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Death by ammonite: fatal ingestion of an ammonoid shell by an Early Jurassic bony fish

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Abstract

A remarkable specimen of the actinopterygian fish *Pachycormus macropterus* from the Early Jurassic (Toarcian) Posidonienschiefer Formation of Germany exceptionally preserves an unusually large ammonite inside its gut. The ammonite was swallowed by the fish, likely by accident, and represents the first direct evidence for an actinopterygian fish consuming an ammonoid. Exceptional aragonite preservation of the conch retaining partial nacreous lustre, combined with only minor acid etching of the shell, strongly indicates that the ammonite was ingested immediately prior to and was directly responsible for the fish's death. The fish's stomach provided a microenvironment protecting the aragonite from chemical dissolution.

1. Introduction

Predator–prey interactions in the fossil record can offer unique and crucial insights into the ecology of extinct organisms and the trophic structure of their ancient ecosystems across deep time. Despite their overall abundance in the Jurassic, the role of ammonites as prey for vertebrate consumers is poorly documented and largely speculative. Although predation on ammonites by both vertebrate and invertebrate predators did occur (Lehman, 1976; Kase *et al.* 1988; Klompaker *et al.* 2009; Hoffman & Keup, 2015), identifying the perpetrator with certainty is problematical as usually only traces of damaged or fragmented conchs are preserved (Martill, 1990). Marine reptiles are often considered as potential ammonite predators (Kauffman & Kesling, 1960; Wetzel, 1960; Kauffman, 2004; Hoffman & Keup, 2015; Gale *et al.* 2017), although bony fishes are frequently overlooked in this role. Martill (1990) and Richter (2009) described bite traces indirectly attributed to durophagous actinopterygians on few Middle Jurassic ammonites from England and Germany. However, more direct evidence (e.g. ammonite remains inside a fish's gut contents) has yet to be described, shedding doubt over the trophic relationship between ammonites and actinopterygian fishes. A single hybodontiform shark tooth found in association with a 'punctured' ammonite from the Late Jurassic of France (Vullo, 2011) represents the only direct evidence for a chondrichthyan feeding on ammonites.

Pachycormidae is a diverse Mid- to Late Mesozoic lineage of stem-teleost fishes ranging in size from 0.3 to 15 m (Wenz, 1968; Martill, 1988; Liston, 2004; Friedman *et al.* 2010). Pachycormid diets and feeding strategies are poorly known: gut contents are known for few taxa and most of these observations are anecdotally based only on a single individual. Early Jurassic genera have been described as teuthophagous (Přikryl *et al.* 2012; Cooper & Maxwell, 2022) or consuming both soft-bodied coleoids and small actinopterygians (Aldinger, 1965; Cooper *et al.* 2022); gastric contents in Middle and Late Jurassic species consist exclusively of small teleosteans (Vetter, 1881; Viohl, 1990; Martill, 1991; Lambers, 1992; Liston, 2008; Maxwell *et al.* 2020). Ammonites were previously theorized to have contributed to the diets of some pachycormids, although no direct evidence has been published (Wild, 1994; Cooper & Maxwell, 2022). Here, we report a specimen of *Pachycormus macropterus* (de Blainville, 1818) from the Early Jurassic of Germany, representing the first direct evidence of an actinopterygian fish consuming a Mesozoic ammonite.

2. Materials and methods

Specimen SMNS 52472 was collected in 1977 from the Fischer Quarry in Zell unter Aichelberg, Germany (Fig. 1). It originates from the early Toarcian (Lower Jurassic) Posidonienschiefer Formation (top of bed number eII₄; *exaratum* Subzone; Riegraf *et al.* 1984) and is referred to the basal asthenocormine pachycormiform, *Pachycormus macropterus* (de Blainville, 1818; Lehman, 1949; Mainwaring, 1978; Cawley *et al.* 2018; Dobson, 2019; Cooper *et al.* 2022).

The specimen was prepared using the transfer method, whereby the original fossil has been embedded into a foreign slab of Posidonienschiefer matrix for improved stability. The skeleton is well-articulated and almost complete, with a total length of 850 mm (Fig. 2). Only the anal fin, pectoral fins and the rostrodermethmoid region of the skull are missing. A small wedge

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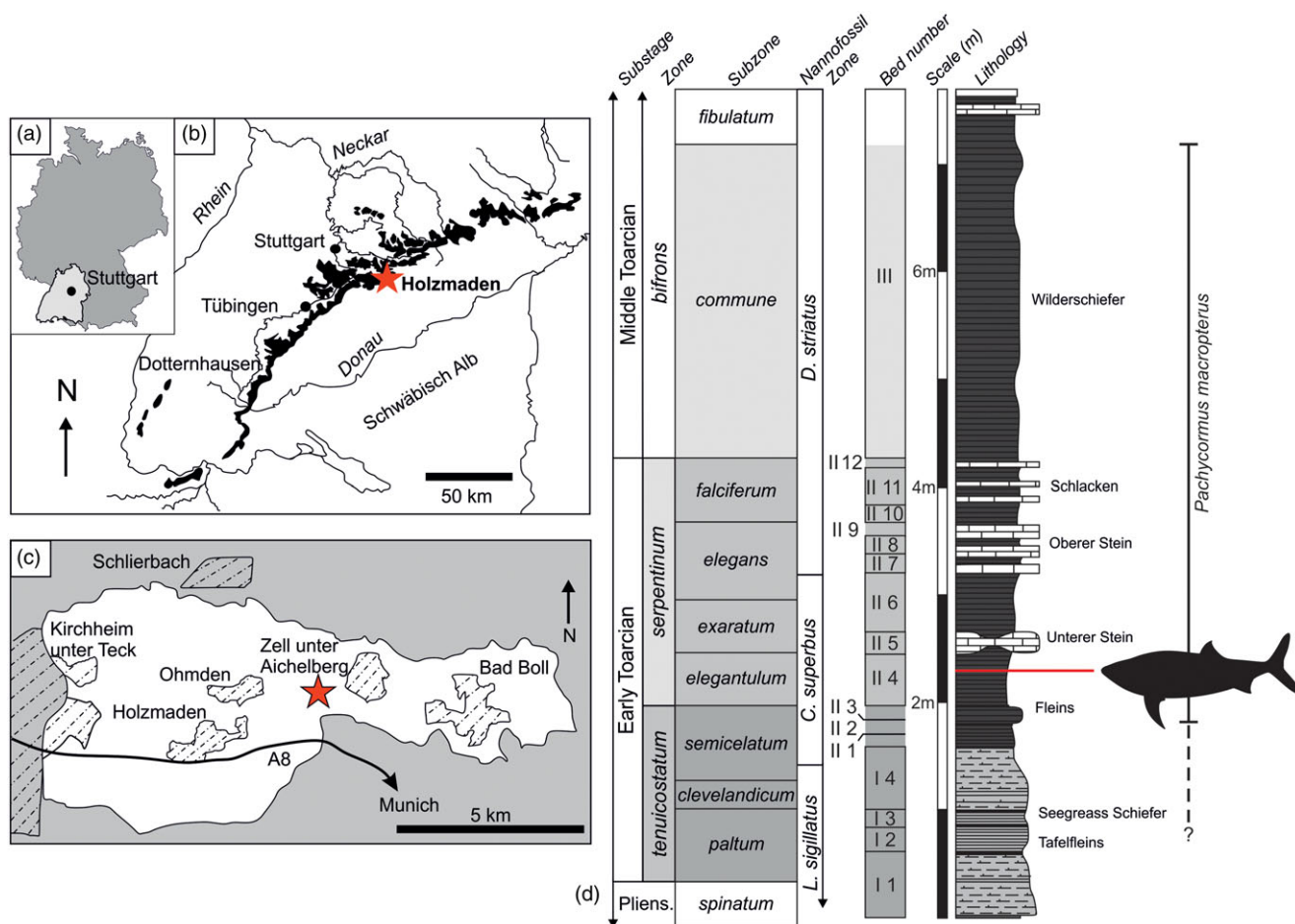


Figure 1. (Colour online) Locality map and simplified stratigraphic log of the Posidonienschiefer Formation at Holzmaden. (a) Map of Germany with the state of Baden-Württemberg highlighted. (b) Extent of Posidonienschiefer formation (Upper Lias) outcrops in Baden-Württemberg with the area of Holzmaden indicated by a star. (c) Simplified map of the Holzmaden area. A star indicates the collection locality of SMNS 52472. (d) Simplified stratigraphic log of the Posidonienschiefer Formation in the Holzmaden area. *Pachycormus macropterus* is distributed between beds ell₃ – ell₁₁ (*serpentinum* – *bifrons* Zones) with the collection horizon of SMNS 52472 indicated. Redrawn and modified from Cooper *et al.* (2022) with biostratigraphy based on Rieggraf *et al.* (1984) and Maxwell *et al.* (2022).

containing the posterior portion of the dorsal fin has been sculpted from plaster. The skull has been compacted dorsal-right laterally, with the skull roof and upper jaws exposed in dorsal view, the elements of the left side in external view and those of the right side in medial view or covered by the skull roof. The vertebral column and unpaired fins are exposed in left-lateral view.

The specimen was examined using a Leica light microscope and photographed with a Nikon Series DMC-FZ72 camera with compact 60X optical macro-lens. Measurements are defined based on Cooper and Maxwell (2022, suppl. fig. 1), and anatomical nomenclature and homologies for the pachycormiform skeleton follow Mainwaring (1978), Lambers (1992) and Dobson (2019). Parameters used to measure the ammonite shell in SMNS 52472 follow Bardin *et al.* (2015).

To assess the relationship between maximum prey size and maximum gape size, we estimated maximum gape size using articular width as a proxy (Mihalitsis & Bellwood, 2017). We divided the mandible length (45 mm) of an uncompacted specimen of *Pachycormus macropterus* (SMNS 4204) by the uncompacted articular width (40 mm) to produce a scaling ratio of 0.88. We then multiplied this scaling ratio by mandible length (measured between the anterior tip of the dentary and the posterior-most margin of the angular) of compacted and/or

disarticulated specimens to provide an estimate for maximum gape size. For maximum prey size, we measured the maximum length and maximum depth/width of each prey taxon identified and used published literature for estimations of maximum body sizes where available (e.g. *Teudopsis* sp. – Doguzhaeva & Mutvei, 2003).

Institutional abbreviations. HAUFF, Urwelt Museum Hauff, Holzmaden, Germany; IGP, Institute of Geology and Palaeontology, Charles University, Prague, Czech Republic; NHMUK, The Natural History Museum London, London, UK; SMNS, Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany.

3. Results

3.a. Placement of the ammonite shell

The ammonite conch (cf. *Eleganticeras* sp.) measures 95 mm in maximum width (Bardin *et al.* 2015). It is positioned just dorsal to the vertebral column of the fish, midway between the skull and dorsal fin, with the aperture of the shell orientated dorsoposterior to the axial skeleton. During compaction, the venter of the body chamber pushed into and deformed the distal margins of the neural spines anterior to the dorsal fin, causing several of them to

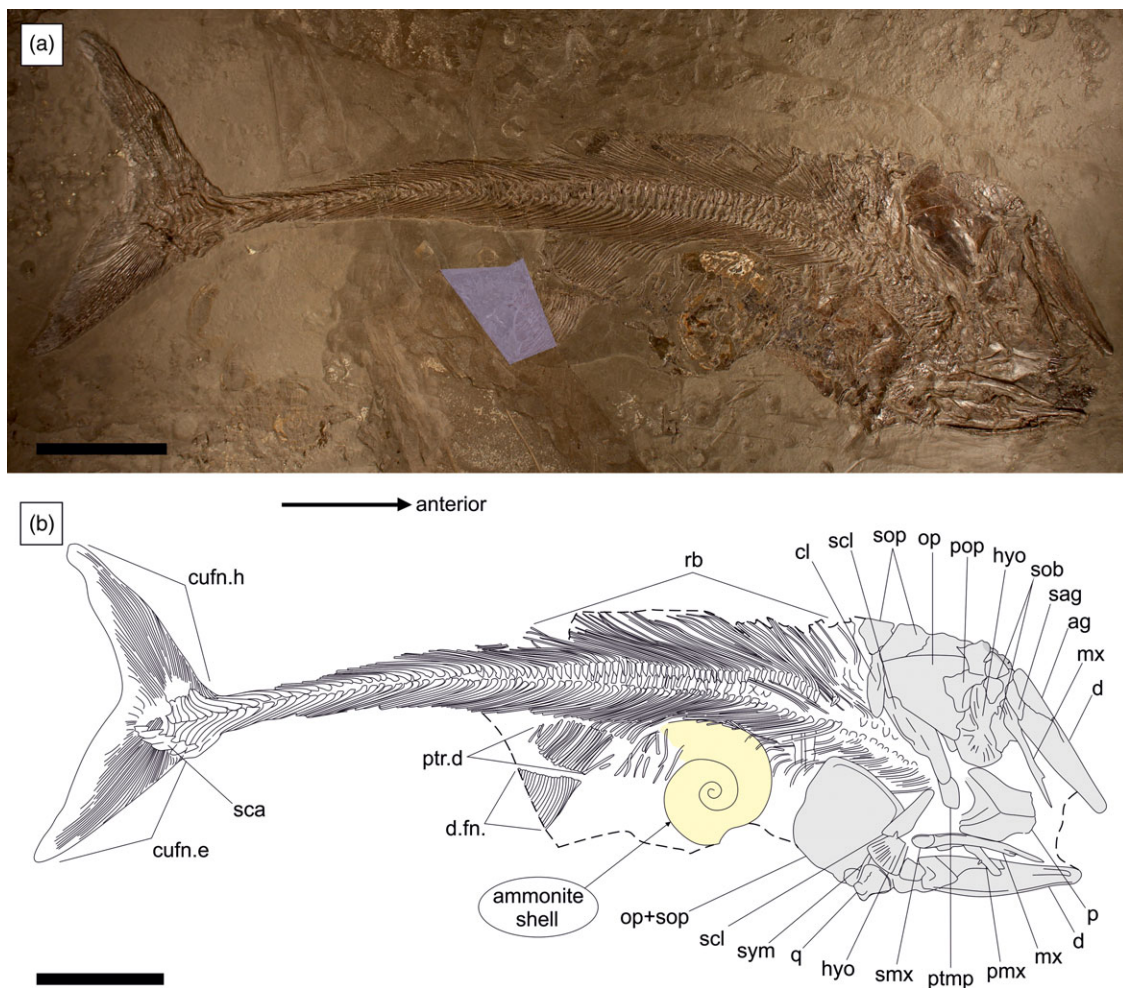


Figure 2. (Colour online) SMNS 52472, *Pachycormus macropterus* (de Blainville, 1818) preserved in left-dorsolateral view with a large ammonite (cf. *Eleganticeras* sp.) inside the gut. (a) Overview of specimen with reconstructed sections highlighted. (b) Schematic line drawing. **Ag** = angular; **cl** = cleithrum; **cufn.e** = epaxial lobe of caudal fin; **cufn.h** = hypaxial lobe of caudal fin; **d** = dentary; **d.fn** = dorsal fin; **hyo** = hyomandibula; **mx** = maxilla; **op** = opercle; **p** = parietal; **pmx** = premaxilla; **pop** = preopercle; **ptmp** = posttemporal; **ptr.d** = pterygiophores of dorsal fin support; **q** = quadrate; **rb** = ribs; **sag** = surangular; **sca** = scaly caudal apparatus; **scl** = supracleithrum; **sob** = suborbital; **sop** = subopercle; **smx** = supramaxilla; **sym** = symplectic. Scale bar equals 100 mm.

break, with the fragments contorted along the ammonite shell margin. At least ten undeformed neural spines are visible underneath the ammonite's body chamber in epirelief. Minor preparation-related breakage towards the rear of the body chamber exposes the distal end of a neural spine underneath the shell, and underneath the bone are the right-lateral body scales. The two rows of supraneurals are perfectly articulated dorsal to the neurals. Although in articulation, the second row of supraneurals overlies the upper (external) surface of the shell. The external face of the ammonite is also partially overlain by the squamation of the fish of the dorsal-left lateral side (Fig. 3). The presence of bones and scales both above and below the shell, in combination with the degree of articulation of the *Pachycormus* skeleton, confirms that the ammonite is situated inside of the fish's body, thus excluding chance association or taphonomic distortion as explanations for its inclusion in the gut. A hypothetical scenario whereby the fish landed on top of or the shell was somehow washed inside of a partially rotting fish carcass lying on the sea floor is unmerited, especially when considering the preservation quality of the ammonite (see section 3.b.).

The placement of the shell is interpreted to result from compaction of the skeleton in a left-dorsolateral direction. The fish carcass, lying dorsoventrally in the sediment with a slight inclination towards the right side, upon burial became compacted, crushing the head dorsoventrally but the postcranium laterodorsally. The tough exterior and structural rigidity of the ammonite conch in the gut, relative to the softer and more ductile nature of the fish's abdominal cavity, caused the shell to shift in the same direction as the axial skeleton, such that it partially penetrated between the unmineralized neural spine – supraneural articulation (SupFig. S1). This would somewhat account for why the supraneurals are perfectly articulated on the top side, but some of the neural spines underneath the shell have fractured with this passive movement of the shell. The presence of telescope fractures cross-cutting the oxycone shell (Fig. 3b) indicates that this movement occurred early in the compaction process (*sensu* Seilacher *et al.* 1976). The ammonite shell was therefore irrefutably ingested by the *Pachycormus* individual while the fish was alive and strongly supports a true ammonite–actinopterygian trophic relationship.

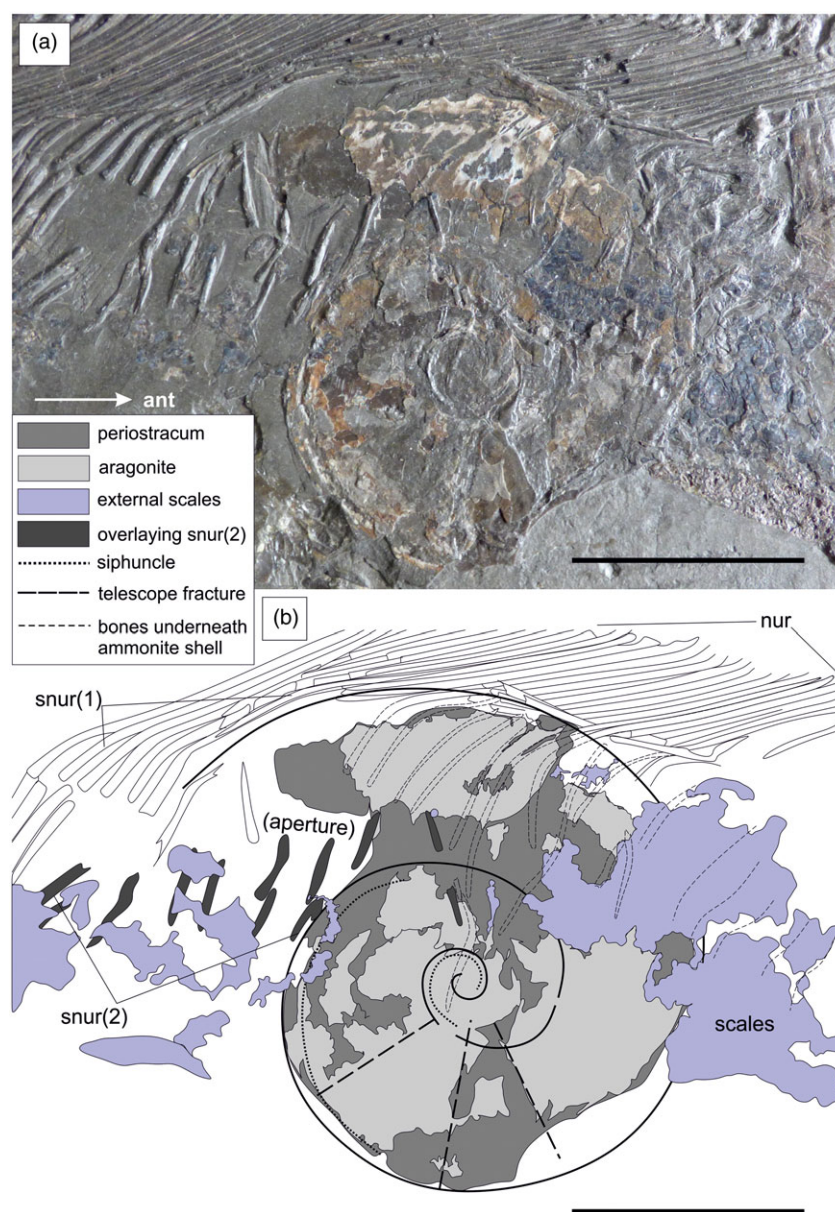


Figure 3. (Colour online) Details of prey ammonite inside the gut of SMNS 52472. (a) Photograph of ammonite conch preserved inside the digestive tract of *Pachycormus*. (b) Line drawing illustrating the ammonite and overlying elements of the skeleton. Bones represented with dashed lines are underneath the ammonite; those with solid lines are either beside or overlaying the shell. Notice the breakage of the neurals (**nur**) and the overlying second row of supraneurals (**snur(2)**); the first row supraneurals (**snur(1)**) are underneath the ammonite. Abdominal scales cover the external surface of both the bones and the ammonite shell. Scale bar equals 50 mm.

3.b. Ammonite preservation and timing of ingestion

Ammonite preservation in the Posidonienschiefer Formation is notoriously unfavourable. Fossil conchs are flattened and largely dissolved, leaving behind only the semi-transparent periostracal films and rare minute patches of original and partially replaced shell fragments (Seilacher *et al.* 1976; Kauffman, 1978; Schmid-Röhl & Röhl, 2003; Muscente *et al.* 2023). The ammonite associated with SMNS 52472 represents a significant exception to this rule, as it preserves large areas of the original shell and retains a nacreous lustre (Fig. 3), allowing us to infer the presence of aragonite (Muscente *et al.* 2023). This is the only known ammonite from the formation to retain this degree of aragonitic preservation, likely the result of the conch being sealed within the fish's gut prior to burial and thereby protecting the original shell material from external chemical dissolution. All of the chance-associated ammonite shells in the surrounding matrix have been extensively dissolved, with only their inorganic periostracum preserved.

The periostracum, external to the aragonite shell, is a strongly contrasting orange-brown colour. The incompletely preserved aragonitic layer is beige-white to cream grey and is more extensively preserved on the body chamber and the dorsoanterior portion of the phragmocone. This layer is rough and patchy, with external surfaces showing small angular pits coupled with cross-cutting scratches and grooves. This damage is not the result of preparation, since equivalent traces are not seen in either the periostracum or surrounding matrix; instead, they most plausibly represent etching traces from the fish's stomach acid. The limited degree of etching suggests that the shell underwent only a very brief period of digestion. The ammonite must have been ingested immediately prior to the fish's death, perhaps within only hours or minutes depending on the corrosive properties in the gastric acids of *Pachycormus*.

Aptychi are absent in SMNS 52472, indicating that the shell was likely vacant at the time of ingestion. The ammonite was likely in an advanced stage of decomposition at the point of ingestion by

Pachycormus, with the air-filled chambers in the phragmocone maintaining the shell's buoyancy in the water column post-mortem. Alternatively, the aptychi may have dislodged while inside of the gut but are now entirely overlain by the bones in the axial skeleton. However, given that the ammonite was ingested shortly before the fish's death, the likelihood of the soft tissues slipping out of the shell while inside of the gut is unlikely.

3.c. Dietary ecology of *Pachycormus* spp

Preserved gut contents are rare in *Pachycormus*, particularly among larger individuals despite the presence of amorphous phosphatic cololites (Table 1). The most readily observed constituent of the gut is the teudopseid coleoid, *Teudopsis* sp. due to its well-mineralized and diagnostic gladii (e.g. Doguzhaeva & Mutvei, 2003), whereas only a single specimen preserves remains of the loligosepiid coleoid *Loligosepia aalensis* (Hauff-D-Pac-1; SupFig. S2). *Loligosepia* and *Teudopsis* do not possess hooklets (Fuchs & Weis, 2008; Fuchs *et al.* 2013) meaning that once the delicate mantle and gladius have been digested, there are no remaining recognizable elements left to pass into the intestine. Examples of gladii and proostraca in the gut of *Pachycormus* therefore represent rare final meals, ingested shortly before death. Abundant in a few specimens are isolated hooklets of the belemnoid coleoid *Clarkeiteuthis conocauda*, which, due to their durable inorganic nature, are more resistant to the effects of gastric corrosion allowing them to form accumulations in the gut, even after the rest of the animal has been fully digested (Přikryl *et al.* 2012). The large ammonite shell inside the gut of SMNS 52472 is therefore a unique occurrence.

Piscivory is rare in *Pachycormus*. Prey fishes predominantly comprise the small teleost *Leptolepis* spp. (Table 1). Two *Pachycormus* specimens from Normandy (NHMUK PV OR 32425; NHMUK PV OR 32427) preserve a small conspecific inside of the gut (Woodward, 1895), suggesting opportunistic cannibalism (Table 1). The majority of prey fishes were ingested head-first (SupFig. S3D), whereas coleoid prey were ingested longitudinally, always posterior-first.

3.d. Gape size in *Pachycormus*

Piscivorous fishes are often considered to be gape-limited, implying that mouth size is the main factor limiting prey size. We defined maximum gape in bony fishes as the articular width between the two opposing rami of the lower jaw (Mihalitsis & Bellwood, 2017), and maximum prey size as the maximum body depth of the largest prey ingested by a successful feed, standardized to the predator's standard length (Table 1).

Maximum gape size ranges in *Pachycormus* from 26 mm (SMNS 87771 = 160 mm SL) to over 126 mm (SMNS 18189 = 840 mm SL) (Table 1), increasing with weak negative allometry ($\log \text{gape} = 0.95(\log \text{SL}) - 0.67$). The estimated gape of SMNS 52472 (111 mm ML) is greater than the maximum diameter of the ingested ammonite shell (95 mm), confirming that this fish was physically capable of swallowing the shell whole in a horizontal orientation. Given that the ammonite is only slightly smaller than the maximum gape of the fish, we infer that the shell was intentionally ingested, rather than as bycatch, because *Pachycormus* had to physically expand its mouth almost fully in order to capture and process this unusually large item. An alternative hypothesis whereby the shell was accidentally swallowed during attempted capture of a different prey item is highly unlikely.

4. Discussion

4.a. Dietary ontogeny in *Pachycormus*

Piscivory appears to be restricted to smaller *Pachycormus* individuals; prey fish are rarely observed in specimens larger than 270 mm SL (Table 1). Larger individuals solely display a teuthophagous diet, with gut contents composed of a variety of soft-bodied coleoids (Table 1) and an apparent preference for vampyropods is consistent with the observed rarity of gut contents in fishes of this size. The shift in dietary preference from piscivory to teuthophagy in *Pachycormus* is correlated with increasing gape. Specimens of *Leptolepis* spp. have a maximum body depth of 26 mm (SC pers. obs.), meaning that even the smallest individuals of *Pachycormus* were capable of swallowing large (≤ 160 mm TL) *Leptolepis*. By contrast, vampyropod and *Loligosepia* coleoids are generally much wider (≥ 45 mm mantle width) and therefore hypothetically were only accessible to larger individuals of *Pachycormus*. Almost all examples of coleoid prey show the gladii orientated longitudinally in the gut and always posterior-first. In these cases, the coleoids' total length exceeds the maximum gape size potential, meaning that the prey, once captured, could only be ingested longitudinally in order to fit through the mouth. Our data suggest that *Pachycormus* was an obligate piscivore as a juvenile and became facultatively teuthophagous at standard lengths ≥ 300 mm. Unlike *Saurostomus* and *Germanostomus*, which frequently consumed loligosepiid and belemnoid coleoids (Cooper & Maxwell, 2022; Cooper *et al.* 2022), teudopseid vampyropods were more common prey items for *Pachycormus* (Table 1). The ammonite in the gut of SMNS 52472 represents a unique exception to the soft-bodied coleoid diet of similar-sized *Pachycormus* individuals.

4.b. Palaeoecological significance and evidence of fatal consumption

Osteichthyan bite traces on ammonites have not been reported in the Posidonienschiefer. Occasionally, small actinopterygians (*Dapedium* and *Pholidophorus*) are found preserved trapped inside of an ammonite body chamber (Jäger, 1990; Fraaye & Jäger, 1995); although whether these fishes were scavenging on the rotting ammonite, feeding on smaller scavengers or seeking refuge remains undetermined (Fraaye & Jäger, 1995; Jäger, 2005). Wild (1994) reported alleged ammonite remains inside the gut of *Saurostomus esocinus*; however, these remains represent fragments of the diplobeliid squid *Clarkeiteuthis conocauda* (Cooper & Maxwell, 2022). An immature *S. esocinus* with a small (2 mm diameter) ammonite larva mixed among larger prey likely represents unintentional bycatch, rather than evidence for *Saurostomus* feeding on zooplankton (Cooper & Maxwell, 2022; fig. 13). A similar unintentional ingestion scenario for SMNS 52472 is implausible, given the diameter of the ammonite relative to the predator's gape size; therefore, SMNS 52472 represents the first irrefutable direct evidence of an actinopterygian intentionally consuming an ammonite.

The absence of aptychi indicates that the ammonite associated with SMNS 52472 was likely in an advanced stage of decomposition or was empty at the moment of ingestion, with the air-filled chambers in the phragmocone maintaining the buoyancy of the shell in the water column. The motion of the floating shell, perhaps mimicking a struggling coleoid or smaller fish, as well as the glimmering nacreous lustre on the externa may have attracted the predator's attention. Alternatively, the *Pachycormus* individual

Table 1. Gut contents in *Pachycormus* spp.

Specimen	Locality	SL	HL	ML	Gut contents	Prey size	Est. gape size	References
SMNS 52472	Zell unter Aichelberg, Baden-Württemberg, Germany eII 6	740 mm	210 mm	125 mm	Large ammonite conch	95 mm diameter	111 mm	This study
SMNS 58389	Ohmden, Baden-Württemberg, Germany eII 4	725 mm	215 mm	120 mm	Coleoid pen fragments (indet.) and small (1–4 mm) isolated actinopterygian bones	Indet.	106 mm	This study
SMNS 51041	Ohmden, eII	–	250 mm	150 mm	Two large (≥ 35 mm width) indeterminate coleoid ink sacs	Indet.	134 mm	This study
SMNS 18189	Holzmaden, eII 4	840 mm	243 mm	142 mm	3 incomplete coleoid pens (indet.) and 1 complete pen (≥ 155 mm \times 35 mm) of <i>Teudopsis</i> sp.	≥ 155 mm length	126 mm	This study
HAUFF-D-PAC-1	Holzmaden, eII 6	540 mm	168 mm	97 mm	Several fragmented gladii and ink sacs of <i>Loligosepia</i> sp. A large belemnite (<i>Passaloteuthis</i> sp.) is protruding from the gut but is chance associated, having impaled the fish post-burial	≥ 100 mm length \times 45 mm width	86 mm	This study (SupFig. S2)
HAUFF-EX-PAC-7	Holzmaden, eII 6	–	180 mm	112 mm	Large <i>Teudopsis subcosta</i> gladius (120 mm \times 39 mm)	≥ 120 mm length	100 mm	This study (Suppl. Fig. S3A–B)
HAUFF-EX-PAC-4	Holzmaden, eII	265 mm	86 mm	50 mm	Indeterminate coleoid mantle fragments	Indet.	45 mm	This study
HAUFF-EX-PAC-3	Holzmaden, eII	600 mm	162 mm	112 mm	2 gladii of <i>Teudopsis</i> sp., (100 mm \times 50 mm) orientated longitudinally. Phosphatized muscle fibres in gut region arranged in cross-hatching pattern	≥ 100 mm length \times 50 mm width	100 mm	This study (SupFig. S3C)
HAUFF-D-PAC-3	Holzmaden, eII	450 mm	143 mm	89 mm	Indeterminate coleoid gladius (90 mm \times 30 mm)	≥ 90 mm length	79 mm	This study
HAUFF-S-PAC-2	‘Holzmaden’	513 mm	220 mm	?	Highly corroded coleoid hooklets	Indet.	?	This study
SMNK-PAL 6680	‘Holzmaden’	670 mm	185 mm	130 mm	Mantle and onychite fragments of an indeterminate belemnoid	≥ 60 mm width	114 mm	This study
IGP 163/1881	‘Holzmaden’	420 mm	n/a	n/a	Isolated belemnoid hooklets likely belonging to <i>Clarkeiteuthis conocauda</i> (Quenstedt, 1849)	Indet.	n/a	Přikryl <i>et al.</i> (2012)
NHMUK PV P 7626	Upper Lias, Ilminster	n/a	n/a	n/a	Isolated bones ascribed to <i>Leptolepis coryphaenoides</i>	n/a	?	Patterson and Rosen, (1977), fig. 32
NHMUK PV OR 32425	Upper Lias of Curcy, Normandy, eII	250 mm	70 mm	41 mm	‘undigested young <i>Pachycormus</i> ’ (<i>P. macropterus</i>)	32 mm width	37 mm	Woodward (1895); pers. obs. SC
NHMUK PV OR 32427	Upper Lias of Curcy, Normandy, eII	270 mm	78 mm	45 mm	‘undigested young <i>Pachycormus</i> ’ (<i>P. macropterus</i>)	32 mm width	40 mm	Woodward (1895); pers. obs. SC
NHMUK PV OR 32431	Upper Lias of Curcy, Normandy, eII	n/a	n/a	n/a	‘ <i>Leptolepis</i> bones in gut’	n/a	?	Woodward (1895)
NHMUK PV OR 32426	Upper Lias of Curcy, Normandy, eII	250 mm	?	?	‘swallowed small fish’ (<i>P. macropterus</i> + Actinopterygii indet.)	32 mm width	≥ 37 mm	Woodward (1895); pers. obs. SC
SMNS 87771	Holzmaden eII	162 mm	55 mm	30 mm	Actinopterygii indet. Isolated bones	n/a	26 mm	This study

HL, head length; ML, mandible length; SL, standard length. ‘?’ denotes an unobtainable measurement, whereas ‘n/a’ is used for missing anatomy and/or unspecified data from previous studies.

may have been scavenging the partial rotting ammonite creature when the shell became caught in the mouth and then swallowed. In this scenario, we surmise that *Pachycormus* did not actively hunt ammonites, rather opportunistically scavenged them. Regardless of the method of consumption, SMNS 52472 evidently represents a case of accidental ingestion of an ammonite conch.

Ingestion of the ammonite shell was undoubtedly fatal. The large size of the conch relative to the stomach, combined with the shell's rigid and brittle structure, would have exerted physiological constraints on the fish's ability to successfully process the ammonite meal. The morphology of the ammonite is highly divergent from the softer, more ductile properties of prey fish and soft-bodied coleoids, which would have been easily compressed by muscular contraction and moved through the digestive tract during peristalsis. As a result, the shell may have become stuck in the foregut, causing the fish the choke and drown, or if passed successfully into the gut, the large shell likely blocked the narrow entrance to the midgut intestine (see Cooper *et al.* 2022, figs 9, 10), resulting in death by congestion or even possibly perforating the stomach wall resulting in internal bleeding. The skeleton shows no evidence of external traumas such as bite traces; the short time frame between ammonite ingestion and death of the consumer – as indicated by the shell's remarkable preservation – strongly implies that the ammonite inside of SMNS 52472 was directly responsible for the fish's death.

5. Conclusions

SMNS 52472 represents the first direct evidence of an actinopterygian fish consuming an ammonite. The large size of the prey suggests that either (1) the shell was attacked as result of mistaken identity or (2) the fish was feeding on the rotting ammonite creature when the shell was accidentally swallowed. The ingestion of the ammonite was almost certainly fatal with SMNS 52472 representing the first documented case for a 'fatal last meal' in a pachycormid fish. A review of gut contents in *Pachycormus* reveals a trend of dietary shift with increased ontogeny, with juveniles being obligate piscivores eventually shifting to facultative teuthophagy in adults. Previous hypotheses on the potential for ammonites to contribute to the diets of bony fishes are strongly supported with new direct evidence. The significance of which reveals a uniquely crucial insight into the recondite and complex trophic relationship between actinopterygian fishes and ammonoid cephalopods in the Mesozoic.

Supplementary material. The supplementary material for this article can be found at [<https://doi.org/10.1017/S0016756823000456>].

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Competing interests. The authors declare none.

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