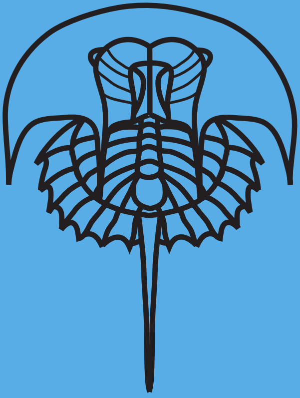

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Part M, Chapter 9B: The Gladius and Gladius Vestige in Fossil Coleoidea

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PART M, CHAPTER 9B: THE GLADIUS AND GLADIUS VESTIGE IN FOSSIL COLEOIDEA

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FOSSIL GLADII AND THEIR SCIENTIFIC HISTORY

At present, approximately eighty fossil gladius-bearing species are considered as valid (excluding those with gladius vestiges). Descriptions of a large majority (95%) include gladius characteristics, and approximately 50% are based solely on the gladius. The gladius is, therefore, the most important character complex in phragmocone-less coleoids, although preservation of soft tissues is very common in association with gladii (see *Treatise Online,* Part M, Chapter 13). Thirty-four of the known gladius-bearing species (43%) are preserved in association with soft parts, eighteen of which (23%) occur in association with extraordinarily well preserved soft parts.

The first reports on fossil gladii all come from the Late Jurassic (Tithonian Altmühltal Formation) Plattenkalks of Solnhofen, Germany. Although wrongly identified as a fish bone, the first gladius was illustrated by Knorr (1749–1755, pl. 22,*2*). The hand-colored, copper engraving shows *Trachyteuthis hastiformis* (Rüppel, 1829) (Fig. 1). König (1825) is credited with being the first to have correctly recognized a fossil gladius, *Plesioteuthis prisca* (Rüppell, 1829), as he classified the pen-like remains as *Loligo.* Rüppell (1829) provided the first descriptions of *Trachyteuthis hastiformis* and *Plesioteuthis prisca.* Since the detailed studies of Münster (1837, 1839, 1846), the so-called Solnhofen archipelago has been known to represent the most diverse coleoid locality. At that time, the gladius of *Trachyteuthis* was considered to be a sepiid cuttlebone, owing to the presence of dorsal granules. Schübler (1832 in Zieten, 1830–1833) presented the first Early Jurassic gladii (*Loligosepia aalensis* Schübler, 1832 in Zieten, 1830–1833), which originated from the Toarcian Posidonia Shales of Holzmaden, Germany.

Eudes-Deslongchamps (1835) found the first gladius outside Germany; his specimen, *Teudopsis buneli* Eudes-Deslongchamps, 1835, originated from the Toarcian of Normandy, France. In 1840, Voltz described Sinemurian gladii from Lyme Regis, England, *Loligosepia bucklandi* (Voltz, 1840), which were at that time the oldest-known gladii. More Jurassic gladii, *Mastigophora brevipinnis* Owen, 1856, from England followed from the Oxford Clay and Kimmeridge Clay (Owen 1855, 1856). Trautschold (1866) presented the first gladii, *Trachyteuthis zhuravlevi* Hecker & Hecker, 1955, from the Russian Late Jurassic. Jurassic gladii from North America have been discovered comparatively late in the history of coleoid research (Hall, 1985).

The first Cretaceous gladius (*Glyphiteuthis ornata* Reuss, 1854) from the Turonian of Bohemia (now the Czech Republic) was published by Reuss (1854). The first gladii from the African platform were recorded during the second half of the nineteenth century. Since the pioneering works of Fraas (1878) and Woodward (1883, 1896) on material from the Cenomanian–Santonian Plattenkalks of Lebanon, our knowledge of late Cretaceous gladii has increased continuously.

Fuchs, Dirk. 2016. Part M, Chapter 9B: The gladius and gladius vestige in fossil Coleoidea. Treatise Online 83:1–23, 14 fig., 2 tables.

FIG. 1. The first illustration of a fossil gladius. The hand-colored copper engraving of KNORR (1749–1755) shows the gladius of *Trachyteuthis hastiformis* (RÜPPEL, 1829) (Octobrachia, Teudopseina) in ventral view (Knorr, 1749–1755, pl. 22,*2*).

Today, the diversity of gladius-bearing coleoids from the Lebanon Plattenkalks is almost as high as in the Solnhofen Plattenkalks.

The first gladii from North America (*Actinosepia canadensis* WHITEAVES, 1897, and *Tusoteuthis longa* LOGAN, 1898) were recorded by WHITEAVES (1897) and LOGAN (1898) from Late Cretaceous (Campanian–Maastrichtian) deposits. In general, gladii from the Early Cretaceous period are rare compared to their relative abundance during the Jurassic and Late Cretaceous. REITNER and ENGESER (1982) discovered the first African gladii (*"Neololigosepia" stahleckeri* REITNER & ENGESER, 1982, and *"Maioteuthis" morroensis* REITNER & ENGESER, 1982) from the Lower Cretaceous (Barremian–Aptian) of Cape Verde. The first gladii from South America (*Teudopsis jeletzkyi* RICCARDI, 2005; Toarcian), Antarctica (*Trachyteuthis* cf. *hastiformis,* a muensterellid gladius; Tithonian), and Australia (*Trachyteuthis willisi* WADE, 1993, and *Muensterella tonii* WADE, 1993; Albian) were described, respectively, by RICCARDI (2005), DOYLE (1991), and WADE (1993).

In 1978, REITNER introduced the first Triassic gladius (*Reitneriteuthis neidernachensis* REITNER, 1978), from the Norian of Bavaria, southern Germany. For a long time, this single specimen was the only Triassic record; however, SCHWEIGERT and FUCHS (2012) recently published a slightly older gladius from the Ladinian Muschelkalk of Germany, named *Germanoteuthis donai* SCHWEIGERT & FUCHS, 2012.

Surprisingly, Cenozoic gladii are virtually unknown. KRETZOI (1942) described a gladius-like structure from the Oligocene of Hungary (*Necroteuthis*), but the exact stratigraphy as well as the morphology of the single specimen has been criticized in the literature (ENGESER, 1988; FUCHS & WEIS, 2008). It is preliminarily considered herein as a sepiid cuttlebone.

GENERAL MORPHOLOGY, TERMINOLOGY, MEASUREMENTS, AND PRESERVATION

Fossil gladii range in length from a few millimeters up to 2 meters. Mesozoic gladii typically occupy the full length of the mantle, as do gladii in extant coleoids. The longest belongs to the Late Cretaceous muensterelloid *Enchoteuthis.* Gladius lengths are defined as very small (<50 mm), small (50–200 mm), medium (201–400 mm), large (401–1500 mm), and very large (>1500 mm).

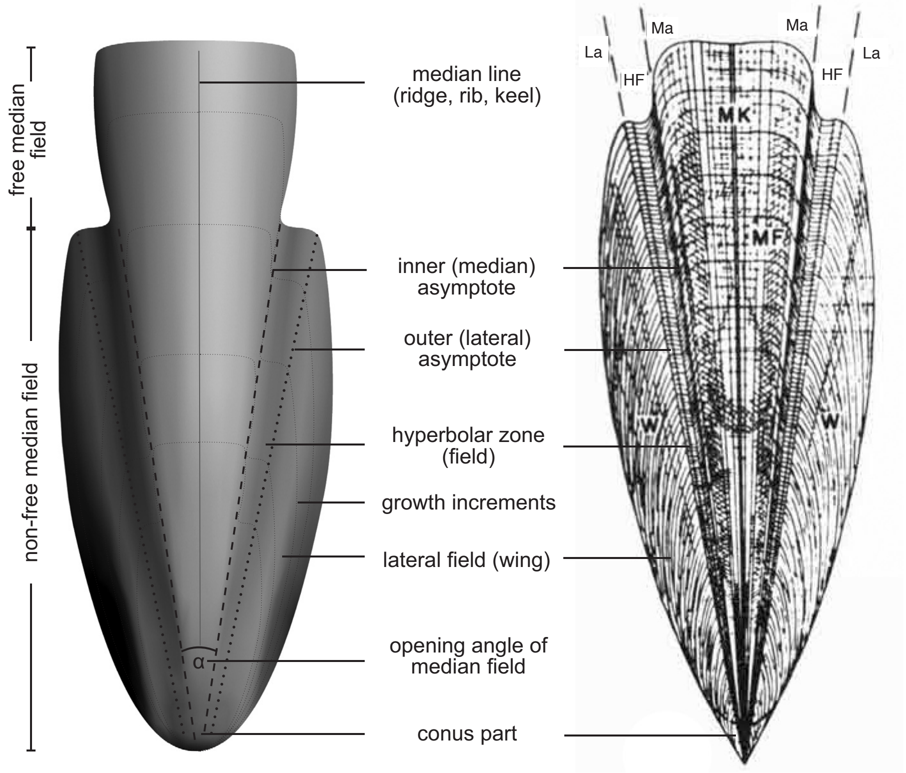

Fig. 2. General morphology and terminology of a fossil gladius; *α,* opening angle; *HF,* hyperbolar field; *La,* lateral asymptote; *Ma,* median asymptote; *MF,* median field; *MK,* lateral asymptote; *W,* wing (adapted from Jeletzky, 1966, fig. 4C; Fuchs & Weis, 2008, fig. 1).

Fossil gladii generally consist of an anteriorly diverging median field and adjoining lateral fields (also termed wings) on both sides (Fig. 2). The lateral fields usually connect to the median field via so-called hyperbolar zones (called re-entrants, notches, arcuated zones, or Bogenstreifung in other terminologies). Functionally, the hyperbolar zones are commonly considered to serve as the main sites of fin attachment (Bizikov, 2004; Fuchs & others, 2015; see *Treatise Online,* Part M, Chapters 9A and 13).

This general morphological subdivision of fossil gladii has been discussed extensively by Jeletzky (1966) and is today undisputed, though terminological inconsistencies exist, particularly concerning the naming of the winglike lateral gladius parts (Table 1). Some confusion has probably been caused by the attempt to find a common terminology for fossil and extant gladii. It is recommended herein that the terms lateral field or wing be used for fossil gladii. Although the term vane is commonly used for extant gladii, this usage is highly problematic since its homologue element in fossil gladii is still obscure (Fuchs & Iba, 2015; see discussion of extant gladii below). Other terms circulating in the literature describe group-specific substructures of either the median field or the lateral fields, as is discussed in more detail below.

The median field, hyperbolar zones, and lateral fields can be determined by the course of growth lines, which correspond to growth increments. The unpaired median field is usually characterized by anteriorly convex (parabolar), the intercalated hyperbolar zones by anteriorly concave (hyperbolar), and the lateral field by laterally convex growth lines. The reversal points of growth lines (i.e.,

TABLE 1. Terminology used to describe the subdivisions of fossil gladii from 1922 to present (new).

Source	Innermost field		———>		Outermost field
Naef, 1922	Mittelplatte	Seitenplatte	Seitenbogenstreifen	Conusfahne	
Roger, 1952	plaque median	plaque lateral	bandelette a stries	conus	
Jeletzky, 1966	median field		hyperbolar zone	wing	
Donovan, 1977	median field		hyperbolar zone	wing/lateral field	
Engeser & Reitner, 1985	Mittelplatte	Seitenplatte	Hyperbolarfeld	Konusfahne	
Donovan & Toll, 1988	median field		hyperbolar zone	vane	
Doyle, 1990, 1991	median field	lateral part	hyperbolar zone	wing	
Haas, 2002	median field	wing			
Fuchs & Weis, 2008, 2010	median field		hyperbolar zone	lateral field	
Fuchs & Larson, 2011a, 2011b	median field	lateral reinforcements	hyperbolar zone	lateral field	
Bizikov, 2004, 2008	rachis	lateral plate		wing	cone flags
Donovan & Boletzky, 2014	median field		hyperbolar zone	lateral field	
Sutton, Perales-Raya, & Gilbert, 2015	median field		vane	wing	cone flags
herein	median field		hyperbolar zone	lateral field	
	central median field	lateral reinforcements	hyperbolar zone	lateral field	

from convex to concave to convex) cause an increased density, often producing narrow bands of very densely spaced increments, the inner (or medial) and outer (or lateral) asymptotes. The inner asymptotes demarcate the median field and hyperbolar zones; the outer asymptotes demarcate the hyperbolar zones and lateral fields. In loligosepiids, the outer asymptotes are more distinct than the inner asymptotes, whereas in teudopseids determination of the outer asymptotes is often more difficult. The opening angle (sometimes called the apical angle, α) of the diverging inner asymptotes indicates the width of the median field (Fig. 2).

Except in one subgroup (see discussion of the teudopseid gladius below), the median field length corresponds to the total gladius length; and from fossil gladii preserved with *in situ* soft tissues, it can also be ascertained that the total gladius length coincides with the mantle length of the animal. Anteriorly, the median field can be straight, convex or concave-rounded, and deeply incised or acute. As a rule, both lateral fields and hyperbolar zones are shorter than the median field. The ratio of the hyperbolar zone length to median field length is a very important and stable diagnostic index that defines the relative length of the hyperbolar zones or the relative length of the anterior free part of the median field. In taxa with weakly arcuated, indistinct hyperbolar zones (and hence poorly developed asymptotes), the hyperbolar zone length is sometimes difficult to determine.

The ratio of the median field width (measured at the anterior end of the hyperbolar zone) to the median field length is closely connected to the opening angle and provides information about the relative median field width. The median field width measured at two-thirds of the median field length is an appropriate mean (particularly for the teudopseid gladius type) for determining the width of the anterior free median field. The slenderness of the entire gladius can be described using the ratio of the maximum gladius width to the median field length. Most fossil gladii are moderate

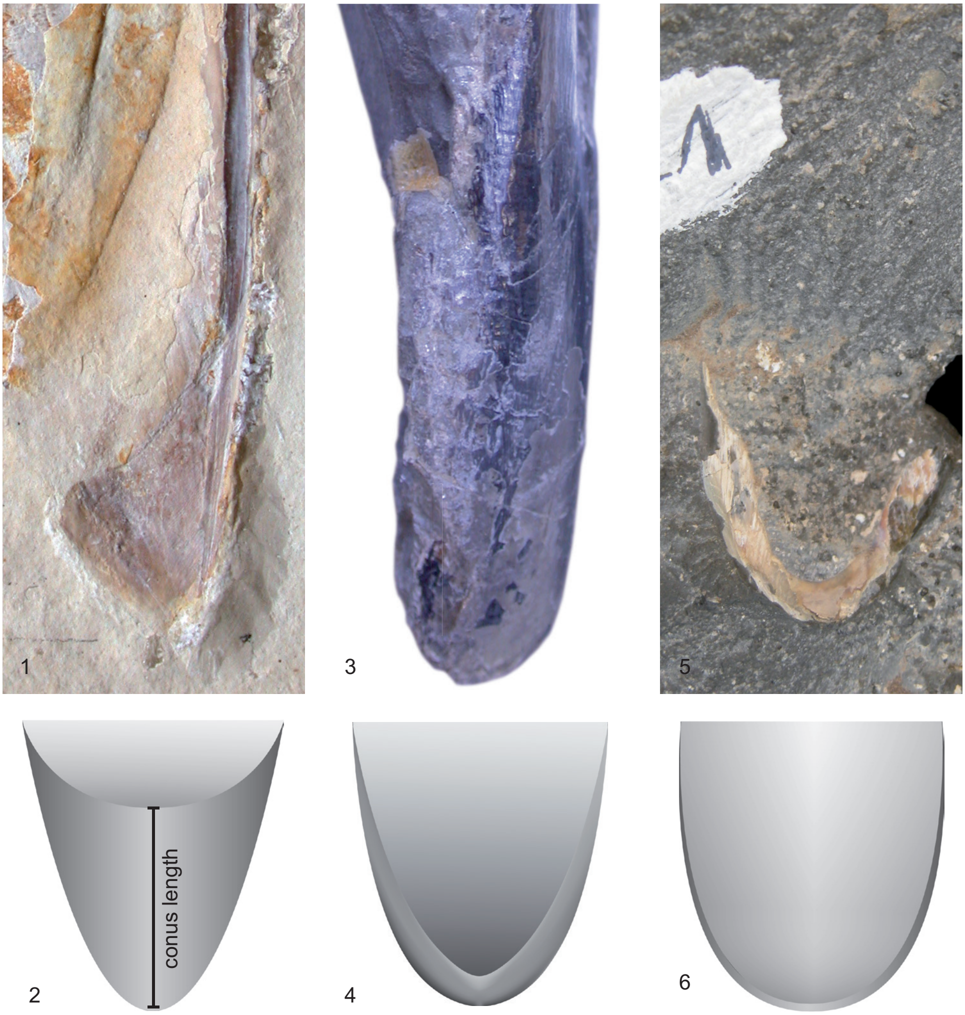

Fig. 3. Conus morphology of fossil gladii. *1, Plesioteuthis prisca* (Rüppel, 1829), Tithonian, Solnhofen Plattenkalks (Senckenberg Museum, Frankfurt, Germany, SMF45-718), lateral view, representing the prototeuthid type of gladius, ×2 (new); *2,* schematic reconstruction of the funnel-like conus in ventral view (new); *3, Loligosepia aalensis,* Toarcian, Posidonia Shales (British Museum of Natural History, London, UK, BMNH C.35729), lateral view, representing the loligosepiid type of gladius, ×2 (Fuchs, 2006a, pl. 11,*B*); *4,* schematic reconstruction of the cup-like conus in ventral view (new); *5, Teudopsis buneli,* Toarcian, Posidonia Shales (Musée National d'Histoire Naturelle, Luxembourg City, Luxembourg, MNHNL TV141), ventral view, representing the teudopseid type of gladius, ×1 (new); *6,* schematic reconstruction of the spoonlike conus in ventral view (new).

in width, and only a few taxa are considered as slender or wide.

Posteriorly, the median field, hyperbolar zones, and lateral fields form a conus, which can be funnel-like or, through ventral reduction or modifications, cup-, spoon-, or patella-shaped (Fig. 3.1–6, see Fig. 8.2, Fig. 9). Rostrum-like posterior projections or septal-like structures—as with modern gladius coni (see *Treatise Online,* Part M, Chapter 9A)—are unknown in fossil gladii (Arkhipkin, Bizikov, & Fuchs, 2012). A rostrum, as observed by Naef (1922) and Jeletzky (1966), has not been confirmed (Fuchs, Klinghammer, & Keupp, 2007; Fuchs & Larson 2011a; Fuchs 2012).

FIG. 4. Unflattened gladius of *Teudopsis subcostata* (MÜNSTER, 1843), Toarcian, Posidonia Shales (Staatliches Museum für Naturkunde, Stuttgart, Germany), in posterior view showing the original curvature of the posterior gladius; note the channel-like hyperbolar zones, ×1 (Fuchs, 2006a, pl. 13,*F*).

The upper (dorsal) surface of the median field can be ornamented with indistinct sets of longitudinal ridges or a pronounced median keel. Diverging ridges can additionally reinforce the stiffness of the median field. These reinforcements can be platelike (and are sometimes called lateral plates), ridge-like, or rib-like. Pronounced keels are usually hollow (i.e., a dorsal keel corresponds to a ventral furrow and vice versa), whereas diverging plates, ridges, or ribs can be solid (i.e., reinforcements leave dorsal and ventral imprints).

Chemically, fossil gladii are commonly preserved as francolite. Desmond DONOVAN (2016) concluded that fossil gladii were originally composed of a chitin-protein mixture (see *Treatise Online,* Part M, Chapter 9C). The median field is built of two to three main layers. The lower (ventral) layers are typified by growth increments, while the outer surface of the uppermost (dorsal) layer is mostly smooth or sometimes granulated (FUCHS, 2012, fig. 7C–D). When slabs or concretions containg fossil gladii are split, the gladius layers may adhere to the slab and counter slab. Ultrastructurally, the gladius layers themselves are of laminar fabric (e.g., HEWITT & WIGNALL, 1988; HEWITT & JAGT, 1999; DOGUZHAEVA & MUTVEI, 2003, 2006; FUCHS & IBA, 2015). Fossil gladii recorded in finely laminated deposits have usually undergone strong compaction. Only in rare cases (e.g., when they are preserved in concretions), the original (unflattened) shape of gladii is preserved (e.g., Toarcian of Luxembourg, UK, and Chile; Albian of Australia; and Campanian of North America). In these three-dimensional specimens, one can see that both the median and lateral fields were originally convex (Fig. 4). Therefore, measurements of flattened specimens and their use in comparative morphology are problematic (FUCHS, ENGESER, & KEUPP, 2007). After compression, the fields are artificially in one plane, the strongly arched conus parts are often longitudinally torn apart, and hyperbolar zones (which were originally channel-like) are leveled as well. Hence, width indices are especially highly dependent on the rate of compaction and contain a significant measurement error. Consequently, details about diverging angles of inner and outer asymptotes must be used with caution: they are useless in longitudinally disrupted specimens. Furthermore, gladii have regularly suffered lateral compression. In such specimens, measurements are useless for morphometric comparisons. As a result of these taphonomic obstacles, intraspecific variability is difficult to assess.

According to FUCHS, KLINGHAMMER, and KEUPP (2007), the gladius of plesioteuthids grows almost isometrically. Digital superimposition of either the growth increments of the same specimen or the gladius outlines of different-sized specimens of the same species is normally possible, suggesting the general absence of a significant growth allometry in all Mesozoic gladius-bearing coleoids. With a single exception, paralarval gladii are still poorly known from the fossil record (HAUG, KRUTA, & HAUG, 2012).

THREE MAIN TYPES OF FOSSIL GLADII

Three different main morphotypes can be recognized in fossil gladii: the prototeuthid, loligosepiid, and teudopseid morphotype. Systematically, these morphotypes characterize

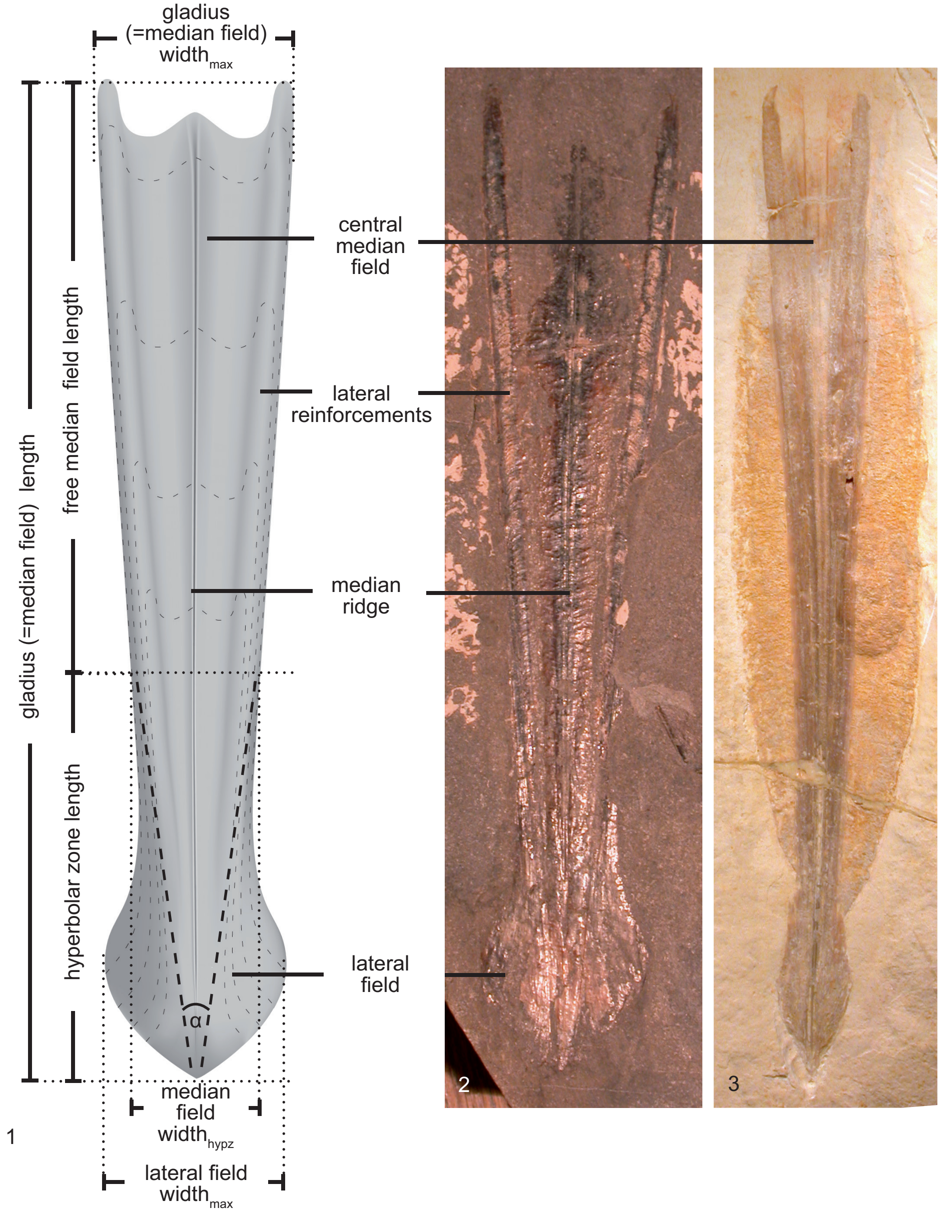

FIG. 5. Detailed morphology and measurements of prototeuthid type of gladius. *1,* Measurements; *α,* opening angle; *hypz,* hyperbolar zone (new); *2, Paraplesioteuthis sagittata* (MÜNSTER, 1843), Toarcian, Posidonia Shales (Urwelt-Museum Hauff, Holzmaden, Germany), dorsal view, ×0.7 (Fuchs, 2006a, pl. 16,*B*); *3, Senefelderiteuthis tricarinata* (MÜNSTER, 1846), Tithonian, Solnhofen Plattenkalks (Black Hills Institute, Hill City, South Dakota, USA), dorsal view, ×0.7 (Fuchs, Iba, & others, 2015, fig. 1F).

the three suborders Prototeuthina NAEF, 1921; Loligosepiina JELETZKY, 1965; and Teudopseina STAROBOGATOV, 1983 (=Mesoteuthoidea *sensu* NAEF, 1922; Mesoteuthina *sensu* JELETZKY, 1966, ENGESER, 1988). The diversity, taxonomy, morphology, and phylogeny of these three suborders have been reconsidered by FUCHS (2006a, 2006b, 2006c); FUCHS, ENGESER, and

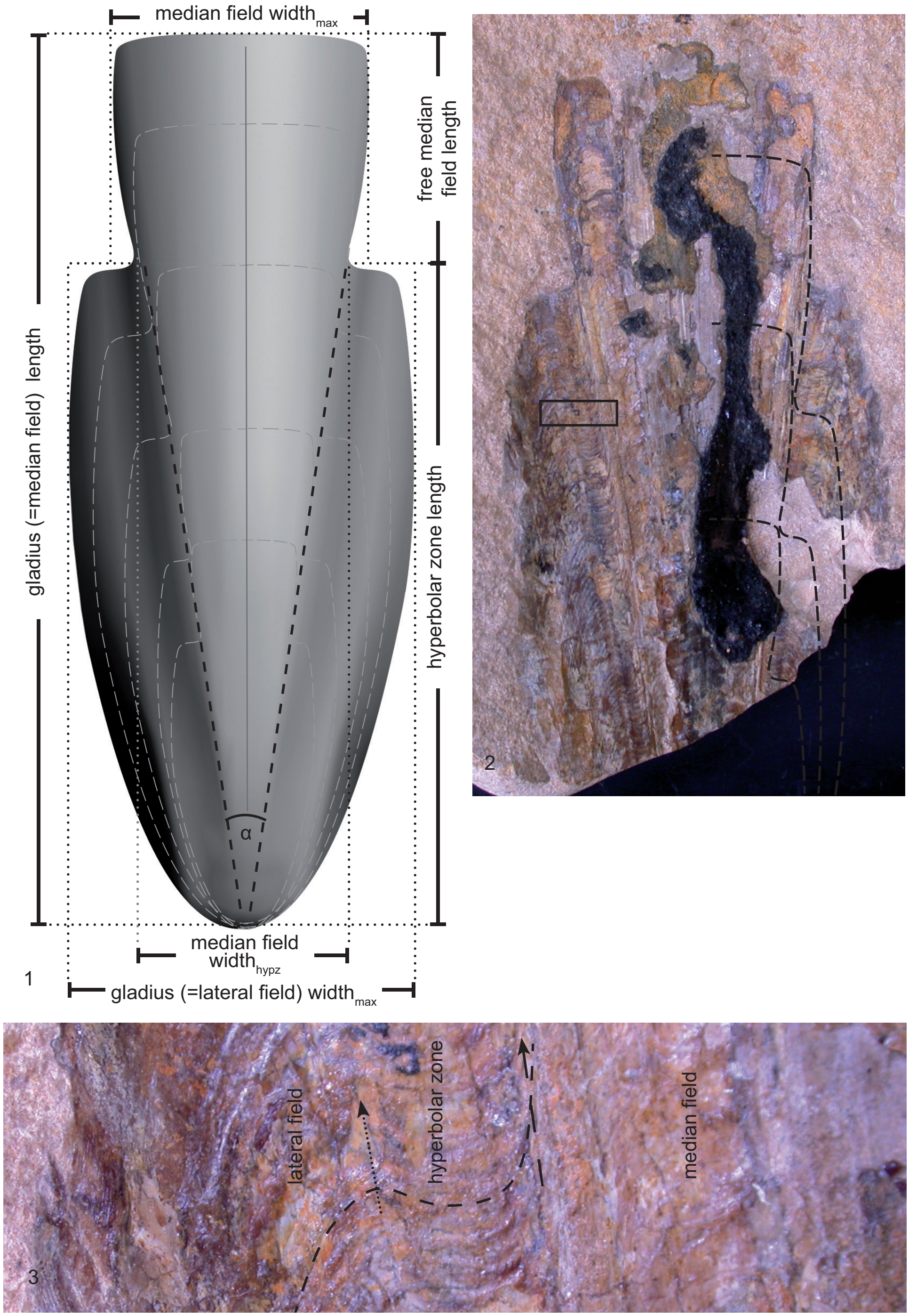

FIG. 6. Detailed morphology and measurements of loligosepiid type of gladius. *1,* Measurements; *α,* opening angle; *hypz,* hyperbolar zone (new); *2–3, Parabelopeltis flexuosa* (MÜNSTER, 1843), Toarcian, Jet Rock Series (British Museum of Natural History, London, UK, C.46819); *2,* ventral view, ×0.5; *3,* close-up view (*rectangular area in 2*), showing course of growth increments at transition from lateral field to hyperbolar zone to median field, ×1.5 (Fuchs, 2006a, pl. 11,*F*).

Keupp (2007); Fuchs, Klinghammer, and Keupp (2007); Fuchs and Schultze (2008); Fuchs and Weis (2008, 2009, 2010); Fuchs and Larson (2011a, 2011b); and Fuchs and others (2016). These studies suggest a remarkable morphological homogeneity on higher systematic levels and a high plasticity on lower levels.

THE PROTOTEUTHID GLADIUS

As illustrated in Figure 5, the triangular median field is generally more slender than in other morphotypes (opening angle 9°–15°), and hyperbolar zones are characteristically indistinct—that is, lateral fields appear to directly adjoin the median field. The maximum gladius width always coincides with the maximum median field width. The hyperbolar zone length is usually less than the 60% of the median field length (hyperbolar zone length:median field length <0.6). Median and lateral reinforcements are present on the median field. Median reinforcements can be platelike, faintly ridge-like, or distinctly rib-like, and either bipartite or unipartite and continuous or discontinuous. Lateral, diverging reinforcements can be solid or hollow and continuous or discontinuous; upper and lower gladius surfaces can therefore differ. In between these reinforced areas, the median field may be very delicate (i.e., thin-layered).

The conus of early prototeuthids (e.g., *Paraplesioteuthis* Naef, 1921, *Senefelderiteuthis* Engeser & Keupp, 1999; *Plesioteuthis* Wagner, 1859) is ventrally closed and therefore funnel-like (Fig. 3.1–2)—in contrast to the loligosepiid and teudopseid type. Cretaceous prototeuthids (e.g., *Dorateuthis* Woodward, 1883) have a distinctly reduced conus (Fuchs & Larson, 2011a). Based on the ventrally closed conus, the prototeuthid gladius appears to represent the most primitive and indeed the earliest known gladii: the Norian *Reitneriteuthis* Schweigert & Fuchs, 2012, and Ladinian *Germanoteuthis* Schweigert & Fuchs, 2012, probably belong to this type (Schweigert & Fuchs, 2012). The last gladius of the prototeuthid type, "*Acanthoteuthis*" *maestrichtensis* van den Binkhorst, 1861, is known from the latest Cretaceous (Maastrichtian).

THE LOLIGOSEPIID GLADIUS

As Figure 6 illustrates, the median field is triangular and both hyperbolar zones and lateral fields are well developed. The maximum gladius width always exceeds the maximum median field width. Hyperbolar zones can be either as long as the lateral fields (Loligosepiidae Regteren Altena, 1949; Geopeltidae Regteren Altena, 1949) or distinctly longer (Mastigophoridae Engeser & Reitner, 1985; Leptotheuthidae Naef, 1921), but the hyperbolar zone regularly exceeds at least 50% of the median field length (hyperbolar zone length:median field length >0.5). The ventrally reduced conus is cup shaped (Fig. 3.3–4). Advanced Mastigophoridae and Leptotheuthidae developed lateral reinforcements on the median field. The loligosepiid morphotype first appears during the Early Jurassic: Sinemurian (*Loligosepia* Quenstedt, 1839) and disappears in the Early Cretaceous: Aptian (*Donovaniteuthis* Engeser & Keupp, 1997).

THE TEUDOPSEID GLADIUS

An anteriorly acute (or weakly rounded) median field is characteristic for the teudopseid gladius type, whose general shape can vary considerably, compared to the loligosepiid and prototeuthid gladius. The hyperbolar zone length is normally less than 60% of the median field length (hyperbolar zone length:median field length <0.6). Hyperbolar zones can be well developed as furrows (e.g., Trachyteuthidae Naef, 1921; Teudopseidae Regteren Altena, 1949) or wide depressions (e.g., Muensterellidae Roger, 1952), or they may be indistinct (e.g., Palaeololiginidae Naef, 1921). A weakly arcuated (and thus indistinct) hyperbolar zone may complicate its recognition. In teudopseid gladii, one must differentiate between two different types of gladius constrictions: those caused by the anterior end of the hyperbolar zones (type 1) and those of the anterior median field (type 2). For example, a weakly arcuated hyperbolar zone and a resulting weak constriction (type 1), coupled with a distinct constriction of the free median field (type 2), as in *Celaenoteuthis* Naef, 1922, and *Palaeololigo* Naef, 1921, may blur the true length of the hyperbolar zone

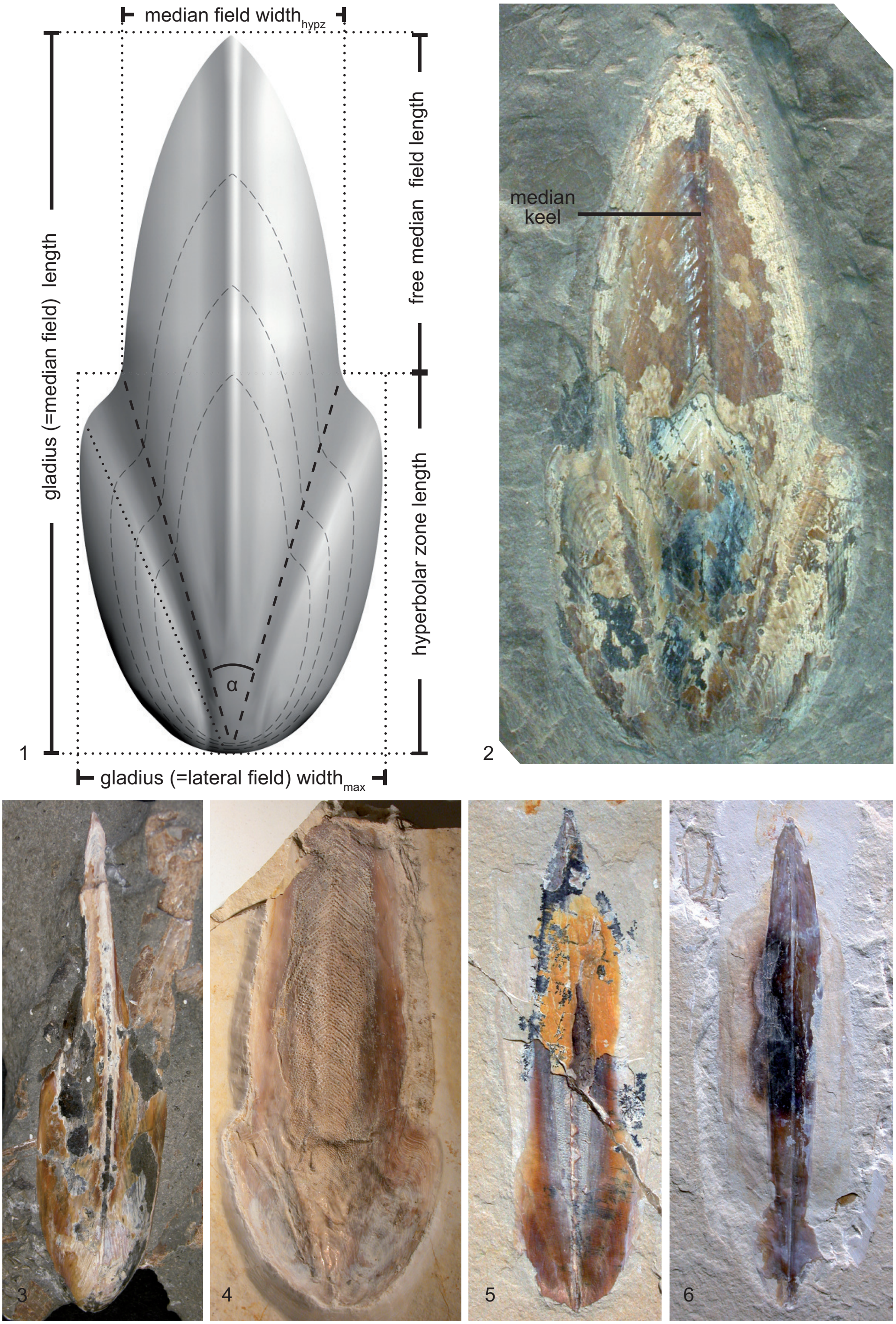

FIG. 7. Detailed morphology and measurements of the teudopseid type of gladius; *1,* measurements; *α,* opening angle; *hypz,* hyperbolar zone (new); *2, Teudopsis subcostata* (MÜNSTER, 1843), Toarcian, Posidonia Shales (Staatliches Museum für Naturkunde, Stuttgart, Germany), dorsal view, ×1 (new); *3, Teudopsis buneli* EUDES-
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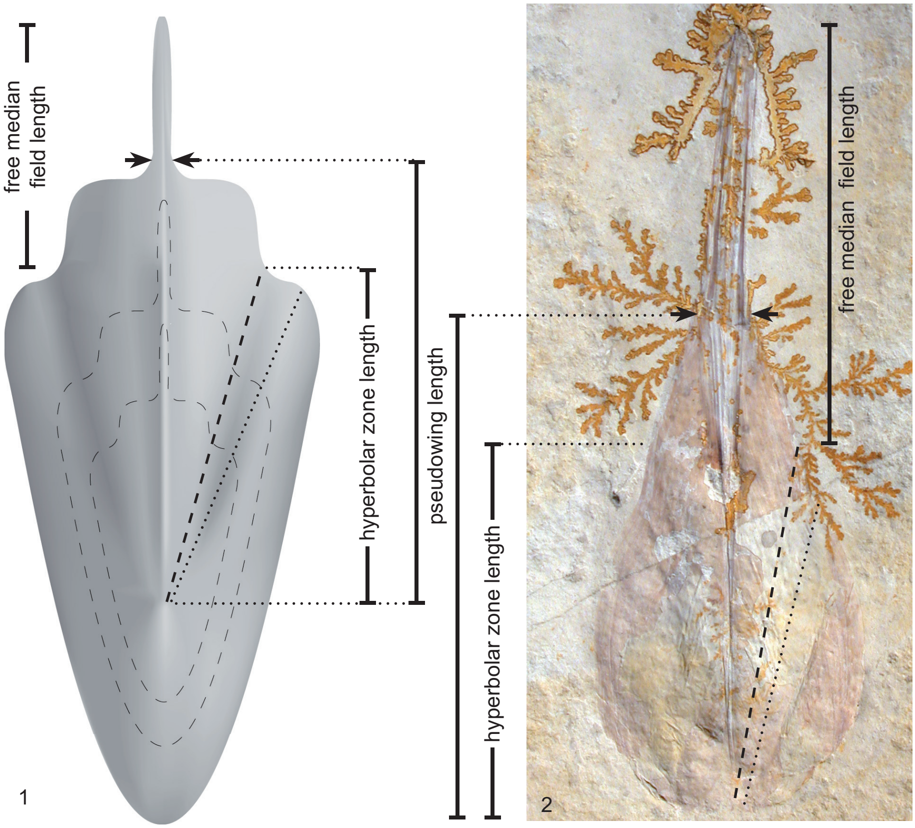

FIG. 8. Constrictions of the free median field suggesting pseudowings (*arrowheads*). *1, Celaenoteuthis incerta* NAEF, 1922, reconstruction, dorsal view (new); *2, Palaeololigo oblonga* (WAGNER, 1859), Tithonian, Solnhofen Plattenkalks (Jura Museum, Eichstätt, Germany, SOS1325), ventral view, ×1.2 (new).

(wing) and simulate false wings (Fig. 8.1–8.2). Recently, FUCHS and others (2016) introduced the term pseudowing for this phenomenon. The anterior median field can thus be wide (e.g., as in many trachyteuthids; rachis-like (shaft-like), as in most muensterellids; or constricted, as in palaeololiginids. In trachyteuthids, the dorsal median field surface is granulated. Similarly, the lateral fields of some muensterellids are granulated. The conus generally appears cup shaped to spoon shaped (Fig. 3.3–3.6), except in the muensterelloid teudopseids.

In the muensterelloids, the teudopseid gladius is modified so that the lateral fields exceed the posterior end of the median field, forming a patella-shaped conus (Fig. 8.1, 9.1–9.2). The median field is hence shorter than the total gladius length. The capulus-like apex marks the posterior end of the median field. This unusual modification

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FIG. 7. *Continued from facing page.*
DESLONGCHAMPS, 1835, Toarcian, Posidonia Shales (Musée National d'Histoire Naturelle, Luxembourg City, Luxembourg, MNHNL TV234), dorsal view, ×0.7 (Fuchs & Weis, 2010, fig. 3); *4, Trachyteuthis* sp., Tithonian, Solnhofen Plattenkalks (H. Tischlinger collection), dorsal view, ×0.7 (new); *5, Glyphiteuthis abisaadiorum* FUCHS & WEIS, 2009, Cenomanian, Lebanon Plattenkalks (Musée National d'Histoire Naturelle, Luxembourg City, Luxembourg, MNHNL CRE042), dorsal view, ×0.9 (Fuchs & Weis, 2009, fig. 2A–C); *6, Rachiteuthis donovani* FUCHS, 2006b, Cenomanian, Lebanon Plattenkalks (Musée National d'Histoire Naturelle, Luxembourg City, Luxembourg, MNHNL CRE039), ventral view, ×0.8 (Fuchs & Larson, 2011b, fig. 14.2).

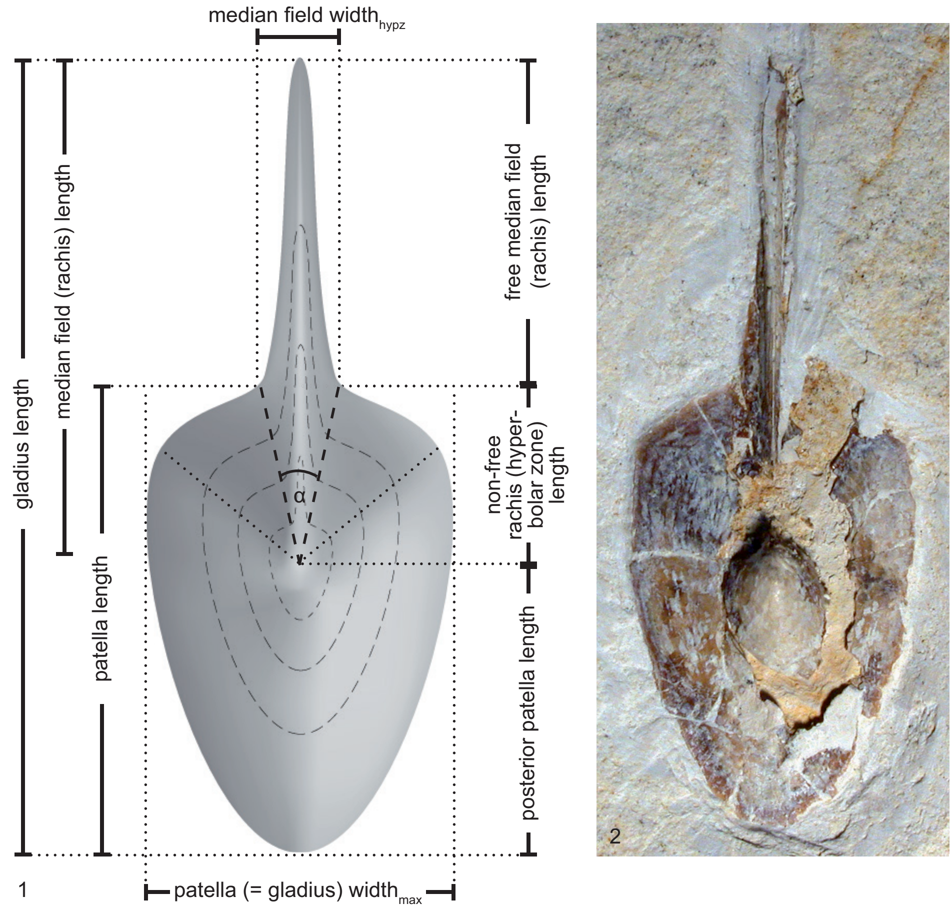

Fig. 9. Detailed morphology and measurements of an aberrant teudopseid type of gladius. *1,* Measurements; *α,* opening angle; *hypz,* hyperbolar zone (new); *2, Muensterella scutellaris* (Münster, 1842), Tithonian, Solnhofen Plattenkalks (Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany), dorsal view, ×2.2 (Fuchs, 2009, fig. 3A).

of an originally cup-shaped conus can be subdivided into an anterior free median field (or rachis) and a posterior patella. The relative length of the free rachis (the ratio of patella length to total gladius length) may be quite long (e.g., *Enchoteuthis*) or conspicuously short (e.g., *Pearciteuthis*). The position of the patella apex is another useful diagnostic character: it can be determined using the ratio of the hyperbolar zone length to the patella length. Specimens of *Enchoteuthis melanae* Miller & Walker, 1968, yielded the longest gladii (up to 200 cm), the largest fossil coleoids to date. The teudopseid gladius type is known from the Early Jurassic (*Teudopsis,* Toarcian) to the Late Cretaceous (*Actinosepia,* Maastrichtian).

STRATIGRAPHIC AND GEOGRAPHIC OCCURRENCES

The fossil record of gladius-bearing coleoids expands from the Middle Triassic (Ladinian) to the Latest Cretaceous (Maastrichtian), ~238 to 65 million years ago. Records of tiny structures from the Lower Permian of Utah (USA), similar to the patella-like gladius of muensterellids, have been interpreted as gladii (Gordon, 1971;

Doguzhaeva & Mapes, 2014), although this interpretation needs further confirmation (Donovan & Toll, 1988; Engeser, 1988; Doyle, Donovan, & Nixon, 1994; Riegraf, Janssen, & Schmitt-Riegraf, 1998).

In addition to a very patchy fossil record during their early history, two larger gaps during the Middle Jurassic (Aalenian–Bathonian) and the Early Cretaceous (Berriasian–Hauterivian) further hamper the understanding of evolutionary transformations of gladius morphotypes. Both gaps span roughly 10–15 million years, which is nevertheless clearly less than the periods with continuous records. Highest diversities occur during the Toarcian (Posidonia Shale of Central Europe), Kimmeridgian to Tithonian (Nusplingen and Solnhofen Plattenkalks), and the Cenomanian (Lebanon Plattenkalks). These evolutionary windows also yielded the best-preserved gladii. Although fossil gladii have been found worldwide, paleobiogeographic implications are limited due to generally poor preservation except in the Konservat-Lagerstätten.

COMPARISON WITH EXTANT GLADII

In contrast to the high morphological plasticity in modern gladii (see *Treatise Online,* Part M, Chapter 9A), the shape and architecture of fossil gladii are remarkably uniform and can be distinguished in the three, major evolutionary lineages mentioned above. Fossil gladii, particularly the loligosepiid and teudopseid types, appear to be thicker and therefore more rigid in comparison to their very brittle and transparent modern equivalents. Fossil gladius coni are proportionally larger than extant coni. Modifications such as the secondary conus and pseudoconus are unknown in their Mesozoic counterparts. Many modern oegopsid gladii exhibit remains of what appears to be septa within their conus (Arkhipkin, Bizikov, & Fuchs, 2012). Such a rudimentary septation is unknown in fossil gladii. Also, a so-called rostrum covering the posterior conus that has been described in several modern gladii is virtually absent in fossil gladii (Arkhipkin, Bizikov, & Fuchs, 2012).

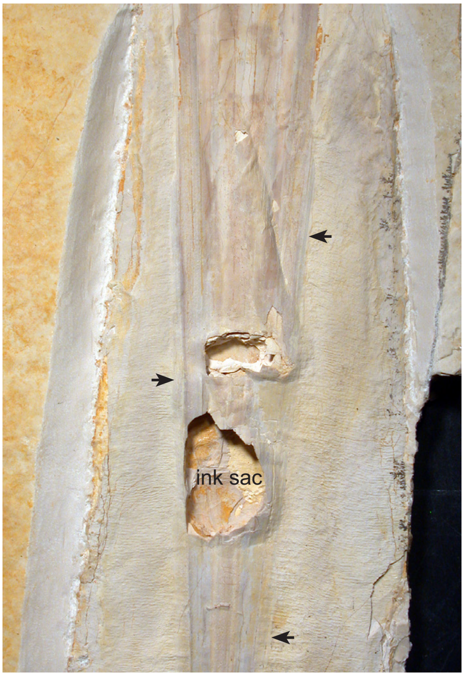

Fig. 10. Marginal attachment of the muscular mantle (*arrowheads*). *Plesioteuthis prisca* (Rüppel, 1829), Tithonian, Solnhofen Plattenkalks (Black Hills Institute of Geological Research, Hill City, South Dakota, USA), dorsal view; note that the muscular mantle does not cover the dorsal gladius surface, ×0.9 (new).

The well-preserved specimens from the Solnhofen and the Lebanon Plattenkalks provide particularly detailed evidence about the gladius-muscle contacts (Fuchs & others, 2015; see *Treatise Online,* Part M, Chapter 13). As in the *Vampyroteuthis* gladius (and the sepiid cuttlebone), but unlike modern squid gladii, the muscular mantle does not cover the dorsal gladius surface. Where known, the muscular mantle is attached to the lateral gladius margins (Fig. 5.3; Fig. 10). Fins usually insert into the hyperbolar zones and/or lateral fields—as in *Vampyroteuthis* Chun, 1903, but unlike in decabrachians (Donovan, Doguzhaeva, & Mutvei, 2003; Fuchs, 2006a; Fuchs & Larson, 2011a, 2011b; Fuchs & others, 2015). Funnel retractor muscles appear to be in contact with the anterior end of the hyperbolar zones (Fuchs, Keupp, & Engeser, 2003; Fuchs & others, 2015).

Table 2. The scientific history of the classification of the Loligosepiina, Teudopseina, and Prototeuthina (new).

Source	Loligosepiina	Teudopseina	Prototeuthina
Naef, 1922	Teuthida		
Jeletzky, 1966	Teuthida	Myopsida	Oegopsida
Donovan, 1977	Vampyromorpha	Myopsida/Sepiida	Oegopsida
Engeser, 1988	Vampyromorpha		
Doyle, Donovan, & Nixon, 1994	Vampyromorpha		Teuthida
Haas, 2002	Octobrachia		
Fuchs, 2006a & herein	Vampyromorpha	Octopoda *s.l.*	Octobrachia *s.l.*

Although paralarval gladii are more or less unknown from the fossil record, growth increments indicate no significant difference between early and late growth stages. This contrasts with growth patterns in at least some extant gladius-bearing families (e.g., Vampyroteuthidae Thiele in Chun, 1915; Loliginidae Lesueur, 1821; Onychoteuthidae Gray, 1849; see *Treatise Online,* Part M, Chapter 9A).

Loligosepiid gladii (e.g., *Parabelopeltis* Naef, 1921; *Doryanthes* Münster, 1846; *Mastigophora* Owen, 1856) resemble the gladius in the extant *Vampyroteuthis* in having a triangular median field and similar hyperbolar zone and lateral field lengths. Further similarities in gladius outlines have been observed between Plesioteuthidae and Ommastraphidae Steenstrup, 1857 (Young, Vecchione, & Donovan, 1998); Muensterellidae and Sepiolidae Leach, 1817 (Bizikov, 2008; Larson, 2010); and Palaeololiginidae and bathyteuthoid teuthids (Donovan & Strugnell, 2010).

WHO WERE THE OWNERS OF MESOZOIC GLADII?

Owing to similarities in the shape of some fossil and teuthid gladii, Mesozoic gladius-bearing coleoids became generally known as fossil teuthids (as indicated by the suffix *-teuthis*). This traditional view, the Decabrachia Theory—held by authorities such as Naef (1922), Jeletzky (1966), and, in part, Donovan (1977)—was criticized by Bandel and Leich (1986), who suggested vampyromorph affinities instead of decabrachian. Subsequently, as Table 2 suggests, the classification of gladius-bearing coleoids as Octobrachia (=Octopodiformes *sensu* Berthold & Engeser, 1987; Vampyropoda *sensu* Boletzky, 1992) received increased acceptance (e.g., Engeser, 1988; Doyle, Donovan, & Nixon, 1994; Haas, 2002; Fuchs, Keupp, & Engeser, 2003; Bizikov, 2004; Fuchs, 2006a, 2006b, 2006c; Fuchs, Engeser, & Keupp, 2007; Fuchs, Klinghammer, & Keupp, 2007; Fuchs & Schultze, 2008; Fuchs & Weis, 2008, 2009, 2010; Fuchs, 2010; Fuchs & Larson, 2011a, 2011b; Fuchs, Keupp, & Schweigert, 2013; Schlögl, Košt'ák, & Hyžný, 2013; Fuchs & others, 2015; Fuchs & Iba, 2015; Klug & others, 2015; Sutton, Perales-Raya, & Gilbert, 2015). The Octobrachia Theory is mainly based on (1) the soft-part morphology—e.g., the presence of only four pairs of arms, uniserial circular suckers, long cirri, and a ventromarginal mantle-gladius contact; and the absence of ventrolateral tentacles, nuchal and funnel-locking cartilages, chitinous rings, teeth, or hooks (see *Treatise Online,* Part M, Chapter 13); (2) the gladius architecture, which is fundamentally different from teuthid gladii (e.g., the absence of rostrum and septation; see Arkhipkin, Bizikov, & Fuchs 2012; *Treatise Online,* Part M, Chapter 9A); and (3) the idea that fin supports of extant octobrachians evolved from a Mesozoic gladius similar to the teudopseid type (see below). Apart from these morphological arguments, the existence of advanced Jurassic teuthids appears to also be stratigraphically dubious, as the forerunners of phragmocone-bearing sepiids and spirulids first appeared during the latest Cretaceous (Haas, 2003; Fuchs, Keupp, & Wiese, 2012; Fuchs & others, 2012).

In light of these arguments—and Young, Vecchione, and Donovan's statement (1998, p. 409) that "as most calcareous coleoid shells probably have a gladius buried within the structure, evolution of a gladius is probably not a difficult step"—fossil and extant gladii appear to be derived from different phragmocone types. Consequently, the repeated appearance of similar gladius shapes might represent a remarkable parallelism in the evolutionary history of the Coleoidea (Fuchs & Iba, 2015).

MORPHOGENETIC ORIGIN AND EVOLUTION OF MESOZOIC GLADII

According to the classical view, the Mesozoic gladius type evolved from a belemnoid shell (Naef, 1921–1923, p. 156). This development implies that (1) major parts of the gladius (especially the median field) correspond to the pro-ostracum, the anterior dorsal projection of a belemnoid shell; (2) the small posterior conus part is equivalent to an orthoconic or slightly cyrtoconic phragmocone; and (3) these early octobrachians lost the ability for shell calcification. The lamello-organic shell layer that mainly composes the belemnoid pro-ostracum is, according to Fuchs and Iba (2015), homologous to the main layer in fossil and extant gladii. A gladius is consequently embedded in every pro-ostracum–bearing belemnoid and the loss of calcification in a given subgroup accordingly exposes a gladius (see also Young, Vecchione, & Donovan, 1998).

Fig. 11. Phragmoteuthida, the putative rootstock of Mesozoic gladius-bearing Octobrachia. *1, Phragmoteuthis bisinuata* (Bronn, 1859), Carnian Fish Shales (Naturhistorisches Museum Vienna, Austria, NHMW 2006z0235/0006), lateral view, ×1.5 (new, photo courtesy of Herbert Summesberger); *2,* reconstruction showing the three-lobed pro-ostracum in ventral view (new).

Owing to the presence of a tripartite (three-lobed) pro-ostracum very similar to the loligosepiid gladius type, Jeletzky (1966, p. 35), Donovan (1977, p. 43), Doyle, Donovan, and Nixon (1994, p. 4), and Fuchs (2006d, p. 121) supposed Triassic phragmoteuthids (Fig. 11.1–11.2) to be the rootstock of gladius-bearing octobrachians. Accordingly, the prototeuthid and teudopseid gladius would have derived from the loligosepiid morphotype. Fuchs (2006a, text-fig. 3,*6–13,* 4,*1–3*) alternatively suggested the prototeuthid gladius to be more ancestral, owing to the retention of a true conus. The opened conus in loligosepiid (and teudopseid) gladii would then instead present a derived feature. Later, Fuchs, Klinghammer, and Keupp (2007) and Schweigert and Fuchs (2012) found additional evidence that the oldest known gladii indeed belong to the prototeuthid morphotype. These observations challenged a phragmoteuthid origin, since the prototeuthid gladius differs from Phragmoteuthida in possessing relatively short

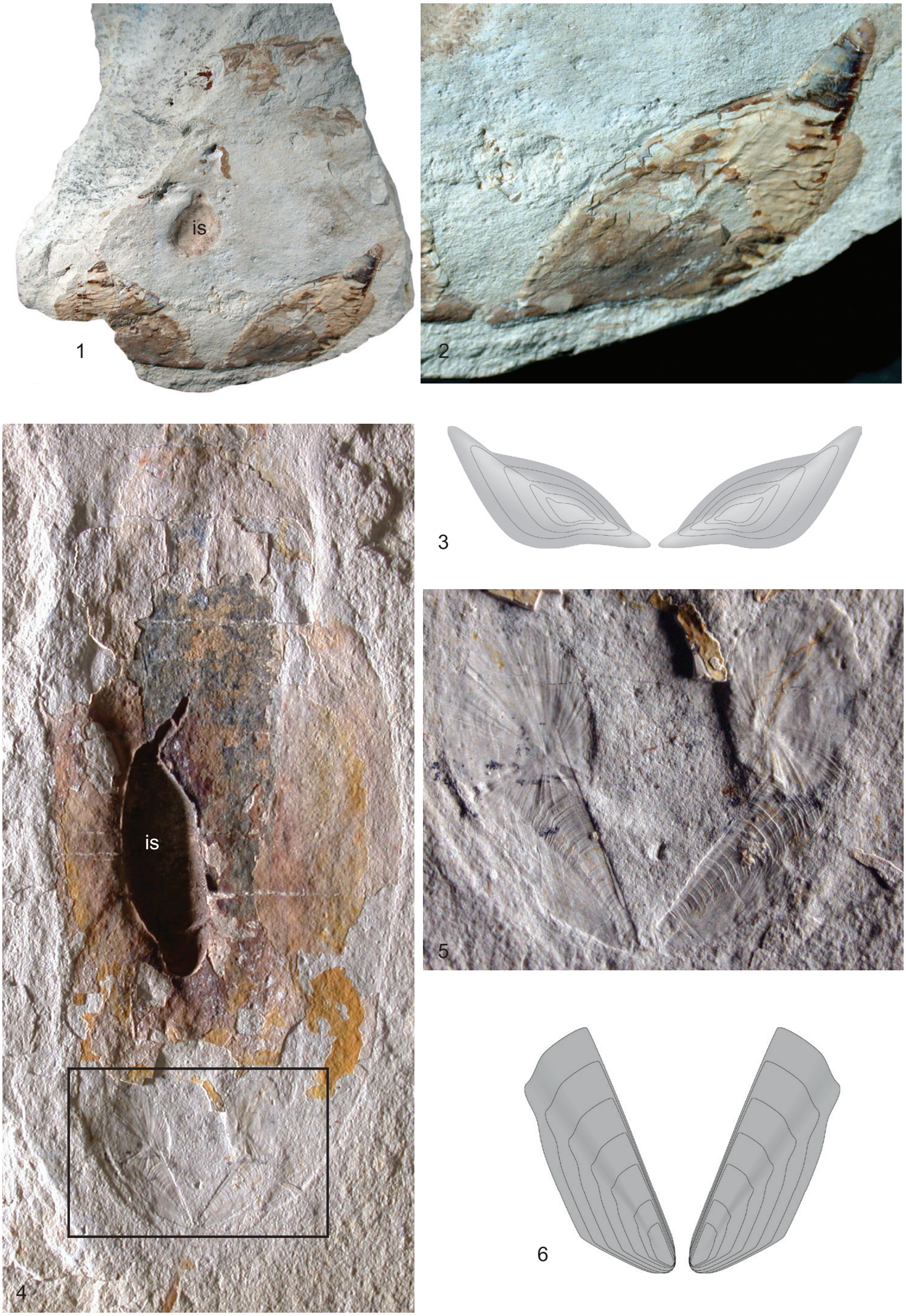

FIG. 12. *For explanation, see facing page.*

lateral fields and poorly developed hyperbolar zones.

In contrast to these higher-level problems, the evolutionary pathways within the Prototeuthina, Loligosepiina, and Teudopseina can be easily reconstructed. The gladius of the Prototeuthina shows clear tendencies towards shortened lateral fields, accompanied by the reduction in the conus length. The gladius of the loligosepiid lineage is typified by gradually widening hyperbolar zones. The Teudopseina divides early into two branches, one with a barely modified gladius (Trachyteuthidae) and one with a reduced anterior median field width (Palaeololiginidae, Muensterellidae). In summary, the morphogenetic origin of the Mesozoic gladius as well as the sister-group relationships between the Prototeuthina, Loligosepiina, and Teudopseina are still obscure, whereas the evolutionary developments are better resolved within the groups.

Fig. 12. Gladius vestiges of Palaeoctopodidae Dollo, 1912. *1, Palaeoctopus newboldi* Woodward, 1896, Santonian, Lebanon Plattenkalks (Musée National d'Histoire Naturelle, Paris, France, MNHN B18834), dorsal view, ×0.8 (Fuchs, Bracchi, & Weis, 2009, fig. 4A); *2,* detail of view *1,* showing the right component of bipartite gladius vestige; *3,* reconstruction of *P. newboldi* (Fuchs, 2009, fig. 4F); *4, Keuppia hyperbolaris* Fuchs, Bracchi, & Weis, 2009, Cenomanian, Lebanon Plattenkalks Musée National d'Histoire Naturelle Luxembourg, Luxembourg, MNHNL CRE045), dorsal view, ; *is,* ink sac, ×1.3 (Fuchs, Bracchi, & Weis, 2009, fig. 5A); *5,* detail of view *1,* with focus on the bipartite gladius vestige (note the pair of radially striated fin cartilages anterior to the vestige); *6,* reconstruction of *K. hyperbolaris* (Fuchs, 2009, fig. 4B).

Fig. 13. Gladius vestiges of fossil (*1–3*) and extant (*4*) Octopodidae. *1, Styletoctopus annae,* Cenomanian, Lebanon Plattenkalks (Museo Civico di Storia Nationale Milano, Italy, MSNM i26323), dorsal or ventral view, ×2.8 (Fuchs, Bracchi, & Weis, 2009, fig. 7A); *2,* detail of view *1* with focus on paired stylets in lateral mantle (Fuchs, Bracchi, & Weis, 2009, fig. 5B); *3,* reconstruction of *S. annae* (Fuchs, 2009, fig. 4H); *4, Enteroctopus dofleini* Wülker, 1910, Japanese waters, ×1 (new).

Fig. 13. *For explanation, see adjacent column.*

FOSSIL RECORD AND EVOLUTION OF GLADIUS VESTIGES

The unpaired fin support of extant cirrate octopods and the paired stylets in the lateral mantle of incirrate octopods are sometimes called the gladius vestige (see *Treatise Online,* Part M, Chapter 9A). This term arose indirectly from proposals made by NAEF (1921–1923, p. 656), who suggested that the fin support evolved from a pro-ostracum–bearing phragmocone, an interpretation that implies derivation from a gladius. Although NAEF (1922, p. 285) stated that "no fossil records of this structure," (i.e., the gladius vestige) were available, we know today that he illustrated the first record of an octobrachian gladius vestige. He interpreted an unpaired structure from the Late Cretaceous (Santonian) of Sâhel Aalma, Lebanon, as a teudopseid gladius (NAEF, 1922, fig. 54b). However, two more fossils introduced later by ROGER (1944a, 1944b) from the same locality have clearly shown that NAEF's specimen represents the left part of an originally paired gladius vestige of *Palaeoctopus newboldi* WOODWARD, 1896 (ENGESER, 1988; FUCHS, 2009; FUCHS, BRACCHI, & WEIS, 2009). Associated soft tissues indicate that the bladelike structures are located close to each other in the dorsal posterior mantle of a sac-like body (Fig. 12.1–12.3). Medially, both parts appear to have no connection; hence, the separation of the shell sac might have been already realized. Therefore, *Palaeoctopus* WOODWARD, 1896, unambiguously belongs to the incirrate lineage (a median connection would implicate affinities either to the cirrate or the octopod stem lineage). The presence of one pair of fins in *Palaeoctopus* indicates that the paleoctopodid gladius vestige still provided sufficient space for fin attachments.

Additional and slightly older bipartite gladius vestiges have been described by FUCHS, BRACCHI, and WEIS (2009) from the Cenomanian of Hâkel, Lebanon (note that a presumed gladius vestige described by FUCHS, IFRIM, and STINNESBECK (2008) from the Turonian of Mexico was subsequently proven to be a fish bone; see SCHULTZE & others, 2010). Whereas the bladelike vestiges of *Keuppia levante* FUCHS, BRACCHI, & WEIS, 2009, and *K. hyperbolaris* FUCHS, BRACCHI, & WEIS, 2009 (Fig. 12.4–12.6) are similar to *Palaeoctopus* in shape and position, the vestiges of coeval *Styleoctopus annae* FUCHS, BRACCHI, & WEIS, 2009 (Fig. 13.1–13.3) are rodlike and located in the lateral mantle, very similar to the situation in *Enteroctopus* ROCHEBRUNE & MABILLE, 1889 (Fig. 13.4) and some other extant Octopodidae ORBIGNY, 1840 in FÉRUSSAC & ORBIGNY, 1835–1848 (e.g., *Benthoctopus* GRIMPE, 1921; *Eledone* LEACH, 1817).

The gladius vestiges of *Keuppia* and *Paleoctopus* differ distinctly in their growth patterns. In *Keuppia,* vestiges grow towards the anterior (similar to gladii)—that is, both growth centers (primordial shells and the shell sacs) are situated close to each other in the posterior mantle (FUCHS, BRACCHI, & WEIS, 2009). In *Palaeoctopus,* in contrast, vestiges grow anteriorly and posteriorly—that is, vestiges grow concentrically around growth centers that are distant from each other.

The main difference between modern and palaeoctopodid gladius vestiges is probably their rigidity. The gladius vestiges of *Palaeoctopus* and *Keuppia* were flat, laminated, and probably chitinous (similar to gladii preserved as francolite). Therefore, fossil vestiges were rather stiff, having a limited flexibility similar to fossil gladii (DOGUZHAEVA & MUTVEI, 2003; FUCHS, 2006a). Modern cartilage-like vestiges, in contrast, are rather soft (DOUBLEDAY & others, 2008; MARQUEZ & RE, 2009). The chemical nature of the *Styletoctopus* rods is still unknown, as their morphology has been reconstructed by the help of imprints.

Vampyroteuthis, the single living species of the Vampyromorpha ROBSON, 1929, suggests by its well-developed gladius that both the U-shaped fin support of the Cirrata GRIMPE, 1916, and the stylets of some Incirrata GRIMPE, 1916, morphogenetically evolved from a gladius (HAAS, 2002; BIZIKOV, 2004). Most workers today accept this development, although a fossil link—such as the clasp- or

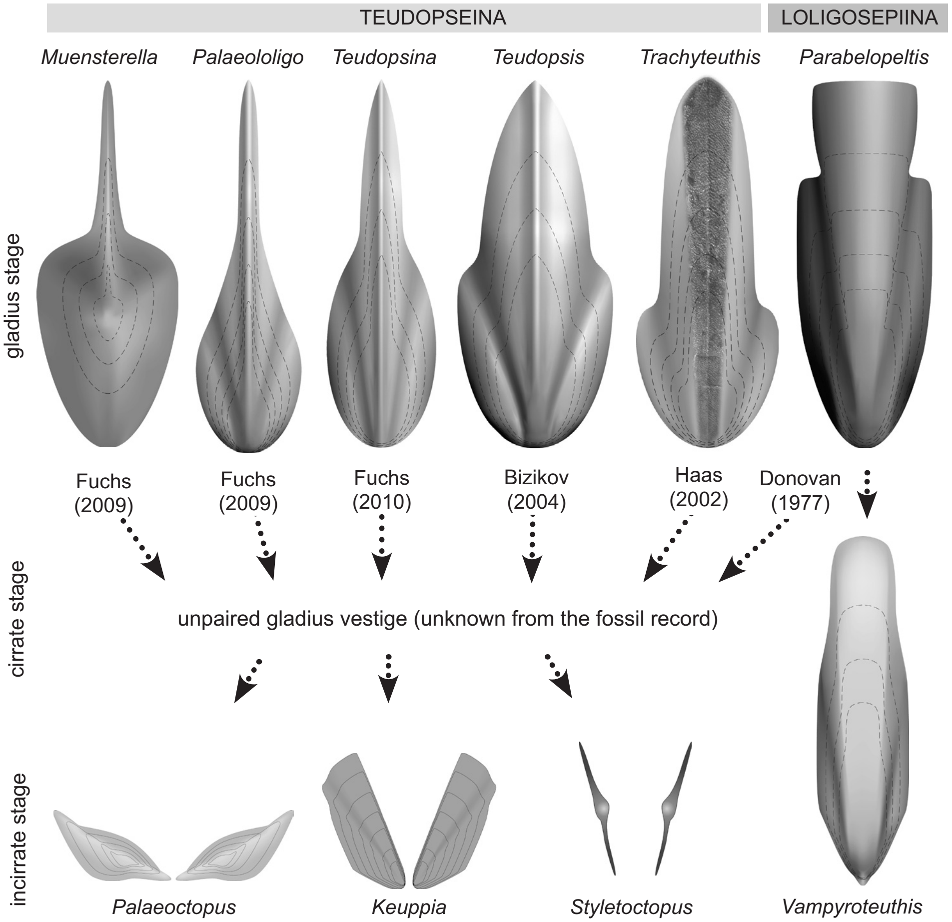

FIG. 14. Different ideas on the morphogenetic origin of extant *Vampyroteuthis* and Cretaceous gladius vestiges (new).

saddle-shaped gladius vestiges of cirrates (or stem-lineage representatives of the Octobrachia)—are still unknown from the fossil record. VOIGHT (1997) accepted that the cirrate fin support represents a modified gladius, but she concluded, on the other hand, that the incirrate rodlets evolved de novo.

Fin-supporting gladius vestiges might have developed from the lateral fields through gradual reduction of the median field to obtain the body plasticity typical for octobrachians (JELETZKY, 1966, p. 50, 88; DONOVAN, 1977, p. 43; HAAS, 2002; BIZIKOV, 2004; FUCHS, 2009; FUCHS, BRACCHI, & WEIS, 2009; FUCHS & WEIS, 2010). This can be inferred from the fact that fin muscles commonly attach to the lateral field-hyperbolar zone area.

DONOVAN (1977) and FUCHS, BRACCHI, and WEIS (2009) regarded a loligosepiid gladius to be the morphogenetic origin (this gladius type has been repeatedly been supposed to lead to the *Vampyroteuthis* type of gladius). HAAS (2002), BIZIKOV (2004), and FUCHS (2009), in contrast, preferred the teudopseid pathway (Fig. 14). According to these authors, a wide median field would be the ideal prerequisite to open and reduce the gladius in a longitudinal direction. Based on this idea, FUCHS (2009) discussed the relative size of the median field in different teudopseid gladii and concluded that the palaeololiginid as well as the muensterellid gladius (both gladius types are modifications of a teudopseid gladius) show clear evidence of a median field reduction—that is, the lateral fields became the dominant gladius parts. In *Palaeololigo,* the reduction affects only the median field width, not the length. FUCHS (2010) recognized in muensterellids, as well as in a recently discovered teudopsid gladius (*Teudopsinia haasi* FUCHS, 2010), a median field reduction that affects both the median field width and length.

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