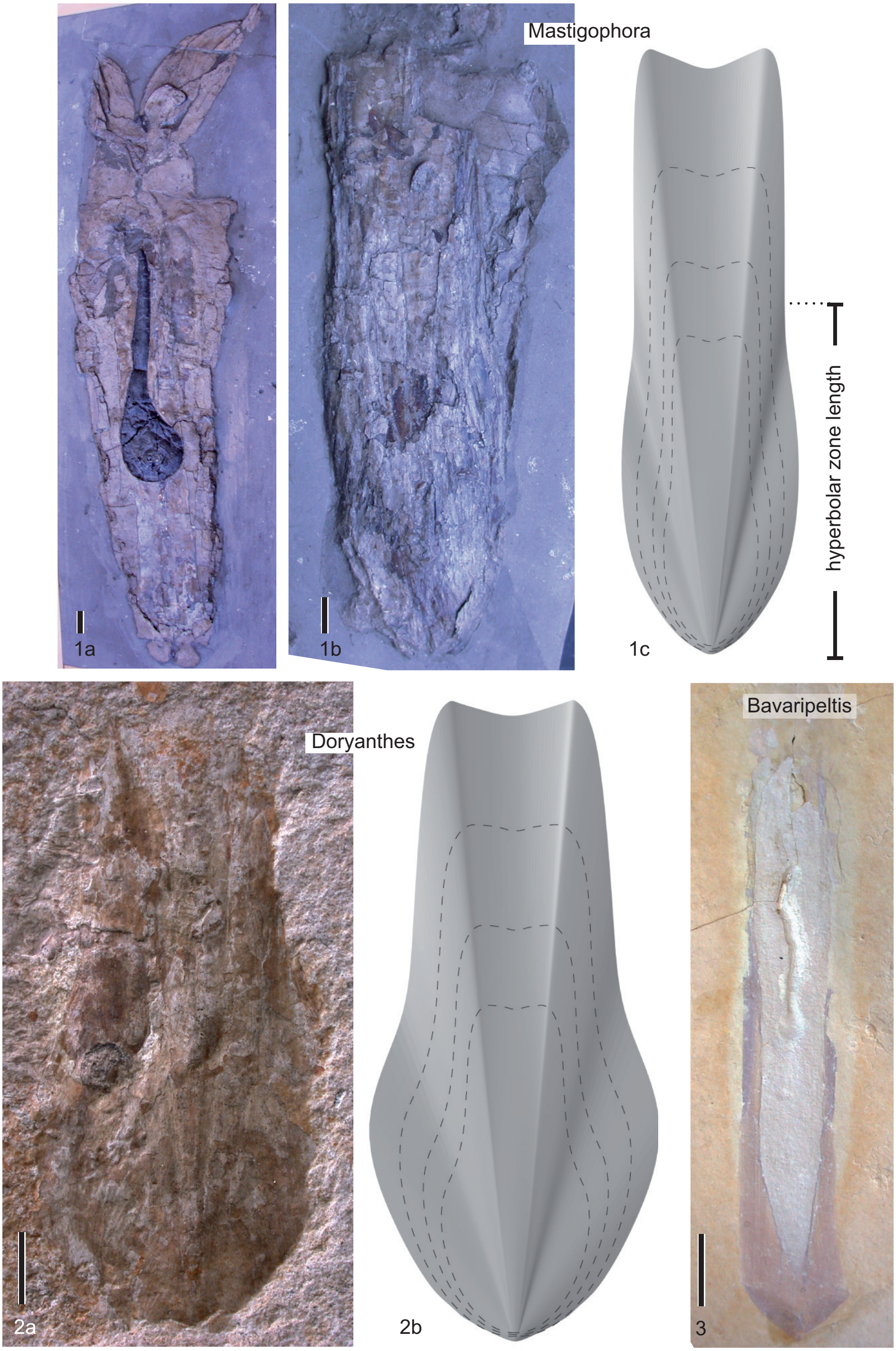


FIG. 10. Mastigophoridae (p. 19).

with suckers; two pairs of fins present during ontogeny. *Oligocene–Holocene* (extant).

Necroteuthis Kretzoi, 1942, p. 126 [*Necroteuthis hungarica;* OD]. Small-sized vampyroteuthids; gladius moderately wide (gladius width$_{max}$ to median field length 0.35–0.45); median field moderately wide (median field width$_{hypz}$ to hyperbolar zone length 0.45–0.55 = opening angle 25°–31°), anterior median field margin distinctly convex; hyperbolar zone weakly arcuated, moderately long (hyperbolar zone length to median field length 0.35–0.45); lateral fields slender to very slender (lateral fields width$_{max}$ to median field width$_{max}$ 0.85–0.95); conus part posteriorly rostrum-like extended (rostral process); soft tissues unknown. *Oligocene:* Hungary.——Fig. 11*a–b*. **N.hungarica,* Kretzoi, 1942, Oligocene, Tard Clay Formation, Hungary. *a,* overview of the holotype (M59/4672), Hungarian Natural History Museum, gladius seen in dorsal view (new; photo courtesy Martin Kostak), *b,* gladius reconstruction (new). Scale bar, 10 mm.

VAMPYROMORPHA *INCERTAE SEDIS*

Nanaimoteuthis Tanabe & others, 2008, p. 400 [**N. jeletzkyi;* M]. Soft parts and gladius unknown; large-sized lower beak; wing weakly expanded; wing fold high; hood very broad, convex, without notch; rostrum sharp with large hook, inner lamella short with crest portion largely covered by outer lamella; soft parts unknown. *Upper Cretaceous (middle Turonian–lower Campanian):* Japan (Hokkaido), Canada (British Columbia).——Fig. 12*a–e*. Lower beak of *N. hikida* Tanabe, Misaki, & Ubokata, 2015. holotype, KMNH IvP 902,001, Santonian, Hokkaido, northern Japan; *a,* right lateral view; *b,* right lateral view after removing parts of the outer lamella (*ol*) to show inner lamella (*il*); *c,* dorsal view; *d,* left lateral view; *e,* frontal view (Tanabe, Misaki, & Ubokata, 2015, fig 6; photo courtesy of Kazushige Tanabe). Scale bars, 10 mm.

Gramadella Fischer & Riou, 1982a, p. 311 [**G. piveteau;* OD]. Mantle bullet-shaped; arms long, about as long as mantle length; one arm pair elongated; head not clearly demarked; fins possibly skirtlike; gladius unknown. *Middle Jurassic (lower Callovian):* France.——Fig. 13,*1*. **G. piveteau,* lower Callovian, La Voulte-sûr-Rhône, France, paratype, MNHN R.3762, scale bar, 10 mm (new).

Proteroctopus Fischer & Riou, 1982b, p. 277 [**P. ribeti;* OD]. Mantle bullet-shaped; arms long, longer than mantle length, dorsal arm pair elongated; interbrachial web absent; suckers biserial; cirri short; head not clearly demarked, dorsally fused with mantle; ink sac absent(?); fins subterminal, nodular, fin cartilage with core; gladius (although poorly known) anteriorly wide. *Middle Jurassic (lower Callovian):* France.——Fig.13,*2*.

Fig. 11. Vampyroteuthidae (p. 21).

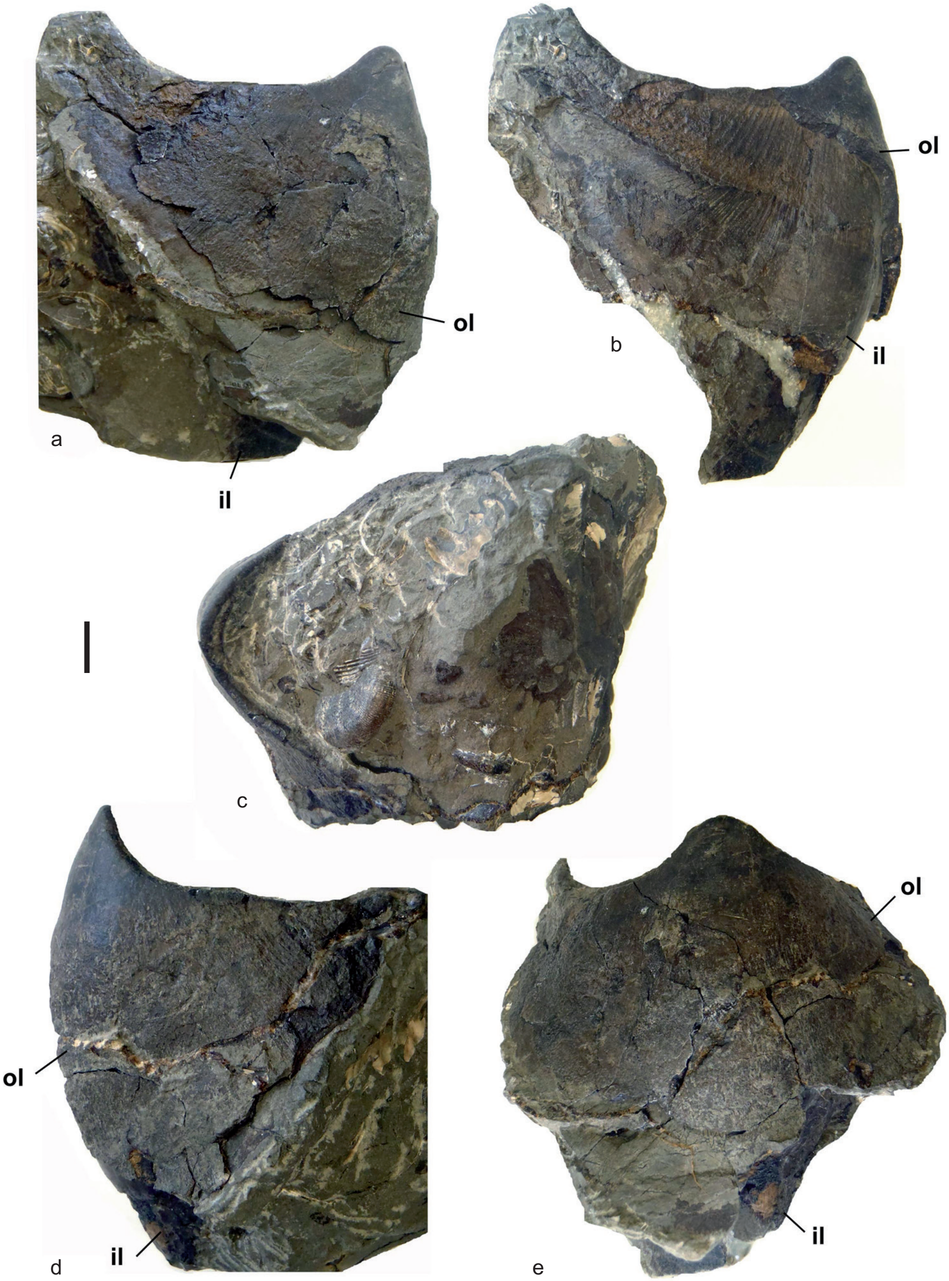


FIG. 12. Vampyromorpha *Incertae Sedis* (p. 21).

P. ribeti, lower Callovian, La Voulte-sûr-Rhône, France, holotype, MNHN 03801, scale bar, 10 mm and applies to all parts (new).

Vampyronassa FISCHER & RIOU, 2002, p. 13 [*V. rhodanica;* M]. Mantle bullet shaped; arms long, almost as long as mantle length; dorsal arm pair elongated; interbrachial web present; fins subterminal, wide nodular; gladius present, but poorly known. *Middle Jurassic (lower Callovian):* France.——FIG. 13,*3*. **V. rhodanica,* lower Callovian, La Voulte-sûr-Rhône, France, holotype, MNHN B.74247, scale bar 10 mm (new).

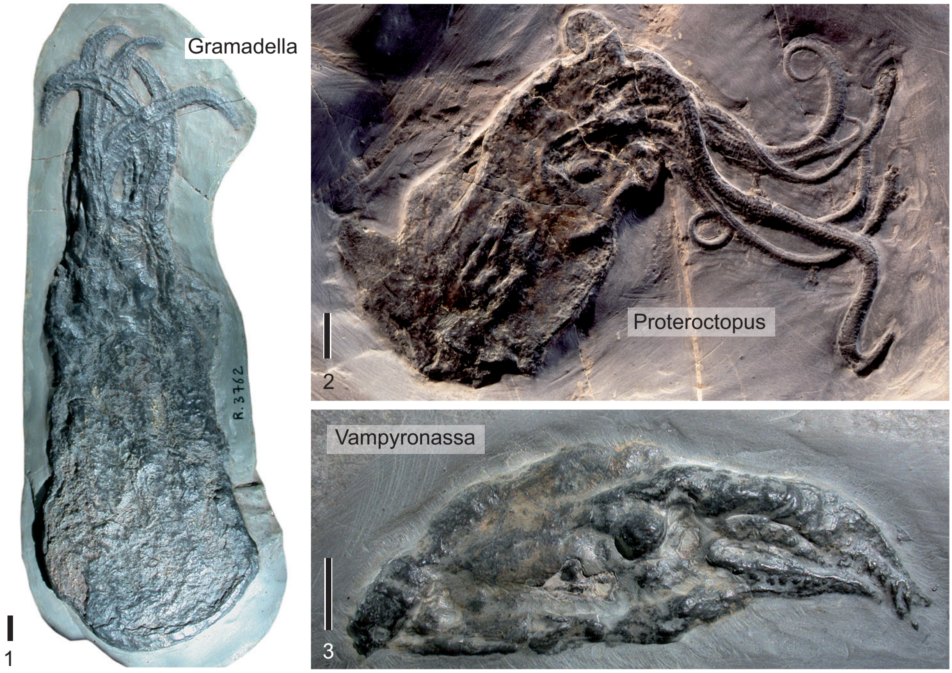


FIG. 13. Vampyromorpha *Incertae Sedis* (p. 21–22).

NOMEN DUBIUM

Provampyroteuthis KANIE, 1998, p. 24 [*P. *giganteus;* M]. Soft parts and gladius unknown; generic diagnosis based on isolated upper and lower beaks whose different morphologies suggest more than one species and genus. *Upper Cretaceous, lower Santonian:* northern Japan (Hokkaido).

Order OCTOPODA Leach, 1817

[Octopoda LEACH, 1817, p. 137] [=Octopodida SWEENEY & ROPER, 1998, p. 576; =Octobrachia *sensu* BOLETZKY, 1999, p. 275]

Coleoids whose dorsolateral arm pair is absent; gladius well developed (mantle length equals gladius length), reduced to unpaired or paired gladius vestiges (mantle length exceeds gladius vestige length), or absent; suckers radially symmetrical, sessile, uniserial, alternating or biserial, sucker rings absent; biserial cirri present or absent; fins (when present) with cartilaginous axial support, position subterminal, shape variable, number either one, or two pairs, or absent; funnel- and mantle-looking cartilages absent.

Suborder TEUDOPSEINA Starobogatov, 1983

[*nom. correct.* ENGESER & KEUPP, 1999, p. 29 *pro* Teudopseoidei STAROBOGATOV, 1983] [=Mesoteuthoidea NAEF, 1921a, p. 534; =Mesoteuthina JELETZKY, 1966, p. 45; =Teudopsidina DOYLE, DONOVAN, & NIXON, 1994, p. 7].

Very small to very large-sized octobrachiates with variable body shape; gladius either well developed (mantle length equals gladius length) or with reduced median field length (mantle length exceeds gladius vestige length), gladius width slender to very wide, maximum gladius width usually situated in posterior gladius part; median field spindle shaped, anteriorly more or less pointed (never straight), with or without pronounced median keel, median field width and thus median field area may vary greatly; hyperbolar zones well developed as furrows or wide depressions, rarely flat indistinct; hyperbolar zone usually moderately long, rarely short or long (hyperbolar zone length to median field length <0.6); lateral fields slender to very wide, shorter than hyperbolar zones, winglike outspread; free median field constriction present or absent; conus part spoon-, cup-, or patella-shaped; suckers where known circular, uniserial; cirri biserial; fins present; head demarcated or fused with dorsal mantle. *Lower Jurassic (Toarcian)–Upper Cretaceous (Maastrichtian).*

Family TEUDOPSEIDAE Regteren Altena, 1949

[*nom. correct.* JELETZKY, 1966, p. 45, *pro* Teudopseoidei REGTEREN ALTENA, 1949, p. 59] [=Beloteuthidae NAEF, 1921a, p. 535, *nom. rejected* JELETZKY, 1966]

Teudopseid gladius with spindle-shaped median field and pronounced median keel, moderately wide (gladius $width_{max}$ to median field length 0.20–0.45); median field length equals gladius length; median field anteriorly distinctly pointed, median field slender to wide (median field $width_{hypz}$ to hyperbolar zone length 0.20–0.80 = opening angle 12°–44°); median field constriction absent; median field area moderately large to large (median field area to gladius area 0.40–0.80); hyperbolar zone distinct, furrow-like, moderately long to long (hyperbolar zone length to median field length 0.40–0.60); lateral fields moderately wide to wide (lateral fields $width_{max}$ to median field $width_{max}$ 1.0–2.50); dorsal granulation absent; conus part spoon- to cup-shaped. [The family is presumed to be the root stock of other teudopseid families; paraphyletic grouping is therefore likely]. *Lower Jurassic (lower Toarcian)–Upper Cretaceous (Cenomanian).*

Teudopsis EUDES-DESLONGCHAMPS, 1835, p. 71 [**T. buneli;* SD WOODWARD, 1851–1856, p. 69] [=*Beloteuthis* MÜNSTER, 1843, p. 59, jr. obj. syn.]. Medium-sized teudopseids; gladius moderately wide (gladius $width_{max}$ to median field length 0.20–0.45); median field moderately wide to wide (median field $width_{hypz}$ to hyperbolar zone length 0.35–0.80 = opening angle 20°–44°); free median field width variable, with or without constriction; median field area moderately large to large (median field area to gladius area 0.50–0.80); hyperbolar zone moderately long to long (hyperbolar zone length to median field length 0.40–0.55); lateral fields flexed towards the venter or winglike outspread, moderately wide (lateral fields $width_{max}$ to median field $width_{max}$ 1.0–2.0); soft parts poorly known. *Lower Jurassic (lower–upper Toarcian, ?Callovian):* France, Luxembourg, Germany, UK, Slovakia, Hungary (?), Argentina, Canada (Alberta).——FIG. 14,*1a–b*. *T. bollensis* (VOLTZ), lower Toarcian, Posidonia Shale Formation, Holzmaden, southern Germany; *a,* gladius in dorsal view, MNHN (Fuchs & Weis, 2010, fig. 4B); *b,* gladius reconstruction based on *T. bollensis* (new). Scale bar, 10 mm.

Teudopsinia FUCHS, 2010, p. 62 [**T. haasi;* M]. Small-sized teudopseids; gladius moderately wide (gladius $width_{max}$ to median field length 0.25–0.35); median field slender (median field $width_{hypz}$ to hyperbolar zone length 0.20–0.30 = opening angle 12°–17°); free median field slender (median field $width_{2/3}$ to median field length 0.10–19); median field area moderately large (median field area to gladius area 0.40–0.55); hyperbolar zone weakly arcuated, long (hyperbolar zone length to median field length 0.50–0.60); lateral fields winglike outspread, wide (lateral fields $width_{max}$ to median field $width_{max}$ 2.20–2.40); soft parts unknown. ?*Upper Jurassic (lower Tithonian), Upper Cretaceous (upper Cenomanian):* ?southern Germany, Lebanon.——FIG. 14,*2a–b*. **T. haasi,* upper Cenomanian, Hâkel, Lebanon; *a,* holotype, MSNM i12627, showing the gladius in dorsal view, (Fuchs, 2010, fig. 2); *b,* gladius reconstruction (new). Scale bar, 10 mm.

Family TRACHYTEUTHIDAE Naef, 1921

[Trachyteuthidae NAEF, 1921a, p. 534] [=Actinosepiidae DOYLE, DONOVAN, & NIXON, 1994, p. 11, *partim*]

Teudopseid gladius with characteristic granules (tubercles) on dorsal median field surface; gladius moderately wide (gladius $width_{max}$ to median field length 0.20–0.49); median field length equals gladius length; median field moderately wide, rarely wide (median field $width_{hypz}$ to hyperbolar zone length 0.40–1.10 = opening angle 23°–58°); free median field slender to wide (median field $width_{2/3}$ to median field length 0.10–0.50), median field constriction rare; median field with or without pronounced median keel, anteriorly rounded, pointed, or serrated; median field area large to very large (median field area to gladius area 0.55–0.95); hyperbolar zone well developed, furrow-like, moderately long to long (hyperbolar zone length to median field length 0.25–0.55); lateral fields slender to wide (lateral fields $width_{max}$ to median field $width_{max}$ 0.80–2.20), winglike outspread; conus spoon shaped; arm length moderately long to long (arm length to mantle length 0.7–1.0); arms equipped with uniserial

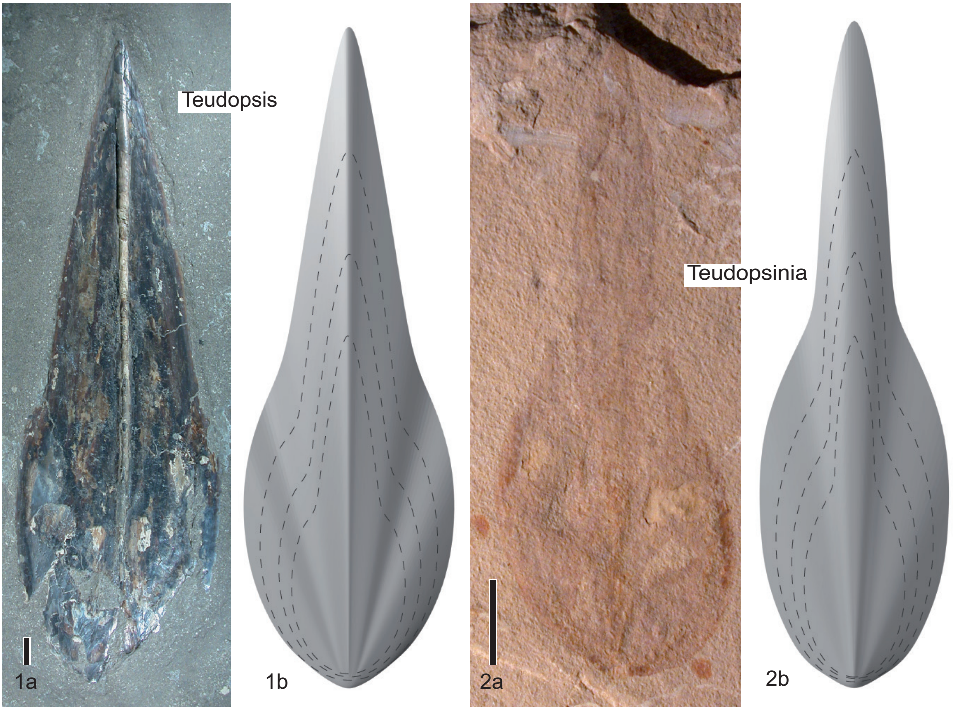


FIG. 14. Teudopseidae (p. 24).

suckers and paired cirri; two pairs of lobate fins. *Middle Jurassic (Callovian)–Upper Cretaceous (Maastrichtian).*

Trachyteuthis MEYER, 1846, p. 598 [**Tr. ensiformis* MEYER, 1846, p. 598; SD DOYLE, DONOVAN, & NIXON, 1994, p. 11; =*Sepia hastiformis* RÜPPELL, 1829, p. 9)] [=*Coccoteuthis* OWEN, 1855, p. 124 (type, *C. latipinnis,* OD); =*Voltzia* SCHEVILL, 1950b, p. 99, (type, *V. palmeri,* OD) =*Pseudoteudopsis* RICCARDI, 2016, p. 918 (type, *P. perezi,* OD.]. Medium- to large-sized teudopseids; gladius moderately wide (gladius $width_{max}$ to median field length 0.30–0.49); median field moderately wide to wide (median field $width_{hypz}$ to hyperbolar zone length 0.40–0.80 = opening angle 23°–44°); free median field slender to wide (median field $width_{2/3}$ to median field length 0.15–0.40), anteriorly rounded or weakly pointed, without median field constriction; median field area large (median field area to gladius area 0.60–0.80); hyperbolar zone distinctly arcuated, moderately long to long (hyperbolar zone to median field length 0.40–0.55); lateral fields moderately wide (lateral fields $width_{max}$ to median field $width_{max}$ 1.20–1.70); granulation fine to very coarse; arms long (arm length to mantle length 0.80–1.0) and slender. *Middle Jurassic (Callovian)–Upper Cretaceous (upper Cenomanian):* UK, Germany, Cuba, Chile, Antarctica, Lebanon, Russia, Australia.——FIG. 15*a–c*. *Trachyteuthis* sp., lower Tithonian, Altmühltal Formation, vicinity of Eichstätt, southern Germany; *a*, *Tr. hastiformis* (RÜPPELL), specimen in dorsal view showing gladius and mantle attachment (note the two pair of fins), JME SOS5762 (Fuchs, Engeser, & Keupp, 2007, fig. 4A); *b*, *Trachyteuthis* sp., gladius showing the dorsal granulation of the median field, Tischlinger collection (new); *c*, gladius reconstruction based on *Tr. nusplingensis* FUCHS, KEUPP, & ENGESER, 2007, upper Kimmerdigian, Nusplingen Formation, Germany (new). Scale bars, 10 mm.

Actinosepia WHITEAVES, 1897, p. 460 [**A. canadensis;* M]. Medium- to large-sized teudopseids; gladius moderately wide (gladius $width_{max}$ to median field length 0.40–0.49); free median field expanded (median field $width_{2/3}$ = gladius $width_{max}$), exceeding maximum lateral field width; median field wide (median field $width_{hypz}$ to hyperbolar zone length 1.00–1.10 = opening angle 54°–58°) with 5–7 radiating, keel-like elevations, anterior median field margin serrated; median field area very large (median field area to gladius area 0.85–0.95); hyperbolar zones well developed, short to moderately long (hyperbolar zone to median field length 0.25–0.35); lateral fields slender (lateral fields $width_{max}$ to median field $width_{max}$ 0.85–0.95); granulation fine to very coarse, granulated area large, reaching lateral margins of the median field;

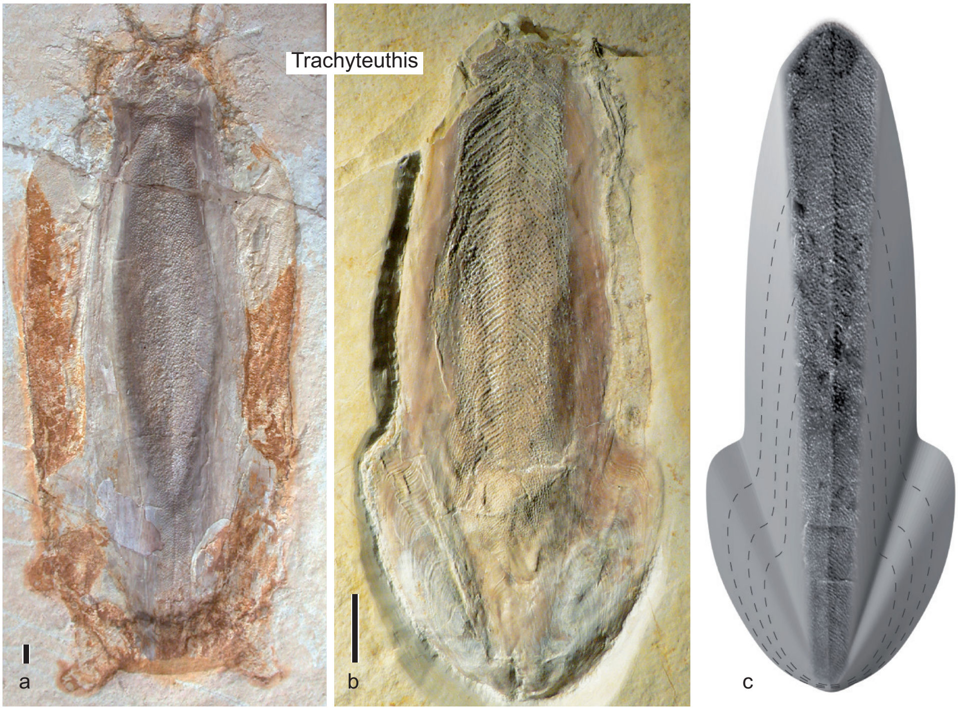


FIG. 15. Trachyteuthidae (p. 25).

soft parts unknown. *Upper Cretaceous (Campanian–Maastrichtian):* Canada, USA.——FIG. 16*a–d*. **A. Canadensis,* Campanian; *a*, uncompressed gladius in right dorsolateral view, Canada (Vancouver Island), Graham Beard collection (new); *b*, specimen showing the uncompressed gladius in left dorsolateral view, Canada (Alberta), BHI5845 (Larson, 2010, fig. 3A; photo courtesy of Neil Larson); *c*, gladius reconstruction (new); *d,* cross section of the gladius demonstrating the absence of a chambered part, Graham Beard collection (new). Scale bars, 10 mm.

Glyphidopsis FUCHS & LARSON, 2011b, p. 823 [**G. waagei;* M]. Small-sized teudopseids; gladius moderately wide (gladius $width_{max}$ to median field length 0.40–0.49); median field moderately wide (median field $width_{hypz}$ to hyperbolar zone length 0.55–0.65 = opening angle 31°–36°), anteriorly pointed, with mediodorsal keel-like elevation; free median field moderately wide (median field $width_{2/3}$ to median field length 0.20–0.29); median field area moderately large to large (median field area to gladius area 0.55–0.65); hyperbolar zone weakly arcuated, moderately long to long (hyperbolar zone length to median field length 0.45–0.55); lateral fields moderately wide (lateral fields $width_{max}$ to median field $width_{max}$ 1.45–1.55); granulation fine; arms long (arm length to mantle length about 1). *Upper Cretaceous (Cenomanian):* Lebanon.——FIG. 17*a–b*. **G. waagei,* Cenomanian, Hâkel, Lebanon; *a,* holotype, BHI 2251, showing the gladius in dorsal view (FUCHS & LARSON, 2011b, fig. 13); *b,* gladius reconstruction (new). Scale bar, 10 mm.

Glyphiteuthis REUSS, 1854, p. 30 [**Gl. ornata* REUSS, 1854, p. 30; M] [=*Libanoteuthis* KRETZOI, 1942, p. 125, 134 (type, *Geoteuthis libanotica* FRAAS, 1878, p. 345)]. Small- to medium-sized teudopseids; gladius moderately wide (gladius $width_{max}$ to median field length 0.20–0.40); median field moderately wide to wide (median field $width_{hypz}$ to hyperbolar zone length 0.40–0.80 = opening angle 23°–44°); anterior median field sharply pointed, with mediodorsal keel-like elevation, granulation variable; free median field slender (median field $width_{2/3}$ to median field length 0.10–0.19), occasionally with median field constriction; median field area large (median field area to gladius area 0.60–0.80); hyperbolar zone weakly arcuated, moderately long (hyperbolar zone length to median field length 0.30–0.40); lateral fields moderately wide (lateral fields $width_{max}$ to median field $width_{max}$ 1.30–1.70); arms moderately long (arm length to median field length 0.70–0.80); head not fused with the dorsal mantle; cephalic cartilage ring shaped. *Upper Cretaceous (lower Cenomanian–Santonian):* Czech Republic, France, Lebanon, Mexico.——FIG. 18*a*. **Gl. ornata* REUSS, middle Turonian, Czech Republic, NMP O6099 (Fuchs, pl. 15,*F*).——FIG. 18*b*. *Gl. freijii* FUCHS & LARSON 2011b, upper Cenomanian, Hâkel, Lebanon, holotype, BHI 2255, showing the gladius

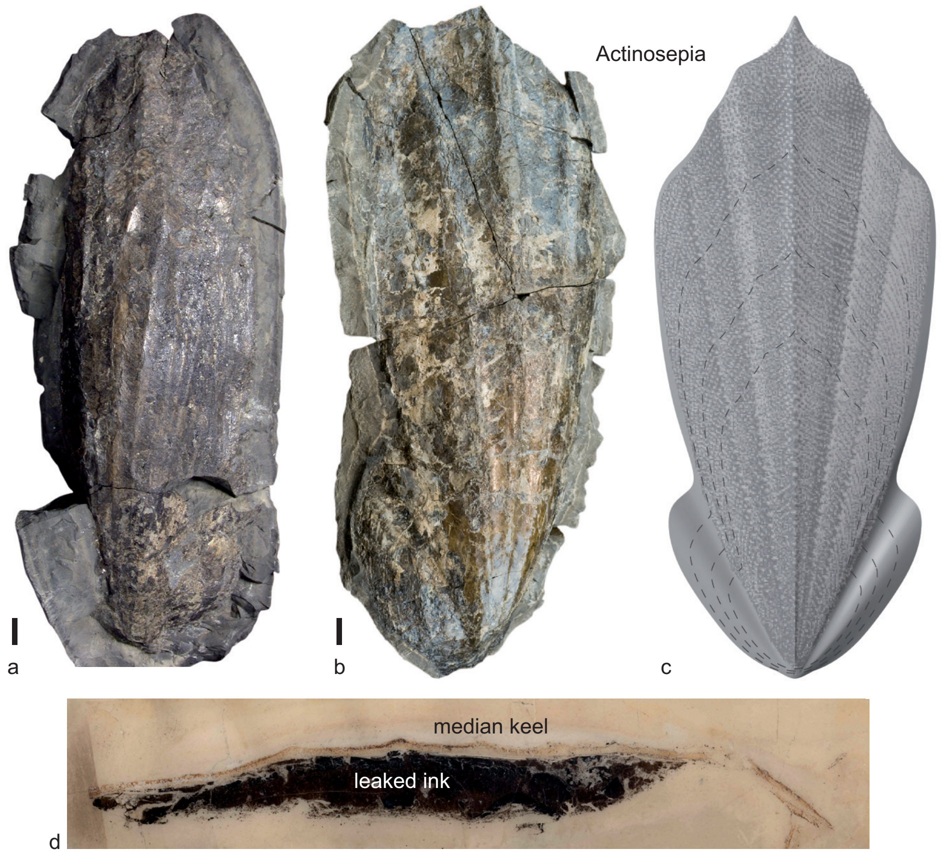


FIG. 16. Trachyteuthidae (p. 25–26).

and fossilized soft tissues (Fuchs & Larson, 2011b, fig. 101,*1*).——FIG. 18*c–d*. *Gl. libanotica* (FRAAS), upper Cenomanian, Hâkel, Lebanon, gladius in dorsal view, BHI 2237 (Fuchs & Larson, 2011b, fig. 4,*1*); *b*, gladius reconstruction based on *Gl. Libanotica* (new). Scale bars, 10 mm.

Paraglyphiteuthis KOSTÁK, 2002, p. 362 [**Glyphiteuthis crenata* FRITSCH, 1910, p. 14; M] [=*Glyphiteuthis* REUSS, 1854, p. 30 (type, *Gl. ornata,* M)]. Medium-sized teudopseids; gladius poorly known; free median field anteriorly sharply pointed, mediodorsal keel ribbed; configuration of hyperbolar zones and lateral fields unknown; soft parts unknown. *Upper Cretaceous (upper Turonian):* Czech Republic.——FIG. 19,*1a–b*. **P. crenata* (FRITSCH), Turonian, Czech Republic; *a*, holotype, NMP O3258, showing mediodorsal fragments of the ribbed keel (new); *b*, close-up with focus on the ribbed median keel (new). Scale bars 10 mm.

Styloteuthis FRITSCH, 1910, p. 12 [**S. convexa,* M; SD BÜLOW-TRUMMER, 1920, p. 251]. Small- to medium-sized teudopseids; gladius poorly known; shape of free median field unknown; posterior part circular in outline; median field moderately wide (median field width$_{hypz}$ to hyperbolar zone length 0.40–0.50 = opening angle 23°–28°), flanks of pronounced median keel finely granulated; hyperbolar zone weakly arcuated; hyperbolar zone length to median field length unknown; lateral fields wide (lateral fields width$_{max}$ to median field width$_{max}$ 2.0–2.10); soft parts unknown. *Upper Cretaceous (upper Turonian):* Czech Republic.——FIG. 19,*2*. **S. convexa,* middle Turonian, Czech Republic, holotype, NMP O3221, showing the posterior gladius fragment in dorsal view; *arrow head* marks granulation, scale bar, 10 mm (new).

Family PALAEOLOLIGINIDAE Naef, 1921

[Palaeololiginidae NAEF, 1921a, p. 535]

Small- to medium-sized (rarely large-sized) teudopseids; gladius leaf to lanceolate in shape, slender to moderately wide (gladius width$_{max}$ to median field length 0.10–0.40); anteriorly acute, posteriorly rounded; median

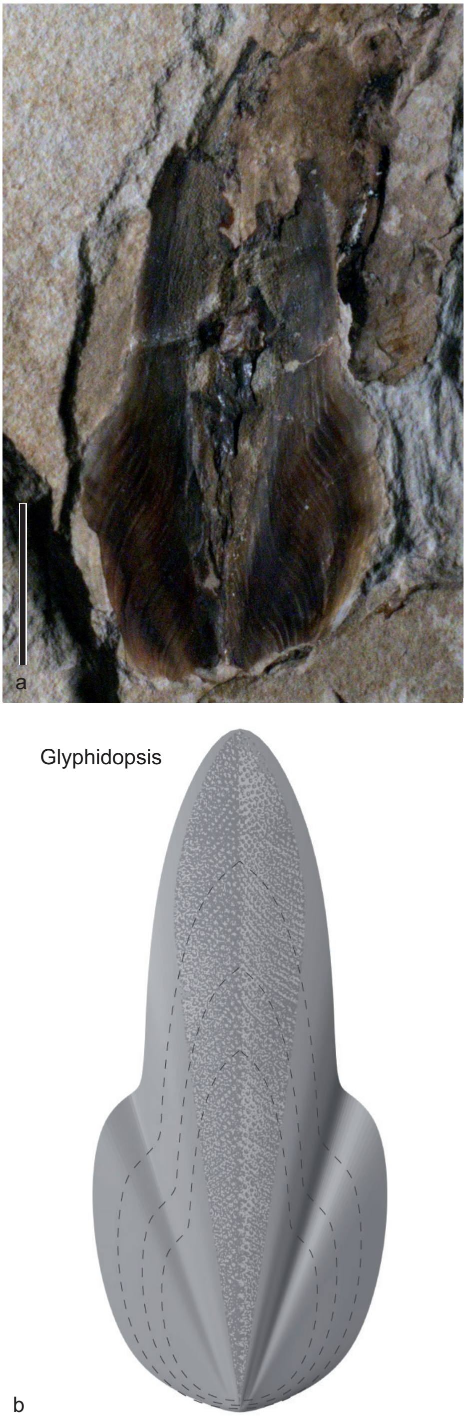


FIG. 17. Trachyteuthidae (p. 26).

field length equals gladius length; median field slender to moderately wide (median field $width_{hypz}$ to hyperbolar zone length 0.40–0.50 = opening angle 23°–38°) with 1–2 diverging ridges and a ridged, ribbed, or keeled midline; free median field very slender to slender (median field $width_{2/3}$ to median field length 0.05–0.15), free median field sometimes constricted suggesting a pseudo-wing; median field area moderately large to large (median field area to gladius area 0.50–0.80); hyperbolar zone indistinct, very weakly arcuated, hyperbolar zone length short to moderately long (hyperbolar zone length to median field length 0.25–0.45); lateral fields moderately wide (lateral fields $width_{max}$ to median field $width_{max}$ 1.20–2.0); conus spoon shaped; arm length moderately long to long. *Upper Jurassic (Tithonian)–Upper Cretaceous (Turonian).*

Palaeololigo NAEF, 1921a, p. 535 [**Teuthopsis oblonga* WAGNER, 1859, p. 276; SD NAEF, 1921b, p. 145]. Usually small-sized teudopseids, rarely large-sized; gladius leaf shaped, moderately wide (gladius $width_{max}$ to gladius length 0.25–0.40); median field moderately wide (median field $width_{hypz}$ to hyperbolar zone length 0.45–0.69 = opening angle 26°–38°); mediodorsal unipartite keel, pronounced, extending from posterior to anterior extremities; free median field distinctly constricted (pseudo-wing length to median field length 0.55–0.65), very slender (median field $width_{2/3}$ to median field length 0.05–0.10), anteriorly pointed; median field area moderately large to large (median field area to gladius area 0.50–0.65); hyperbolar zone indistinct, weakly arcuated, moderately long (hyperbolar zone length to median field length 0.35–0.45); lateral fields moderately wide (lateral fields $width_{max}$ to median field $width_{max}$ 1.40–1.70); arms moderately long to long (arm length to mantle length 0.55–0.85). *Upper Jurassic (lower Tithonian):* southern Germany.——FIG. 20,*1a–c*. *Palaeololigo* sp., lower Tithonian, Altmühltal Formation, vicinity of Eichstätt, southern Germany; *1a, P. albersdoerferi* (ENGESER & KEUPP, 1999), specimen with imprints of arms and fins, dorsal view, Resch personal collection, scale bars, 10 mm (new; photo courtesy of Udo Resch); ——FIG. 20,1*b–c*, **P. oblonga* (WAGNER), JME SOS1325; *b,* the gladius in ventral view (Fuchs & others 2016, fig. 8.2); *c,* gladius reconstruction based on *P. oblonga,* dorsal view (new). Scale bars, 10 mm.

Marekites KOSTÁK, 2002, p. 360 [**Styloteuthis? vinarensis* FRITSCH, 1910, p. 13; M]. Small- to medium-sized teudopseids; relative gladius width uncertain since free median field unknown; gladius posteriorly elliptical in shape; median field slender

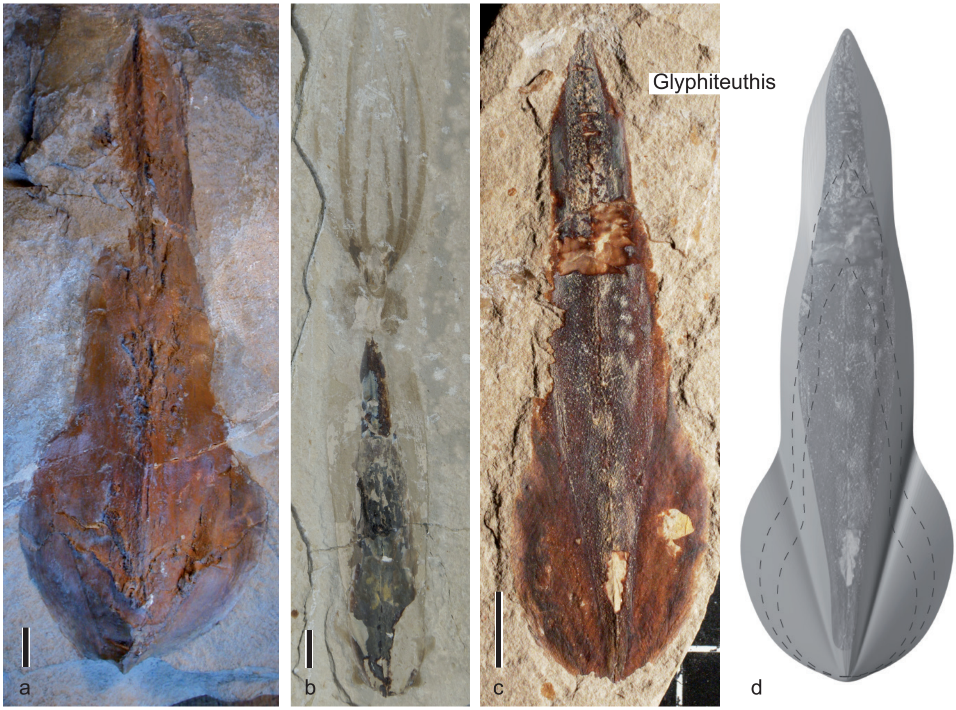


FIG. 18. Trachyteuthidae (p. 26–27).

to moderately wide (median field width$_{hypz}$ to hyperbolar zone length 0.20–0.45 = opening angle 12°–25°); central median field rachis-like with two diverging and one median ridge-like reinforcements; relative hyperbolar zone length unclear, possibly parallel sided over long distance; hyperbolar zone weakly arcuated, indistinct; lateral fields moderately wide (lateral fields width$_{max}$ to median field width$_{max}$ 1.30–1.80); soft parts unknown. *Upper Cretaceous (upper Cenomanian–upper Turonian):* southern Italy (Sicily), Czech Republic.——FIG. 20,*2a–b. M. vinarensis* (FRITSCH), middle Turonian, Czech Republic; *a,* holotype, NMP O3223, showing the posterior gladius fragment in dorsal view (new); *b*, gladius reconstruction based on *M. vinarensis,* scale bar, 10 mm (new).——FIG. 20,*2c. M. nebrodensis* FUCHS & others, 2016, Upper Cenomanian, Italy, MSNC 4496, scale bar, 10 mm (new).

Rachiteuthis FUCHS, 2006b, p. 8 [**R. donovani;* M]. Small-sized teudopseids; gladius slender (gladius width$_{max}$ to gladius length 0.10–0.19), lanceolate in shape; median field slender (median field width$_{hypz}$ to hyperbolar zone length 0.25–0.34 = opening angle 14°–19°); free median field very slender to slender (median field width$_{2/3}$ to median field length 0.05–0.15); distinct lateral ridges and a median keel extend from posterior to anterior extremities; free median field with or without constriction; median field area moderate to large (median field area to gladius area 0.70–0.80); hyperbolar zone weakly arcuated, short to moderately long (hyperbolar zone length to median field length 0.25–0.35); lateral fields moderately wide (lateral fields width$_{max}$ to median field width$_{max}$ 1.55–1.90); mantle torpedo shaped; fins rhomboidal; arms moderate in length (arm length to mantle length 0.70–0.80) and slender. *Upper Cretaceous (upper Cenomanian):* Lebanon.——FIG. 21*a–c. *R. donovani,* upper Cenomanian, Lebanon; *a,* paratype, MSNM i25135, with fossilized soft parts (Fuchs, 2006b, pl. 5A); *b,* holotype, MSNM i25142, showing gladius in dorsal view (Fuchs, 2006b, pl. 4A); *c,* gladius reconstruction based on *R. donovani* (new). Scale bars, 10 mm.

Superfamily MUENSTERELLOIDEA Roger, 1952

[Muensterelloidea *nom. transl.* FUCHS & SCHWEIGERT, 2018, p. 207, *ex* family Muensterellidae ROGER, 1952, p. 741]

Small- to very large-sized teudopseids; gladius length not necessarily as long as mantle length; posterior gladius conus part limpet shaped, anteriorly with short projection or long rachis-like extension; lateral fields moderately wide to wide, extent posteriorly behind the apex forming the posterior part of the patella; median field therefore

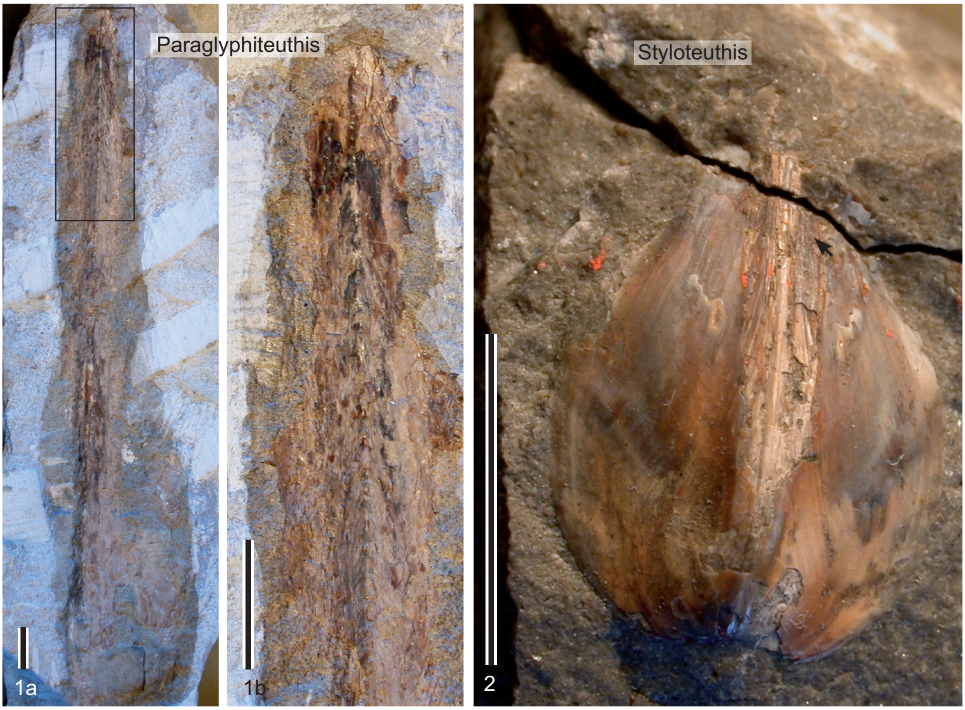


FIG. 19. Trachyteuthidae (p. 27).

reduced in length, not reaching posterior gladius end (median field length to gladius length <1); median field area very small to moderately large (median field area to gladius area <0.45); free median field length, hyperbolar zone length and position of patella apex variable; patella moderately wide to very wide (lateral fields width$_{max}$ (=patella width) to median field width$_{max}$ >1.50), patella margin serrated or smooth; patella with or without dorsal ornamentation (tubercles, radiating ribs, spines); fins present; ink sac present.

Family MUENSTERELLIDAE Roger, 1952

[*nom. correct.* ENGESER, 1988, p. 91 *pro* Münsterellidae ROGER, 1952, p. 741] [=Kelaenidae NAEF, 1921a, p. 535; =Celaenidae NAEF, 1922, p. 150; =Kelaenidae JELETZKY, 1966, p. 45]

Small- to medium-sized muensterelloids, gladius length equals mantle length; gladius moderately wide to wide (patella width to gladius length 0.25–0.65); median field moderately long to long (median field length to gladius length 0.60–0.90); median field very slender to wide (median field width$_{hypz}$ to hyperbolar zone length 0.15–0.80), always wider than median keel or ridge; free median field constriction may be present or absent; free median field shorter than patella length (patella length to gladius length >0.50); median field area moderate to very small (median field area to gladius area 0.05–0.45); patella moderately wide to very wide (patella width to median field width$_{max}$ 1.50.0–6.0), long oval to circular in shape (patella width to patella length 0.45–1.10), position of apex variable; hyperbolar zone well developed either as wide depression or furrow; hyperbolar zone length moderately long to long (hyperbolar zone length to median field length 0.35–0.55); patella margin smooth or serrated; dorsal ornamentation such as radial ribs, tubercles, or spines may be present. *Middle Jurassic (Callovian)–Upper Cretaceous (Turonian).*

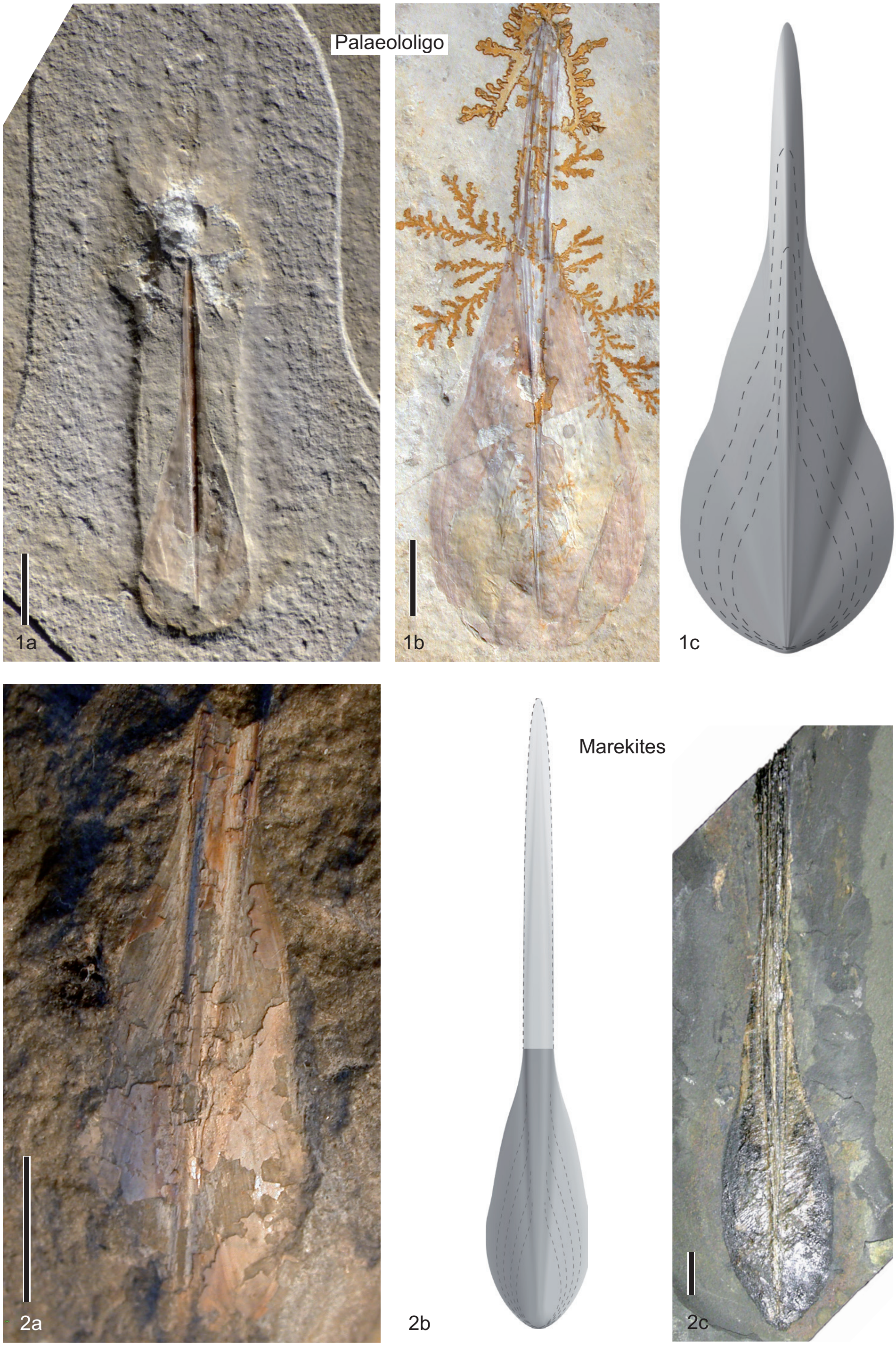


FIG. 20. Palaeololiginidae (p. 28–29).

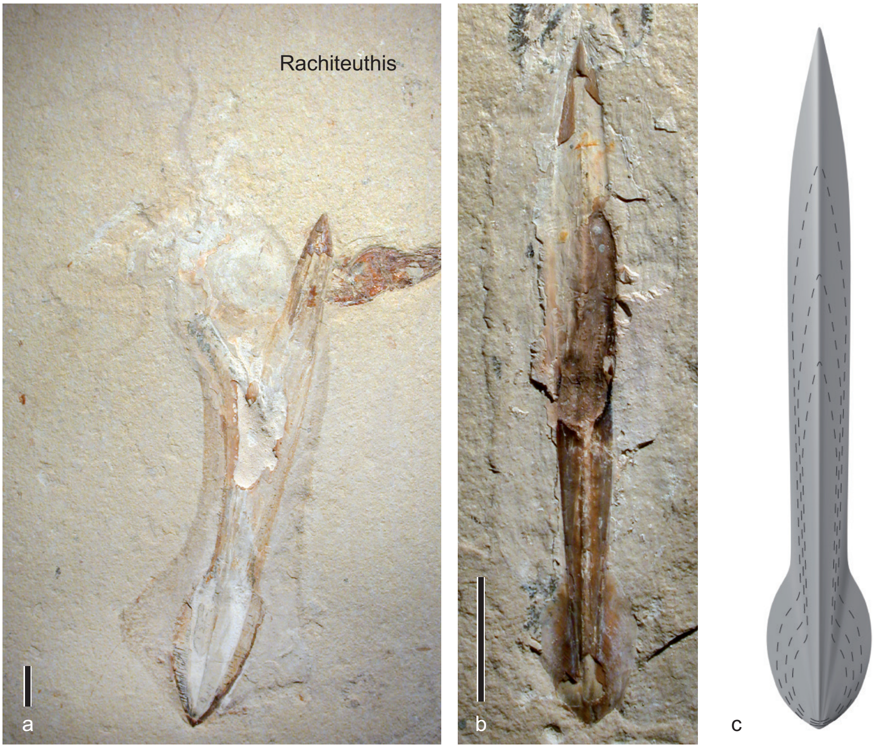


FIG. 21. Palaeololiginidae (p. 29).

Muensterella SCHEVILL, 1950a, p. 117 [**Kelaeno arquata* MÜNSTER, 1842, p. 96; SD BÜLOW-TRUMMER, 1920, p. 266; =*Kelaeno scutellaris* MÜNSTER, 1842, p. 96] [=*Kelaeno* MÜNSTER, 1842, p. 95, name invalidated, ICZN Opinion 1860, 1997; =*Listroteuthis* NAEF, 1922, p. 153]. Predominantly small-sized muensterelloids (rarely moderate or large in size); gladius moderately wide (patella width to gladius length 0.25–0.40); median field moderately long to long (median field length to gladius length 0.65–0.80); median field very slender to moderately wide (median field $width_{hypz}$ to median field length 0.15–0.40 = opening angle 9°–23°); median field with unipartite dorsal keel; free median field gently constricted, anteriorly pointed, length slightly shorter than patella (patella length to gladius length 0.55–0.65); median field area small (median field area to gladius area 0.10–0.20); patella very wide (patella width to median field $width_{max}$ 4.0–6.0), long oval in outline (patella width to patella length 0.45–0.75), position of apex anterior or central (hyperbolar zone length to patella length 0.35–0.60); hyperbolar zone moderately long (hyperbolar zone length to median field length 0.35–0.45); patella margin smooth or faintly serrated; radial ribs present, but very rare; tuberculation unknown; spines present, but very rare; arms conspicuously short; body squat shaped; fins skirtlike. [*Kelaeno arquata* is today universally recognized as a younger synonym of *K. scutellaris.*] *Upper Jurassic (upper Kimmeridgian)–Upper Cretaceous middle Turonian):* Germany, Antarctica, Texas (USA).——FIG. 22,*1a–c*. **M. scutellaris* (MÜNSTER), lower Tithonian, Altmühltal Formation, vicinity of Eichstätt, southern Germany; *a,* specimen with fossilized soft tissues, BSPG MC-21 (Fuchs, Keupp, & Engeser, 2003, pl. 1,*1*); *b,* gladius in dorsal view, BSPG collection (Fuchs, 2009, fig. 3A); *c,* gladius reconstruction based on *M. scutellaris* (new). Scale bars, 10 mm.

Celaenoteuthis NAEF, 1922, p. 153 [**C. incerta;* M]. Small- to medium-sized muensterelloids; gladius moderate in width (patella width to gladius length 0.35–0.45); median field triangular with narrow, rachis-like anterior projection, moderately wide (median field $width_{hypz}$ to hyperbolar zone length 0.45–0.55 = opening angle 25°–31°); median field long (median field length to gladius length 0.85–0.95); free median field distinctly constricted producing the anterior rachis, moderately long to long (pseudo-wing length to median field length 0.65–0.75), free median field length slightly shorter than patella (patella length to gladius length 0.55–0.65); median field area small to moderate (median field area to gladius area 0.35–0.45); patella moderately wide (patella width

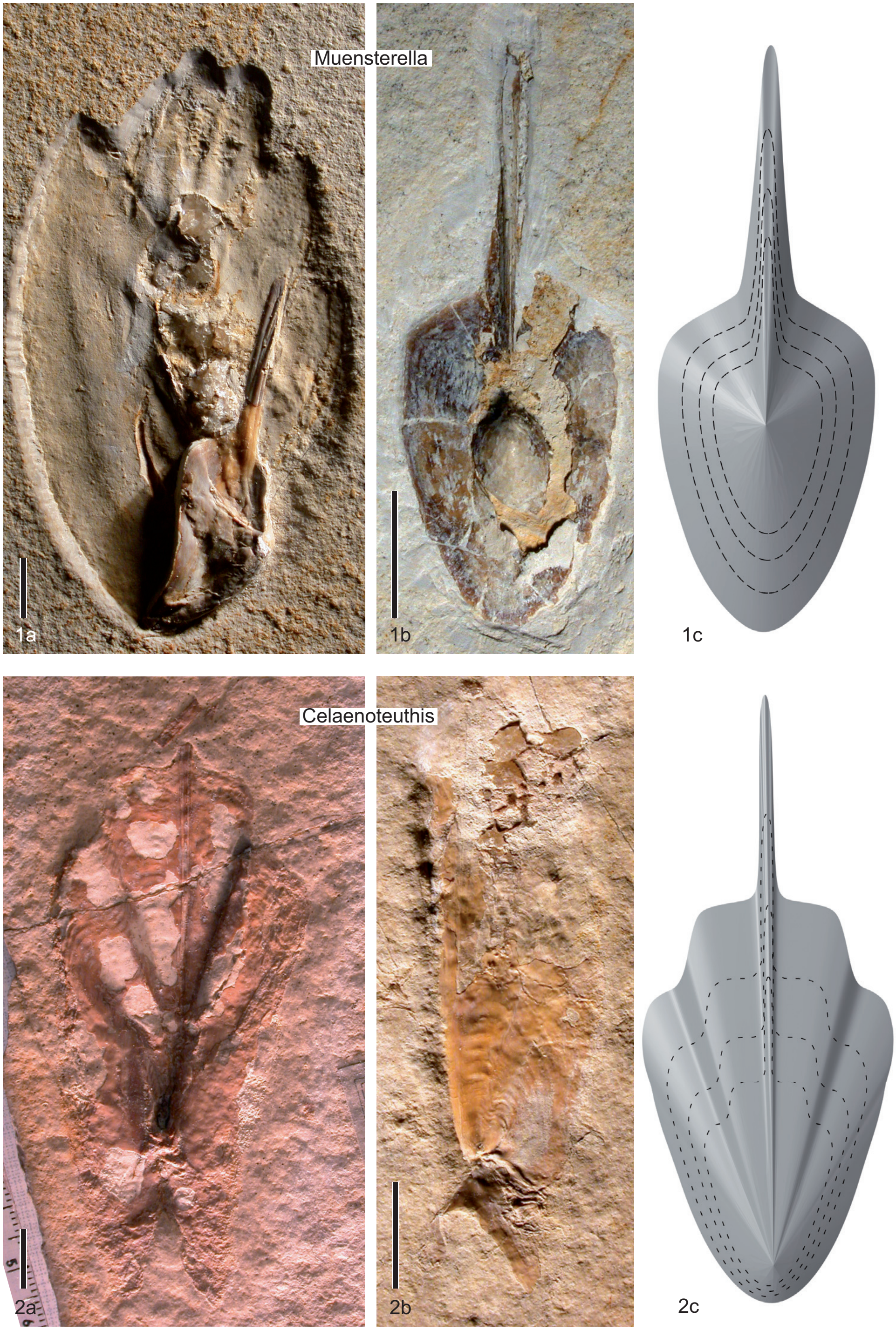


FIG. 22. Muensterellidae (p. 32–34).

to median field width$_{max}$ 1.65–1.75), long oval in outline (patella width to patella length 0.65–0.75), apex located in posterior position (hyperbolar zone length to patella length 0.75–0.85); hyperbolar zone distinctly curved, furrow-like, moderately long to long (hyperbolar zone length to median field length 0.45–0.55); patella margin smooth; radial ribs, tuberculation, and spines absent; gladius length equals mantle length. *Upper Jurassic (lower Tithonian):* southern Germany.——FIG. 22,*2a–c*. **C. incerta,* lower Tithonian, Altmühltal Formation, vicinity of Eichstätt, southern Germany; *a*, gladius in ventral, MfNB MB.C18846 (Fuchs, 2009, fig. 3C); *b*, gladius in lateral view (new); *c*, gladius reconstruction (new). Scale bars, 10 mm.

Engeseriteuthis FUCHS & others 2019, p. 74 [**E. arcuatus;* M]. Small- to medium-sized muensterelloids with distinctly arcuated hyperbolar zones; gladius moderately wide to wide (patella width to gladius length 0.45–0.55); median field wide (median field width$_{hypz}$ to hyperbolar zone length 0.75–0.85 = opening angle 41°–46°); median field long (median field length to gladius length 0.75–0.85); free median field constricted, anteriorly rounded, length slightly shorter than median field (patella length to gladius length 0.50–0.55); median field area small (median field area to gladius area 0.30–0.39); patella wide (patella width to median field width$_{max}$ 2.35–2.45), circular in outline (patella width to patella length 0.90–1), apex located in posterior position (hyperbolar zone length to patella length 0.60–0.70); hyperbolar zone distinctly curved, furrow-like, moderately long (hyperbolar zone length to median field length 0.35-0.45); patella margin smooth; radial ribs, tuberculation, and spines absent; gladius length equals mantle length. *Upper Jurassic (upper Kimmeridgian):* southern Germany.——FIG. 23,*1a–b*. **E. arcuata*, upper Kimmeridgian, Geisental Formation, Schamhaupten, southern Germany; *a,* gladius in ventral, holotype, JME SOS Scha709 (Fuchs & others, 2019, fig. 11a); *b,* gladius reconstruction (new). Scale bar, 10 mm.

Etchesia FUCHS, 2017, p. 340 [*E. martilli;* M]. Small-sized muensterelloids; gladius spearhead-like, very wide (ratio patella width to gladius length 0.85–0.95) without rachis-like anterior projection; median field wide (median field width$_{hypz}$ to hyperbolar zone length 0.70–0.80 = opening angle 39°–44°); median field long (median field length to gladius length 0.85–0.95); free median field gently constricted, anteriorly blunt, slightly shorter than patella (patella length to gladius length 0.55–0.65); median field area small (median field area to gladius area 0.35-0.40); patella wide (patella width to median field width$_{max}$ 2.25–2.35), wide oval in shape (patella width to patella length 1.40–1.50), apex shifted close to posterior gladius rim (hyperbolar zone length to patella length 0.75–0.85), hyperbolar zone a wide depression, long (hyperbolar zone length to median field length 0.50–0.60; patella margin distinctly serrated; dorsal surface ornamented with radial ribs and tubercles; spines unknown; soft tissues unknown. *Upper Jurassic (lower Tithonian):* UK.——FIG. 23,*2a–b*. **E. martilli,* lower Tithonian, Kimmeridge Clay, Kimmeridge Bay, UK; *a,* gladius in ventral, holotype, MJML K1802 (Fuchs 2017, fig. 2); *b,* gladius reconstruction (new). Scale bar, 10 mm.

Listroteuthis NAEF, 1922, p. 153 [**Celaeno conica* WAGNER, 1859, p. 276; M] [=*Muensterella* SCHEVILL, 1950a, p. 117 (type, *M. scutellaris* (MÜNSTER, 1842)]. Small-sized muensterelloids; gladius moderately wide (patella width to gladius length 0.45-0.55); median field moderately wide (median field width$_{hypz}$ to hyperbolar zone length 0.45–0.55 = opening angle 25°–31°), median field moderately long (median field length to gladius length 0.60–0.70); median field with bipartite dorsal keel; free median field gently constricted, anteriorly pointed, length shorter than patella (patella length to gladius length 0.65–0.75); median field area very small to small (median field area to gladius area 0.15–0.25); patella very wide (patella width to median field width$_{max}$ 2.60–2.70), oval in outline (patella width to patella length 0.65–0.75), patella apex centered (hyperbolar zone length to patella length 0.45–0.55); hyperbolar zone moderately long to long (hyperbolar zone length to median field length 0.45–0.55); patella margin smooth; radial ribs, tuberculation, and spines absent; soft parts poorly known. *Upper Jurassic (lower Tithonian):* southern Germany.——FIG. 24,*1a–b*. **L. conica,* lower Tithonian, Mörnsheim Formation, Daiting, southern Germany; *a,* gladius in dorsal view, neotype (Fuchs & others, 2019, fig. 13A-C); *b,* gladius reconstruction (new). Scale bars, 10 mm.

Muensterellina FUCHS & others, 2019, p. 69 [**M. johnjagti;* M]. Small-sized muensterelloids; gladius wide (patella width to gladius length 0.55–0.65); median field moderately long (median field length to gladius length 0.60–0.70); median field wide to very wide (median field width$_{hypz}$ to hyperbolar zone length 1.10–1.20 = opening angle 58°–62°), free median field anteriorly rounded, distinctly shorter than patella (patella length to gladius length 0.60–0.70); median field area very small (median field area to gladius area 0.05–0.15); patella moderately wide (patella width to median field width$_{max}$ 1.70–1.80), circular in outline (patella width to patella length 0.90–1), apex central (hyperbolar zone length to patella length 0.45–0.55); hyperbolar zone moderately long (hyperbolar zone length to median field length 0.45–0.55); patella margin weakly serrated; patella ornamented with radiating ribs; tuberculation and spines unknown; soft parts unknown. *Middle Jurassic (upper Callovian):* UK.——FIG. 24,*2a–b*. **M. johnjagti,* middle Callovian, Oxford Clay, Christian Malford, UK; *a,* gladius in dorsal view, holotype, NMHUK PI CC 1740 (FUCHS & others, 2019, fig. 14A); *b,* gladius reconstruction (new). Scale bar, 10 mm.

Tyrionella FUCHS & others, 2019, p. 71 [*T. fauseri;* M]. Small-sized muensterelloids; gladius wide

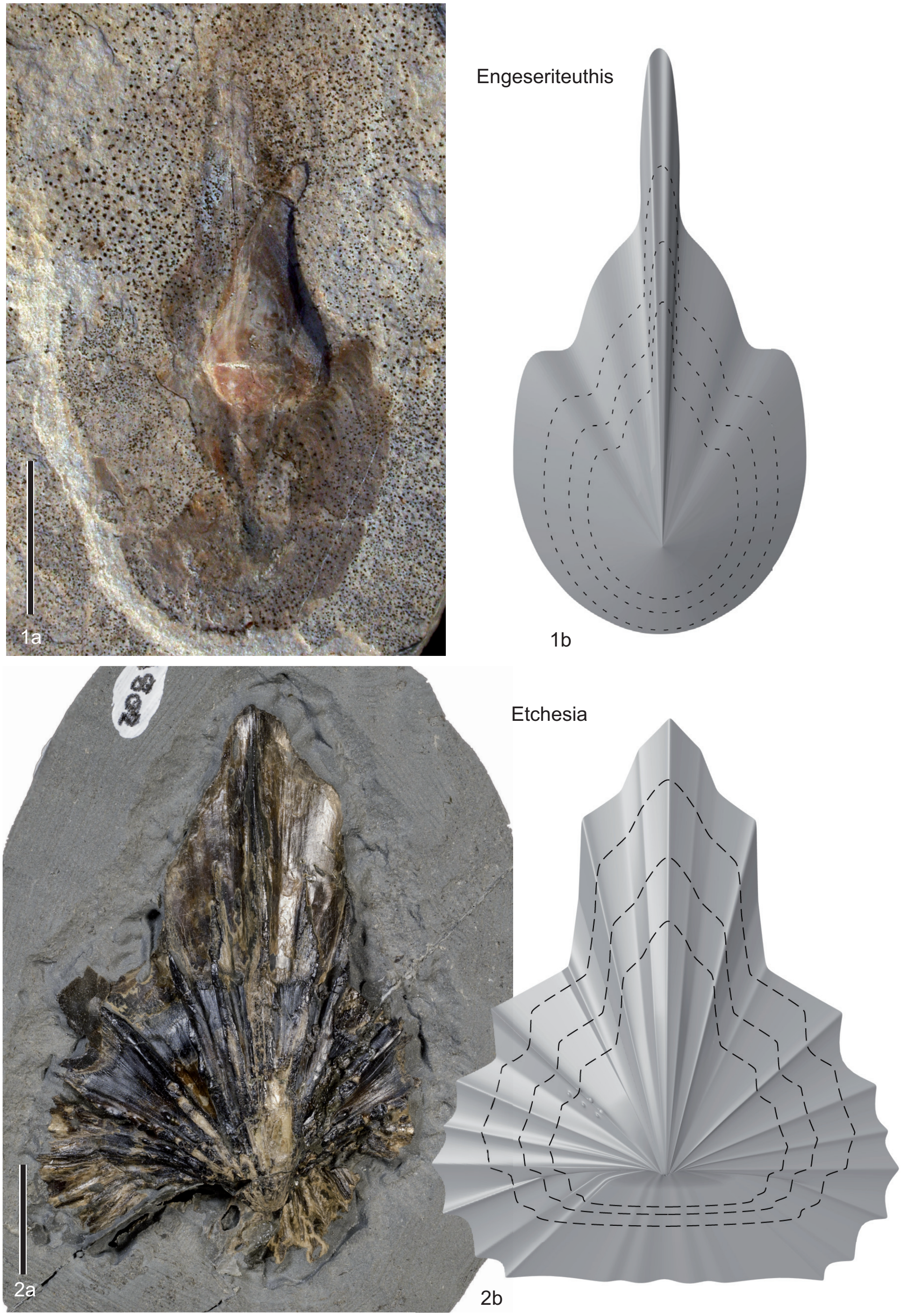


FIG. 23. Muensterellidae (p. 34).

(patella width to gladius length 0.55–0.65); median field wide to very wide (median field $width_{hypz}$ to hyperbolar zone length 1.15–1.25 = opening angle 60°–64°), moderately long (median field length to gladius length 0.60–0.70), ornamented with diverging ridges; free median field gently constricted, length shorter than patella (patella length to gladius length 0.55–0.65); median field area small (median field area to gladius area 0.25–0.35); patella moderately wide (patella width to median field $width_{max}$ 1.75–1.85), circular in outline (patella width to patella length 0.95–1.05), patella apex centered (hyperbolar zone length to patella length 0.45–0.55); hyperbolar zone moderately long (hyperbolar zone length to median field length 0.35–0.45); patella margin smooth; radial ribs, tuberculation, and spines absent; soft parts unknown. *Upper Jurassic (lower Tithonian).* southern Germany.——FIG. 25*a–b.* **T. fauseri,* lower Tithonian, Altmühltal Formation, Schernfeld, southern Germany; *a,* gladius in ventral view, holotype, PIMUZ 31910, (FUCH & others 2019, fig. 15A–C); *b,* gladius reconstruction (new). Scale bar, 1 mm.

Family ENCHOTEUTHIDAE Larson, 2010

[*nom. corr.* FUCH & others, 2019, p. 42, *pro* Enchoteuthididae LARSON, 2010, p. 96]

Large- to very large-sized muensterelloids; gladius length most probably equals mantle length; gladius slender to moderately wide (patella width to gladius length 0.15–0.30); median field reduced to very slender rachis (median field $width_{hypz}$ to hyperbolar zone length 0.10–0.19 = opening angle <12°); median field long (median field length to gladius length 0.75–0.95); free median field constriction absent; free median field slightly longer than patella (patella length to gladius length < 0.50), rachis cross section dorsally rounded, dorsally keeled; ventrally with a pair of distinct ventral and ventrolateral ridges (quadripartite); median field area small (median field area to gladius area 0.20–0.35); patella very wide (patella width to median field $width_{max}$ 4.50–7.0), long oval (patella width to patella length <0.80), apex never in anterior position (hyperbolar zone length to patella length >0.50); hyperbolar zone well developed as wide depression, short to moderately long (hyperbolar zone length to median field length 0.25–0.35); patella margin smooth; radial ribs, tubercles, or spines unknown; soft parts unknown.

Enchoteuthis MILLER & WALKER, 1968, p. 176 [**E. melanae;* M] [=*Kansasteuthis* MILLER & WALKER, 1968, p. 179 (type, *Kansasteuthis lindneri,* M; =*Niobrarateuthis* MILLER, 1957, p. 810, *partim* (type, *N. bonneri,* M)]. Large- to very large-sized muensterelloids; gladius slender to moderately wide (patella width to gladius length 0.15–0.25); median field reduced to a very slender rachis (median field $width_{hypz}$ to hyperbolar zone length 0.10–0.19 = opening angle 6°–11°); median field long (median field length to gladius length 0.75–0.85); free median field slightly longer than patella (patella length to gladius length 0.40–0.50), parallel sided, rachis cross section dorsally rounded, ventrally with a pair of distinct ventral and ventrolateral ridges (quadripartite); non-free rachis dorsally keeled; median field area small (median field area to gladius area 0.20–0.30); patella very wide (patella width to median field $width_{max}$ 4.50–6.80), long oval in outline (patella width to patella length 0.35–0.50), apex centered to slightly shifted posteriorly (hyperbolar zone length to patella length 0.50–0.60); hyperbolar zone moderately long (hyperbolar zone length to median field length 0.25-0.35); patella margin smooth; radial ribs, tuberculation, spines unknown; soft parts unknown. *Lower Cretaceous (upper Albian)–Upper Cretaceous (upper Campanian):* Australia, Canada, USA.——FIG. 26*a–c.* **E. melanae,* Santonian-Campanian, Niobrara Formation, USA; *a,* holotype, FHSM 13049, showing the posterior conus part (Larson, 2010, fig. 10; photo courtesy of Neil Larson); *b,* gladius reconstruction based on *E. melanae* (new); *c,* cross section of the free rachis, KU 151925, showing ventral and ventrolateral keels (Larson, 2010, fig. 13; photo courtesy of Neil Larson). Scale bars, 1 mm.——FIG. 26*d. E. cobbani* (LARSON, 2010), holotype, BHI 4138, showing the gladius in dorsal view (Larson, 2010, fig. 17A; photo courtesy of Neil Larson).

Niobrarateuthis MILLER, 1957, p. 810 [**N. bonneri;* OD]. Large-sized muensterelloids; gladius moderately wide (patella width to gladius length 0.20–0.30); median field reduced to a very narrow rachis (median field $width_{hypz}$ to hyperbolar zone length 0.15–0.25 = opening angle 9°–14°); median field long (median field length to gladius length 0.90–0.95); free median field (rachis) distinctly longer than patella (patella length to gladius length 0.30–0.40); rachis cross section solid, dorsally rounded (except its keeled posterior end); median field area small (median field area to gladius area 0.30–0.39); patella very wide (patella width to median field $width_{max}$ 4.55–4.65), oval in outline (patella width to patella length 0.65–0.75), apex shifted posteriorly (hyperbolar zone length to patella length 0.85–0.95); hyperbolar zone moderately long (hyperbolar zone length to median field length 0.30–0.40); patella margin smooth; radial ribs, tuberculation, spines unknown; soft parts unknown. *Upper Cretaceous (upper Santonian–lower Campanian):* USA.——FIG. 27,*1a–b.* **N. bonneri,* uppermost Santonian/lowermost Campanian,

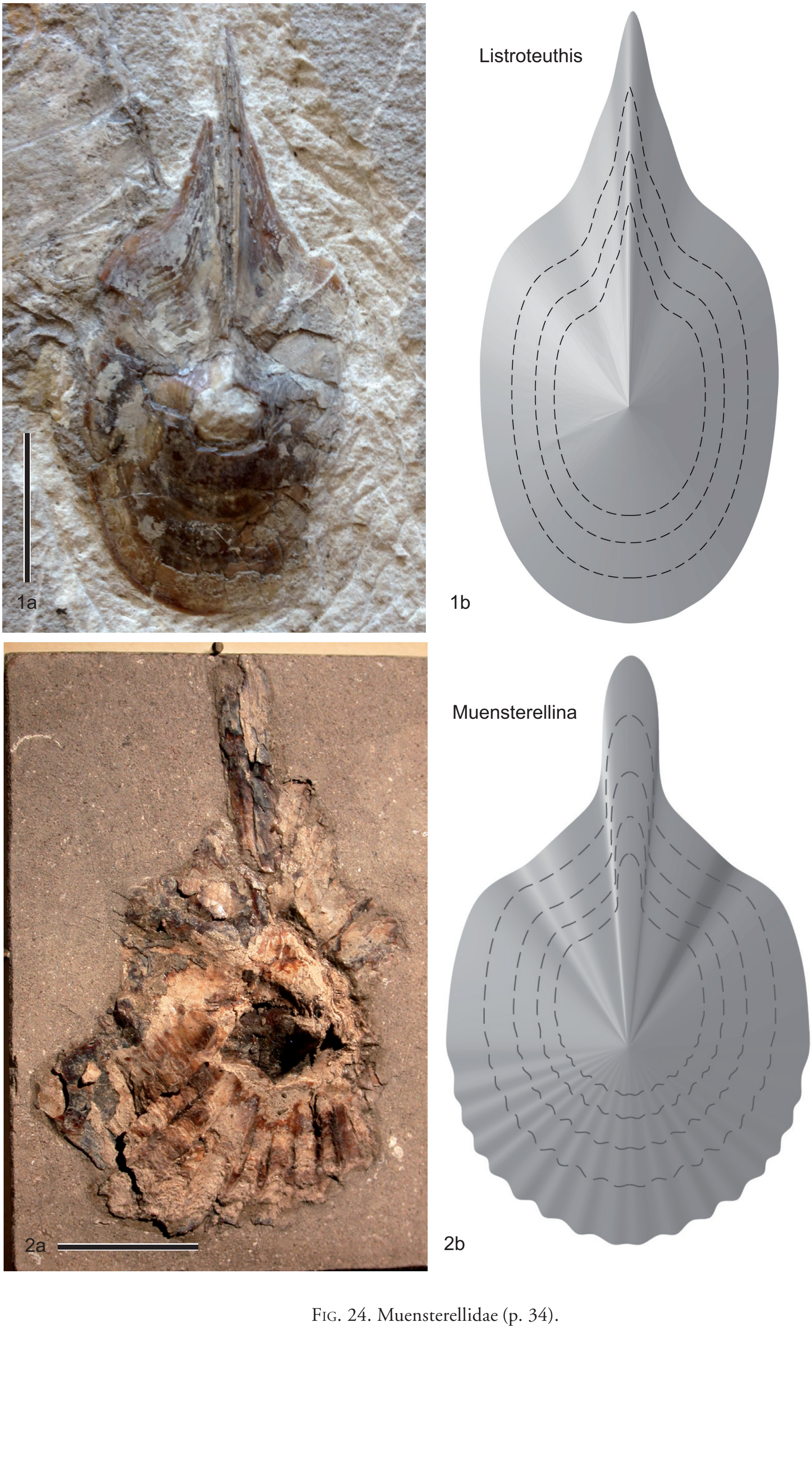


FIG. 24. Muensterellidae (p. 34).

FIG. 25. Muensterellidae (p. 34–36).

Niobrara Formation, Kansas, USA; *a,* holotype, FHKSCM 7959, showing the patella in dorsal view (new; photo courtesy of Neil Larson); *b,* gladius reconstruction (new). Scale bar, 100 mm.

ENCHOTEUTHIDAE *INCERTA SEDIS*

Tusoteuthis LOGAN, 1898, p. 497 [**T. longa;* M; *nom. dub.*]. Large- to very large-sized muensterelloids; gladius poorly known; free median field unknown; patella possibly spindle shaped, position of apex unknown. *Upper Cretaceous (upper Santonian–lower Campanian):* USA.——FIG. 27,*2a–b.* **T. longa,* uppermost Santonian/lowermost Campanian, Niobrara Formation, Kansas, USA; *a,* holotype, KU 113463, showing mounted fragments of posterior gladius (Larson, 2010, fig. 15A; photo courtesy of Neil Larson); *b,* gladius reconstruction, length of rachis as well as position of apex assumed (new). Scale bar, 10 cm.

Family PATELLOCTOPODIDAE Fuchs & Schweigert, 2018

[Patelloctopodidae FUCHS & SCHWEIGERT, 2018, p. 207]

Small-sized muensterelloids; gladius length probably shorter than mantle length (vestigial); gladius vestige limpet-like, wide to very wide (patella width to gladius length >0.60); median field wide to very wide (median field width$_{hypz}$ to hyperbolar zone length >0.75 = opening angle >40°), short (median field length to gladius length <0.40); free median field constriction indistinct; free median field reduced in length, distinctly shorter than patella length (patella length to gladius length >0.70); median field area very small (median field area to gladius area <0.15); patella wide to very wide (patella width to median field width$_{max}$ 2.30–3.70), circular (patella width to patella length 0.85–1.10); position of apex anterior (hyperbolar zone length to patella length <0.20); hyperbolar zone well developed, length variable; patella margin usually serrated; dorsal ornamentation such as radial ribs present either with or without tubercles; spines unknown; fins unknown, but most probably present; ink sac unknown.

Patelloctopus FUCHS & SCHWEIGERT, 2018, p. 209 [**P. ilgi;* M]. Small-sized muensterelloids; gladius vestige with a high-conical circular patella and very short, nose-like anterior projection; gladius vestige very wide (patella width to gladius length 0.85–0.95); median field very wide (median field width$_{hypz}$ to

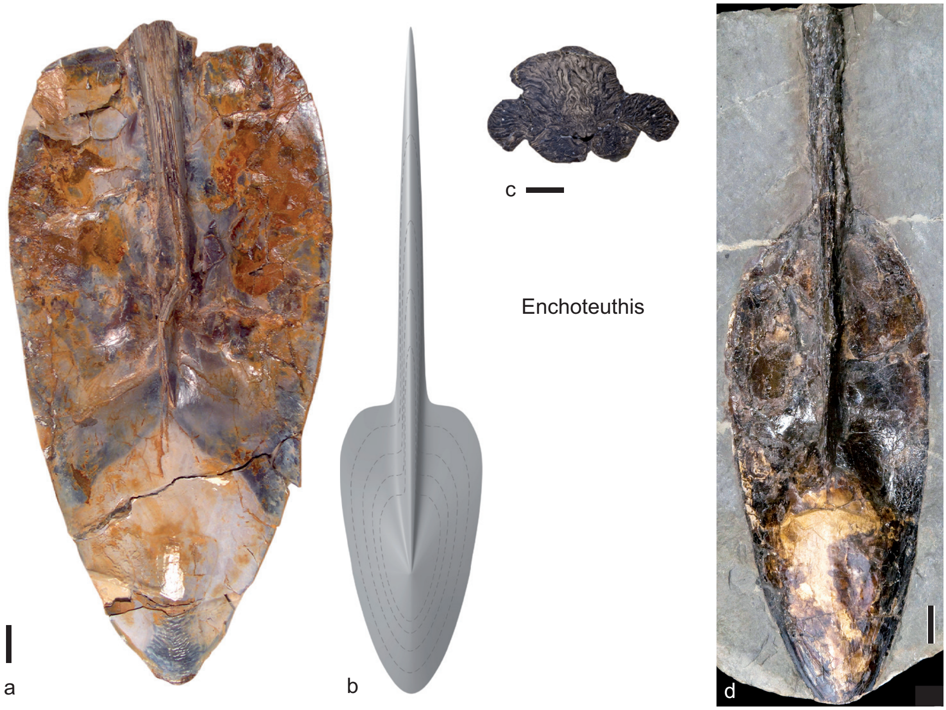


FIG. 26. Enchoteuthidae (p. 36).

hyperbolar zone length 1.55–1.65 = opening angle 76°–79°), short (median field length to gladius length 0.25–0.35); free median field anteriorly rounded, very short (patella length to gladius length 0.80–0.90); median field area very small (median field area to gladius area <0.10); patella very wide (patella width to median field width$_{max}$ 3.55–3.65), circular in outline (patella width to patella length 1.0–1.10), apex located in anterior position (hyperbolar zone length to patella length 0.15–0.25); hyperbolar zone moderately long to long (hyperbolar zone length to median field length 0.45–0.55); patella margin serrated, posterior rim incised; radial ribs and tuberculation present; spines unknown; soft tissues unknown. *Upper Jurassic (upper Kimmeridgian)*: southern Germany.——FIG. 28,*1a–b*. **P. ilgi*, upper Kimmeridgian, Nusplingen Formation, Nusplingen, southern Germany; *a,* paratype, SMNS 70340, showing the gladius vestige in dorsal view; *b,* reconstruction of the vestigial gladius (new). Scale bar, 10 mm.

Pearceiteuthis HEWITT & JAGT, 1999, p. 317 [**P. buyi;* M]. Small-sized muensterelloids; gladius wide (patella width to gladius length 0.60–0.70) without distinct anterior projection; median field very wide (median field width$_{hypz}$ to hyperbolar zone length >2.0 = opening angle >90°); short (median field length to gladius length 0.25–0.35); free median field gently constricted, anteriorly pointed, significantly shorter than patella (patella length to gladius length 0.65–0.75); median field area very small (median field area to gladius area 0.05–0.15); patella wide (patella width to median field width$_{max}$ 2.35–2.45), circular in outline (patella width to patella length 0.85–0.95), apex shifted close to anterior gladius rim (hyperbolar zone length to patella length <0.10), median field (median field length to gladius field length 0.31) and hyperbolar zone length therefore very short (hyperbolar zone length to median field length 0.08); patella margin distinctly serrated; dorsal surface ornamented with radial ribs; tuberculation and spines unknown; soft tissues unknown. *Middle Jurassic (upper Callovian):* UK.——FIG. 28,*2a–b*. **P. buyi,* upper Callovian, Oxford Clay, Christian Malford, UK; *a,* holotype, NHMUK PI OR34468, showing the gladius vestige in dorsal view; *b,* reconstruction of the vestigial gladius (new). Scale bar, 10 mm.

PUTATIVE MUENSTERELLOIDEA

Eoteuthoides KOSTÁK, 2002, p. 363 [**Styloteuthis caudata* FRITSCH, 1910, p. 13; OD]. Gladius anteriorly rachis-like posteriorly blade- or patella-like; median field consists only as a keeled rachis, possibly not reaching posterior gladius end, anterior free rachis unknown; hyperbolar zone indistinct; lateral fields spindle shaped, extending posteriorly behind rachis possibly forming a patella-like

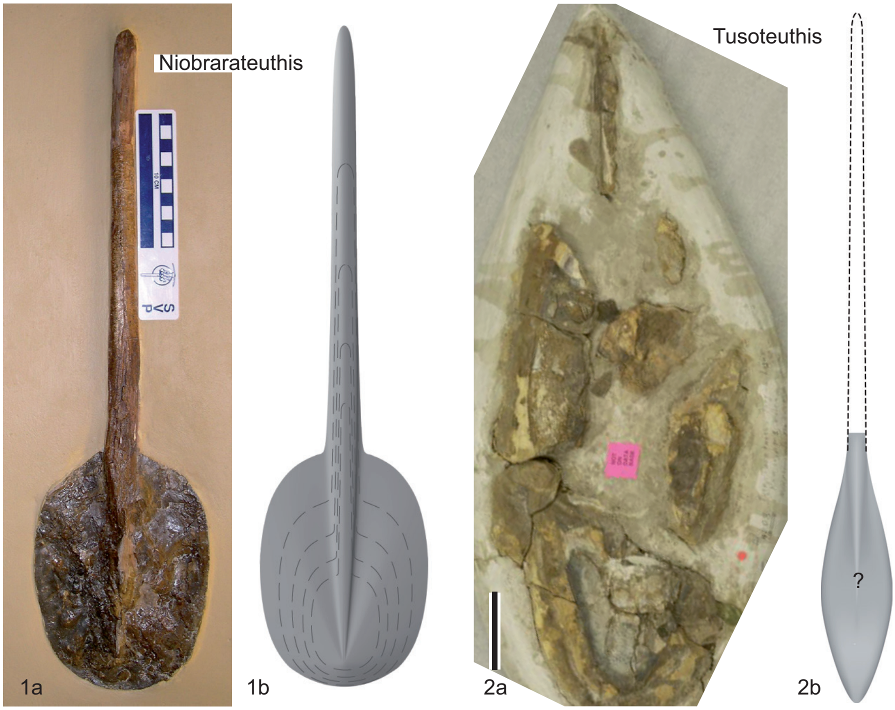


FIG. 27. Enchoteuthidae and Enchoteuthidae *Incerta Sedis* (p. 36–38).

conus, apex in posterior position (non-free rachis lengthins to patella length >0.90). *Upper Cretaceous (upper Turonian):* Czech Republic.——FIG. 29*a–b*. **Eo. caudata* (FRITSCH), *upper Turonian,* Czech Republic; *a,* holotype, NMP O3222, showing the posterior gladius, scale bar 1 mm (new); *b,* gladius reconstruction (new).

Suborder CIRRATA Grimpe, 1916

[Cirrata GRIMPE, 1916, p. 353] [=Cirroteuthoidea Naef, 1922, p. 284; =Cirromorphina JELETZKY, 1966, p. 5; =Cirroctopoda YOUNG, 1989, p. 202; =Cirrina SWEENEY & ROPER, 1998, p. 576].

Gladius reduced to an unpaired gladius vestige, which is distinctly shorter than mantle length; median field reduced in width and length; suckers uniserial; cirri biserial; fins present; dorsal mantle fused with head. ?*Upper Cretaceous (Santonian–Campanian)–Holocene.*

Family UNDETERMINED

Paleocirroteuthis TANABE & others, 2008, p. 402 [**P. haggarti;* M]. Soft parts and gladius unknown; large-sized lower beak; wing (outer lamella) elongated; hood rounded; inner lamella elongated without infold of lateral wall; rostrum either sharp with small hook or blunt with weak hook; outer lamella wide, large, and thick. *Upper Cretaceous (Santonian–lower Campanian):* Canada (British Columbia).——FIG. 30*a–b*. **P. haggarti,* holotype, CDM 994.59.9, Santonian, Haslam Formation, Courtenay, Vancouver Island, Canada; frontal (*a*), right lateral (*b*) views (Tanabe & others, 2008, fig. 5.*2,5*; photo courtesy of Kazushige Tanabe). Scale bars, 10 mm.

Suborder INCIRRATA Grimpe, 1916

[Incirrata GRIMPE, 1916, p. **353**] [=Octopoda LEACH, 1817 *sensu* YOUNG, 1989, p. 202; =Incirrina GRIMPE, 1916 *sensu* SWEENEY & ROPER, 1998, p. 577].

Gladius reduced to paired gladius vestiges or absent (where present distinctly shorter than mantle length), shape blade- or stylet-like; suckers uniserial or alternating; cirri absent; fins present in ancestral forms, absent in extant representatives; dorsal mantle fused with head. *Upper Cretaceous (Cenomanian)–Holocene).*

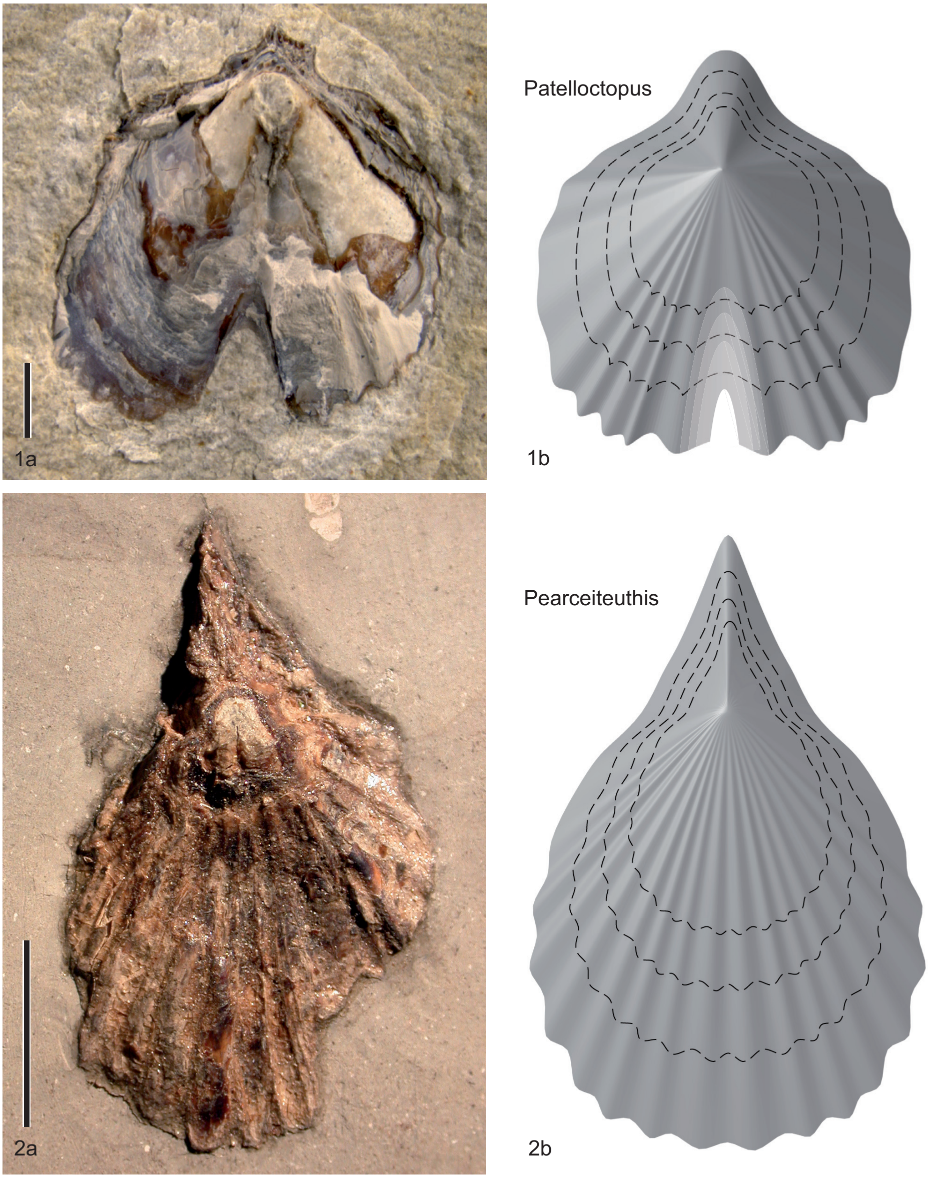


FIG. 28. Patelloctopodidae (p. 38–39).

Family PALAEOCTOPODIDAE Dollo, 1912

[Palaeoctopodidae DOLLO, 1912, p. 126]

Incirrates with oval to spherical mantle outlines; arms very long (ratio to mantle length >1); suckers circular, biserial or alternating, cirri absent; ink sac present; fins subterminal, basal fin cartilage present; gladius vestige bipartite, bladelike, without median connection, located in dorsal posterior mantle, growth nucleus either central or posteromarginal. *Upper Cretaceous (Cenomanian–Santonian):* Lebanon.

Palaeoctopus WOODWARD, 1896a, p. 567 [**Calaïs newboldi* WOODWARD, 1896b, p. 229; OD (M)]. [=*Calaïs* WOODWARD, 1896b, p. 229; *nom. inval.*

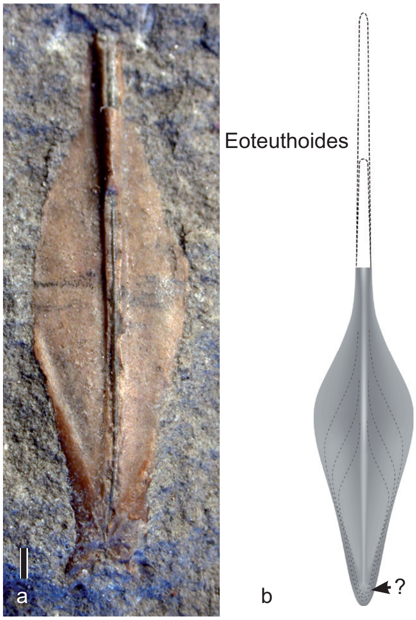


FIG. 29. Putative Muensterelloidea (p. 39–40).

(insect); =*Parateudopsis* ENGESER & REITNER, 1986, p. 9]. Mantle outline spherical; gladius vestige with anterior and posterior nose-like projections, growth increments concentrically around a central nucleus; arms very long (ratio to mantle length >1); fins subterminal, oar-like. *Upper Cretaceous (Santonian):* Lebanon.——FIG. 31,*1a–c*. **P. newboldi* (WOODWARD), Santonian, Lebanon; *a,* overview of the holotype, NHMUK C32324, note the weak imprints of fins (new); *b,* MNHN B18834, showing the bipartite gladius vestige (new); *c,* gladius vestige reconstruction (new). Scale bars, 10 mm.

Keuppia FUCHS, BRACCHI, & WEIS, 2009, p. 67 [**K. levante;* OD]. Mantle outline oval; gladius vestige without anterior and posterior projections, growth increments concentrically around a posterior nucleus; arms very long (ratio arm length to mantle length >1), fin cartilage present. *Upper Cretaceous (upper Cenomanian):* Lebanon.——FIG. 31,*2a–c*. **K. levante,* upper Cenomanian, Lebanon; *a,* overview of the holotype, MSNM i2632 (Fuchs, Bracchi, & Weis, 2009, fig. 2A); *b,* close-up of the posterior mantle to show the bipartite gladius vestige (Fuchs, Bracchi, & Weis, 2009, fig. 4D); *c,* gladius vestige reconstruction of *K. levante* (new).——FIG. 31,*2d,* gladius vestige reconstruction of *K. hyperbolaris* (new). Scale bars, 10 mm.

Family OCTOPODIDAE d'Orbigny, 1840

[*nom. correct.* WOODWARD, 1851 in 1851–1856, p. 76, *pro* family Octopidae D'ORBIGNY, 1840, p. 30]

Incirrates with sac-like body; suckers alternating, cirri absent; dorsal mantle fused with head; ink sac present; fins absent; gladius vestige stylet-like located in the lateral mantle or absent. *Upper Cretaceous (Cenomanian)–Holocene.*

Styletoctopus FUCHS, BRACCHI, & WEIS, 2009, p. 73 [**St. annae;* M]. Gladius vestige paired, stylet-like, widely separated in the lateral mantle. *Upper Cretaceous (Cenomanian):* Lebanon.——FIG. 32*a–c*. **St. annae,* Cenomanian, Lebanon; *a,* overview of the holotype, MSNM i26323 (Fuchs, Bracchi, & Weis, 2009, fig. 7A); *b,* close-up of the mantle to show the paired stylets (Fuchs, Bracchi, & Weis, 2009, fig. 7B); *c,* gladius vestige reconstruction (Fuchs, Bracchi, & Weis, 2009, fig. 4E). Scale bars 10 mm.

ICHNOTAXA ASSIGNED TO OCTOPODIDAE

Oichnus BROMLEY, 1981, p. 60 [**O. simplex;* BROMLEY, 1981, p. 60; OD]. Drilling holes found in shells of molluscs, decapod crustaceans, barnacles; positions

FIG. 30. Family Undetermined (p. 40).

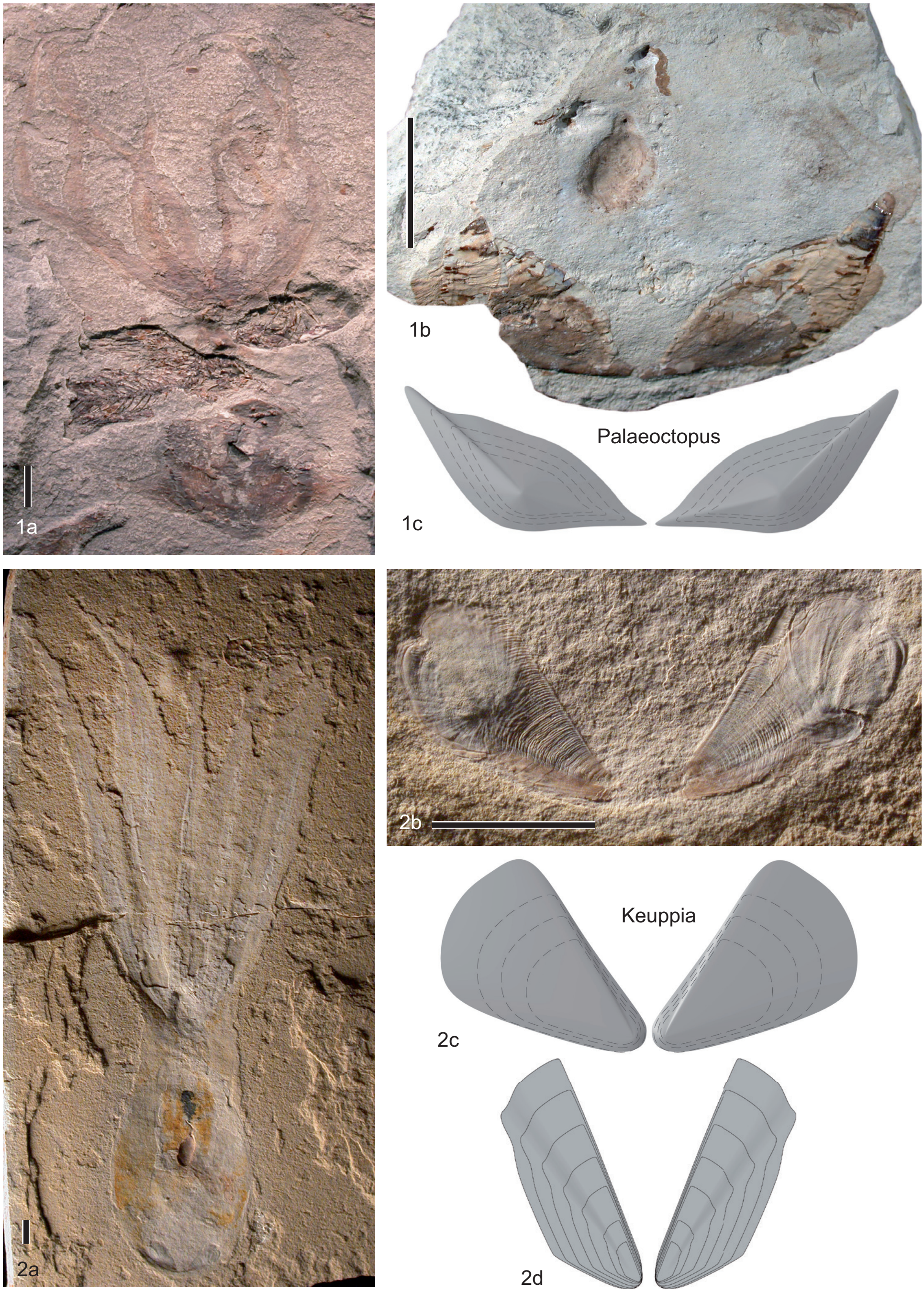


FIG. 31. Palaeoctopodidae (p. 41–42).

stereotypic; shape circular to semicircular, diameter millimeter-sized, cylindriconical, external edge beveled, rounded, short groove leads in the hole. *Lower Eocene–Holocene.* North Sea, Mediterranean Sea, USA, Japan.——FIG. 33. *O. ovalis* BROMLEY, 1993, p. 170, Pliocene, USA, octopod drilling hole in a crab shell, scale bar, 0.1mm (Klompmaker & others, 2013, Fig. 3C; photo courtesy A. Klompmaker).

Family ARGONAUTIDAE Cantraine, 1841

Females with external shell-like egg case in which females live, calcitic shell paper-thin, convolute, unchambered, externally sculptured; rodlike gladius vestige absent.

Argonauta LINNAEUS, 1758, p. 708 [**A. argo;* SD MONTFORT, 1810, p. 7]. Venter width variable, angled, bordered by paired keels; keels with nodes or spines; flanks with flat-topped sigmoidal radial ribs, with or without nodules. *Miocene–Holocene. middle Miocene–Pliocene:* Japan, New Zealand, Austria, Italy, Cyprus, Red Sea; *Holocene* (extant): circumglobal in tropical and subtropical surface waters.——FIG. 34,*1. A. joanneus* HILBER, 1915, holotype, UMJ collection, middle Miocene (Langhian), Steiermark, Austria, left lateral view, scale bar, 10 mm (Fuchs & Lukeneder, 2014, fig. 6a; photo courtesy of Martin Gross).

Izumonauta KOBYASHI, 1954a, p. 31 [**I. latus;* M]. Venter comparatively broad, angled, bordered by low-noded keels, flanks with radial rows of granules or tubercles. *middle–upper Miocene:* Japan, New Zealand.——FIG. 34,*2a–c*. **I. latus,* holotype, UMUT CM 0481, middle Miocene, Fujina Formation, Shimane Prefecture, Japan; left lateral (*a*), posterior (*b*), and anterior (*c*) views (new; photo courtesy of Yasuhiro Ito). Scale bars, 10 mm.

FIG. 32. Octopodidae (p. 42).

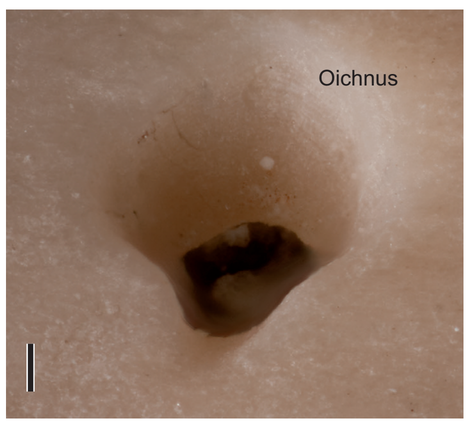


FIG. 33. Octopodidae Ichnotaxa (p. 42–44).

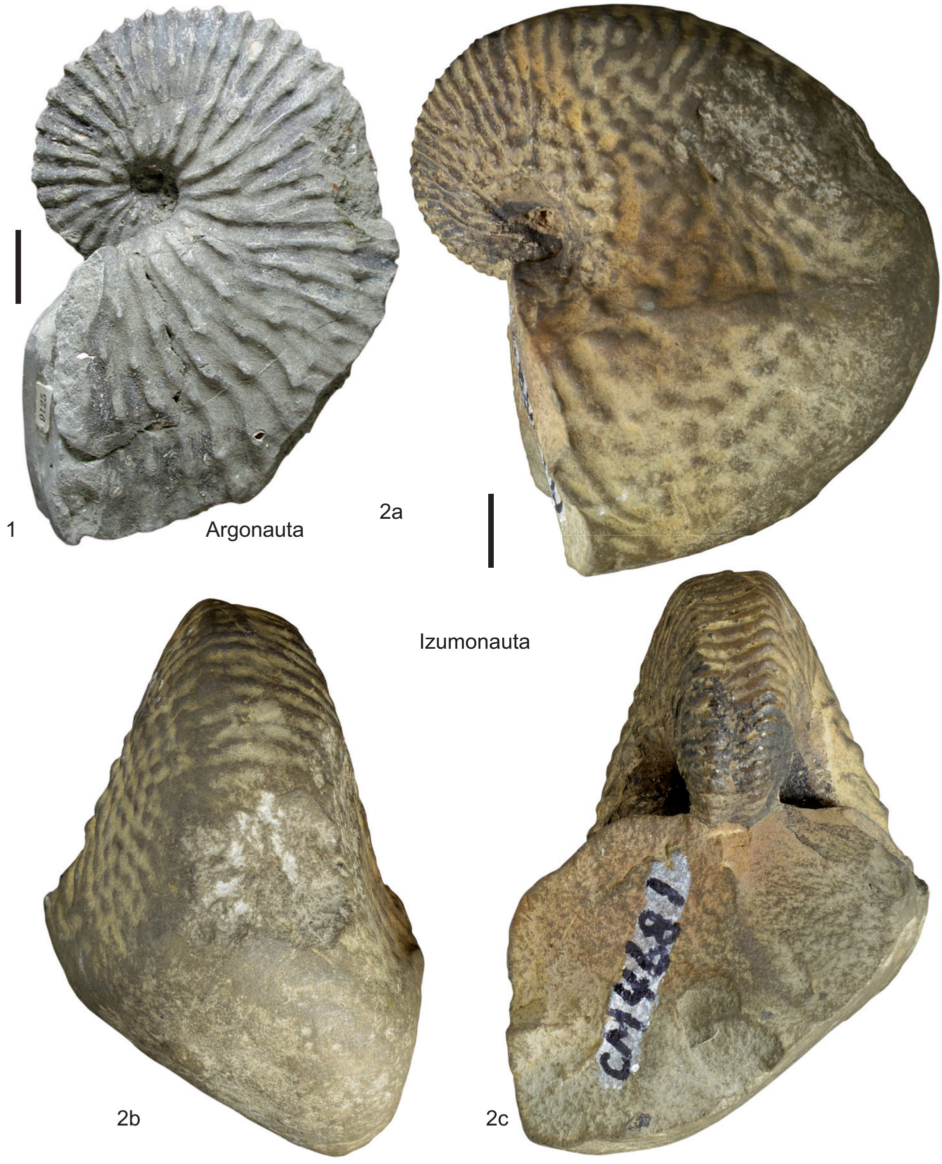


FIG. 34. Argonautidae (p. 44).

Kapal MARTIN, 1929, p. 221 [**K. batavus;* M] Venter comparatively broad, bordered by pronounced noded keels, flanks with radial ribs. *middle Miocene:* Indonesia (Sumatra).——FIG. 35*a–c*. **K. batavus,* holotype, RGM.6739, middle Miocene, Sumatra; left lateral (*a*), anterior (*b*), and posterior (*c*) views (new; photo courtesy of Ronald Pouwer). Scale bar, 1 mm.

Mizuhobaris NODA, OGASAWARA, & NOMURA, 1986, p. 18 [**Nautilus izumoensis* YOKOYAMA, 1913, p. 2; OD]. Egg case lacking peripheral keels, venter rounded; flanks smooth except fine growth increments. *middle Miocene:* Japan, USA (southern California).——FIG. 36,*1a–c*. **M. izumoensis* (YOKOYAMA), IGPS 98924, middle Miocene, Fujina Formation, Shimane Prefecture, Japan; right lateral (*a*), apertural (*b*), and left lateral (*c*) views. (Noda, Ogasawara, & Nomura, 1986, pl. 9,*3A–C*). Scale bars, 10 mm.

Obinautilus KOBAYASHI, 1954b, p. 182 [*O. pulcher;* OD]. Venter very narrow, slightly depressed with peripheral angulations, without distinct keels,

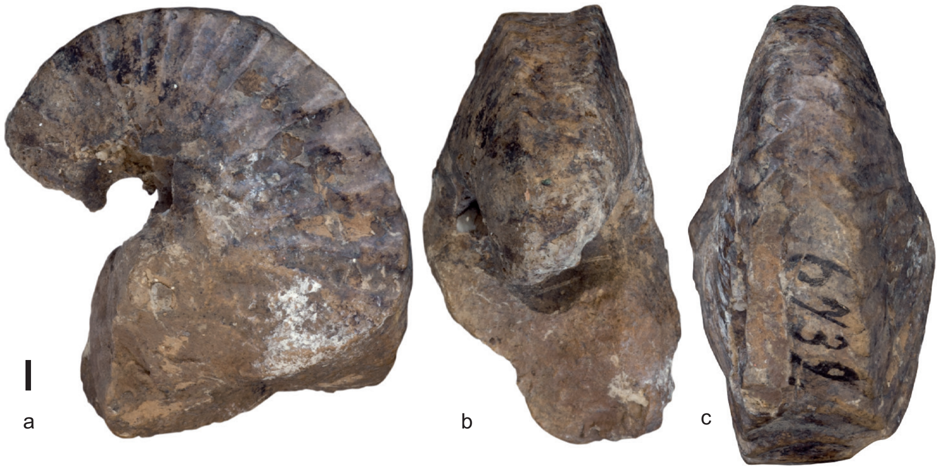


FIG. 35. Argonautidae (p. 45).

nodules absent; flanks rather smooth. *Oligocene–Pliocene:* Japan, Iran.——FIG. 36,*2a–c*. **O. pulcher,* holotype, UMUT CM 08493, Oligocene, Nichinan Formation, Miyazaki Prefecture, Japan; left lateral (*a*), anterior (*b*), and posterior (*c*) views (new; photo, Yasuhiro Ito). Scale bars, 10 mm.

ABBREVIATIONS OF MUSEUM REPOSITORIES

BHI: Black Hills Institute, Hill City, USA
BSPG: Bayerische Staatssammlung für Paläontologie und Geologie, München, Munich, Germany
CDM: Courtenay and District Museum and Paleontology Center, Vancouver Island, Canada
FHKSCM: Fort Hays Kansas State College Museum Hays, USA
FHSM: Fort Hays Kansas State University, Sternberg Museum, Hays, USA
GPIT: Geologisch Paläontologisches Institut, Eberhart Karls Universität Tübingen, Germany
IGPS: Institute of Geology and Paleontology, Tohhoku University, Sendai, Japan
JME: Juramuseum Eichstätt (Germany)
KMNH: Kitakyushu Museum of Natural History and Human History, Kitakyushu, Japan
KU: Kansas University, Natural History Museum, Lawrence, USA
LWL: Museum fur Naturkunde, Westfälisches Landesmuseum, Münster, Germany
MfNB: Museum für Naturkunde, Berlin, Germany
MJML: Museum of Jurassic Marine Life, Kimmeridge, UK
MSNM: Museo Civico di Storia Naturale Milano, Italy
NHMUK: National History Museum of London, UK
NMP: National Museum Prague, Czech Republic
MNHN: Musée National d´Histoire Naturelle, Paris, France
MNHNL: Musée National d´Histoire Naturelle de Luxembourg, Luxembourg
PIMUZ: Paläontologisches Institut und Museum, Universität Zürich, Switzerland
RGM: Naturalis, National Museum of Natural History, Leiden, The Netherlands
SMNS: Staatliches Museum für Naturkunde Stuttgart, Germany
UMH: Urweltmuseum Hauff, Holzmaden, Germany
UMJ: Universal Museum Johanneum, Graz, Austria
UMUT: University Museum, University of Tokyo, Japan

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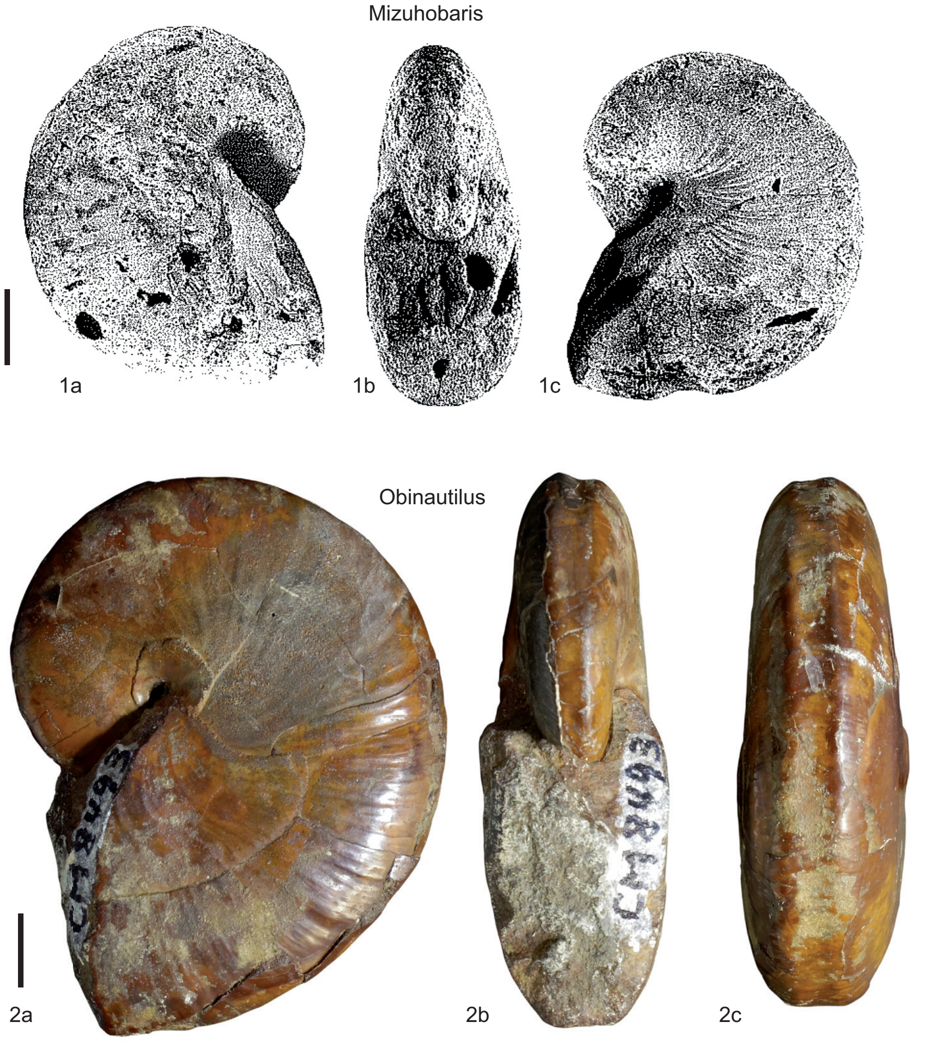

FIG. 36. Argonautidae (p. 45–46).

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