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Desmond T. Donovan and Dirk Fuchs

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PART M, CHAPTER 13: FOSSILIZED SOFT TISSUES IN COLEOIDEA

DESMOND T. DONOVAN[1] & DIRK FUCHS[2]

[[1]University College London, desmond.donovan@virgin.net; [2]Department of Earth and Planetary Sciences, Hokkaido University, dfuchs@mail.sci.hokudai.ac.jp]

INTRODUCTION

SOURCES OF MATERIAL

In general, fossilization of (non-mineralized) soft tissues of animals is rare in the geological record. Fossilized soft tissues are found only where there have been certain sedimentary environments, characterized by low-energy conditions and fine-grained sediments (usually), and where rapid burial occurred under appropriate geochemical conditions.

Surprisingly, in the case of the mainly soft-bodied Coleoidea, we are able to access a morphological paleo-database that is remarkably precise and more detailed than in any other group of marine animals. This data is locked in the so-called Konservat-Lagerstätten. The majority of fossil coleoids showing soft parts come from the evolutionary windows listed below.

1. The Lower Carboniferous (Mississippian) Bear Gulch Limestone in Montana (USA) recently yielded the oldest soft parts of coleoids (MAPES, WELLER, & DOGUZHAEVA, 2010).
2. The Upper Carboniferous (Pennsylvanian) Mazon Creek biota of the Francis Creek Shale of Illinois (USA) yielded impressions of soft tissues in nodules (JOHNSON & RICHARDSON 1968; DOGUZHAEVA, MAPES, & MUTVEI, 2007).
3. The Lower Jurassic (Toarcian) Posidonia Shales of southern Germany (and their equivalent formations in central Europe), an anoxic, black shale formation, yielded mainly the phosphatized muscular mantle (NAEF, 1922; FUCHS, 2006a).
4. The Middle Jurassic Oxford Clay Formation at Christian Malford (Wiltshire, England) yielded fossilized muscular mantle and arm tissues in laminated, carbon-rich shales (DONOVAN, 1983; VECCHIONE & others, 1999; WILBY & others, 2004, 2008; FUCHS, 2014). This locality is now lost. Important collections are in the British Museum (Natural History), London, and the City Museums and Art Gallery, Bristol, and isolated specimens can be encountered further afield.
5. Laminated marls of Middle Jurassic age (lower Callovian, *Gracilis* Zone) of the Rhône valley (France) from an outcrop 800 m east of La Voulte-sur-Rhône (Ardèche, France) has yielded a diverse fauna, including coleoids with three-dimensionally preserved soft parts. Descriptions and references are given by FISCHER and RIOU (1982a, 1982b, 2002). The fossil coleoids are found in nodules and are replaced by a suite of minerals, including calcite, apatite, pyrite + chalcopyrite, and galena (WILBY, BRIGGS, & RIOU, 1996). According to these authors, further work remains to be done on these fossils, which may reveal internal structures.
6. The Upper Jurassic (Kimmeridgian–Tithonian) Plattenkalks of southern Germany (generalized herein as the Solnhofen Plattenkalks) include a conglomerate of different, shallow-marine basins (e.g., Solnhofen, Eichstätt, Mühlheim, Daiting, Painten, Schamhaupten, Brunn), each of which differs slightly in stratigraphy, lithography, taphonomy, and

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faunal composition (Schweigert, 2007). Generally, these deposits consist, in part, of very fine grained, lithographic limestones that may preserve a diverse set of different soft tissues or their impressions (Bandel & Leich, 1986; Fuchs, Keupp, & Engeser, 2003; Klug & others, 2005; Fuchs, 2006a; Fuchs, Klinghammer, & Keupp, 2007; Keupp & others, 2010). They are perhaps the most famous source of fossils in the world. Coleoids have been collected since the second half of the 18th century (Knorr, 1773), and many specimens are housed in collections worldwide.

7. The Upper Cretaceous Fish Beds (=Plattenkalks) of Lebanon, although known since the 19th century, are an indispensible source for understanding the paleobiology of coleoids. As in the Solnhofen Plattenkalks, soft parts are characterized by high-fidelity preservation (Roger, 1946; Fuchs 2006b; Fuchs, Bracchi, & Weis, 2009; Fuchs & Weis, 2009; Fuchs & Larson, 2011a, 2011b). Many museums have material. Two stratigraphic levels have yielded cephalopods: the rocks at Hâkel, Hjoûla, , and Nâmmoura (Cenomanian), about 45 km north-northeast of Beirut, and those at Sâhel Alma (Santonian), about 22 km northeast of Beirut. The fossil market today offers a large number of soft-body coleoids from the Cenomanian localities.

No preserved tissues or impressions of soft parts have been reported from Permian, Triassic, or Cenozoic rocks. This leaves some gaps in our knowledge of fossil Coleoidea.

TYPES OF PRESERVATION

The soft anatomy of fossil Coleoidea is known from three kinds of preservation: fossilized tissues, impressions of soft parts preserved in sediment, and impressions of soft tissues on mineralized shells. Processes of fossilization are discussed in the chapter on taphonomy (see *Treatise Online,* Part M, Chapter 16).

Fossilized tissues comprise mostly muscular tissue. Apart from the ink sac, by far the most frequently found fossilized coleoid soft tissue (Fig. 1), the muscular mantle, is also very commonly found, with the arms and fins occurring less often in the fossil record. Even the highly delicate inner organs of the respiratory, circulatory, excretory, digestive, and reproductive system have been preserved in rare instances. A list of fossilized soft tissues is given in Table 1.

Most impressions of soft parts are known from the fine-grained limestones of the Solnhofen region (Upper Jurassic) and Lebanon (Upper Cretaceous). A few examples are known from other Lagerstätten, such as the Lower Jurassic Posidonia Shales. Nonmineralized soft tissues that are functionally associated with the phragmocone (such as siphuncular tissues or attachment scars on the phragmocone) will be considered in *Treatise Online,* Part M, Chapter 8A.

MUSCULAR MANTLE

Phosphatized mantle musculature has been observed in phragmocone- and gladius-bearing coleoids. The mantle musculature is rarely entirely conserved, but imprints in the sediment usually help to get an impression of the general body outline. As in modern forms, the mantle length typically corresponds to the shell length (except in octopods with gladius vestiges).

The detailed structure of the muscular mantle in Recent Coleoidea is described in *Treatise Online,* Part M, Chapter 3, Anatomy of Recent Forms (Nixon, 2011). Kear, Briggs, and Donovan (1995) have shown that this structure was already present in several Jurassic fossil genera. Muscular mantle can often be recognized with the naked eye, or under low magnification, by the transversely striated appearance produced by the alternation of circular and radial muscle (Fig. 1–2). Fine lines represent the radial muscle. Diagrams of mantle structure in Recent coleoids can give the impression that bands of radial muscle are continuous around the mantle (see *Treatise Online,* Part M, Chapter 3, Fig. 27). In fossil mantles—for example, in *Loligosepia* Quenstedt, 1839 (Fig. 1); *Plesioteuthis* Wagner, 1859; *Trachyteuthis* Meyer, 1846; or *Muensterella* Schevill, 1950—they extend for short distances, a centimeter or two, rather than forming continuous lines. It is uncertain whether this is a more primitive state than in Recent coleoids.

In Recent coleoids, mantle-shell contacts are various (see *Treatise Online,* Part M, Chapter 9A). The mantle can be attached to the shell margin (*Vampyroteuthis* Chun, 1905; *Sepiida* Gray, 1849; *Sepiolida* Leach, 1817) or the dorsal surface of the shell (*Loliginida* Lesueur, 1821, and *Oegopsida* d'Orbigny, 1842 in Ferussac & d'Orbigny, 1839–1848); as in octopods, it can also envelope the shell rudiments (i.e., gladius vestiges). In Mesozoic gladius-bearing coleoids, the mantle is attached exclusively to the lateral margins of the gladius (Fig. 2; Fuchs, Iba, & others, 2015; see also *Treatise Online,* Part M, Chapter 9B). A head-mantle fusion, which is typical for some Recent coleoids, has been observed in palaeoctopods *Palaeoctopus* Woodward, 1896, and *Keuppia* Fuchs, Bracchi, & Weis, 2009, and presumed in a few gladius-bearing coleoids from La Voulte-sur-Rhône and the Lebanon Plattenkalks: *Proteroctopus* Fischer & Riou, 1982; *Vampyronassa* Fischer & Riou, 2002; *Rachiteuthis* Fuchs, 2006 (Table 1; Fuchs 2006a, 2006b; Fuchs, Bracchi, & Weis, 2009; Fuchs & Larson, 2011a).

ARM CROWN

The number of arms is the most important diagnostic feature at superordinal level; thus, the arm crown is the central character complex for the classification of fossil coleoids. It is, therefore, of substantial interest and also a subject of some controversy.

The first coleoid arms were recorded by Münster (1834). Biserial hooklike imprints led him to recognize the fossil's cephalopod nature. The arm crown came from the Tithonian Solnhofen Plattenkalks and belonged to *Acanthoteuthis speciosa* Münster, 1839, hence a phragmocone- and hook-bearing belemnoid.

Fig. 1. Phospatized muscular mantle of *Loligosepia aalensis* (Schübler in Zieten, 1830–1833), Lower Jurassic (lower Toarcian), Schömberg, Germany (Staatliches Museum für Naturkunde, Stuttgart, Germany), ×0.5 (Fuchs, Keupp, & Schweigert, 2013, fig. 1).

The first evidence of hookless arms was reported by Münster (1837), based on phosphatized arm tissues of gladius-bearing *Trachyteuthis,* also from the Solnhofen Plattenkalks.

TABLE 1. List of fossilized soft tissues known in phragmocone- and gladius-bearing coleoid genera; *x,* character known; *?,* character reported, but questionable; *CC,* cephalic cartilage ; *CLA,* cirri-like appendages; *CS,* circulatory system; *ES,* excretory system; *HMF,* head-mantle fusion; *MM,* muscular mantle; *NFC,* nuchal- and funnel-locking cartilage; *RepS,* reproductive system; *RS,* respiratory system; *TP,* tentacular pockets; *footnotes,* (*continued on facing page*)

Genera	MM	HMF	Arms	Tentacles	TP	Circular suckers	Onychites	CLA	Sucker rings	Arm web	Funnel
Phragmocone-bearing											
Jeletzkya[1]	x				x						
Gordoniconus[2]				?			x				
Pohlsepia[3]	x		x								
Phragmoteuthis[4]	?						x				
undet. belemnoid	x										
Clarkeiteuthis	x		x				x				
Passaloteuthis[5]	x		x				x				
Acrocoelites[6]	x		x				x				
Hibolithes[7]							x				
Belemnotheutis	x		x			x	x				
Acanthoteuthis	x		x			x	x				
Sueviteuthis[8]	x		x				x				
Gladius-bearing											
Prototeuthina											
Plesioteuthis	x	?	x	?		x		x		?	x
Senefelderiteuthis	x		x								
Dorateuthis	x		x								
Boreopeltis	x		x	?							
Rhomboteuthis	x		x	?		x				x	
Romaniteuthis	x		x	?		x					
Loligosepiina											
Vampyronassa	x		x			x					
Proteroctopus	x	x	x								
Gramadella	x		x	?					?		
Loligosepia	x		x								
Jeletzkyteuthis[9]	x										
Geolpeltis[10]	x										
Parabelopeltis[11]	x										
Mastigophora	x		x	?		x					x
Doryanthes[12]			?								
Bavaripeltis	x										
Leptotheuthis	x		x			x		?		?	
Teudopseina											
Trachyteuthis	x		x	?				?		?	
Glyphiteuthis	x		x			x					?
Glyphidopsis[13]	x		x								
Palaeololigo[14]	x		x								
Rachiteuthis	x	x	x								x
Muensterella	x	?	x			x					
Gladius vestige											
Keuppia	x		x			x					
Palaeoctopus	x	x	x			x					
Styletoctopus[15]	x		x								

(Continued on facing page.)

TABLE 1. *Continued from facing page.*

author-date citations for genera: *1,* Johnson & Richardson, 1968; *2,* Mapes, Weller & Doguzhaeva, 2010; *3,* Kluessendorf & Doyle, 2000; *4,* Mojsisovics, 1882; *5–6,* Lissajous, 1915; *7,* Montfort, 1808; *8,* Reitner & Engeser, 1982; *9,* Doyle, 1990; *10,* Regteren Altena, 1949; *11,* Naef, 1921; *12,* Münster, 1846; *13,* Fuchs & Larson, 2011b; 14, Naef, 1921; *15,* Fuchs, Bracchi, & Weis, 2009.

Fins	CC	Fin cartilage	NFC	Buccal mass	Beaks	Esophagus	Stomach	Crop	RS	CS	ES	RepS
x												
	?											
			?									
									x			
					x							
x	x		?	x		x						
x	x			x	x		x		x			
				x			x		x			
x	x			x	x	x	x	x	x			?
x				x			x		x			
x												
x												
x												
							?					
x												
				x								
				x	x							
x					x				x			x
x	x	x		x	x		x		x			
				x								
x	x	x		x					x			
x	x	x					x	?				
	x	x		x			x		x	?	?	?

FIG. 2. Phospatized muscular mantle. *Plesioteuthis prisca* (RÜPPELL, 1829), Upper Jurassic (lower Tithonian), Eichstätt, Germany (Bayerische Staatssammlung für Paläontologie und Geologie, Münich), detail of posterior mantle; note transversally striated muscular mantle attached to lateral margin of gladius (*arrows*), ×2 (adapted from Fuchs, Iba, & others, 2015, fig. 1).

The first arm crowns discovered outside the Solnhofen Plattenkalks came from the Callovian Oxford Clay of Christian Malford, UK (Owen, 1843).

At present, thousands of specimens showing hook-bearing and hookless arm crowns have accumulated in public and private museums. Preserved arm crowns are best known from Callovian deposits of Christian Malford (England) and La Voulte-sur-Rhône (France), as well as from the Solnhofen (Tithonian) and Lebanon (Cenomanian–Santonian) Plattenkalks. The first report of a complete arm crown from early Jurassic times has been recently reported by Fuchs, Keupp, and Schweigert (2013). The oldest record of arms comes from the Lower Carboniferous Bear Gulch Formation (Mapes, Weller, & Doguzhaeva, 2010).

Fossils of many genera with preserved arm crowns have been collected (see Table 1). In less well preserved, phragmocone-bearing taxa, the arm crowns can often be reconstructed indirectly by the presence of associated arm hooks (onychites). Because the arms of gladius-bearing taxa were not equipped with chitinous armatures (see discussion below), arm crown reconstructions are based exclusively on phosphatized arms or their impressions.

Most characteristic are the stellate (star-like) impressions of eight arms in *Plesioteuthis* (Fig. 3a). In these instances, the animal approached the bottom with the body axis nearly vertical. After the arm crown had made its impression in the sediment, the animal fell over and came to rest next to the impression. Although Recent squid do not normally hold the arms spread out, Kier (1982, fig. 1) showed that such a flared attitude is adopted immediately before prey capture. *Plesioteuthis* may have pursued prey into toxic bottom water, but this is perhaps not very likely: in Recent squid, the flared position is held for less than 1 second in the normal capture sequence. Remains of prey (e.g., crustaceans, small fish) have not been observed associated with these fossils. Most probably, the flared posture was adopted in dead or dying animals, which may be seen in side view next to the stellate impressions. The stellate impressions show the middle part of each arm and, in some instances, the distal tips. The proximal sections did not make an imprint, presumably because of the curvature of the arms as they were flared outward.

Vokes (1941) described eight-pointed stellate impressions in sediment from the Upper Cretaceous Mowry Shale of Montana (USA), which are not associated with body fossils (Fig. 3b). Brown & Vokes (1944) named these trace fossils *Asterichnites octoradiatus* Brown & Vokes, 1944, and compared them with the *Plesioteuthis* imprints. The Mowry imprints differ from the Solnhofen ones in having pointed ends, and, in some, the sediment is drawn up toward the oral region at the inner end of each arm, a feature not reported from Solnhofen. Brown and Vokes (1944, p. 665) cited Drew (1911), who recorded that female *Doryteuthis* Münster, 1846, "bounces over the bottom on the tips of her arms just previous to selecting a place for sticking the egg string." Brown and Vokes (1944, pl. 1) figured rows of stellate impressions, which could be held to support the bouncing hypothesis for their trace fossils. They thought that the evidence for such an origin for *Asterichnites* Brown & Vokes, 1944, was plausible, but not conclusive. The pushed-up sediment at the inner end of each impression must have been formed by the arms being drawn together on the rebound, which could help the (presumed) jet in raising the animal off the sea floor. The differences between *Asterichnites* and *Plesioteuthis* may be due to the former having been made by a living animal and the latter by a dead one. On balance, the case for interpreting *Asterichnites* as a coleoid artifact is strong: it is difficult to think of any other animal group with a structure which would make such impressions. Klug and others (2015) recently discussed how very different arm arrangements in *Plesioteuthis* might reflect behavior.

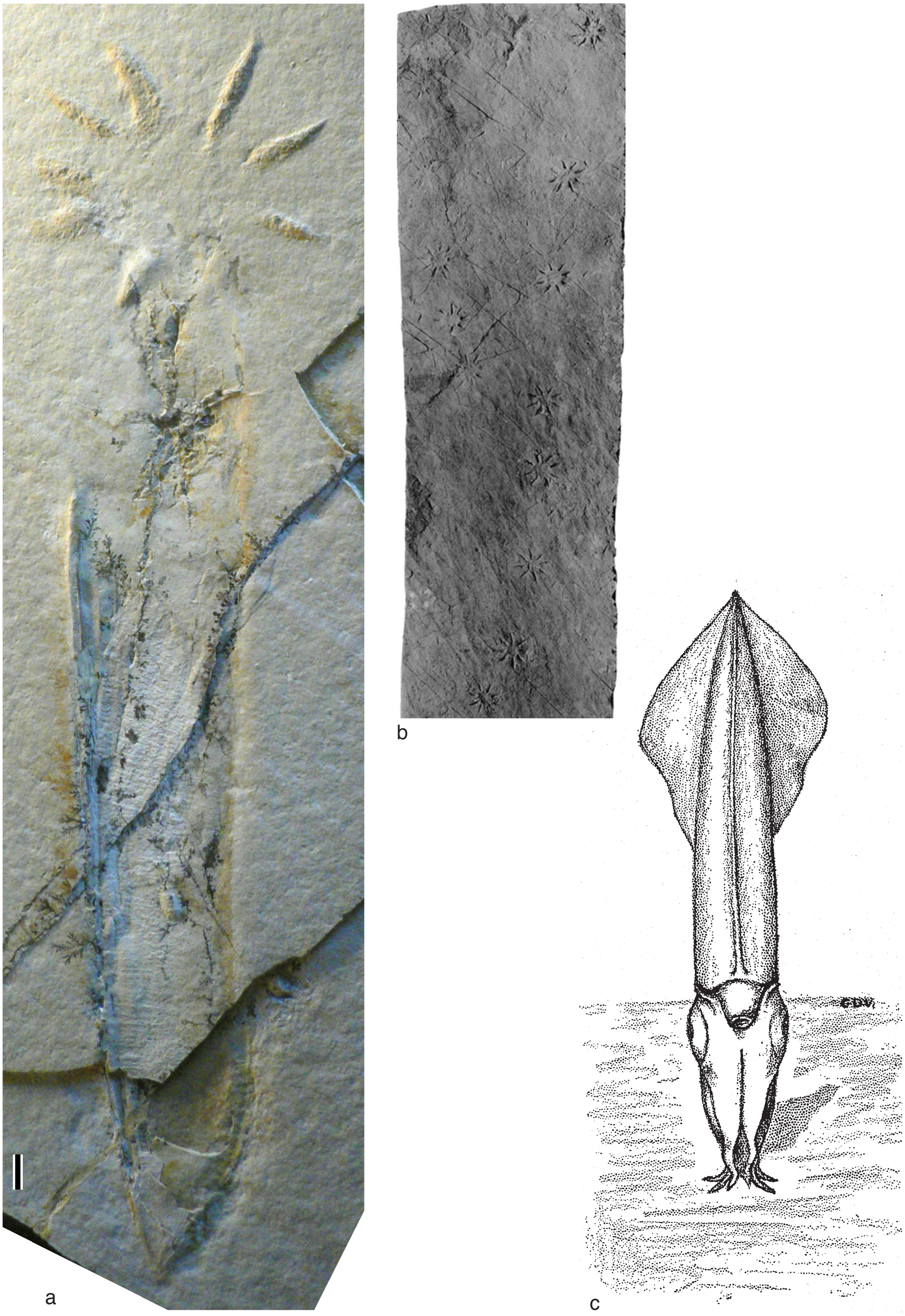

FIG. 3. Stellate arm imprints. *a, Plesioteuthis prisca* (RÜPPELL, 1829), Upper Jurassic (lower Tithonian), Eichstätt region, Germany (Naturhistorisches Museum, Vienna), body in right lateral view, ×0.5 (new); *b, Asterichnites octoradiatus* BROWN & VOKES, 1944, Mowry shale, Upper Cretaceous, Montana, USA, impressions in rows, slab dimensions, 53 by 16 inches (Brown & Vokes, 1944); *c, Doryteuthis (Loligo) pealleii* (LESUEUR, 1821), selecting a place for depositing eggs (Brown & Vokes, 1944).

PHOSPHATIZED ARM MUSCULATURE

The general arrangement of muscles in the arms of coleoids does not differ significantly. It consists basically of transverse muscle surrounded by bundles of longitudinal muscle fibers, with envelopes of spirally arranged oblique muscle and an outer sheath of longitudinal muscle (Kier & Thompson, 2003; see *Treatise Online,* Part M, Chapter 3, Fig. 29).

SEM pictures of the arm tissue of *Belemnotheutis* Pearce, 1842, from Christian Malford (UK) show muscle fibers with different orientations: longitudinal, transverse, and radial (Kear, Briggs, & Donovan, 1995). Arms from the Posidonia Shales, as well as the Solnhofen and Lebanon Plattenkalks, are similarly preserved as a whitish film (Fig. 4), which probably represents apatite, but the structure has not been analyzed in detail.

ARM LENGTH AND THICKNESS

While arm length appears to be more or less constant in phragmocone-bearing belemnoids (arm length:mantle length = 0.2–0.4), arm lengths are highly variable in gladius-bearing coleoids (Fig. 5). Taxa such as *Plesioteuthis; Muensterella; Leptotheuthis* Meyer, 1834; and *Mastigophora* Owen, 1856, had the shortest arms (arm length:mantle length = 0.2–0.28). *Loligosepia* and *Dorateuthis* Woodward, 1883, typify a moderate arm length (arm length:mantle length = 0.45). Taxa such as *Glyphiteuthis* Reuss, 1854; *Trachyteuthis;* and *Senefelderiteuthis* Engeser & Keupp, 1999, had the longest arms (arm length:mantle length = 0.7–0.8). The closely related taxa *Plesioteuthis, Dorateuthis,* and *Senefelderiteuthis* demonstrate that significant differences in arm length must have occurred at the family level. The palaeoctopodid genus *Keuppia* Fuchs, Bracchi, & Weis, 2009, exhibits arm lengths distinctly longer than the mantle.

The arm thickness is apparently correlated with the arm length. Shorter arms are relatively thicker than longer arms, which generally appear filamentous. Arms taper evenly from the base to the tip.

Fig. 4. Fossilized arm crown. *Loligosepia aalensis* (Schübler in Zieten, 1830–33), Lower Jurassic (lower Toarcian), Bachhausen, Germany (Westfälisches Landesmuseum, Münster, Germany); note the loss of one arm (*dotted line*), presumably due to accident, ×0.5 (Fuchs, Keupp, & Schweigert, 2013, fig. 2d).

ARM DIFFERENTIATION

In phragmocone-bearing belemnoids, arm differentiation is likely due to the variable hook armatures on different arms (see *Treatise Online,* Part M, Chapter 10). In gladius-bearing coleoids, a slight differentiation may have existed in form of an elongation of the dorsal arm pair (arm pair I), which has been described from various taxa (Fig. 5, 7). Haas (2002), Fischer and Riou (2002), Fuchs (2006a, 2014), and Fuchs and Larson (2011a, 2011b) observed elongated dorsal arm pairs from the Callovian of

FIG. 5. Different arm lengths. *a, Plesioteuthis prisca* (RÜPPELL, 1829), Upper Jurassic (lower Tithonian), Eichstätt, Germany (Staatliches Museum für Naturkunde, Stuttgart, Germany), left lateral view, note the short arms, ×0.5; *b, Mastigophora aff. brevipinnis* OWEN, 1856, Middle Jurassic (lower Callovian), La Voulte-sur-Rhône, France (Musée National d'Histoire Naturelle, Paris, France), ventral view, note the short arms, ×3 (Fuchs, 2006a); *c, Glyphiteuthis freijii* FUCHS & LARSON, 2011, Upper Cretaceous (Cenomanian), Hâkel, Lebanon (Black Hills Institute of Geological Research, Hill City, South Dakota, USA), ventral view, note the long arms, ×0.8 (Fuchs & Larson, 2011b, fig. 10,*1*).

La Voulte-sur-Rhône (*Vampyronassa, Mastigophora*), the Tithonian Solnhofen Plattenkalks (*Plesioteuthis, Trachyteuthis*), and the Cenomanian Plattenkalks of Lebanon (*Dorateuthis, Glyphiteuthis*).

ARM WEB

An interbrachial web has been assumed for taxa such as *Rhomboteuthis* FISCHER & RIOU, 1982; *Plesioteuthis; Trachyteuthis;* and *Leptotheuthis.* From taphonomical circumstances, Bandel and Leich (1986) reconstructed comparatively short arm webs not longer than one-third of the total arm length. Fischer and Riou (1982a) provided evidence in a three-dimensionally preserved specimen.

NUMBER OF ARMS

No doubt exists that belemnoids typically possessed ten hook-bearing arms. This is easily inferred from frequent records of, for example, *Belemnotheutis antiqua* Pearce, 1842, from the Callovian Oxford Clay of Christian Malford (U.K.); *Clarkeiteuthis conocauda* (Quenstedt, 1849) (formerly *Phragmoteuthis concauda*) from the Toarcian Posidonia Shales of Germany; or *Acanthoteuthis speciosa* from the Tithonian Solnhofen Plattenkalks (Donovan & Crane, 1992; Garassino & Donovan, 2000; Fuchs, Boletzky, & Tischlinger, 2010; Fuchs, Donovan, & Keupp, 2013). *Acrocoelites (Toarcibelus) raui* (Werner, 1912) from the Posidonia Shales also indicates that true belemnitids with a calcitic rostrum possessed ten arms (Reitner & Urlichs, 1983).

Less agreement exists concerning the number of arms in gladius-bearing coleoids. Traditionally, workers assumed ten arms, mainly owing to the presence of a teuthid-like gladius. Both Naef (1922) and Jeletzky (1966), surprisingly, avoided discussing the true arm number and postulated five arm pairs (including a pair of tentacles; see below). In fact, no arm crown consisting of ten unambiguous (hookless) arms is known from the fossil record. Even extraordinarily well preserved arm crowns never yielded more than eight arms (Donovan, 1983; Bandel & Leich, 1986; Fuchs, Keupp, & Engeser, 2003; Fuchs, 2006a, 2006b; Fuchs, Klinghammer, & Keupp, 2007; Fuchs & Larson, 2011a, 2011b; Fuchs 2014; Fuchs, Keupp, & Schweigert, 2013). Arm crowns consisting of only eight arms have been identified in each of the three subgroups of Mesozoic gladius-bearing coleoids: Prototeuthina, Loligosepiina, and Teudopseina (see Fig. 6–7, Table 1).

Recently, Fuchs and Larson (2011a, 2011b) and Fuchs, Keupp, and Schweigert (2013) demonstrated that accidentally lost arms can be identified, based on arm stubs, thereby enabling complete and incomplete arm crowns to be distinguished (Fig. 4). The critique that a fifth arm pair might have regularly been lost in gladius-bearing coleoids is therefore unjustified.

TENTACULAR ARMS

The term “tentacle” is reserved for the modified fourth ventrolateral arm pair of Recent decabrachians. Each tentacle consists of a proximal suckerless stalk and a distal club armed with multiserial suckers and occasionally hooks on the oral surface (see Nixon, 2011, *Treatise Online,* Part M, Chapter 3).

Though belemnoid coleoids have frequently been interpreted to possess tentacle-like arm pairs (e.g., Naef, 1922; Riegraf & Hauff, 1983; Mapes, Weller, & Doguzhaeva, 2010; Stevens, 2010), direct evidence (e.g., tentacular club, ventrolateral position) is still weak (see *Treatise Online,* Part M, Chapter 10).

Likewise, reports on true tentacles in gladius-bearing coleoids are questionable. Naef (1922, fig. 39, 43, 52) usually indicated their existence in his sketches. However, reliable evidence of their existence is weak. Although the presence of tentacles has been widely adopted (e.g., Roger, 1952), reinvestigations of Naef’s specimens failed to confirm his presumptions (Bandel & Leich, 1986; Young, Vecchione, & Donovan, 1998; Fuchs, Klinghammer, & Keupp, 2007; Fuchs, Engeser, & Keupp, 2007; Fuchs, 2014). Fischer and Riou (1982a, 1982b) identified tentacle-like structures in their new genera *Romaniteuthis, Rhomboteuthis,* and *Gramadella* from the Callovian of La Voulte. However, the identification of the position of these structures (whether they are in ventral or dorsal position) was considered premature. Reinvestigations of Fischer and Riou’s (1982a, 1982b) material raised questions about the existence of true tentacles, suggesting instead the presence of

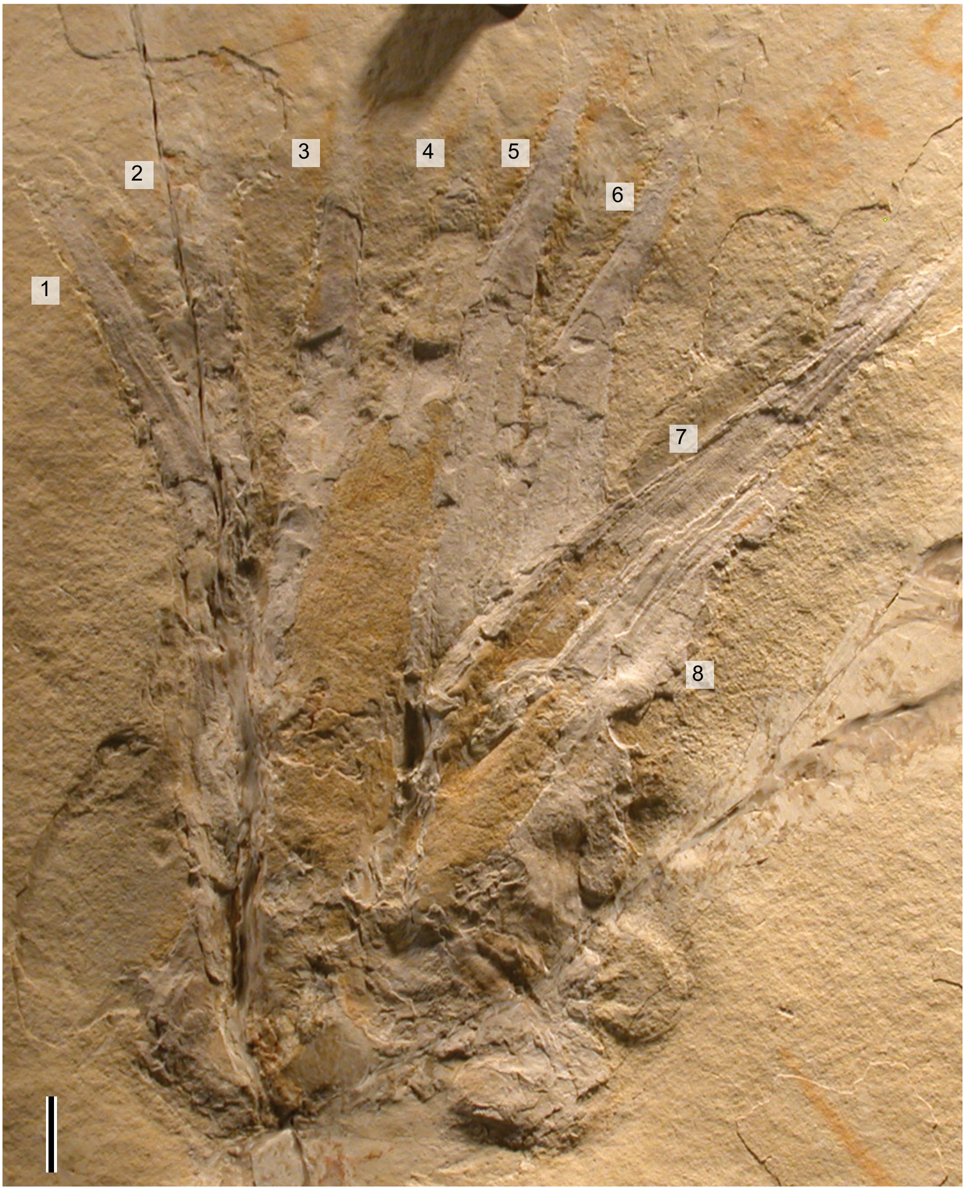

FIG. 6. Arm crown of *Leptotheuthis gigas* MEYER, 1834, Upper Jurassic (lower Tithonian), Eichstätt, Germany (Bürgermeister Müller Museum, Solnhofen, Germany); numbers correspond to the number of preserved arms, ×0.5 (new).

an elongated arm pair in the dorsal position (FUCHS, 2014). In addition, the so-called tentacular stalks in *Mastigophora* described by VECCHIONE and others (1999) allow for alternative interpretations (DONOVAN, 1983; HAAS, 2002; FUCHS, 2014). The regular occurrence of an elongated dorsal arm pair in Mesozoic gladius-bearing coleoids shows that future assumptions of true tentacles must be accompanied by a trustworthy identification of their ventrolateral position within the arm circle.

FIG. 7. Arm crown of *Dorateuthis syriaca* WOODWARD, 1883, Upper Cretaceous (Santonian), Sâhel Aalma, Lebanon, (British Museum of Natural History, London, UK); note ventral arms are shortest and dorsal arms are longest, ×0.5. Abbreviations, *ld,* left dorsal; *ldl,* left dorsolateral; *lv,* left ventral; *lvl,* left ventrolateral; *rd,* right dorsal; *rdl,* right dorsolateral; *rv,* right ventral; *rvl,* right ventrolateral (Fuchs & Larson, 2011b, fig. 3,*3*).

Concerning the apparent lack of tentacles in the fossil record, supporters of the so-called Decabrachia Theory argue that tentacles might have been retracted into tentacular pockets (VECCHIONE & others, 1999). FUCHS and LARSON (2011a, 2011b) studied a large number of gladius-bearing coleoids from the Lebanon Plattenkalks and failed to detect any structures that might correspond to tentacular pockets. A tangle of retracted arm musculature in the head region would have had the same preservation potential as outspread arms, particularly in the light of the extraordinary soft-part preservation in these limestones. If *Plesioteuthis* had possessed a pair of ventrolateral tentacles, the starlike imprints would have consisted of ten imprints because sinking of a dead body in a head-down position would have caused the tentacles to slide from their pouches (KEAR, BRIGGS, & DONOVAN, 1995).

Among Recent oegopsids, few taxa (e.g., *Octopoteuthis* RÜPPELL, 1844: *Gonatopsis* NESIS, 1971; *Lepidoteuthis* JOUBIN, 1895) are known to resorb their tentacles during ontogenesis. So far, juvenile specimens of *Plesioteuthis* or *Dorateuthis* have yielded no evidence of tentacles. As eight arms have been observed in various families in each of the three fossil suborders, it appears unlikely that the ontogenetical loss of tentacles is a common feature of Mesozoic gladius-bearing coleoids.

ARM ARMATURE

Suckers along the arms have been described from various gladius-bearing coleoids (BANDEL & LEICH, 1986; FISCHER & RIOU, 1982a, 1982b, 2002; FUCHS, BRACCHI, & WEIS, 2009; FUCHS, KEUPP, & ENGESER, 2003; FUCHS, 2006a, 2006b; FUCHS & LARSON, 2011a; FUCHS, 2014; see Table 1). La Voulte specimens with three-dimensionally preserved suckers show that in *Rhomboteuthis, Mastigophora* (Fig. 8a), and *Vampyronassa* suckers were uniserial and most probably sessile (FISCHER & RIOU, 1982a, 2002; FUCHS, 2014). Imprints of uniserial, circular suckers have also been described for taxa from the Solnhofen Plattenkalks, and taxa from the Lebanon Plattenkalks even yielded phosphatized remains of uniserial or alternating circular suckers (Fig. 8b–c).

FUCHS, BOLETZKY, and TISCHLINGER (2010) found uniserial suckers in *Acanthoteuthis* WAGNER in MÜNSTER, 1839. Their finding confirmed previous assumptions by MANTELL (1852) and DONOVAN and CRANE (1992) that belemnoid arms were equipped with both suckers and hooks (Fig. 9).

Hooks (onychites) on either side of the suckers are known to occur only in phragmocone-bearing belemnoids (see discussion of onychites in *Treatise Online,* Part M, Chapter 10). Although hooks in association with gladius-bearing forms were assumed (WAGNER, 1860; DOGUZHAEVA & MUTVEI, 2003), this assumption has been clearly rejected by NAEF (1922), JELETZKY (1966), ENGESER and CLARKE (1988), and FUCHS, HEYNG, and KEUPP (2013).

Based on X-ray examination of specimens from La Voulte, FISCHER and RIOU (1982a) assumed the presence of ringlike structures along the arms, the only such observation to date. BANDEL and LEICH (1986) rigorously argued against the presence of sucker rings. In addition, sucker rings have never been observed in either gladius- or phragmocone-bearing taxa in the finely laminated limestones from Holzmaden, Christian Malford, Solnhofen, or Lebanon (FUCHS 2014; FUCHS, HEYNG, & KEUPP, 2013): such chitinous structures as sucker rings would be expected to have left the same imprints as did belemnoid hooks.

Filament-like appendages in close association with suckers have been reported only from gladius-bearing coleoids (BANDEL & LEICH, 1986; FUCHS & LARSON, 2011a). Particularly, the long filaments observed in *Glyphiteuthis* and *Plesioteuthis* led FUCHS and LARSON (2011a) and KLUG and others (2015) to interpret them as octopod cirri. Although HAAS (2002) presumed cirri in *Palaeoctopus,* FUCHS, BRACCHI, and WEIS (2009) found no clear evidence of cirri either in *Palaeoctopus* or in *Keuppia.* This observation suggests an early loss of cirri in the evolution of the Octopoda.

FIG. 8. Fossilized suckers. *a, Mastigophora aff. brevipinnis,* Middle Jurassic (lower Callovian), La Voulte-sur-Rhône France (collection of H. Tischlinger), lateral view, note the uniserial row of pyritized suckers, ×2; *b, Plesioteuthis prisca,* Upper Jurassic (lower Tithonian), Wintershof, Germany (Juramuseum Eichstätt, Germany), note the uniserial row of sucker imprints, ×1.5; *c, Keuppia levante* FUCHS, BRACCHI, & WEIS, 2009, Upper Cretaceous (Cenomanian), Hâkel, Lebanon (Oberösterreichisches Landesmuseum Linz, Austria), note alternating circular suckers on oral arm surfaces, ×1.5 (new; UV-photograph by H. Tischlinger).

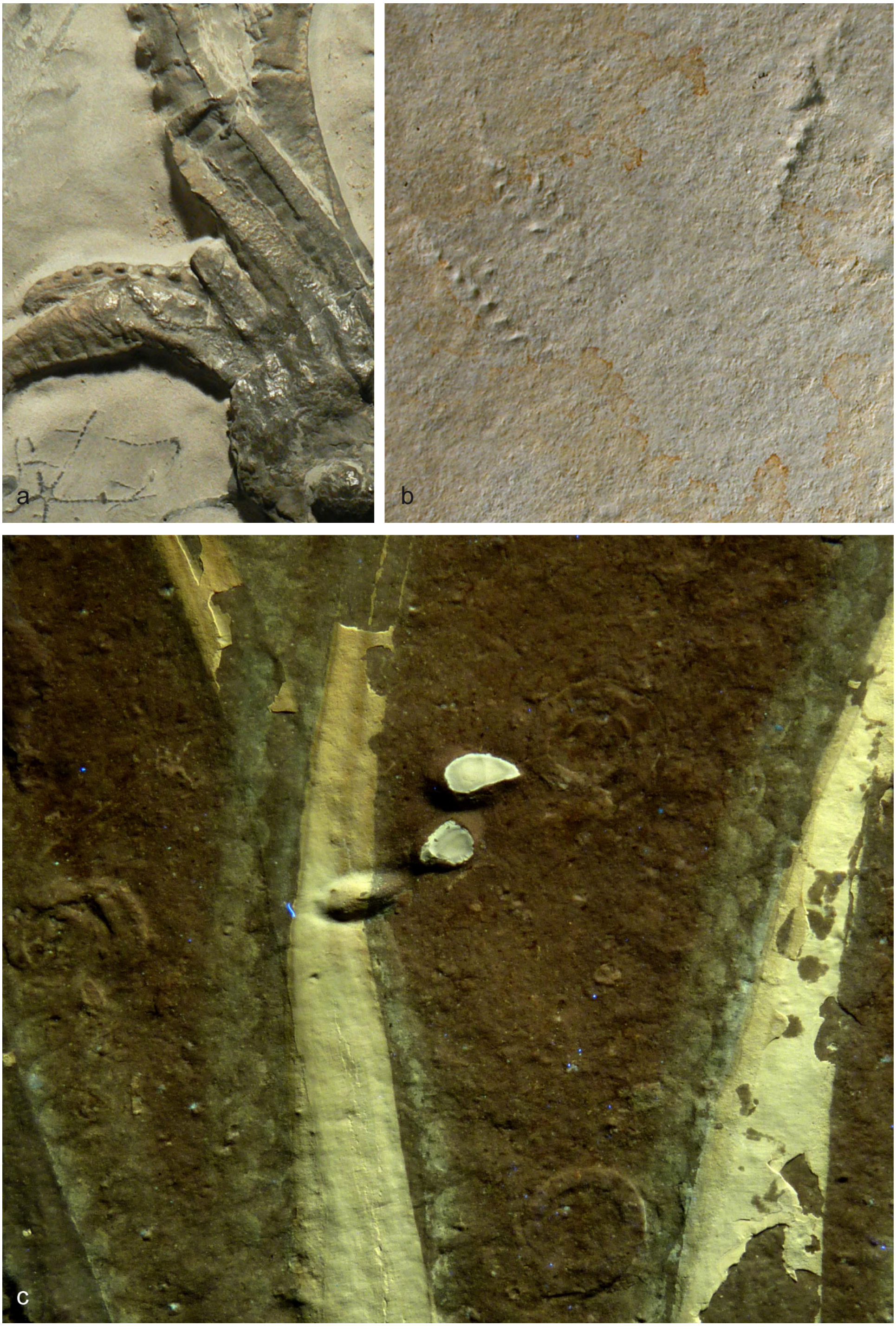

FIG. 8. *For explanation, see facing page.*

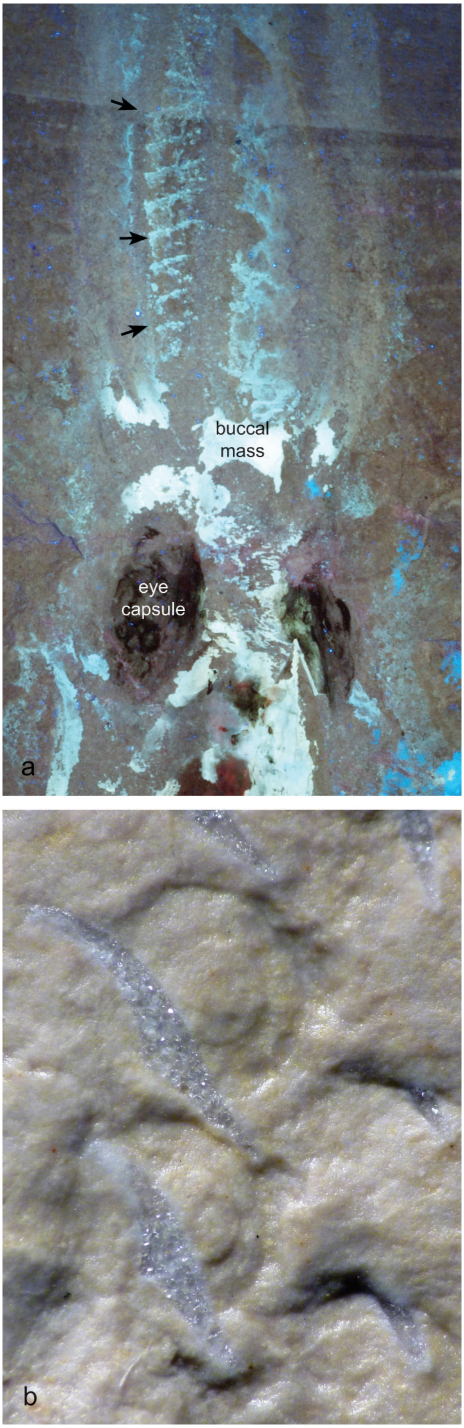

FIG. 9. Fossilized cirri and sucker-hook association. *a, Glyphiteuthis* sp., Upper Cretaceous (Cenomanian), (*Continued on adjacent column.*)

FUNNEL

Preservation of the funnel is rare compared to other muscular structures. When preserved, the funnel is distinguishable mainly in laterally embedded specimens. Such specimens include *Plesioteuthis* (Fig. 10a) from the Solnhofen Plattenkalks and *Rachiteuthis* (Fig. 10b) from the Lebanon Plattenkalks (FUCHS, 2006b). However, dorsally embedded specimens of *Mastigophora* from La Voulte-sur-Rhône (Fig. 5b; FUCHS, 2014) and *Glyphiteuthis* from Lebanon also exhibit their funnel. In specimens of *Muensterella* from Solnhofen, a strand of fossilized muscular tissue, which is usually running in anterior-posterior direction, might be interpreted as the funnel retractor (Fig. 11c; FUCHS, KEUPP, & ENGESER, 2003).

FINS

Although fins in phragmocone-bearing belemnoids were indicated in most reconstructions (e.g., NAEF, 1922; SEILACHER & WIESENAUER, 1978; MONKS, HARDWICK, & GALE, 1996), clear records of fins were long unknown (YOUNG, VECCHIONE, & DONOVAN, 1998; FUCHS 2006a). Longitudinal grooves in the belemnoid rostrum proper have been commonly interpreted as fin attachment sites (STEVENS, 1965; SCHLEGELMILCH, 1998). Recently, however, KLUG and others (2014, 2016) observed semicircular spots of phosphatized muscles that most likely correspond to fins in the posterior mantle region of *Acanthoteuthis* from the Solnhofen Plattenkalks.

In contrast to belemnoids, the existence of fins in gladius-bearing coleoids is

FIG. 9. *Continued from adjacent column.*
Hadjoula, Lebanon (Black Hills Institute of Geological Research, Hill City, South Dakota, USA), UV-photograph showing head and arms equipped with filamentous cirri (*arrow heads*), ×1 (Fuchs & Larson, 2011b, fig. 12,*2*); *b, Acanthoteuthis speciosa* MÜNSTER, 1839, Upper Jurassic (lower Tithonian), Eichstätt, Germany; arm with biserial hooks and uniserial suckers (collection of H. Tischlinger), ×10 (Fuchs, Boletzky, & Tischlinger, 2010, fig. 1F).

FIG. 10. Fossilized funnels (indicated by *arrows*). *a, Plesioteuthis prisca* (RÜPPELL, 1829), Upper Jurassic (lower Tithonian), Eichstätt, Germany (Bayrische Staatssammlung für Paläontologie und Geologie, Munich, Germany), left lateral view, ×0.5; *b, Rachiteuthis donovani* FUCHS, 2006, Upper Cretaceous (Cenomanian), Hâdjoula, Lebanon, (Museo Civico di Storia Naturale di Milano, Milan, Italy), left lateral view, ×2 (Fuchs, 2006b, pl. 5*A*).

unquestionable. Fins are described from a number of taxa, and those are known to exhibit a large variety of fin shapes (Fig. 11; DONOVAN 1983, 1995; FUCHS, KEUPP, & ENGESER, 2003; FUCHS 2006a, 2006b; FUCHS, ENGESER, & KEUPP, 2007; FUCHS & LARSON, 2011b; Table 1).

The oldest evidence of fin impressions comes from the Mazon Creek Lagerstätte (KLUESSENDORF & DOYLE &, 2000). Fin impressions are more frequently recorded in taxa from La Voulte, Christian Malford, Solnhofen, and Lebanon.

In most instances, the outline of fins has been imprinted in the sediment; phosphatized fin musculature is relatively rare. Fins are usually subterminal, separated from each other, and attached (indirectly through the shell sac) to the gladius. Terminal fins are so far unknown. The shape of the fins varies: fins may be ear-shaped, as in *Mastigophora* (Fig. 11a), *Rhomboteuthis, Vampyronassa, Proteroctopus, Plesioteuthis* (Fig. 11b), *Trachyteuthis* (Fig. 11d), *Glyphiteuthis,* and *Dorateuthis*; skirtlike, as in *Muensterella* (Fig. 11c); winglike, as in *Boreopeltis* ENGESER &

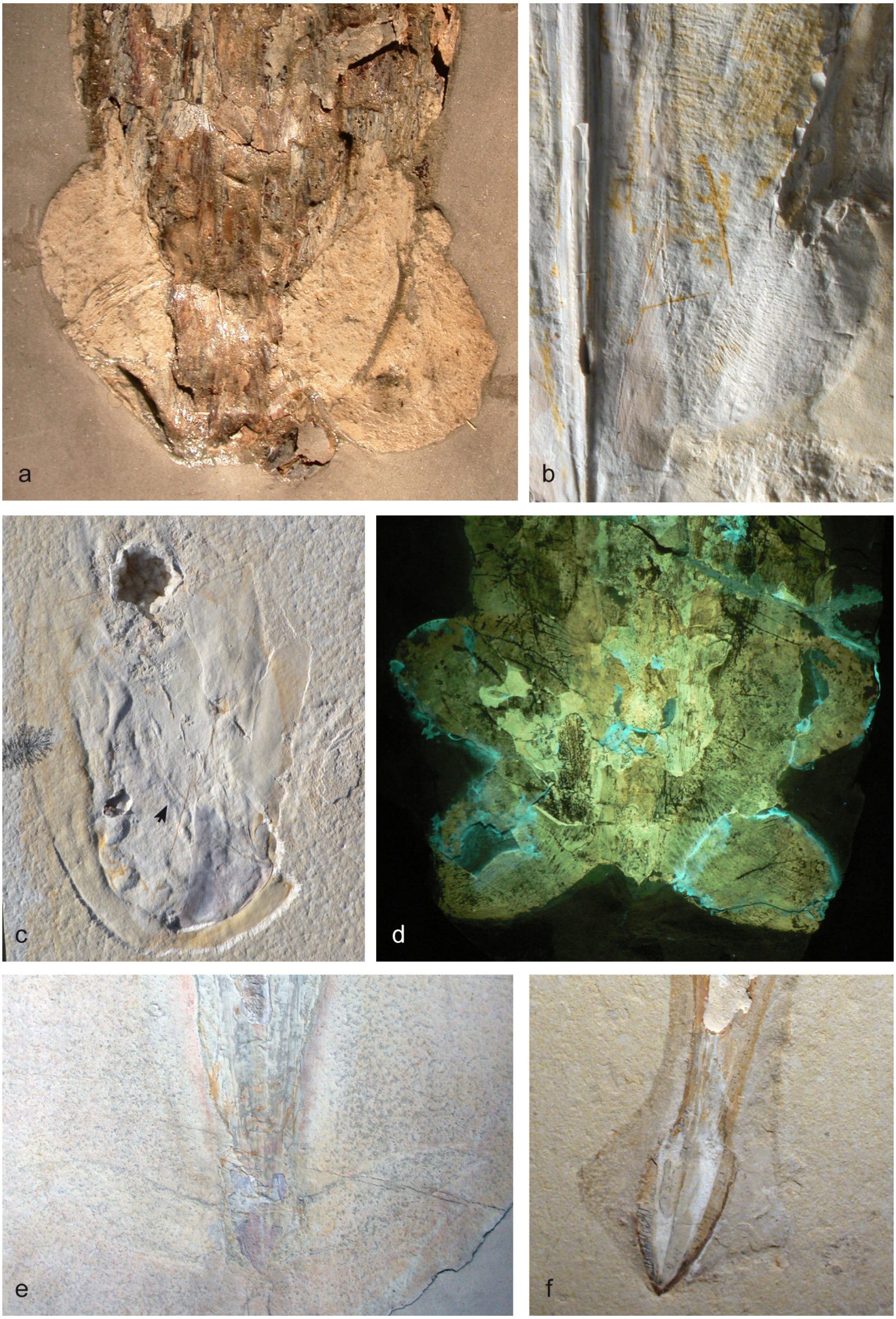

FIG. 11. Fossilized fin musculature. *a, Mastigophora aff. brevipinnis* OWEN, 1856, Middle Jurassic (upper Callovian), Christian Malford, UK (British Museum of Natural History, London, UK), dorsal view, ×0.5 (Fuchs, Iba, & others, 2015, fig. 8C); *(Continued on facing page.)*

Reitner, 1985 (Fig. 11e); or rhomboidal, as in *Rachiteuthis* (Fig. 11f).

Three genera, *Plesioteuthis* (Plesioteutidae), *Glyphiteuthis* (Trachyteuthidae), and *Trachyteuthis* (Trachyteuthidae), are characterized by the possession of two pairs of ear-shaped fins (Donovan, Doguzhaeva, & Mutvei, 2003; Fuchs 2006a; Fuchs, Engeser, & Keupp, 2007; Fuchs & Larson, 2011a; Klug & others, 2015). Those of *Trachyteuthis* show a pattern of bifurcating bundles of muscle fibers, similar to that in Recent coleoids (Young & Vecchione, 1996, fig. 7). Skirtlike fins, such as those reconstructed by Naef (1922) or Bandel and Leich (1986) for *Trachyteuthis* are, therefore, no longer tenable (Donovan, Doguzhaeva, & Mutvei, 2003; Fuchs, Engeser, & Keupp, 2007).

Several specimens of *Mastigophora, Trachyteuthis, Glyphiteuthis,* and *Rachiteuthis*, which show phosphatized fin musculature, indicate that the fin bases are either attached to the hyperbolar zones of the gladius (Donovan, 1983; Donovan, Doguzhaeva, & Mutvei, 2003; Fuchs 2006a; Fuchs & Larson, 2011a) or to the lateral fields, as in *Plesioteuthis* (Fig. 11b). Fins have also been described in palaeoctopodids *Palaeoctopus* and assumed in *Keuppia* from the Late Cretaceous Lebanon Plattenkalks (Woodward 1896; Fuchs, Bracchi, & Weis, 2009). Owing to the presence of a medially separated gladius vestige, both genera belong to the incirrate lineage, indicating that the loss of fins occurred comparatively late in the evolution of octopods (Fuchs, Bracchi, & Weis, 2009). The presence of fin *Anlagen* in Recent cirrate embryos supports this assumption.

CARTILAGINOUS STRUCTURES

In Recent coleoids, the most notable cartilaginous structures comprise the cephalic (cranial), the branchial, the nuchal- and funnel-locking, and the fin cartilages (see *Treatise Online,* Part M, Chapter 9A). Fossil evidence of cartilaginous structures includes clear evidence of the cephalic and the fin cartilage. Neither nuchal- nor funnel-locking cartilages for decabrachian coleoids are known so far from the fossil record, at least in gladius-bearing coleoids (Fuchs & others, in press). Klug & Fuchs (2010) and Klug & others (2016) presumed the existence of nuchal cartilage in an undetermined belemnoid from the Hettangian of Great Britain and in *Acantoteuthis.*

CEPHALIC CARTILAGE

In Recent forms, the cephalic cartilage (or eye capsules) encases the central nervous system. Foramens allow the nerves, blood vessels, and the esophagus to pass through this so-called skull.

The fossil record of cephalic cartilage is based largely on the relative arrangement of imprints in the head region of fossil coleoids (e.g., Naef 1922). However, in some instances, the cephalic cartilage is either substantially preserved or left a detailed staining of its outline.

Münster (1846) was probably the first to correctly identify the remains of cephalic cartilage from the Lower Jurassic Plattenkalks. The oldest evidence of cephalic cartilage was reported from the Upper Cretaceous Eudora Shale (Oklahoma, USA) by Doguzhaeva and

Fig. 11. *Continued from facing page.*
b, Plesioteuthis prisca, Upper Jurassic (lower Tithonian), Eichstätt, Germany (collection of H. Keupp), detail of right fin to show striation caused by fin muscles, ×1.5 (Fuchs, Iba, & others, 2015, fig. 1A); *c, Muensterella scutellaris* (Münster, 1842), Upper Jurassic (lower Tithonian), Eichstätt, Germany (Bergér Museum Eichstätt), left lateral view showing imprints of skirtlike fins, with *arrow* marking position of funnel retractor ×0.25 (new); *d, Trachyteuthis* sp., Upper Jurassic (lower Tithonian), Eichstätt, Germany (collection of H. Tischlinger), dorsal view, ×0.25 (new; UV-photograph by H. Tischlinger); *e, Boreopeltis sagittata* Engeser & Reitner, 1985, Upper Jurassic (lower Tithonian), Eichstätt, Germany (British Museum of Natural History, London, UK), ventral view, ×0.5 (new); *f, Rachiteuthis donovani* Fuchs, 2006, Upper Cretaceous (Cenomanian), Hâdjoula, Lebanon, (Museo Civico di Storia Naturale di Milano, Italy), lateral view, ×0.5 (Fuchs, 2006b, pl. 5A).

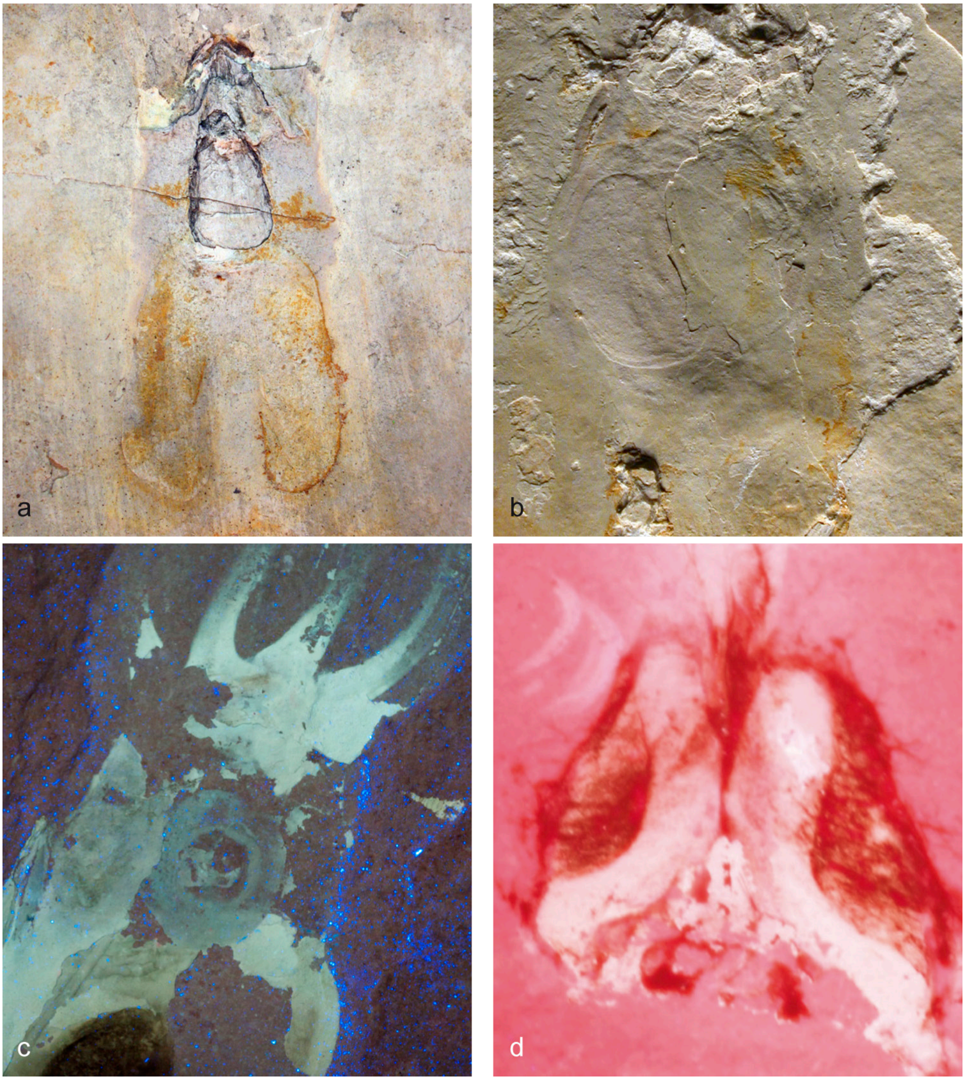

Fig. 12. Fossilized cephalic cartilages. *a–b, Plesioteuthis prisca* (Rüppell, 1829), Upper Jurassic (lower Tithonian), Eichstätt, Germany; *a,* (Bayrische Staatssammlung für Paläontologie und Geologie, Munich, Germany), original of Münster, 1846, elliptical structures posterior to dorsoventrally compressed upper and lower beak represent the cephalic cartilage, ×1 (new); *b,* (Staatliches Museum für Naturkunde, Stuttgart, Germany), laterally compressed eye capsules, ×1.5 (new). *c–d,* UV-photographs, Upper Cretaceous (Cenomanian), Hâkel, Lebanon (Black Hills Institute of Geological Research, Hill City, South Dakota, USA); *c, Glyphiteuthis* sp. Reuss, 1854, right lateral view of the head with ring-shaped eye capsule, ×1 (Fuchs & Larson, 2011b, fig. 12,*3*); *d, Dorateuthis syriaca* Woodward, 1883, ventral view, note the boomerang-shaped eye capsules, ×2 (Fuchs & Larson, 2011a, fig. 4,*6*).

others (2010). It occurs together with imprints of hooks indicating that this cephalic cartilage belongs to a phragmocone-bearing belemnoid. In gladius-bearing coleoids, Jurassic records of cephalic cartilages are observable in association with *Plesioteuthis* (Münster, 1846; Klinghardt, 1932) and Cretaceous records with *Dorateuthis, Glyphiteuthis,* and *Rachiteuthis* (Fuchs & Larson, 2011a, 2011b).

The cephalic cartilage of *Plesioteuthis* (Fig. 12a–b), *Glyphiteuthis* (Fig. 12c), *Dorateuthis* (Fig. 12d, Fig. 14), and *Rachiteuthis* appears

FIG. 13. Fossilized fin cartilages. *a–b,* Upper Cretaceous (Cenomanian), Hâkel, Lebanon (Black Hills Institute of Geological Research, Hill City, South Dakota, USA); *a, Glyphiteuthis libanotica* (FRAAS, 1878), dorsal view of posterior part of gladius, remains of fin cartilages visible on either side of hyperbolar zones, ×1 (Fuchs & Larson, 2011b, fig. 7,*4*); *b, Rachiteuthis donovani* FUCHS, 2006, dorsal view of posterior part of gladius, remains of fin cartilages visible on either side of the lateral fields, ×2 (Fuchs & Larson, 2011b, fig. 14,*4*); *c, Keuppia levante* FUCHS, BRACCHI, & WEIS, 2009, Upper Cretaceous (Cenomanian), Hâdjoula, Lebanon (Museo Civico di Storia Naturale di Milano, Italy), dorsal view of the bipartite gladius vestige, radiating encrustations are interpreted to be the fin cartilage, ×3 (Fuchs, Bracchi, & Weis, 2009, fig. 4D).

as circular eye capsules that are similar to Recent incirrate *Eledone* LEACH, 1817.

FIN CARTILAGE

In some Recent coleoids, paired fin cartilage supports the fins like a rigid base. Fossil fin cartilages have so far been described in gladius-bearing *Glyphiteuthis* (Fig. 13a) and *Rachiteuthis* (Fig. 13b; FUCHS & LARSON, 2011a), as well as in the palaeoctopodid *Keuppia* (Fig. 13c; FUCHS, BRACCHI, & WEIS, 2009). They appear as

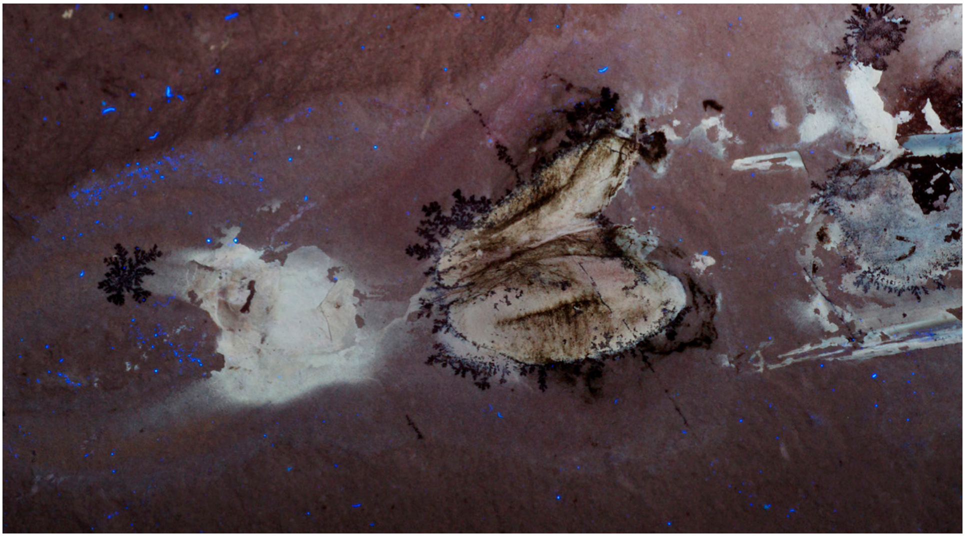

FIG. 14. Fossilized buccal mass. *Dorateuthis syriaca* WOODWARD, 1883, Upper Cretaceous (Cenomanian), Hâkel, Lebanon (Black Hills Institute of Geological Research, Hill City, South Dakota, USA), the circular buccal mass is located between the arm stubs and the circular eye capsules, ×1 (new; UV-photograph by N. Larson).

white, circular encrustations attaching the lateral field of the gladius or the bipartite gladius vestiges. The encrustations are fluorescent, indicating phosphatized tissues. The presence of basal fin cartilage in Late Cretaceous incirrates is in accordance with the presumed late reduction of fins in their evolution (FUCHS, BRACCHI, & WEIS, 2009).

TISSUES OF THE DIGESTIVE SYSTEM

BUCCAL MASS

The spherical buccal mass, or the mandibular muscle complex, lies in the hollow center of the arm bases and envelops the lower and upper beaks (for the preservation of beaks and radulae, see *Treatise Online,* Part M, Chapter 12).

Fossilized mandibular muscles frequently occur in gladius-bearing specimens from the Solnhofen (*Plesioteuthis; Senefelderiteuthis; Boreopeltis; Bavaripeltis* ENGESER & KEUPP, 1997; *Leptotheuthis*) and Lebanon (*Dorateuthis* [Fig. 14], *Glyphiteuthis, Rachiteuthis, Keuppia*) Plattenkalks (FUCHS 2006a; FUCHS, BRACCHI, & WEIS, 2009; FUCHS & LARSON, 2011a, 2011b). Evidence of belemnoid buccal masses can be observed only in *Acanthoteuthis* from the Solnhofen Plattenkalks (KLUG & others, 2011). If the buccal mass is not preserved substantially, its former position can at least be determined by calcitic druses, which have been diagenetically formed within the hollow buccal mass.

ESOPHAGUS

The esophagus has been observed exclusively in *Dorateuthis* from the Lebanon Plattenkalks (LUKENEDER & HARZHAUSER, 2004; FUCHS & LARSON, 2011a). In a single specimen, one can see how the esophagus remains pass through the cephalic cartilage (Figs. 12d).

STOMACH, INTESTINE, AND CROP

In contrast to belemnoids, fossil evidence of the muscular alimentary canal often occurs in gladius-bearing specimens from the Solnhofen Plattenkalks: *Plesioteuthis, Senefelderiteuthis, Boreopeltis, Muensterella* (Fig. 15a) and from the Lebanon Plattenkalks: *Dorateuthis* (Fig. 15b–c), *Glyphiteuthis, Keuppia* (NAEF,

Fig. 15. Fossilized remains of the digestive system. *a, Muensterella scutellaris* (Münster, 1842), Upper Jurassic (lower Tithonian), Eichstätt, Germany (Naturhistorisches Museum, Vienna, Austria), left lateral view of mantle, with part of the meandering alimentary canal visible, ×1 (new); *b–c, Dorateuthis syriaca* Woodward, 1883; *b,* Upper Cretaceous (Cenomanian), Hâkel, Lebanon (Black Hills Institute of Geological Research, Hill City, South Dakota, USA), left lateral view, note the anterior stringlike structure with coarsely chopped food and the spot of finely chopped food in posterior mantle, ×0.5 (Fuchs & Larson, 2011a, fig. 5,*4*); *c,* Upper Cretaceous (Santonian), Sâhel Aalma, Lebanon (Musée National d'Histoire Naturelle, Paris, France), left lateral view, ×1 (new).

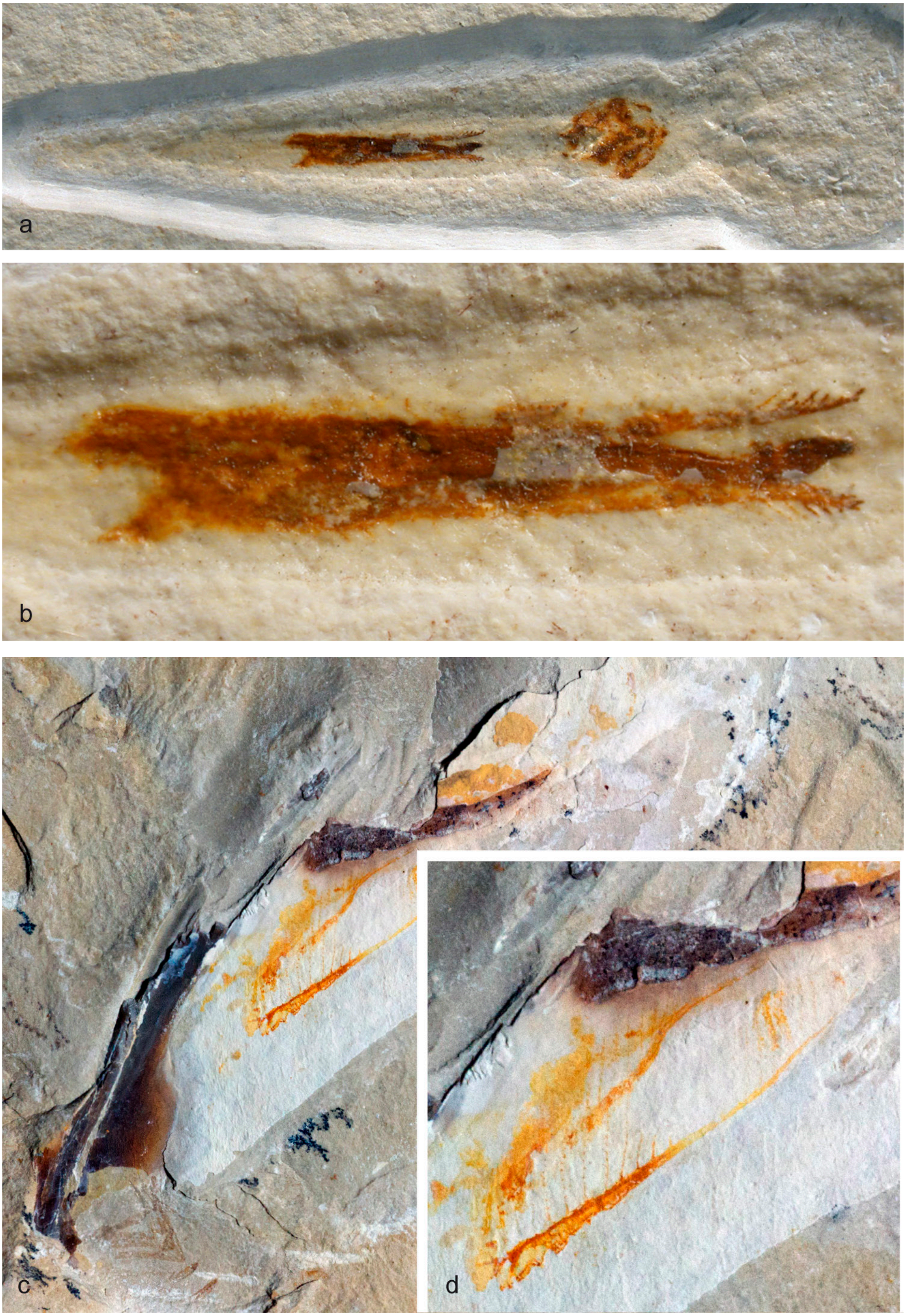

Fig. 16. Fossil remains of gills. *a–b, Plesioteuthis prisca* Rüppell, 1829, Upper Jurassic (lower Tithonian), Eichstätt, Germany (Bayerische Staatssammlung für Paläontologie und Geologie, Münich); *a,* overview, ×1; *b,* close-up of the gills, ×4 (new); *c–d, Rachiteuthis donovani* Fuchs, 2006, Upper Cretaceous (Cenomanian), Hâdjoula, Lebanon (Black Hills Institute of Geological Research, Hill City, South Dakota, USA), right lateral (*c*), ×1, and close-up (*d*) views of gills, ×2 (adapted from Fuchs & Larson, 2011b, fig. 16,*1–3*).

1922; Klinghardt, 1932; Roger, 1946; Lukeneder & Harzhauser, 2004; Keupp & others, 2010; Fuchs & Larson, 2011a, 2011b).

The former position of the stomach is mostly indicated by an accumulation of chopped food remains, usually consisting of fish bones, belemnite hooks, or fragments of crustacean cuticles. In *Dorateuthis,* Fuchs & Larson (2011a) recorded different spots of coarse and fine food particles; from the more anterior coarse particles, they presumed the existence of a crop (Fig. 15b).

In rare cases, the stomach can be identified by deep saclike holes in the posterior mantle. Some specimens of *Dorateuthis* appear to have preserved the cuticular lining of the stomach (Fig. 15c). A specimen of *Muensterella* nicely shows parts of the digestive canal. The meandering tube is swelled and, in contrast to the surrounding mantle, longitudinally striated. It might be interpreted as a crop or the intestine (Fig. 15a).

TISSUES OF THE RESPIRATORY, CIRCULATORY AND EXCRETORY SYSTEM

GILLS

In contrast to *Nautilus* Linnaeus, 1758 in 1758–1759, which has two pairs of gills, Recent coleoids possess only one pair (see *Treatise Online,* Part M, Chapter 3). The term "Dibranchiata," which was therefore introduced by Owen (1836) for endocochleate cephalopods, was longtime rejected by paleontologists; because they thought that this delicate soft part character cannot be proven in the coleoid fossil record.

However, first assumptions about featherlike imprints in the lateral mantle of *Plesioteuthis* were mentioned by Klinghardt (1932) from the Solnhofen Plattenkalks. Later, Bandel and Leich (1986) confirmed the preservation potential of gills in the Solnhofen Plattenkalks and made clear that early coleoids were already dibranchiates. Mehl (1990) pointed out that imprints of gills are actually quite abundant in Solnhofen, but they are often hidden between the phosphatized mantle musculature; additionally, he figured the first gills of *Senefelderiteuthis* (see his fig. 2), which he identified as *Plesioteuthis*. Keupp and others (2010) presented the first gills of *Trachyteuthis,* likewise from the Solnhofen Plattenkalks.

Reitner and Mehl (1989) used radiography to reveal the first phosphatized gills. Their specimen comes from the Toarcian Posidonia Shales of Holzmaden and belongs to phragmocone-bearing *Clarkeiteuthis conocauda* (Quenstedt, 1849). Although Reitner (2009) argued that only the cartilaginous skeleton of the gill apparatus has been preserved in this specimen, the longitudinal axis clearly corresponds to the primary gill vessel, while the series of paired, lappetlike appendages branching off from this axis is equivalent to the branchial lamellae.

The first evidence of gills from the Lebanon Plattenkalks was recorded in the palaeoctopodid *Keuppia* (Fuchs, Bracchi, & Weis, 2009) and gladius-bearing coleoids *Dorateuthis, Glyphiteuthis,* and *Rachiteuthis* (Fuchs & Larson, 2011a, 2011b). The gill relicts are regularly visible as yellowish stains, which represent pyritized rather than phosphatized structures (Fig. 16b). A similar mineralization has been observed by Keupp (2006) and Keupp and others (2010) in *Plesioteuthis* and *Trachyteuthis* gills from the Solnhofen Plattenkalks (Fig. 16a). According to Fuchs and Larson (2011a, 2011b), *Dorateuthis* and *Rachiteuthis* even exhibit branchial lamellae with very short, second-order side branches, possibly corresponding to the third-order branchial vessels.

BLOOD VESSEL, BRANCHIAL HEARTS, BLOOD SINUS, AND NEPHRIDIA

Riegraf (1987) found a pattern of blood vessels most probably imprinted on the inner surface of an isolated ink sac from the Posidonia Shales of Holzmaden. Similar reticulated structures can also be observed in specimens from the Solnhofen and Lebanon Plattenkalks (e.g., stomach, eye capillaries, Fig. 12d).

Fig. 17. *For explanation, see adjacent column.*

Fuchs, Wilby, and others (2015) recorded a characteristic arrangement of yellowish staining in small octopods from Lebanon, which led them to conclude an almost complete venous blood system consisting of pyritized afferent gill vessels, branchial hearts, vena cava, and blood sinus (Fig. 17a). Large portions of these stains are overlain by a pair of similarly stained triangles, which were interpreted as nephridial sacs.

TISSUES OF THE REPRODUCTIVE SYSTEM

GONADS

Except for the gonad capillary system as described by Fuchs, Wilby, and others (2015) in small octopods from Lebanon, reports on fossilized gonad tissues are rare. Roger (1946) indicated the presence of gonads preserved in *Dorateuthis* from the Lebanon Plattenkalks, but this observation needs confirmation.

NEEDHAM SAC

In Recent coleoid males, sperm packages are stored in an expanded region of the genital duct, the Needham sac. So far, a fossilized Needham sac has been reported only in a single specimen of gladius-bearing *Trachyteuthis* from the Solnhofen Plattenkalks (Keupp & others, 2010). The relict consists of a spirally enrolled and segmented cord (Fig. 17b). The cord has been determined as the Needham sac and the segments as the spermatophores.

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Fig. 17. Fossilized tissues of the circulatory, excretory, and reproductive systems; *a,* palaeoctopodid, Upper Cretaceous (Cenomanian), Hâdjoula, Lebanon (collection of R. Smith), ×5 (Fuchs, Wilby, & others, 2015, fig. 2A); *b, Trachyteuthis* sp. Meyer, 1846, Upper Jurassic (upper Kimmeridgian), Painten, Germany (collection of H. Keupp), close-up view of the middle part of the body showing spirally coiled Needham sac with segmented spermatophores, ×10 (Keupp & others, 2010, fig. 2).

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