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Article

Evidence for fish predation on a coleoid cephalopod from the Lower Jurassic Posidonia Shale of Germany

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With 4 figures

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Abstract: A specimen of the Early Jurassic actinopterygian fish *Pachycormus* sp. from the Lower Jurassic Posidonia Shale of Germany has a well preserved filling of the alimentary canal. The region interpreted as the stomach contains numerous hooklets that can be referred to the coleoid cephalopod *Phragmoteuthis* Mojsisovics, 1882. The presence of arm hooklets clearly demonstrates predation on coleoid cephalopods by actinopterygian fishes.

Key words: Taphonomy, Cephalopoda, Actinopterygia, predation, Jurassic, Germany.

1. Introduction

A specimen of the actinopterygian fish *Pachycormus* sp. (IGP 163/1881) in the collections of the Institute of Geology and Palaeontology, Faculty of Science, Charles University in Prague, is notable for the preservation of stomach contents in the lumen of the gut. Pachycomids were large to very large pelagic predators typified by fusiform bodies, a prominent rostrum, sickle-shaped pectoral fins and a deeply forked caudal fin. The group also includes some more elongate taxa including the giant filter feeder *Leedsichthys* (Martill, 1988); they were adapted for fast swimming (Webb 1984; Lombardo & Tintori 2005) and were among the top bony fish predators, together with some elasmobranches and marine reptiles. This study documents the preserved prey remains in specimen IGP 163/1881.

1.1. Palaeoecological setting

The Lower Jurassic (Toarcian) Posidonia Shale fauna is famous for the exceptional preservation of crinoids, crustaceans, cephalopods, fish, sharks, ichthyosaurs, crocodiles and other marine reptiles (Nudds & Selden 2008) and, as such, represents a marine fossil Konservat Lagerstätten.

2. Material and methods

The specimen described here is a single individual of *Pachycormus* sp. preserved in left lateral aspect on a slab of typical Posidonia Shale and has an estimated standard length of ca. 420 mm (Fig. 1a). The slab is enclosed in a wooden frame and is housed in the collection of the Institute of Geology and Palaeontology, Faculty of Science, Charles University

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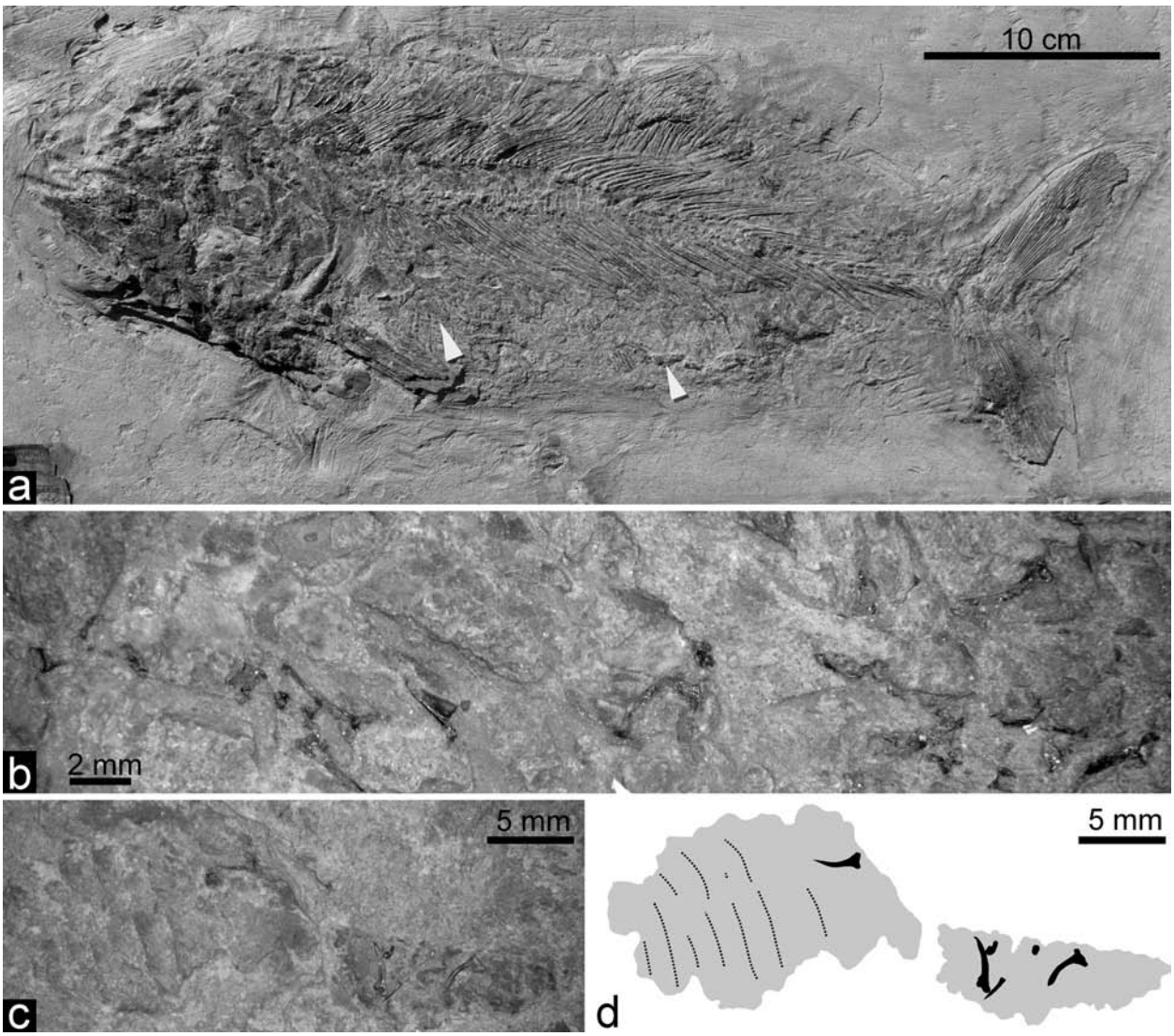

Fig. 1. a – Almost complete fish *Pachycormus* sp., specimen No. IGP 163/1881; arrows show clusters with preserved onychites. **b** – A close-up view of the cluster closely behind the head. **c** – A close-up view of the gut fills. **d** – An interpretation of (c).

in Prague, specimen number IGP 163/1881.The skeleton is articulated although parts of the dorsal and the pectoral fins and dorsal part of the skull are missing. The fossil was studied using a binocular microscope and photographed with a Panasonic DMC FZ-30 digital and microscope camera.

2.1. Preservation

The specimen is partly preserved as an external mould (these bones are probably on a missing counter slab) and partly as original bone (Fig. 1a). The specimen is pyritized in certain parts (skull, neural spines and in the caudal region). The body is huge. On the skull, it is possible to recognize a narrow lower jaw with a single row of uniform teeth, the branchiostegal rays (at least nine), the opercular area, the cleithra and the posterior part of the neurocranium. The anterodorsal part of the skull is incompletely preserved, being heavily crushed and partly mouldic. The pectoral girdle is preserved with the left pectoral fin articulated with the ventral part of the girdle. The fin is well preserved proximally but distally it is an external mould. Nevertheless, its scythe-like shape is clearly recognizable. Typical for Pachycormidae, the pelvic fins and their supportive skeleton are not developed. The dorsal fin commences in advance of the anal fin but it is incompletely preserved. The number of dorsal fin rays is at least

twelve. The anal fin is incompletely preserved, with just the supporting skeleton present. The fin rays in the fins are unsegmented, but bifurcate continuously becoming thinner distally. The notochordal canal is open. Numerous strong ribs are developed in the abdominal part of the body. In the caudal skeleton a fused, fan-like hypural plate in present the ventral portion, with four free hypurals in the dorsal part, and six epurals. In several areas the scales are preserved; these scaled areas are located behind the head, in the pectoral region and close to the tail.

Two clusters of blackish, dark, hook-like elements (see arrows in Fig. 1) are preserved in the abdominal cavity. The hooks are located inside of the fish, at the surface of the sediment which lies between the ribs of left and right side. The first cluster is largest with a length of ca. 20 mm and is preserved in the ventral portion, close to the skull, alongside the pectoral fin (Fig. 1b); it probably represents the stomach (or portion of the intestine that lie beside the stomach). The second, smaller cluster (the length about 13 mm) is preserved between the first cluster and the anal fin and is an elongate prominence (Fig. 1c). In front of the second cluster, a slightly elevated area with transverse imprints of striation (Fig. 1c, d) is preserved, probably representing part of an impression of the spiral valve.

Many well preserved chitinous hooklets are present especially in the stomach area. Although probably not all of them are exposed, their number exceeds 60 (at least 55 in the stomach area and 11 in the spiral valve area). Hooklet morphology is somewhat variable (see below and Fig. 2).

3. Interpretation and discussion

Palaeoecological trophic reconstructions are the terminal stages of studies of fossil ecosystems (e.g., Maisey 1994; Martill et al 1994; and others). The fragmentary character of information available (e.g., partial knowledge of soft tissues with possible functional morphological adaptations; incomplete list of members of a trophic net and others) makes such reconstructions encumbered by a large portion of inaccuracy. Such reconstructions are based on circumstantial evidence with different information levels. The most authentic data are called "frozen behavior" (Boucot 1990). Such significant features (e.g., prey specimens in predators' stomachs) are used for realistic reconstruction, but they are extremely rare. In many fossil assemblages, trophic relationships where supposed just on the basis of relative occurrences of the members of the assemblage in particular strata or surface slabs. In such cases, organisms inhabited the same living space, e.g., they where members of the same shoal (Viohl 1994). In such type of fossils the organism is interpreted to pertain preserved at a close distance or with intimated action. The last category is highly speculative, and all possible sources of information (e.g. taphonomy, sedimentology or functional anatomy) must be valorized before the final conclusions. Viohl (1994) supposed sharing of the same shoal for specimens which lie closely together and were supposedly killed by the same event.

Although in literature were previously briefly mentioned fish specimens with preserved remains of a cephalopod prey preserved *in situ* from the Jurassic (Berckhemer 1937; Carroll 1988; Böttcher 1989; Wild 1994; Etches & Clarke 2010), such specimens still represent unique palaeobiological documentations.

The location of the prey items is in agreement with location of the stomach in extant actinopterygians of similar body plan; and a majority of preserved prey remains studied within fossil fish predators is also located in this area (e.g. Maisey 1994; Wilby & Martill 1992; Přikryl & Novosad 2009). The second cluster is represented by gut fill preserved *in situ* within a distal part of the alimentary canal. The filling is in longitudinal form, probably emulating the shape and structure of the walls of the gut. Apart from the well preserved hooklets, the gut contains no other discernible remains.

Arm hooklets are typical for some Recent squids. In the Early Jurassic, only belemnoids – i.e., belemnites (Belemnitida Gray, 1849), phragmoteuthids (Phragmoteuthida Jeletzky, 1965) and belemnoteuthids (Belemnoteuthida *sensu* Donovan 1977 and Engeser & Reitner, 1981) had arms with hooks. In some belemnoteuthids (genus *Belemnotheutis* Pearce, 1842), also both the suckers and hooklets have been reported to be present in the arm (Donovan & Crane 1992; Fuchs et al. 2010). It is notable that the major diversification of belemnoteuthids started in the Middle Jurassic. The Early Jurassic taxa referred to Belemnoteuthida s.l. are poorly known and include the problematic genera *Chitinobelus* Fischer, 1981 and *Chondroteuthis* Bode, 1933, with imperfectly known arm crowns. Considering this, the hooklets recorded in *Pachycormus* probably do not belong to true belemnites (Belemnitida), but rather to phragmoteuthids (see below).

Belemnoid coleoid cephalopods possess usually ten similar arms-bearing hooklets (Riegraf 1996; Fuchs 2006; Doguzhaeva et al. 2007). A belemnoid arm hooklet consists of three basic parts – base, shaft and curved uncinus (see Kulicki & Szaniawski 1972;

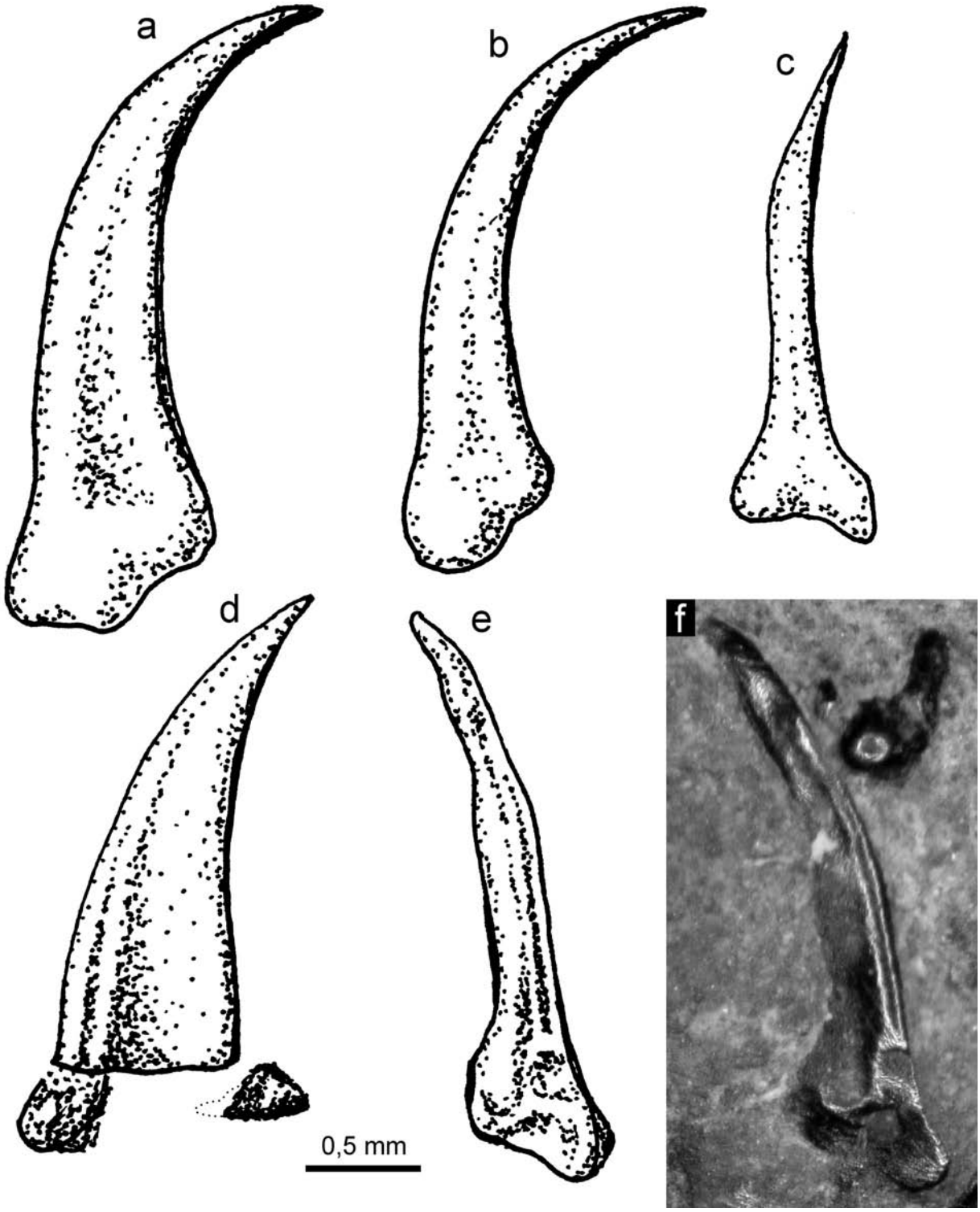

Fig. 2. Variability of onychites preserved within the alimentary canal of the *Pachycormus* sp.

Engeser 1987; Engeser & Clarke 1988), ranging in length from 1 mm to 5.8 mm (Donovan 2006). The hooklets are arranged in two parallel rows on the inner arm surface. According to Pollard (1968, based on Crick 1907: figured specimen of „*Belemnoteuthis*" *montefiorei* = *Phragmoteuthis montefiorei*), the number of hooks per arm varies with the length of the arm, but the average number appears to be about thirty (15 pairs). Donovan (2006) reported the number of 20-25 pairs of hooklets on each phragmoteuthid arm. However, more complete records from the Lower Jurassic of northern Italy (Garassino & Donovan 2000) show a larger number of hooks in this coleoid which exceed 31 pairs of between 1 mm to 4 mm in length (length of arms 50-70 mm).

The size and shape of hooks varies within one arm. Smaller hooks (1-1.5 mm) are usually developed in proximal and distal ends of the arms. Larger ones (2-4 mm) are typical for the middle part of the arm. The shape is also highly variable, e.g., relatively short straight spinose one with a marked base, longer slender form with a gentle to strong curve, laterally flattened. Belemnite hooks are characterized by a strongly curved uncinus (see Klug et al. 2010). Ends of the hooks are bent terminally, meeting the axis of the proximal part at an angle of 20°. In this respect, they are markedly different from the hooks of phragmoteuthids; these are much straighter due to the elongate shaft. In some phragmoteuthids (i.e., *Phragmoteuthis ticinensis* Rieber, 1970), the hooks are very similar to belemnitid hooks. In other species of *Phragmoteuthis*, more straight or stylet-like hooks can be observed. In the material studied, no typical belemnite hook with strongly curved uncinus has been recorded. Slightly curved hooks (Fig. 2) found in the *Pachycormus* stomach area are almost identical to those found in the middle to distal parts of an arm of common species of *Phragmoteuthis* (e.g. *Phragmoteuthis conocauda* Quenstedt, 1849).

In IGP 163/1881, the alimentary canal contains 1-3 mm-sized hooks from the proximal, middle and distal parts of the arms. Hook variability (Fig. 2) suggests ingestion of a complete arm(s). The length of the arms can be estimated at about 50-60 mm (see above), the total length of the belemnoid specimen did not exceed 20 cm. The number of hooks observed suggests feeding of at least two arms. Although some hooks are not visible, the number of swallowed belemnoid arms probably did not exceed three.

Belemnoid hooks, and belemnoid prey remains in general, were mainly recorded in the stomachs of marine reptiles (mainly ichthyosaurs) (e.g., Pollard 1968; Rieber 1970; Keller 1976; Massar & Young 2005; Delsate et al. 2008; Lomax 2010) and in non-spiral coprolites referred to ichthyosaurs (Garassino & Donovan 2000). Other marine predators reported are plesiosaurs (Wahl 1998). Predation on belemnoids by fishes has been reported by Berckhemer (1937), Riegraf & Reitner (1979: 300, however, without any reference to literature); Carroll (1988), Böttcher (1989), and Wild (1994).

The ichnologic point of view. According to Hunt et al. (1994), all fossil residues preserved *in situ* in the intestinal canal (gut) fall to the category of cololites (*syn*. coeloliths). As stated above, the studied fish specimen bears cololites at two locations: 1) a cololite with perfectly preserved belemnite hooks in the stomach area; 2) a roughly cylindrical cololite between the stomach and the anus with partly corroded hooks. In its shape and size, the second cololite resembles numerous finds interpreted (chiefly correctly) as coprolites, i.e., fossil feces. These were described from sediments of a broad range of ages, composition and environments, occurring outside fossil bodies. Herein, we suggest the term "pre-coprolite" for a cololite "just prepared" for extruding from the body. The typical feature of the pre-coprolite is finished morphology, i.e. the organization and formation of the undigested remains into the final coprolite form (in the qualitative and architectural sense). They still lie inside the alimentary canal, but, in fact, the digestive process was completely finished (Fig. 3). Presumably, these forms may be similar in size, shape, consistency and composition to "true coprolites" of the same animal. As shown by the described specimen, such subgroup of cololites may be clearly different to the cololites preserved in other parts of alimentary canal. Furthermore, the definition and study of pre-coprolites can offer a possibility to identify makers of free fecal pellets (i.e. coprolites).

We hope that the research of whole group of coprolites and cololites, which (after a relatively fruitful research in the 19th century; e.g. Buckland 1829) became the by far most understudied group of trace fossils (Hunt et al. 1994 and references therein), can be supported by the search for "pre-coprolites" in future.

Preservation. The hooks are quite well preserved in the anterior portion of the digestive canal; signs of biological digestion are observable at the shaft base in some specimens. The good condition of them suggests

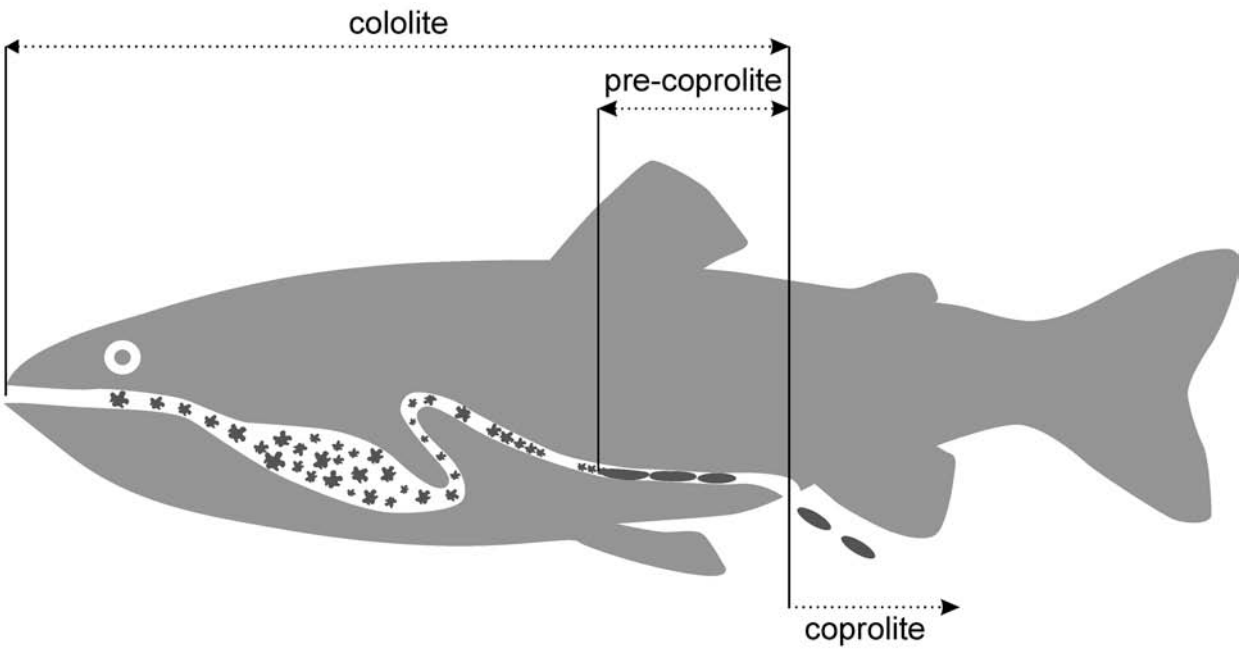

Fig. 3. The usage of the terms cololite, pre-coprolite, and coprolite.

freshness of the prey without long time of working of digestive juices. A different state of preservation was recorded inside the pre-coprolite. The hooks recorded in the pre-coprolite and in the spiral valve area show marked signs of digestion (Figs. 1c, d, 2e, f). These corroded hooks, which are generally resistant, suggest the presence of extraordinarily aggressive digestive juices in the stomach (but probably not in the gut).

Spiral valve imprint. The elevated area situated anteriorly from the cololite bears transversal striae, and may represent the imprint of a spiral valve into the gut contents. The imprint is short (cca 15 mm long) and shallow and it probably does not represent a complete section (in length nor diameter) of the gut with the valve. Seven imprints of spirals declined at an angle of about 60 degrees to the antero-posterior axis are preserved in external view (see also interpretative Fig. 1d) with each imprint representing one turn of the spiral. In modern fishes, spiral valves are restricted to elasmobranchs (Cailliet et al. 1986), lungfishes (e.g. Purkerson et al. 1975; Hassanpour & Joss 2009), *Acipenser* (Macallum 1886), *Polyodon* (Maroni et al. 2009), *Lepisosteus* (Macallum 1886), *Amia* (Macallum 1886; Hilton 1900) and *Latimeria* (Helfman et al. 1997). In fossil representatives, a spiral valve was present in some elasmobranchs (Williams 1972, figs. 4-5) and possibly in other groups, but indications are mainly indirect, having the character of coprolites (e.g. Broughton et al. 1978) or cololites (Williams 1972; Chron et al. 1978). The specimen described here thus represents the first possible evidence of the presence of a spiral valve in Pachycormidae. Another specimen recording the presence of the spiral valve in the pachycormid fishes is housed in the Museum Werkforum in Dotternhausen (illustrated in Jäger 2005, fig. 64). This local museum displays a specimen of *Saurostomus esocinus* Agassiz, 1833 (Fig. 4) with preserved filling of the digestive tract. In the terminal portion of the gut, a spiral valve is clearly distinguishable.

4. Conclusions

We present a new view on fish predation on the basis of uniquely preserved specimen of a fish and associated hooklets of a belemnoid, both recorded together *in situ*. Both pachycormid fishes (Bürgin 2000) and belemnoids (see above) were prey items of Mesozoic marine reptiles. This clearly documents the position of smaller belemnoids (i.e., phragmoteuthids) in the Early Jurassic trophic chain.

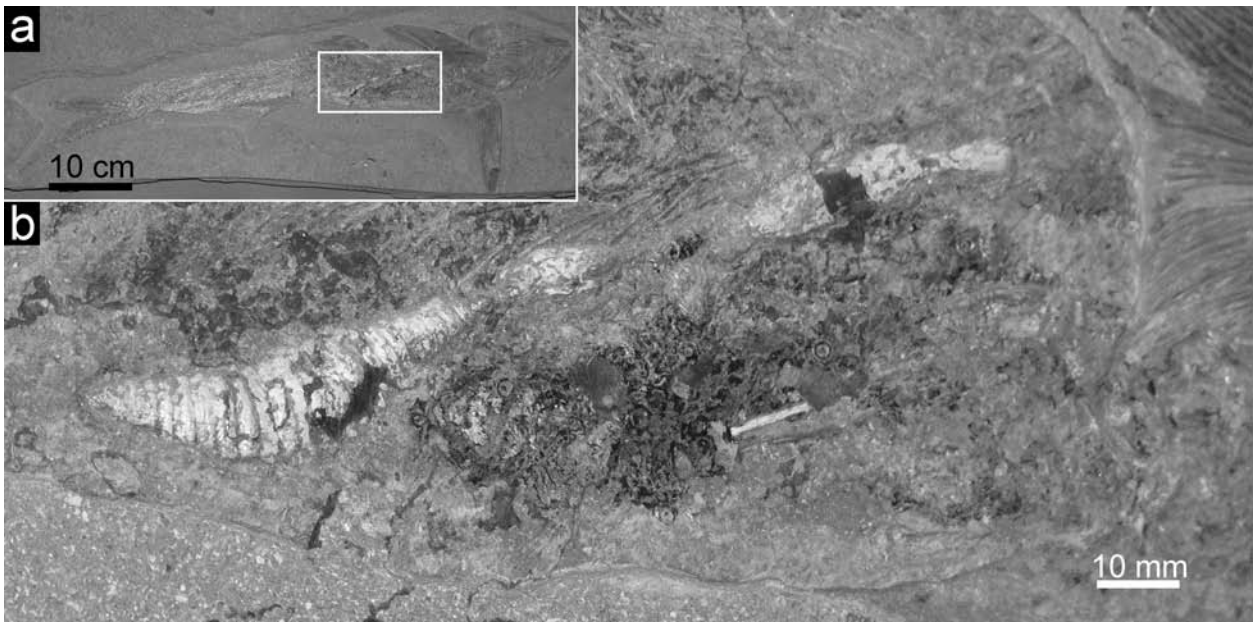

Fig. 4. *Saurostomus esocinus* Agassiz, 1833. Specimen housed in the Museum Werkforum at Dotternhausen, Germany (cement mill HOLCIM). The specimen is installed in the exposition, a catalogue number is unknown. **a** – Overall view. **b** – Detail of the white box in (a).

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