

Direct evidence of hybodont shark predation on Late Jurassic ammonites

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Abstract Sharks are known to have been ammonoid predators, as indicated by analysis of bite marks or coprolite contents. However, body fossil associations attesting to this predator–prey relationship have never been described so far. Here, I report a unique finding from the Late Jurassic of western France: a complete specimen of the Kimmeridgian ammonite *Orthaspidoceras* bearing one tooth of the hybodont shark *Planohybodus*. Some possible tooth puncture marks are also observed. This is the first direct evidence of such a trophic link between these two major Mesozoic groups, allowing an accurate identification of both organisms. Although *Planohybodus* displays a tearing-type dentition generally assumed to have been especially adapted for large unshelled prey, our discovery clearly shows that this shark was also able to attack robust ammonites such as aspidoceratids. The direct evidence presented here provides new insights into the Mesozoic marine ecosystem food webs.

Keywords Ammonites · Hybodont sharks · Predation · Jurassic · France

Introduction

Direct evidence of predation activity is rarely observed in the fossil record (e.g. preservation of gut contents; Kear 2006; Kriwet et al. 2008) and is especially important in

order to establish ancient predator–prey relationships. Most of previous reports of vertebrate predation on ammonoids consist of bite marks present on shells from various geological periods (e.g. Middle Jurassic of France; Martire and Torta 2000). Numerous case studies have shown that such marks were caused by Carboniferous ctenacanthiform sharks (Mapes and Hansen 1984; Hansen and Mapes 1990; Mapes et al. 1995; Mapes and Chaffin 2003), Jurassic semionotid fishes (Martill 1990), or Cretaceous mosasaurid reptiles (Kauffman and Kesling 1960; Hewitt and Westermann 1990; Kauffman 1990, 2004). However, teeth lost by the predator while catching prey and sunk into the shell represent a peculiar taphonomic condition that has never been observed so far. Such a direct evidence for a trophic relationship between the aspidoceratid ammonite *Orthaspidoceras* and the hybodontiform shark *Planohybodus* is described here on the basis of a fossil specimen coming from the Kimmeridgian of western France. A cast of the original specimen (specimen 42K7 of the Vaubourg private collection, Aytré, France) is housed in the Muséum d'Histoire naturelle of La Rochelle (MHNLR RYV 1).

Geological setting

The specimen discussed here was found in the Upper Kimmeridgian (Mutabilis Zone, Lallierianum Subzone) deposits that are exposed at the Pointe du Rocher near Yves, south of La Rochelle (Charente-Maritime, western France) (Fig. 1). This Upper Jurassic section was described in detail by Fürsich and Oschmann (1986). The benthic macrofauna is well developed, with numerous shell beds of the small oyster *Nanogyra virgula*. With the exception of the common ammonite *Orthaspidoceras*, the pelagic fauna is scarce. As revealed by surface collected fossils, sharks

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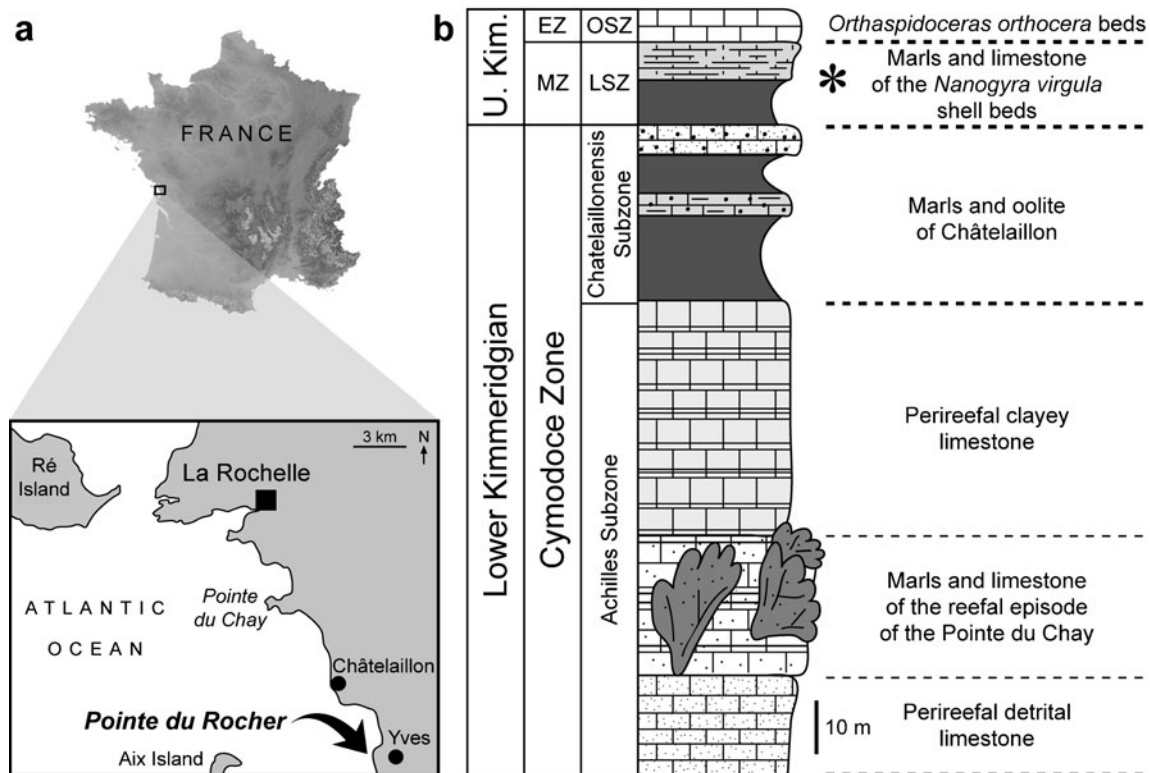


Fig. 1 Location (a) of the Pointe du Rocher at Yves (Charente-Maritime, western France) and stratigraphical position (b) of the studied specimen within the Kimmeridgian (Upper Jurassic) series

south of La Rochelle (*asterisk*). EZ Eudoxus Zone, LSZ Lallierianum Subzone, MZ Mutabilis Zone, OSZ Orthocera Subzone

are only represented by the hybodont *Planohybodus*. In addition, some rare vertebrate remains indicate the presence of various fishes (e.g. semionotids, pycnodontids, ichthyodectiforms), turtles, thalattosuchians, and ichthyosaurs. Sedimentological and palaeontological data suggest a rather shallow shelf palaeoenvironment characterized by low energy conditions (Fürsich and Oschmann 1986).

Description

The ammonite is preserved as an uncrushed internal mould, showing the phragmocone and most of the body chamber (diameter, 118 mm; whorl width, 56 mm). It is characterized by a rounded whorl section and by a row of strong, spiny lateral tubercles slightly bent towards the umbilicus. The mould displays some small shallow depressions or perforations that may correspond to puncture marks (Fig. 2a). An elongated bean-shaped mark (6 mm in width) is present in the posterior part of the body chamber (Fig. 2b). Another falciform mark (3 mm in width) with tapered ends can be observed in the dorsal region of the shell, close to the shark tooth (Fig. 2c). The non-preservation of the shell does not permit observation of

other damages (e.g. shell cracks and crushed portions of the shell).

The tooth of *Planohybodus* shows a high (9.2 mm) and robust main cusp flanked by a pair of lateral cusplets (only the distal one is preserved here) (Fig. 2c). The crown is labiolingually flattened. Numerous longitudinal folds develop from the base of the crown up to the middle of the main cusp. The tip of the main cusp is broken. The tooth is not impressed into the ammonite but is situated a few millimetres above the surface of the internal mould.

It must be noted that two more *Planohybodus* teeth were present adjacent to the tooth described above. Unfortunately, they were destroyed by the amateur palaeontologist who discovered and prepared the ammonite.

Discussion

The ammonite *Orthaspidoceras lallierianum* is very common in the early Late Kimmeridgian deposits of the Pointe du Rocher. In the northern part of the Aquitaine Basin, this endemic and monotaxic *Orthaspidoceras* fauna developed in distal, quiet, rather shallow water environments (Fürsich and Oschmann 1986; Hantzpergue 1989, 1995). The dense

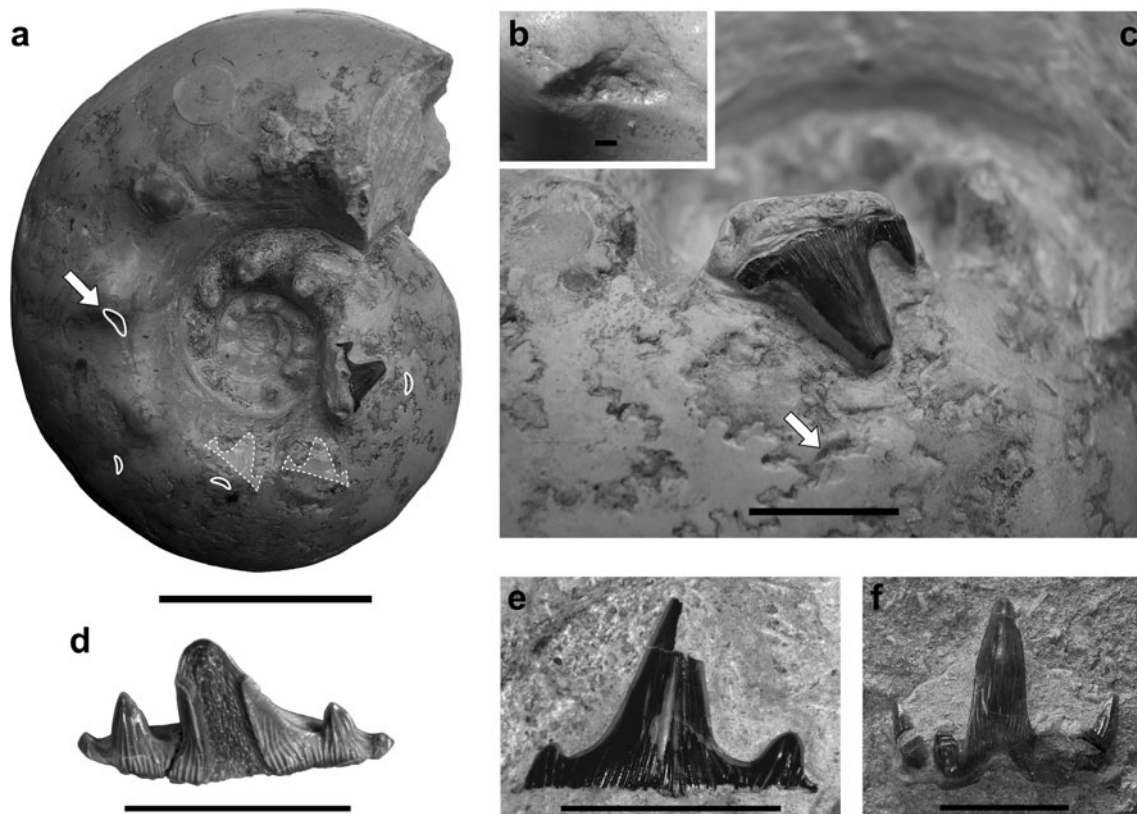


Fig. 2 Direct evidence of hybodont shark predation on ammonites and tooth morphology of ammonoid predators. *Scale bars* represent 50 mm (**a**), 10 mm (**c-f**), and 1 mm (**b**). **a** Internal mould of the ammonite *Orthaspidoceras* associated with a tooth of the hybodont shark *Planohybodus* (42K7; cast MHNLR RYV 1) from the Late Kimmeridgian of the Pointe du Rocher, western France. The two *dotted outlines* indicate the approximate position of the two other teeth that were originally preserved on this specimen. The *arrow* indicates the hole that is interpreted as a tooth puncture mark; other marks are more hypothetical. **b** Close-up of 42K7 showing the possible tooth mark indicated in **a** by the arrow. **c** Close-up of 42K7 showing the

morphology of the *Planohybodus* tooth and a sickle-shaped mark (*arrow*) on the ammonite mould (tooth puncture mark?). Isolated *Planohybodus* teeth (MHNLR GRE 1 and MHNLR CHA 1) from the Early Kimmeridgian of Ré Island (**d**) and Châtelaillon (**e**) (La Rochelle ablerea, western France) displaying unusual damage on the main cusp probably due to predation activity on hard-shelled prey items such as ammonites. **f** Cladodont tooth (USNM 14107) of the ctenacanthiform shark *Glikmanius*, a Carboniferous predator of ammonoids, showing a general morphology similar to that of *Planohybodus* teeth

Orthaspidoceras populations may have constituted the major prey source for the predators of the pelagic realm able to attack shelled organisms. The marine reptiles found at the Pointe du Rocher correspond to long-snouted predator forms (an indeterminate species of the thalattosuchian *Steneosaurus* with slender teeth and an indeterminate ichthyosaur) that may have preyed upon unshelled items such as small to medium-sized fishes. The same remark can be made about the large ichthyodectiform fish present in this locality. The more robust dentition of *Planohybodus* suggests that this shark was a more generalist predator that could include ammonites in its prey range. This assumption is confirmed by the new specimen described here. For the first time, a body fossil belonging to the predator that attacked the ammonite is preserved in association with the shell. The hybodont tooth associated to the ammonite is very similar to those of *Planohybodus grossiconus* from the

Bathonian of Western Europe (Rees and Underwood 2008) as well as that from the Kimmeridgian of southern England described as “*Hybodus*” sp. 2 (now to be referred to *Planohybodus* sp.) (Underwood 2002).

Taken as a whole, what hybodont sharks ate remains somewhat unclear. Some demersal forms, such as *Ptychodus* or *Tribodus*, have a highly specialized grinding-type dentition which indicates obvious durophagous feeding habits, with a prey spectrum likely dominated by benthic invertebrates (Kauffman 1972; Maisey and Carvalho 1997; Vullo and Néraudeau 2008). Recently, Whitenack and Motta (2010) noted that there are no dietary data for hybodont sharks. However, the stomach content of a unique specimen of *Hybodus hauffianus* from the Toarcian Posidonia Shale of Holzmaden displays over 250 belemnite guards (Levy 2009). The clutching-type teeth of *H. hauffianus* have a relatively low, robust, multicusped

crown, especially in the posterolateral tooth rows (Duffin 1997). Such a dental morphology would rather suggest that this species preferentially fed upon shelled prey items. Results of performance testing undertaken by Whitenack and Motta (2010) also indicate that such teeth were suited for durophagy.

On the other hand, an exhaustive review of predation on cephalopods through time was provided by Mapes and Chaffin (2003). It is generally assumed that the vertebrates which have most likely preyed upon shelled cephalopods corresponded to durophagous forms with crushing or grinding dentitions, such as the Late Paleozoic petalodonts or the Jurassic hybodont *Asteracanthus* among selachians (Walker and Brett 2002; Mapes and Chaffin 2003). The specimen discussed here unambiguously shows that sharks with tearing-type dentition were able to catch and bite shelled cephalopods. This is in accordance with previous studies that have assigned the bite marks observed on the Carboniferous ammonoid *Gonioloboceras goniolobum* to the ctenacanthiform shark *Glikmanius occidentalis* (Mapes and Chaffin 2003). Indeed, this early shark has cladodont teeth (Fig. 2f) that are strikingly similar to those of *Planohybodus* (Ginter et al. 2005). The tooth crowns of these two taxa display convergent morphological features such as the strong labiolingual compression, longitudinal folds of the enamel present on both faces, and sharp lateral cusplets. Such teeth are especially efficient for puncturing prey. In the case of predation on ammonoids, Mapes and Chaffin (2003) described in detail a hypothetical scenario of such an attack: the predator strategy would have been to puncture gas chambers of the shell and thus to cause a buoyancy control problem, making prey vulnerable. With the exception of the indentation observed at the level of the body chamber (plus a few ambiguous marks), no major damage can be detected on the conch of the *Orthaspidoceras* specimen dealt with herein. It is difficult here to determine whether the hybodont shark (i.e. *Planohybodus*) attacked and bit an alive *Orthaspidoceras* individual (healthy or not) or scavenged on a dead animal. However, it is worth to note that the preserved tooth (plus the two removed teeth) and the assumed indentations are located in the dorsal part of the shell, suggesting that the attack may have come from above.

Unlike in most aspidoceratids with two spine rows, the shell of *Orthaspidoceras* displays on each side only one row of periumbilical short, spiny tubercles. Their function can be regarded as defence against predators (Checa and Martin-Ramos 1989). Added to the globular shape of the conch (i.e. sphaerocone type), these massive tubercles may have also increased the sturdiness of the shell (Ward 1981; Kröger 2002).

Two isolated *Planohybodus* teeth from the underlying Lower Kimmeridgian deposits (Cymodoce Zone) outcrop-

ping around La Rochelle (Ré Island and Châtelailon) display some damage that might be linked to the feeding habits of this shark (Fig. 2d, e). Both teeth, moreover perfectly preserved, show a main cusp of which the apex is snapped clean through, suggesting that it broke whilst the shark was biting a hard-shelled prey. In one of the teeth, the intensity of the impact even caused the loss of a large fragment on the labial face of the crown. The Cymodoce Zone deposits of the La Rochelle area have yielded a rich ammonite fauna dominated by medium- to large-sized, robust forms (e.g. *Lithacosphinctes*, *Paraspidoceras*, *Physodoceras*, *Rasenioides*) that lived in open marine environments (Hantzpergue 1989, 1995). Such observations suggest that the predation behaviour of *Planohybodus* in these Early Kimmeridgian ecosystems was probably similar to that directly inferred from the Pointe du Rocher specimen here described.

As underlined by Whitenack and Motta (2010), the relation between tooth morphology and biological role should be used with more caution for inferring feeding habits from the dentition type. Indeed, the tooth morphology of *Hybodus* (robust clutching-type teeth) and *Planohybodus* (more slender tearing-type teeth) would have rather suggested dental adaptations for predation on ammonites (hard-shelled prey items) and belemnites (unshelled, soft prey items), respectively. Surprisingly, exceptional direct evidence from the fossil record shows that the prey range of such sharks was actually much broader and sometimes unexpected in accordance to the dentition features.

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References

- Checa A, Martin-Ramos D (1989) Growth and function of spines in the Jurassic ammonite *Aspidoceras*. *Palaeontology* 32:645–655
- Duffin CJ (1997) The dentition of *Hybodus hauffianus* Fraas, 1895 (Toarcian, Early Jurassic). *Stuttgarter Beitr Naturk B* 256:1–20
- Fürsich FT, Oschmann W (1986) Storm shell beds of *Nanogyra virgula* in the Upper Jurassic of France. *N Jb Geol Paläont Abh* 172:141–161
- Ginter M, Ivanov A, Lebedev O (2005) The revision of “*Cladodus*” *occidentalis*, a late Palaeozoic ctenacanthiform shark. *Acta Palaeontol Pol* 50:623–631
- Hansen MC, Mapes RH (1990) A predator-prey relationship between sharks and cephalopods in the Late Paleozoic. In: Boucot AJ (ed) *Evolutionary paleobiology of behavior and coevolution*. Elsevier, Amsterdam, pp 189–192
- Hantzpergue P (1989) Les ammonites kimméridgiennes du haut-fond d'Europe occidentale. *Biochronologie, Systématique, Evolution, Paléobiogéographie*. *Cahiers de Paléontologie CNRS*:1–428

- Hantzpergue P (1995) Faunal trends and sea level changes: biogeographic patterns of Kimmeridgian ammonites of the Western European Shelf. *Geol Rundsch* 84:245–254
- Hewitt RA, Westermann GEG (1990) Mosasaur tooth marks on the ammonite *Placenticerus* from the Upper Cretaceous of Alberta, Canada. *Can J Earth Sci* 27:469–472
- Kauffman EG (1972) *Ptychodus* predation upon a Cretaceous *Inoceramus*. *Palaeontology* 15:439–444
- Kauffman EG (1990) Mosasaur predation on ammonites during the Cretaceous—an evolutionary history. In: Boucot AJ (ed) *Evolutionary paleobiology of behavior and coevolution*. Elsevier, Amsterdam, pp 184–189
- Kauffman EG (2004) Mosasaur predation on Upper Cretaceous nautiloids and ammonites from the United States Pacific coast. *Palaios* 19:96–100
- Kauffman EG, Kesling RV (1960) An Upper Cretaceous ammonite bitten by a mosasaur. *Contr Mus Paleontol Univ Mich* 15:193–248
- Kear BP (2006) First gut contents in a Cretaceous sea turtle. *Biol Lett* 2:113–115
- Kriwet J, Witzmann F, Klug S, Heidtke UHJ (2008) First direct evidence of a vertebrate three-level trophic chain in the fossil record. *Proc R Soc B* 275:181–186
- Kröger B (2002) Antipredatory traits of the ammonoid shell—indications from Jurassic ammonoids with sublethal injuries. *Paläontol Z* 76:223–234
- Levy Z (2009) The possible trophic control on the construction and function of the aulacocerid and belemnoid guard and phragmone. *Rev Paléobiol* 28:131–137
- Maisey JG, Carvalho MR (1997) A new look at old sharks. *Nature* 385:779–780
- Mapes RH, Chaffin DT (2003) Predation on cephalopods: a general overview with a case study from the Upper Carboniferous of Texas. In: Kelley PH, Kowalewski M, Hansen TA (eds) *Predator–prey interactions in the fossil record*. Topics in geobiology 20. Kluwer/Plenum, New York, pp 177–213
- Mapes RH, Hansen MC (1984) Pennsylvanian shark–cephalopod predation: a case study. *Lethaia* 17:175–183
- Mapes RH, Sims MS, Boardman DR II (1995) Predation on the Pennsylvanian ammonoid *Gonioloboceras* and its implications for allochthonous vs. autochthonous accumulations of goniatites and other ammonoids. *J Paleontol* 69:441–446
- Martill DM (1990) Predation on *Kosmoceras* by semionotid fish in the Middle Jurassic Lower Oxford Clay of England. *Palaeontology* 33:739–742
- Martire L, Torta S (2000) Pseudoborings in ammonite molds: the combined result of predation and taphonomic-reworking (Bajocian, Normandy, N. France). *Palaios* 15:356–362
- Rees J, Underwood CJ (2008) Hybodont sharks of the English Bathonian and Callovian (Middle Jurassic). *Palaeontology* 51:117–147
- Underwood CJ (2002) Sharks, rays and a chimaeroid from the Kimmeridgian (Late Jurassic) of Ringstead, southern England. *Palaeontology* 45:297–325
- Vullo R, Néraudeau D (2008) When the “primitive” shark *Tribodus* (Hybodontiformes) meets the “modern” ray *Pseudohypolophus* (Rajiformes): the unique co-occurrence of these two durophagous Cretaceous selachians in Charentes (SW France). *Acta Geol Pol* 58:249–255
- Walker SE, Brett CE (2002) Post-Paleozoic patterns in marine predation: was there a Mesozoic and Cenozoic marine predatory revolution? In: Kowalewski M, Kelley PH (eds) *The fossil record of predation*. The paleontological society papers 8. Paleontological Society, Pittsburgh, pp 119–193
- Ward P (1981) Shell sculpture as a defensive adaptation in ammonoids. *Paleobiology* 7:96–100
- Whitenack LB, Motta PJ (2010) Performance of shark teeth during puncture and draw: implications for the mechanics of cutting. *Biol J Linn Soc* 100:271–286