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PART M, CHAPTER 20: PATHOLOGY OF FOSSIL AND EXTANT COLEOID SHELLS

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INTRODUCTION

The term pathology refers to growth anomalies of single individuals of a population (or in the fossil record of an assemblage) that are caused by exogenic, e.g., injuries due to predator and prey interactions, parasite infection, or the colonization of the shell during live time by epizoans (*syn vivo* epizoans = epibole; excluded post-mortem epizoans = epicole) or by endogenic processes, such as infections or illness (Davis, Klofak, & Landman, 1999; Buikstra, Cook, & Bolhofner, 2017). Shufeldt (1892) proposed the term paleopathology for occurrences of pathologies in fossils. Observable phenotypic, such as morphological reactions of an affected individual, are called symptoms, while several anomalies of a single individual can be described as complex syndromes (Landman & Waage, 1986). It follows that only the reactions of the living individual to the disturbing factor(s) should be considered to characterize pathological symptoms. These reactions are responsible for morphological deviations from the so-called normal phenotype of a given population. In this regard, Hölder (1956, p. 1) proposed “normality is fiction” and is best understood as the mean value of a morphological character. While the reactions, when preserved in mineralized hard parts, can be described, the disturbing factor or pathogen can only in rare cases be identified by, for instance, specific bite traces or shell breakage (Hoffmann & Keupp, 2015). The same holds true for non-mineralized pathological tissues such as fins or tentacles that show abnormal growth pattern. Paleopathology of cephalopods—specifically of the extinct, externally shelled ammonoids—has received proportionately large attention (Keupp, 2012). This is surprising as shell regeneration mechanisms in ectocochleate cephalopods is strongly limited in contrast to endocochleate Coleoidea, whose shell is fully covered by regenerative epithelium. Nevertheless, records of pathological coleoids—with their internal, mostly aragonitic or purely organic skeletons and a phylogenetic trend of skeleton reduction—are comparably scarce. Most records come from belemnites and their low-magnesium calcite rostra. First records of pathological belemnite rostra date back to, e.g., Blainville (1827), Raspail (1829), Duval-Jouve (1841), d’Orbigny (1842), and Quenstedt (1845–1849, 1856–1857), with a detailed review by Keupp (2012) and Hoffmann & others (2018a). Most earlier authors regarded such phenomena as monstrous or cripple-forms. First attempts for an etiological interpretation—even though not very convincing today—were applied by Duval-Jouve (1841) and Abel (1916).

For coleoid cephalopods, three categories of syndromes can be distinguished based

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on their causes: 1) Regeneration of injuries including inflammatory infection, often caused by unsuccessful predator attack; 2) prod traces due to motion; and 3) parasitosis.

Growth anomalies due to tumor formation that eventually caused the death of the animal have been observed in modern cephalopods (*Octopus*) (Jullien, 1940; Sparks, 1972; Gestal & others, 2019), which is in contrast to many other extant mollusks such as bivalves and gastropods (Sparks, 1972). Due to their internal skeleton, coleoid cephalopods are not affected by sessile organisms that occupy, for example, external shells such as those of nautiloids and ammonoids (Keupp, 2012; Hoffmann & Keupp, 2015; see Meischner (1968) for pernicious epibionts). Along these lines, the discussion of the orientation of *syn vivo* attachment of cirripeds to belemnite rostra (ichnogenus: *Rogerella*) by Seilacher (1968) and Seilacher and Gishlick (2015) is herein regarded as a postmortem phenomenon due to the lack of any reaction of the host animal (Keupp, 2012). Clearly, another advantage of an internal skeleton is related to injuries of the phragmocone. In nautiloids and ammonoids, with their external shell, an injury of the phragmocone results in uncontrolled flooding of the chambers which in turn results in drowning and/or shell implosion, which is lethal to the animal. Only two exceptions were reported for nautiloids (Kröger & Keupp, 2004; Tsujino & Shigeta, 2012). In contrast, the internal shell of coleoids is protected by tissue and stays in the body (namely, the mantle sac) after being fractured; for example, due to a predator attack. If the animal survived, such fractures were often successfully repaired.

Postmortem modifications of coleoid skeletons such as epicoles, diagenesis (compaction and pressure solution), epigenetic deformations (impacts, tectonic stress) are summarized under the term pseudopathologies (Keupp 2002, 2012 and references therein) and will be not discussed herein.

PATHOLOGIES IN EXTANT COLEOIDS: THE SHELLS OF *ARGONAUTA, SEPIA*, AND *SPIRULA*

ARGONAUTA LINNAEUS, 1758 in 1758–1759

Although argonauts (paper nautiluses) reduced all remains of the molluscan shell, at least the females of these incirrate octopuses evolved a substitution shell, which is secreted by a pair of modified arms and used as a brood chamber. These thin-walled, calcitic egg cases of female argonauts are known to bear regenerated injuries (Fig. 1.1) (see especially Montfort, 1808, p. 127–128; Rang, 1837; Beneden, 1839; Power, 1839, 1856; Keupp, 2012). It should be noted that Rang (1837) published data belonging to Jeanette Power without permission. Power first presented her observations from 1832–1833, in which she broke off parts of the female's shell and documented its repair process, to the scientific academy of Paris in 1834. She sent her shells to Rang afterwards. That she was the first to report on shell repair in argonauts was acknowledged by Owen (1839). Though seemingly external, the shell can be seen as being internal since it is enveloped by a large, flag-like membrane of the dorsal arms. Therefore, regeneration mechanisms resemble those of endocochleates rather than ectocochleates; namely, that new shell material was added only from the outside starting with a shiny substance (Owen 1839). In this way, argonauts are capable of agglutinating a broken piece of shell even though it is in the wrong orientation (Adams, 1848; see Hoffmann & others 2018b for an example of *Spirula* Lamarck, 1799 shell fragments agglutinated into the repair shell).

Results of a supposedly endogenous incident on the shell of *Argonauta hians* Lightfoot, 1786 have been figured by Keupp (2012, Fig. 443). The initial part of the egg case is unsculptured and conus-shaped (Fig. 1.2). Subsequent regular grown parts

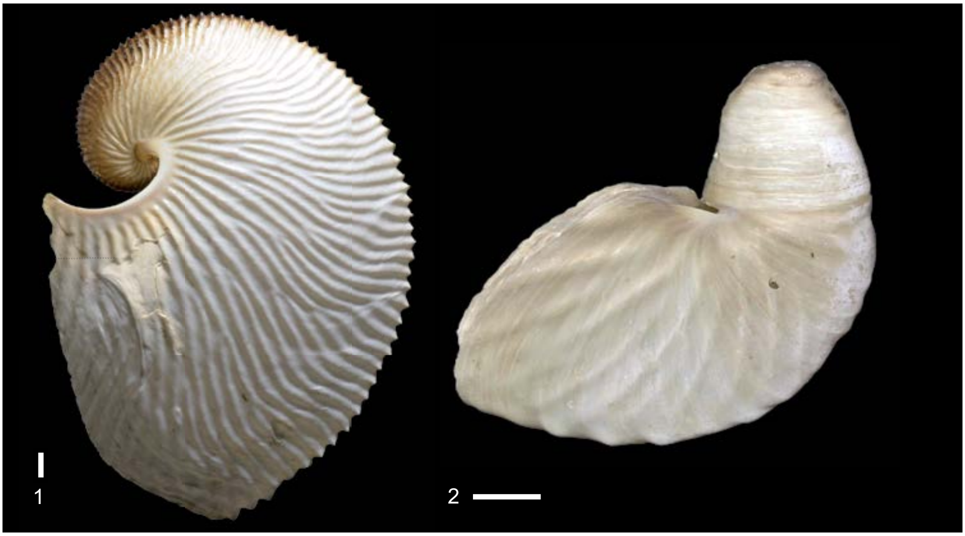

FIG.1. Pathologies of extant argonaut egg cases. *1, Argonauta argo* LINNAEUS, 1758 in 1758–1759, Bavarian State collection, SNSB BSPG 2014 XXI 88001, injured shell margin repaired, Phillipines (new); *2, Argonauta hians* LIGHTFOOT, 1786, collection of Yasunari Shigeta, Tokyo, showing abnormally grown initial part, Philippines; scale bars, 10 mm (Keupp, 2012, fig. 443).

are sculptured and mounted approximately rectangular to the pathologic initial part. Broken and repaired shells were also reported by HOYLE (1886), SMITH (1903), BOLETZKY (1983), TREGO (1993), and FINN (2018). The last author, in a recent review, recognized over 50 species based on shell morphology. FINN (2018) proposed that ecological, biological, or traumatic events considerably affect shell growth and morphology, sometimes resulting in shell patterns typical for a different species, while genetic analyses recognize only four valid species. In contrast to conchiferan molluscs, shell-less argonauts are capable of substituting their (brood) shell (HOLDER, 1909a, 1909b; ALLISTON, 1983).

SEPIIDA GRAY, 1849

Basically, three causes of growth anomalies of mineralized hard parts (e.g, cuttlebone, statoliths) can be recognized:

1) Injuries, often triggered by sublethal predator attacks (RUGGIERO, 1980; BATTIATO, 1983; BELLO & PAPARELLA, 2002, 2003; KEUPP, 2012). Ventro-dorsal bite attacks often puncture and/or fracture the chambered part of the cuttlebone (Fig. 2.1–2.2). The healing process of this injury may result in a variety of phenomena. Fractures of the dorsal shield are provisionally repaired by deposition of organic cement, which may induce more or less uncontrolled mineralized proliferations. During this regeneration process, septa become crowded through growth retardation (BELLO & PAPARELLA, 2003). On the one hand, cicatrization may generate kinks and, in post-traumatic growth periods, longitudinal furrows in the chambered part (WIEDMANN & BOLETZKY, 1982), or on the other hand, a temporary change of the cuttlebone growth direction (BOLETZKY & OVERATH 1991) (Fig. 2.3).

2) Independent from preceding injuries of the cuttlebone, tumorigenic developments of the associated mantle tissue may likewise produce longitudinal furrows similar to those caused by shell repairs (BOLETZKY, personal communication) (Fig. 2.4).

3) Metabolic disturbances by environmental factors (BOLETZKY & OVERATH,

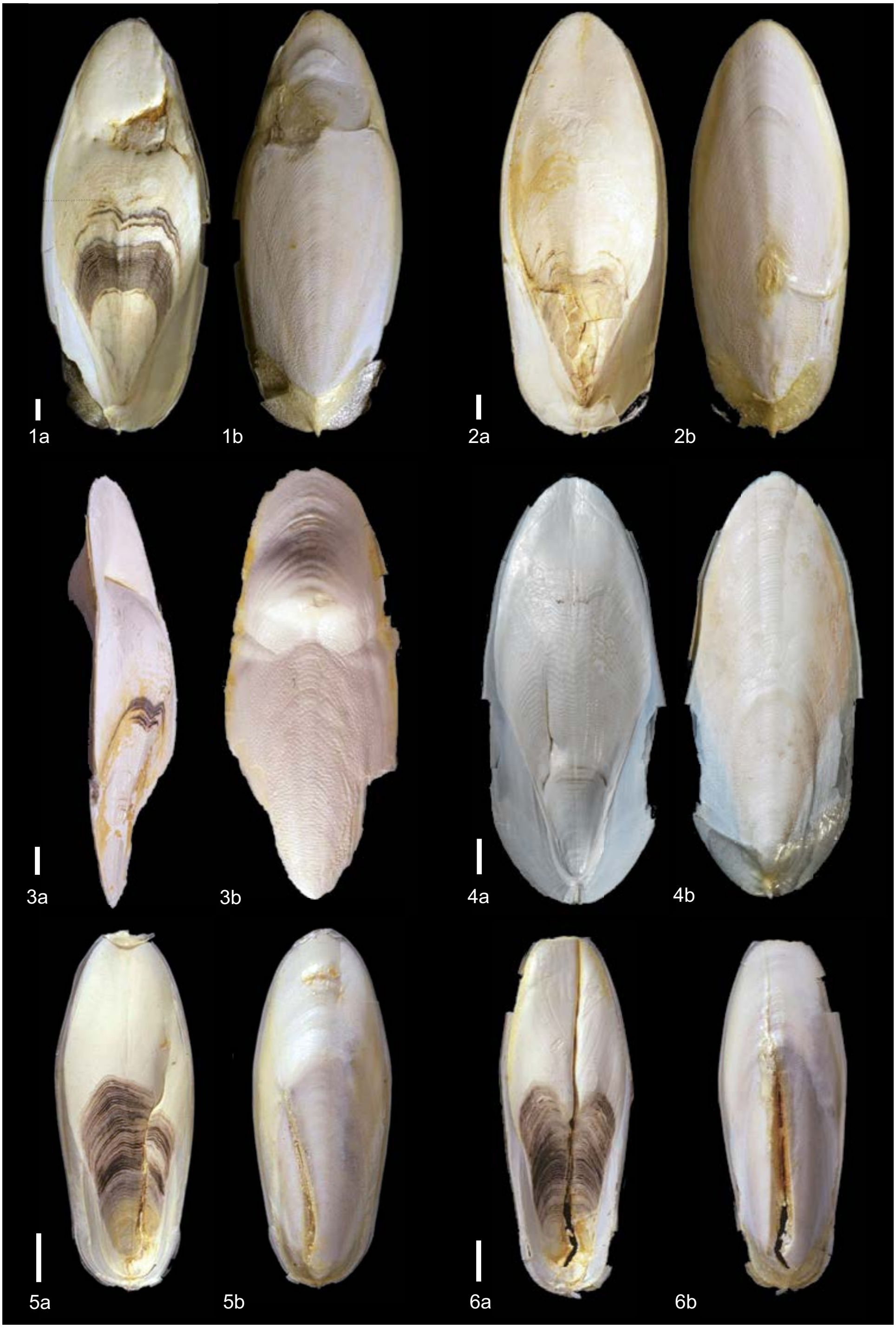

FIG. 2. *(For explanation, see facing page).*

1991; Maneja, Piatkowski, & Melzner, 2011a, 2011b). Distinct evidence of environmental disturbances, such as ocean acidification of hard parts exclusively comes from experiments with reared cuttlefishes (Gutowska, Pörtner, & Melzner, 2008; Gutowska & Melzner, 2009; Gutowska & others, 2010; Hu, 2016; Sykes & others, 2019). Boletzky and Overath (1991) have shown that changes in water chemistry causes significant mineralization problems of a whole population of *Sepia officinalis* Linneaus, 1758 in 1758–1759. In juveniles, this problem becomes particularly evident through densely packed organic-rich septa, and more dramatically, through longitudinally ruptured cuttlebones (Fig. 2.5–2.6). The presence of organic repair cements show that animals have survived ruptured cuttlebones at least for some time. Similarly, aragonitic statoliths respond to experimental hyperacidification with malformations (Maneja, Piatkowski, & Melzner, 2011a, 2011b) (Fig. 3). Incorporation of organic-rich and densely packed septa visible as dark lamella (Boletzky & Overath, 1991) point to incomplete mineralization processes, which may also occur as a consequence of environmental metabolic disorders (Fig. 2.1a).

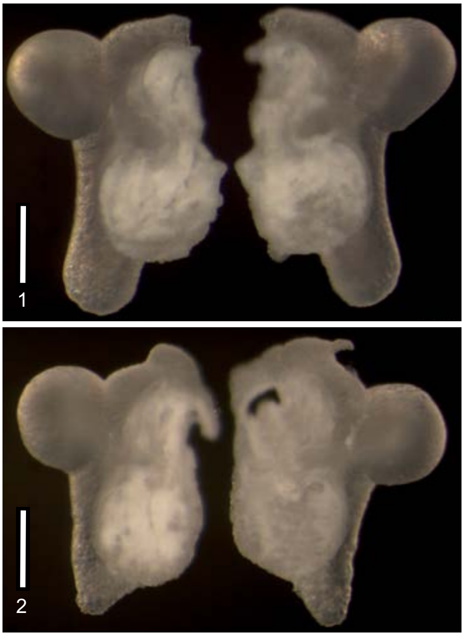

Fig. 3. Pathology of sepiid statoliths (*Sepia officinalis* Linneaus 1758 in 1758–1759). *1,* reared under normal conditions (380 ppm CO_2); *2,* reared under hyperacidic conditions (4000 ppm CO_2); scale bars, 200 µm (Keupp 2012, fig. 445).

SPIRULIDA HAECKEL, 1896

To date, only two descriptions of pathologic shells of the meso-pelagic rams horn squid *Spirula spirula* Linneaus, 1758 in 1758–1759 exist (Keupp, 2012; Hoffmann & others, 2018b). Anomalies of the spirulid shell include:

1) Regenerated injuries putatively after predator attacks—they may occur in individual chambers or may induce irregularly thickened precipitations of carbonate in the apertural region (Hoffmann & others, 2018b) (Fig. 4.1).

2) Infestation of parasites (?trematodes) and subsequent development of blisters (Keupp, 2012; Hoffmann & others, 2018b) (Fig. 4.2).

3) Endogenic early ontogenetic disturbances exemplified by degenerated initial chambers (Keupp, 2012) (Fig. 4.3).

4) Abnormal dorsal mantle attachment scars on the inner shell surface. Originally rectangular insertions detach, turn about 20° and reattach, resulting in an unusual pentagonal scar outline (Keupp, 2012) (Fig. 4.4).

Fig. 2. Pathologies of extant sepiid cuttlebones, ventral views (*a*), dorsal views (*b*). *1, Sepia officinalis* Linnaeus, 1758 in 1758–1759, SNSB BSPG 2014 XXI 88010, repaired injuries caused by predator attacks, ?Mediterranean Sea (Keupp, 2012, fig. 418, left); *2, Sepia officinalis*, SNSB BSPG 2014 XXI 88013, ventrolateral aspect, repaired injuries caused by predator attacks, ?Mediterranean Sea (Keupp, 2012, fig. 420, left); *3, Sepia officinalis*, SNSB BSPG 2014 XXI 88018, growth anomaly, Mediterranean Sea (Keupp, 2012, fig. 423); *4, Sepia officinalis*, SNSB BSPG 2014 XXI 88017, appearance of a dark conchiolin-rich septum marks a growth disturbance, Mediterranean Sea (Keupp, 2012, fig. 426); *5–6, Sepia officinalis*, SNSB BSPG 2014 XXI 88047, 88048, longitudinally disrupted (aquarium reared) provisionally repaired, scale bars, 10 mm (Keupp, 2012, fig. 427).

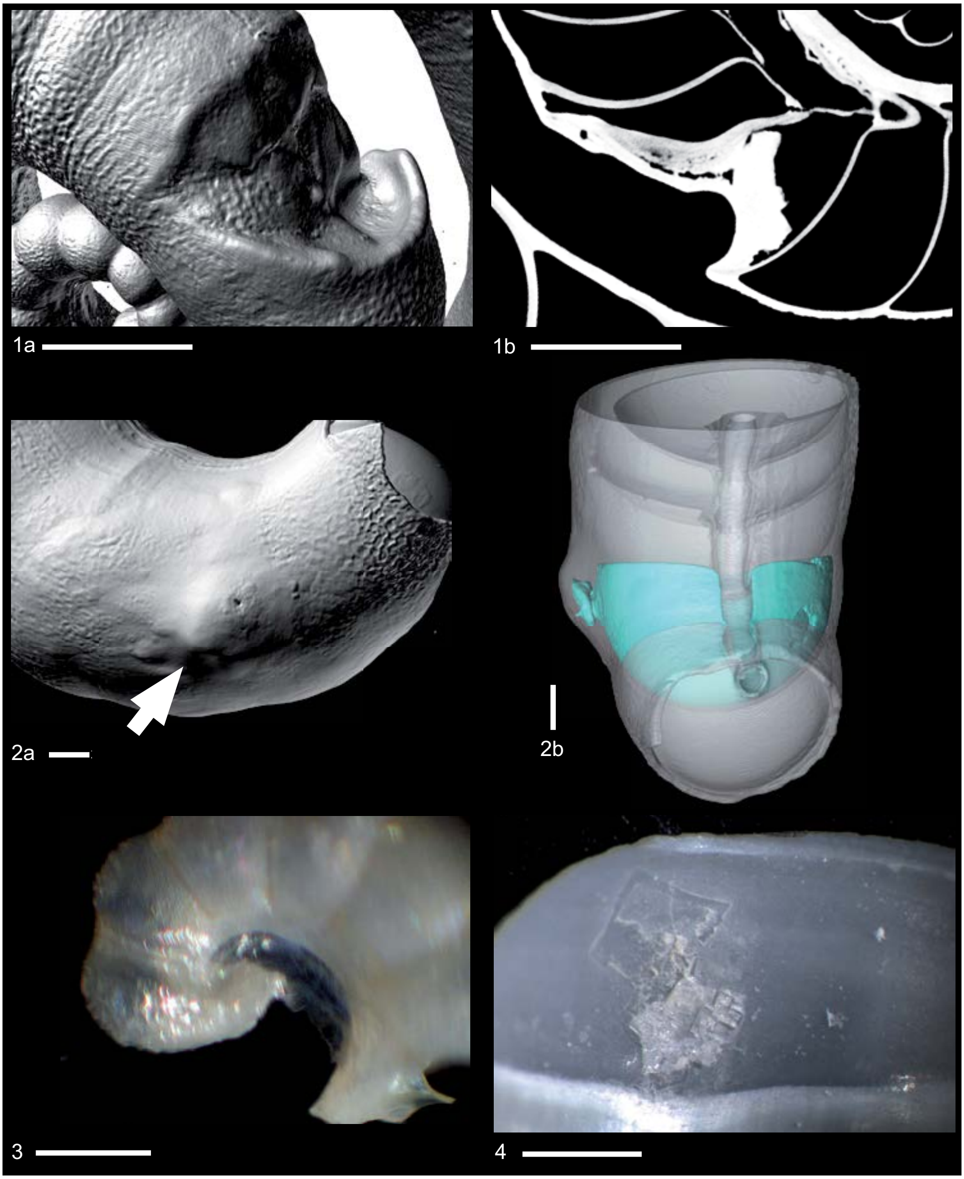

FIG. 4. Pathology of extant spirulid shells (*Spirula spirula* LINNEAUS, 1758 in 1758–1759). *1a–b,* Ruhr-University Bochum, RUB-Pal 11250, specimen with crushed chamber 15, which is significantly reduced in whorl height, CT-based surface rendering image and remnants of shell material in the chamber (*a*); CT-based orthoslice image (*b*); Fuerteventura, Canary Islands; scale bars, 1 mm (Hoffmann & others, 2018b, fig. 3E–F); *2,a–b,* SNSB BSPG 2014 XXI 88005, specimen with a blister (*a*), CT-based surface rendering image, *arrow* points toward the affected surface area, note the vanished surface crenulation, translucent shell with the connecting strand in the middle (siphuncle) and the chamber with blister in blue-green; CT-based volume rendering (*b*); Gran Canaria, Canary Islands; scale bars, 1 mm (Hoffmann & others, 2018b, fig. 4D, K); *3,* SNSB BSPG 2014 XXI 88064, abnormal protoconch, Canary Islands; scale bar, 0.5 mm (Keupp, 2012, fig. 433 left); *4,* SNSB BSPG 2014 XXI 88065, specimen with dislocated and slightly rotated dorsal attachment scar, Mozambique, scale bar, 1 mm (Keupp, 2012, fig. 437 right).

PATHOLOGIES IN FOSSIL COLEOIDS

As far as we know, paleopathologies of the mineralized or chitinous internal coleoid skeleton were described for the following groups: a) Hematitida, b) Aulacoceratida, c) Belemnitida, and d) Octobrachia. Argonauts, sepiids, and spirulids with evidence of growth anomalies are thus far unknown from the fossil record.

HEMATITIDA DOGUZHAEVA, MAPES, & MUTVEI, 2002 (CARBONIFEROUS)

Hematites barbarae Flower & Gordon, 1959 from the Lower Carboniferous (Mississippian) represents the oldest coleoid to date (Gustomesov, 1976; Doguzhaeva, Mapes, & Mutvei, 2010). As far as we are aware of, no true or regenerated injury or paleopathology have been described for this group. Most specimens, however, show a truncation already described by Flower and Gordon (1959). That *syn vivo* truncation only affects the protoconch (initial chamber) and the first few chambers of the phragmocone. The space that contained the phragmocone parts was filled with rostrum material after the truncation took place. The rostrum itself seems not to be involved in the truncation process. Because the truncation occurs regularly, a primarily less mineralized embryonic shell enhancing the truncation process seems more likely to explain that phenomenon instead of assuming a pathology (Fig. 5.1) (Doguzhaeva, Mapes, & Mutvei, 2002; Keupp, 2012).

AULACOCERATIDA STOLLEY, 1919 (PERMIAN–LOWER JURASSIC)

Keupp and Fuchs (2014) regarded the taxon Aulacoceratida as paraphyletic, based on the observation of significant differences in the formation and regeneration of the ribbed rostra of the Aulacoceratidae Mojsisovics, 1882 and Dictyoconitidae Gustomesov, 1978 compared to the Xiphoteuthidae Bather in Blake, 1892 with a smooth rostrum surface. Both types of rostra (smooth and ribbed) are aragonitic and show healed injuries most likely due to predator attacks. For the first time, Keupp (2012) described healed injuries for the Upper Triassic *Aulacoceras sulcatum* Hauer, 1860 found in Timor (Fig. 5.2–5.4). Here, the longitudinal ribs are composed of radial segments. Thickening of the segments during growth takes place by a centripetal elongation of each segment. Accordingly, bite traces of a juvenile rostrum of *Aulacoceras* Hauer, 1860, without significant damage of the shell secreting mantle epithelia, remain visible on the adult rostrum surface (Fig. 5.4). In cases in which the mantle epithelium is significantly affected, problems in the symmetric formation of the ribs may occur or the ribs completely disappear. Instead of ribs, irregular grainy mineralization takes place (Fig. 5.3).

The smooth Xiphoteuthidae rostra grow thicker by a successive, concentric addition of layers, analog to the calcitic belemnite rostra. Accordingly, growth anomalies during early ontogenetic stages will be leveled out during growth. Mojsisovics (1871) reported a pathological specimen of *Atractites* Gümbel, 1861 from Alpine Lower Jurassic deposits. The juvenile part of the rostrum was broken, but all parts remained in the mantle sac. During the post-traumatic healing process, a newly secreted rostrum layer formed a knee-shaped rostrum. More than 100 years later, Keupp (2012) reported a similar case for *Atractites lanceolatus* Bülow, 1915 from the Ladinian (Upper Triassic) of Timor (Fig. 5.5). A small hole, about 4 mm in diameter, with rounded ridges was reported by Keupp (2012; (Fig. 5.6) from a Hettangian *Atractites alpinus* Gümbel, 1861 from Timor. The presence of a backward-oriented effluence channel potentially indicates an inflammation of the mantle sac epithelium with ulceration after a puncture injury. The potential of a parasite infestation is rejected, based on the lack of a blister-like

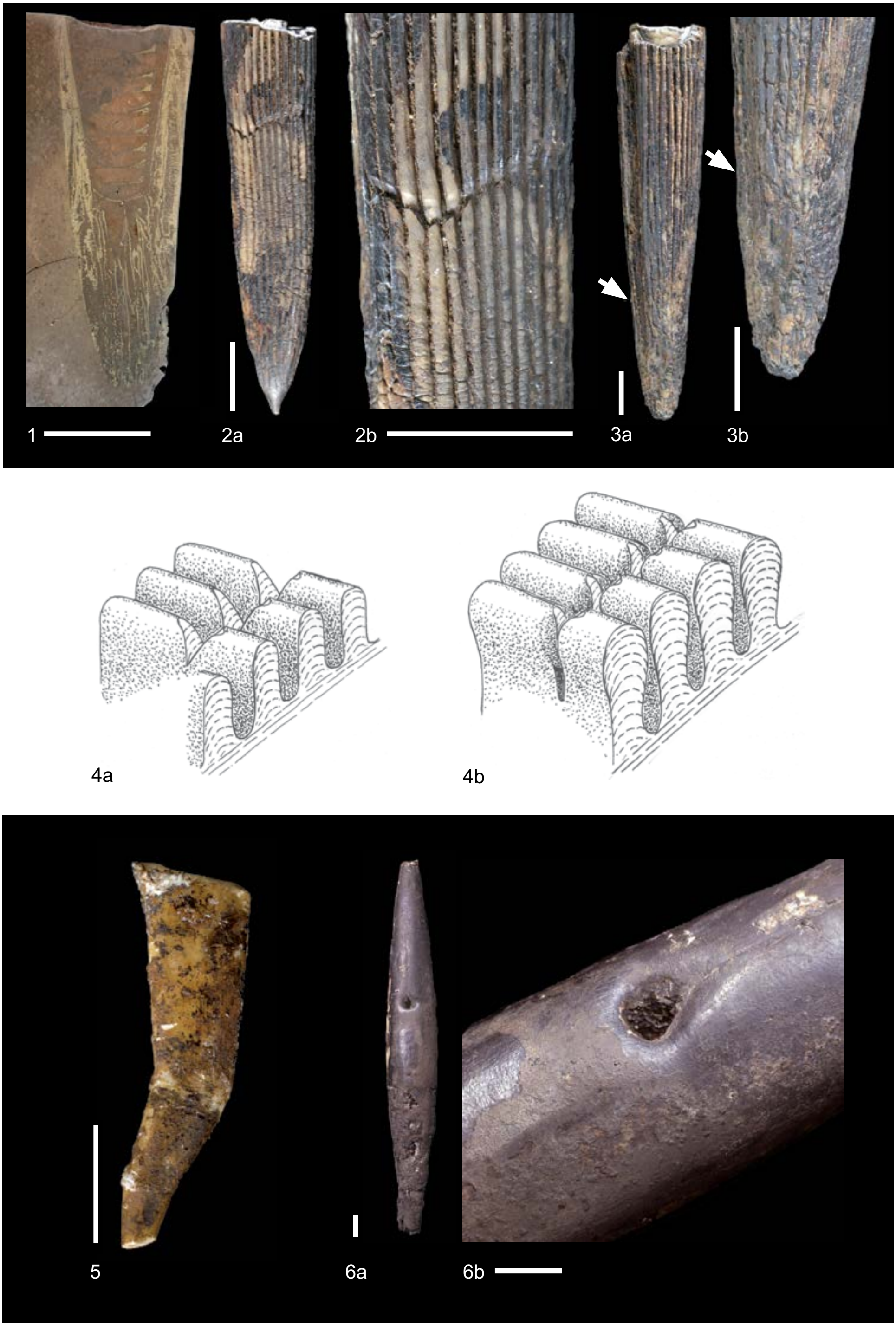

FIG. 5. *(For explanation, see facing page).*

structure, which would characterize the typical host reaction to such an infestation.

BELEMNITIDA ZITTEL, 1895 (UPPER TRIASSIC–CRETACEOUS)

For the low-magnesium calcite rostra of belemnites, a variety of anomalies were reported. The majority of these anomalies result from mechanical injuries, and less so due to parasitic infestations. Early descriptions, e.g., ABEL (1916), DAQUÉ (1921), TASNADI-KUBASCA (1962), and RICHTER (1993), argued that broken rostra are due to mechanical stress induced during active digging in the sediment or due to colliding with animals during fast backward swimming. SCHWEGLER (1939) was the first to discuss predator attacks instead of purely mechanic reasons for the breakage. Following his lines of arguments, we can compare the fractures of belemnite rostra with the often described injuries of the sepiid cuttlebone (see RUGGIERO, 1980; BATTIATO, 1983; KEUPP, 2012). The nektonic lifestyle of belemnites and the counterweight function of the rostrum that allows a horizontal swimming position make injuries due to digging behavior highly unlikely (see JENNY & others, 2019). Further, examples of prod trace-related injuries are rare. KEUPP (2002, 2012) introduced an example of a juvenile rostrum of *Belemnitella* D'ORBIGNY, 1840 with a broad, shallow, slightly curved longitudinal furrow beginning from the apex. The morphology of this unique furrow suggests that due to a strong kick *syn vivo* against the apex (rostrum tip), a long chip of rostrum material was separated from the main part of the rostrum. The originally sharp ridges became rounded during the regenerative reaction of the animal secreting additional material. Follow the suggestion of VALLON, RINDSBERG, and MARTIN (2015), we herein restrict the use of the term mark to physical (abiogenic) sedimentary structures, e.g., load casts or flute marks but not bite marks or scratch marks. Moreover, the term trace is defined as a morphologically recurrent structure resulting from the life activity of organisms modifying the substrate (BERTLING & others 2006). Accordingly, with the use of bite trace and prod trace, we infer the biogenic origin of these structures.

The deposition of concentric growth layers in belemnites, analog to the aragonitic structures in Xiphoteuthididae, results in a successive attenuation of the primary morphology of the injury due to the deposition of post-traumatic growth layers. In addition to invasive methods (polished section, thin section), non-invasive methods (CT, MRT) were recently applied for etiological analyses (MIETCHEN & others, 2005; HOFFMANN & others, 2018a).

During the regeneration process of unsuccessful predator attacks or putative parasite infestations, recurrent patterns (symptoms) in different taxa were observed. KEUPP (2012), in the style of the normed anomalies for ectocochleate cephalopods (nautiloids, ammonoids) of HÖLDER (1956), introduced *forma aegra* types for such symptoms that could be classified in an open nomenclature. Depending on the intensity of the injury, different *forma aegra* types in different combinations may occur during the regeneration process (e.g., KEUPP, 2016). Short descriptions of the *forma aegra* types developed for belemnite rostra are provided below.

Fig. 5. Pathologies of hematitid (*1*) and aulacoceratid (*2–6*) rostra. *1, Hematites barbarae* FLOWER & GORDON, 1959, longitudinally sectioned specimen with truncated apical part of the phragmocone, lower Serpukhovian, Chainman Shale, USA, scale bar 10 mm (new, photo, Royal Mapes); *2a–b, Aulacoceras sulcatum* HAUER,1860, SNSB BSPG 2014 XXI 83420, specimen overview (*a*) and close-up (*b*) with regenerated rostrum; Norian, Timor, scale bars, 1 mm (Keupp & Fuchs, 2014, fig. 2d–e); *3a–b, Aulacoceras sulcatum*, SNSB BSPG 2014 XXI 83419, specimen overview (*a*) and close-up (*b*) with degenerated ribs (indicated by *arrows*), Norian, Timor, scale bars, 1 mm (Keupp, 2012, fig. 373 right); *4a–b,* schematic regeneration mechanisms of the ribbed rostrum, traumatic stage (*a*), and later regenerated stage (*b*); *5, Atractites lanceolatus* BÜLOW, 1915, SNSB BSPG 2014 XXI 83262, specimen with regenerated fracture, Ladinian, Timor, scale bar, 1 mm (Keupp, 2012, fig. 372b); *6a–b, Atractites alpinus* (GÜMBEL, 1861), SNSB BSPG 2014 XXI 83263, specimen overview (*a*) and close-up (*b*) with partially regenerated bite trace, Ladinian, Timor, scale bars, 1 mm (Keupp, 2012, fig. 374).

forma aegra angulata (Fig. 6.1)—characterized by multiple rostrum fractures in which the dislocated rostrum fragments are covered by post-traumatic growth layers. Depending on size and position of the fragments within the mantle sac, bends of variable angles within a plane, or screw-like in different planes, result. Such characteristic fractures have been described by a number of authors (e.g., Duval-Jouve, 1841; Kabanov, 1967; Doyle, 1990; Kraus, 2000; Keupp, 2002, 2012; Mietchen & others, 2005; Hüne & Hüne, 2008). The phenomenon also includes rostra with fragments of a crushed rostrum being oriented sub-parallel to each other (see Moosleitner, 2012; Keupp, 2012, fig. 397). In at least one rostrum known thus far, this resulted in a reversal of the growth direction of the rostrum towards the head of the animal.

forma aegra anomalosulcata (Fig. 6.2)—presumably forms due to proliferating scar tissue of the mantle sac epithelium. The scar tissue forms ridges made of organic material that in turn result in furrows on the rostrum surface oriented perpendicular to the regular longitudinal furrows.

forma aegra bullata (Fig. 6.3)—enclosing a hollow space, possibly indicating the earlier presence of an endoparasite. The locally proliferating mineralization of the rostrum can lead, in rare cases, to the formation of a second rostrum paralleling the primary rostrum (Keupp 2012, fig. 405; Hoffmann & others 2018a).

forma aegra clavata (Fig. 6.4)—more or less club-shaped rostra that are thicker and shorter compared to normal forms. Such forms are the result of broken juvenile rostra. Depending on when the fracture occurred and its severity, this syndrome can range from slightly to heavily deformed rostra. Often the earliest parts of the phragmocone, including the initial chamber, are involved (Keupp, 2012, top of fig. 381). Extreme shortenings of the rostrum results in a more drop-shaped morphology (Kabanov, 1967; Keupp, 2012).

forma aegra collata (Fig. 6.5)—flap-like outgrowth at the subapical rostrum area without injury. The symptom is reported from a variety of Jurassic and Cretaceous belemnites and possibly resulted from a parasitic infestation (Keupp, 2012). The infestation causes the formation of a collar (Latin: *colla*) which is regarded as an effluence channel and potentially indicates an inflammation of the mantle sac epithelium.

forma aegra dissulcata (Fig. 6.6)—perturbations of the course of ventral, longitudinal furrows of the rostrum. The formation of such furrows is presumably strongly linked with the position of the central blood vessel system (Stevens, 1965). Accordingly, S-shaped or laterally displaced furrows (Kabanov, 1967; Keupp, 2012) indicate temporary dislocations of the soft body. These dislocations may be caused by traumatic events, such as a predator attack or may be due to an intrinsic disturbance.

Fig. 6. Pathologies of belemnitid rostra and their symptoms defined as *forma aegra* (*f.a.*) types. *1, Hibolithes hastatus* (Montfort, 1808), SNSB BSPG 2014 XXI 83117, Oxfordian, Germany (Keupp, 2012, fig. 395.4); *2, Hibolithes jaculoides* (Swinnerton, 1937), SNSB BSPG 2014 XXI 8364, Upper Hauterivian, northern Germany (Keupp, 2012, fig. 401 left); *3a–b, Neoclavibelus subclavatus* (Voltz, 1830), SNSB BSPG 2014 XXI 83264, overview (*a*) and MR image (*b*) Upper Toarcian, Bavaria, Germany (Keupp, 2012, fig. 404); *4, ?Belemnitella* sp., SNSB BSPG 2014 XXI 83204, Campanian, northern Germany (Keupp, 2012, fig. 391); *5a–b, Belemnellocamax mamillatum* (Nilsson, 1826), SNSB BSPG 2014 XXI 8392, lateral view (*a*) and apical view (*b*), Lower Campanian, Ignaberga, Sweden (Keupp, 2012, fig. 403); *6,* juvenile *Hibolithes* sp., SNSB BSPG 2014 XXI 83280, Hauterivian, Provence, France (Keupp, 2012, fig. 406); *7, Cylindroteuthis spicularis* (Phillips, 1865), SNSB BSPG SHK 2014 XXI 83064, Lower Oxfordian, near Moscow, Russia (Keupp, 2012, fig. 382); *8, ?Hibolithes* sp., SNSB BSPG 2014 XXI 83383, Lower Oxfordian, near Krakow, Poland (Keupp, 2012, fig. 392); *9, Belemnitella* sp., SNSB BSPG 2014 XXI 83175, Upper Campanian, northern Germany (Keupp, 2012, fig. 398); *10a–b, Belemnitella mucronata* (Schlotheim, 1813), SNSB BSPG 2014 XXI 8391, lateral view (*a*) and apical view (*b*), Campanian, northern Germany (Keupp, 2012, fig. 402); *11, Pachyteuthis excentrica* (Young & Bird, 1822), SNSB BSPG SHK 2014 XXI 8374, Lower Callovian, near Kursk, Russia; scale bars, 10 mm (Keupp, 2012, fig. 388).

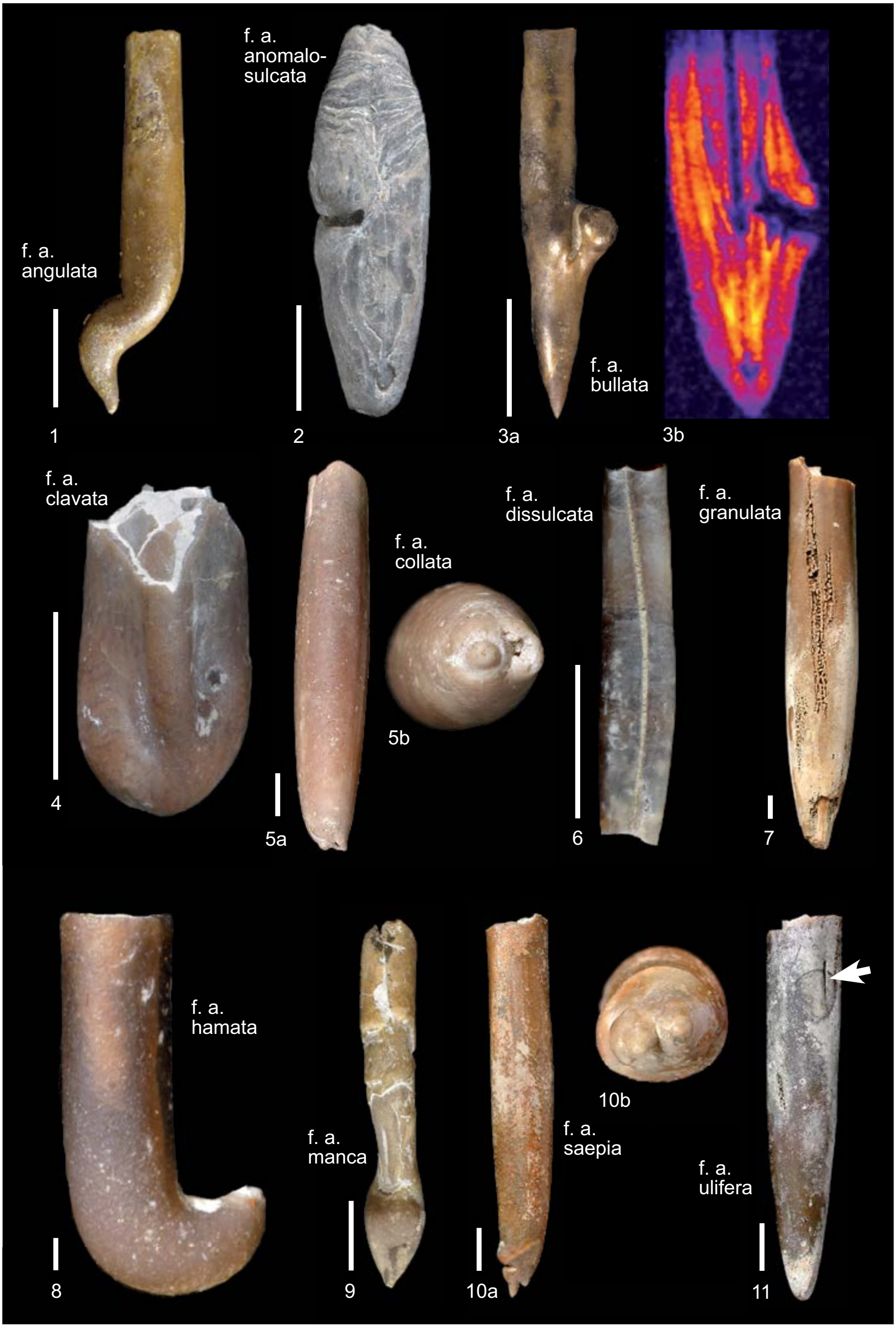

FIG. 6. *(For explanation, see facing page).*

forma aegra granulata (Fig. 6.7)—injured mantle epithelium with a limited ability of growth layer secretion, the causes of which can be similar to those of *forma aegra manca* (see below). Although injured and restricted in its function, in these cases, the mantle is able to secrete calcite grains enriched in organic matter (Keupp, 2012, fig. 382). Those irregular calcite deposits result in a rough, granular rostrum surface. Isolated fragments of the injured mantle epithelium can form irregular proliferating spherulithic aggregates (Keupp, 2012, fig. 384). In rare cases, these isolated mantle epithelium could form free pearls—specifically, when the epithelium forms a closed shell sac-like structure that could survive for a limited time in the nutritive body fluid

forma aegra hamata (Fig. 6.8)—hook-shaped rostra, as reported by Blainville (1827), and is often the result of rostrum fractures during early ontogenetic stages. Parts of the broken rostrum become dislocated and post-traumatic growth is more to one side than to the other, which results in a change of growth direction (Duval-Jouve, 1841; Radwanska & Radwanski, 2004; Moosleitner, 2006; Keupp, 2012). In cases in which the rostrum becomes significantly shorter, a transitional form between *forma aegra hamata* and *forma aegra clavata* exists (Keupp, 2012).

forma aegra manca (Fig. 6.9)—mechanical injury of the mantle sac epithelium which leads to a partial lack of growth layers. This is clearly related to the disabled secretion function of the injured epithelium. The symptom is often observed at the apical area of the rostrum. There, the apex (tip of the rostrum) is often incompletely developed, with juvenile, pre-traumatic parts forming the apex. The rostrum may be thinner in the area where the lateral epithelium is injured, thus becoming scepter-shaped (Keupp, 2012).

forma aegra saepia (Fig. 6.10)—duplication or multiplication (up to five known thus far) of the rostral tip (e.g., Finzel, 1963; Schmid, 1963; Miertzsch, 1964; Keupp, 2002, 2012; Mietchen & others, 2005; Hoffmann & Weissmüller, 2018). Keupp (2012) argued that due to trauma (mechanical injuries) or parasites, parts of the apex-forming mantle epithelium was separated into locally independent secretion centers that formed several apices.

forma aegra ulifera (Fig. 6.11)—more or less linear scratching traces on the surface of belemnite rostra that belong to the ichnocategory of bite traces. Most important is the distinction between postmortem (Riegraf, 1973; Hölder, 1973) and *syn vivo* bite traces. The latter should cause regenerative reactions of the bitten animal. Bite traces could also remain visible in the post-traumatic growth layers due to scarring, including the formation of scar tissue of the mantle sac epithelium.

PATHOLOGICAL ARM HOOKS

Belemnoid coleoids were equipped with a large number (about 400, 40 per arm) of so-called micro-hooks. In contrast, some groups—presumable the males—developed a pair of mega-hooks, sometimes called onychites (see Fuchs & Hoffmann, 2017). Because these chitinous hooks were only partly covered with tissue, mechanical damage of their distal parts could not regenerate. Hooks modified due to trauma are accordingly not expected. Kulicki and Szaniawski (1972), however, reported a malformed hook (*Longuncus longus* Kulicki & Szaniawski, 1972) from Tithonian deposits of Poland, presumable due to endogenic perturbations.

OCTOBRACHIA HAECKEL, 1866

The internal skeleton of Octobrachia, the so-called gladius, is analogous to the modern ten-armed teuthids. The Mesozoic gladii, found in Fossil-Lagerstätten such as the famous limestones in southern Germany or Lebanon, belong to octobrachiate coleoids (Fuchs, 2016). During the Jurassic and Cretaceous, these forms were widely distributed in the shelf areas of the oceans and were part of the food web. Specifically, Keupp

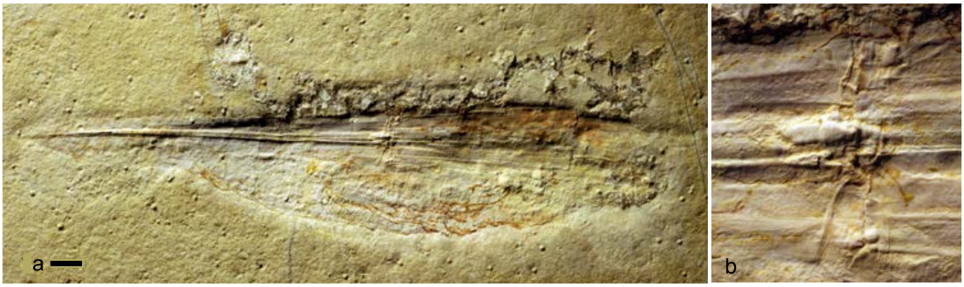

FIG. 7. Pathologies of octobrachian gladii. *Plesioteuthis prisca* (RÜPPELL, 1829), SNSB BSPG 2014 XXI 85026, overview (*a*) and close up (*b*) of the healed fracture, Tithonian, Altmühltal Formation, Solnhofen, Bavaria, Germany, scale bar, 10 mm (Keupp, 2012, fig. 449).

(2012) reported on stomach contents of predatory fishes (prionolepid teleosts) from the Cenomanian of Lebanon that contained complete gladii of *Rachiteuthis* FUCHS, 2006. Broken gladii of plesioteuthid coleoids were reported from the Upper Jurassic Solnhofen Limestones (Germany), suggesting that large predators caught their prey but did not completely digest it (KEUPP, 2012, fig. 447). In rare cases, coleoids survived the predator attack and could regenerate their gladius fractures, indicated by small ridges perpendicular to the length axis of the gladii (DIETL & SCHWEIGERT, 2001 for Upper Jurassic *Plesioteuthis* WAGNER, 1859 from the Nusplingen Limestones (Germany); KEUPP, 2012, for *Plesioteuthis* from Solnhofen (Fig. 7); and SCHWEIGERT & others, 2011 for *Trachyteuthis* MEYER, 1846).

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