

Bite traces of a large, mosasaur-type(?) vertebrate predator in the lower Turonian ammonite *Mammites nodosoides* (Schlüter, 1871) from the Czech Republic

Martin Mazuch^a, Martin Košťák^{a,*}, Radek Mikuláš^b, Adam Culka^c, Ondřej Kohout^a, John W.M. Jagt^d

^a Institute of Geology and Palaeontology, Faculty of Science, Charles University Prague, Albertov 6, Prague 2, 128 43, Czech Republic

^b Institute of Geology of the Czech Academy of Sciences, Rozvojová 135, Praha 6, 165 00, Czech Republic

^c Institute of Geochemistry, Mineralogy and Mineral Resources, Faculty of Science, Charles University Prague, Albertov 6, Prague 2, 128 43, Czech Republic

^d Natuurhistorisch Museum Maastricht, De Bosquetplein 6-7, 6211 KJ Maastricht, the Netherlands

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ABSTRACT

A specimen of the acanthoceratid ammonite *Mammites nodosoides* from the lower Turonian of the Bohemian Cretaceous Basin shows signs of having been preyed upon by a reptile, probably with a mosasaur-like dentition. Based on these traces, a new ichnotaxon, *Nihilichnus quadripertitus* Mikuláš, isp. nov., is erected. Several bite traces are arranged into two convergent, straight rows, which would rule out sauropterygian reptiles or fishes as agents. Jaw margins appear to contour the ammonite aperture, suggesting an attack directed at the apertural part with the head and arm crown. The lethal nature of the bite(s) inflicted is supported by the crushed anterior, albeit not anteriormost, portion of the body chamber. Spacing, size and angle of these traces, as well as the angle of convergence between both rows would suggest that the agent was a medium-sized (up to 6 m) member of the marine lizard family Mosasauridae, and more specifically, of the subfamily Tethysaurinae. However, a representative of another closely related subfamily, the Yaguarasaurinae (which includes the genus *Romeosaurus*), cannot be ruled out. The bite marks on the present ammonite shell contribute to a palaeoecological evaluation of tethysaurines (in particular with regard to food adaptations) and to a better picture of the palaeogeographical distribution of early Turonian mosasauroids across central European shelves.

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1. Introduction

Ammonite shells with signs of predation by vertebrates are rare fossils across the globe. That these cephalopods played a role as prey items of ichthyosaurs and plesiosaurs has been documented by studies of stomach contents (Kauffman, 1981; Sato and Tanabe, 1998; Klompmaker et al., 2009). Bite marks in Jurassic and Cretaceous ammonite shells have been linked basically to predatory attacks by representatives of two major vertebrate groups, i.e., fishes (Martill, 1990) and reptiles (Kauffman and Kesling, 1960; Kauffman, 1990, 2004; Andrew et al., 2010; Rivera-Sylva et al., 2012; Kauffman

and Sawdo, 2013). With the exception of North America, where mosasauroid predation on ammonites has been studied on the basis of a larger sample of specimens, there are very few examples from elsewhere (North Africa, Europe; Gale et al., 2017). However, other authors have cast doubt on the mosasauroid nature of bite marks on ammonites (Kase et al., 1998; Seilacher, 1998; Machalski, 1999) and have suggested that these might represent homing scars of patellogastropods (limpets). In a subsequent paper by Tsujita and Westermann (2001), an extensive lot of ammonite material from the upper Campanian Bearpaw Formation of Alberta, Canada (e.g., *Placenticerus*) was described and discussed and the limpet homing scar interpretation was refuted as sole agent of these marks in ammonites.

The record of mosasauroid predation on ammonites by Gale et al. (2017) concerns a specimen of the lower Turonian species *Pseudaspidoceras madagascariensis* (Basse, 1954) from Morocco. Those authors considered the small-sized mosasaurid *Tethysaurus*

* Corresponding author.

E-mail addresses: mazuch@natur.cuni.cz (M. Mazuch), martin.kostak@natur.cuni.cz (M. Košťák), mikulas@gli.cas.cz (R. Mikuláš), adam.culka@natur.cuni.cz (A. Culka), kohout.ondra@seznam.cz (O. Kohout), john.jagt@maastricht.nl (J.W.M. Jagt).

to have produced these bite marks. Stratigraphically, this Moroccan record corresponds to the mosasaur-like type of predation from the Czech Republic presented herein (see below). The existence of mosasauroid predators in the Bohemian Cretaceous Basin (BCB) as early as the early Turonian has already been pointed out on previous occasions, based on isolated skeletal material. The present bite marks in an ammonite shell from this basin appear to constitute the first European record of such.

2. Geological and stratigraphical setting

The present ammonite (registration number CHMHZ-Mch0001) comes from the locality of Měcholupy (also spelt Mischelup and Michelob in older literature; see Fig. 1), which is the type locality of *Mammites nodosoides* (see Wright and Kennedy, 1981), having been recovered from the Bílá Hora Formation and, more precisely, from the so-called ‘Malnice Beds’, an informal term of regional stratigraphical value. Historically, several small quarries, in close proximity to each other and with identical lithology, were exploited around the village of Měcholupy in the nineteenth century. This explains why the exact position of the section from which this specimen was recovered is unknown. The specimen was part of the collection mentioned by Laube and Bruder (1887), which suggests that it had been collected in the second half of the nineteenth century. The exact date of collection is not mentioned on the original label, which lists only locality and lithostratigraphical position, e.g., ‘Malnitzer Schichten’ (= Malnice Beds). Lithologically, the levels that yield material of *M. nodosoides* are developed as spongilitic calcareous, silty marlstones to limestones (‘opuka’ in regional terminology) in this area. Based on this index taxon, these strata are of late early Turonian age (*Mammites nodosoides* ammonite Zone).

3. Methods

Scanning electron microscopy: In order to determine any changes in the original composition of the present specimen, SEM observations were made (JEOL JSM-6380LV). Small samples, removed from the fossil and coated with gold, were monitored

using the secondary electron imaging method in high vacuum mode.

Raman spectroscopy: The sample used for Raman microspectrometric analysis was a fragment (8 × 6 × 2 mm) of altered shell, with one surface light coloured and the opposite side significantly darker grey/brown in colour. Several point analyses were performed on both surfaces. The analyses were performed using a Renishaw InVia Reflex Raman spectrometer coupled with a Leica microscope using a 50×/0.75 objective. The excitation was provided by the 785 nm line of diode laser. The spectra were recorded at low-energy settings: 0.1–0.5% laser power (ca. 0.1–0.6 mW power at sample), so as to avoid detector saturation due to a significant amount of laser-induced fluorescence. The spectra were recorded either over the first-order spectral range of 100–1800 cm⁻¹ or narrowed range of 850–1150 cm⁻¹ where the ν₁ bands of the minerals are located. The scanning parameters were as follows: 10 s acquisition time for 1 scan, and 30 scans (wide range) or 40 scans (narrowed range) were taken in each analysis to improve the signal-to-noise ratio. The instrument was calibrated using a silicon standard and correct Raman band positions were checked using a benzonitrile standard. The spectra were viewed and baseline-corrected using the GRAMS/AI 9.1 spectroscopy software package.

Other methods: A Canon EOS 5DMkIII and 70D camera was used for further image display and recording. Image processing was performed in Corel graphics programs. Measurements of the entire shell and individual details were performed using a digital caliper.

Abbreviation: CHMHZ – Chlupáč’s Museum of Earth History, Faculty of Science, Charles University, Prague.

Notes on terminology: The authors are aware of the current disagreement regarding the use of the phrase ‘bite marks’, rather than ‘biting traces’ which has been used in professional ichnological papers during the past two decades. Unfortunately, zoo-palaeontologists, forensic zoologists and other specialists who deal with structures created by teeth on solid objects (most often on bones) have not adopted this practice (compare Zonneveld et al., 2022). For this reason, we shall use both variants according to the preferences of who wrote the paragraph or sections below.

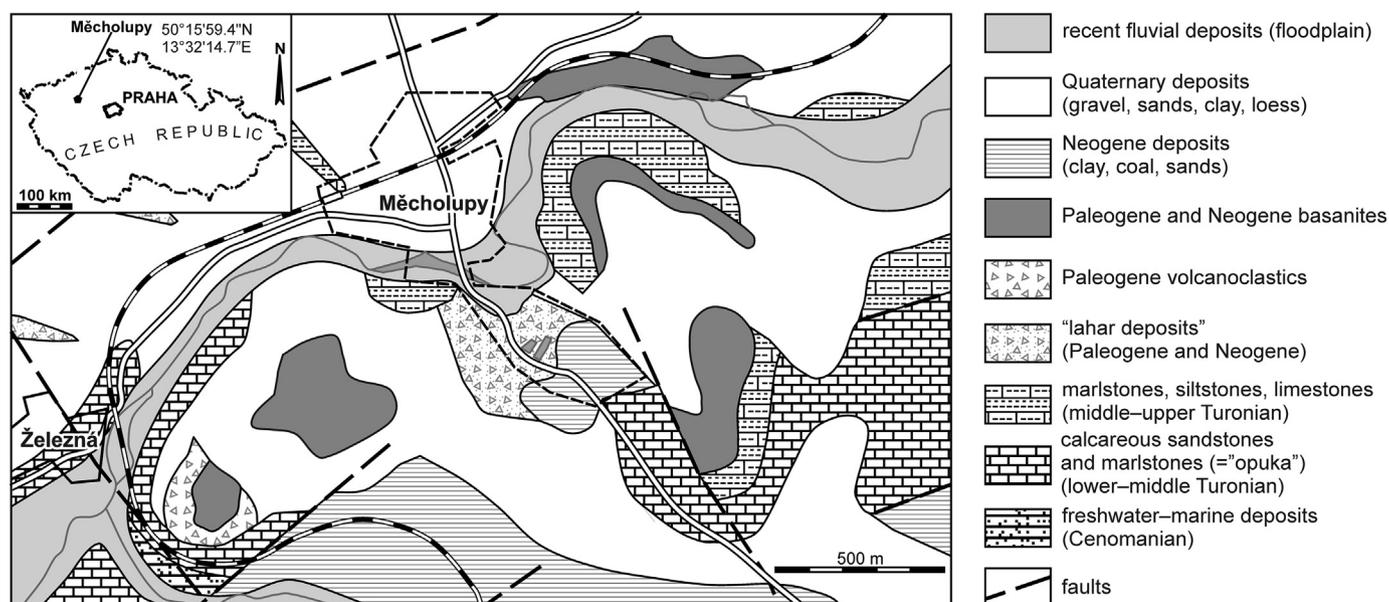


Fig. 1. Geographical position of the locality of Měcholupy (inset: black pentagon) and detailed geological map of its environs (simplified after online Geological maps of the Czech Geological Survey, Prague; <https://mapy.geology.cz/geocr50/>).

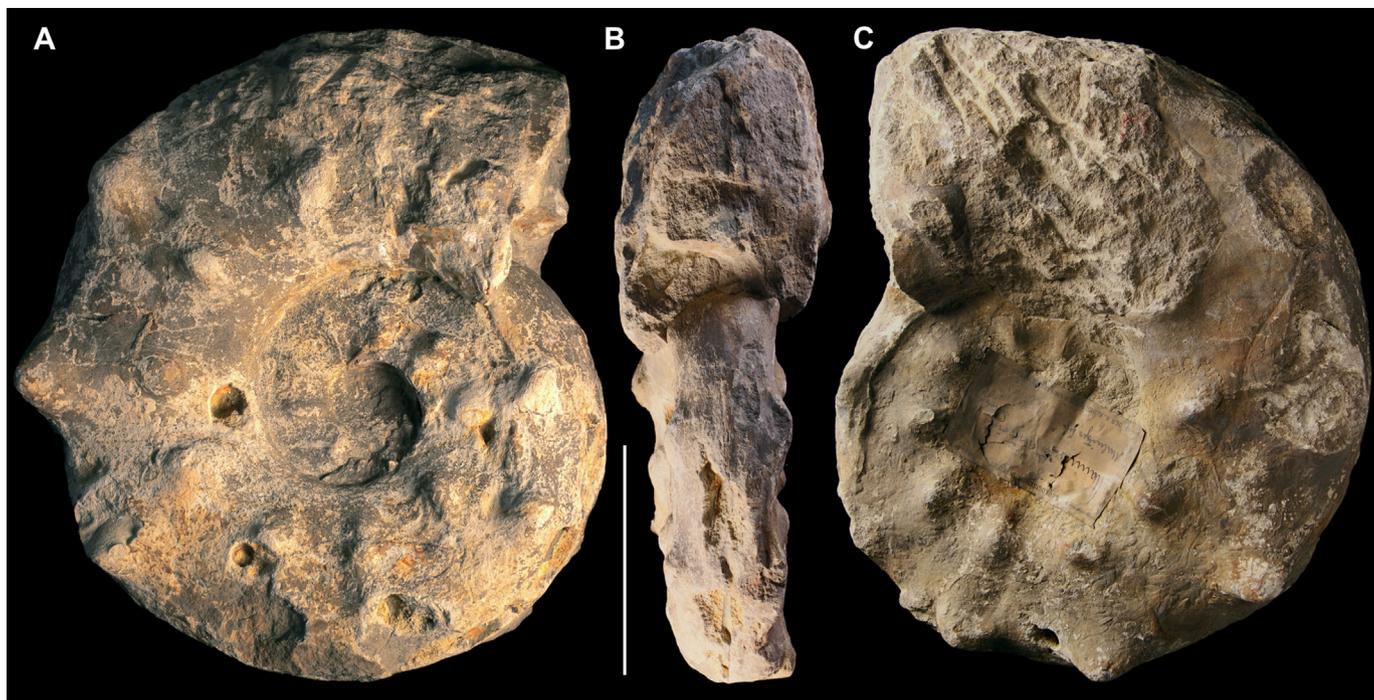


Fig. 2. *Mammites nodosoides* (Schlüter, 1871) (specimen CHMHZ-Mch0001) from the lower Turonian at Měcholupy (Czech Republic; Fig. 1), in left lateral (A), apertural (B) and right lateral (C) views.

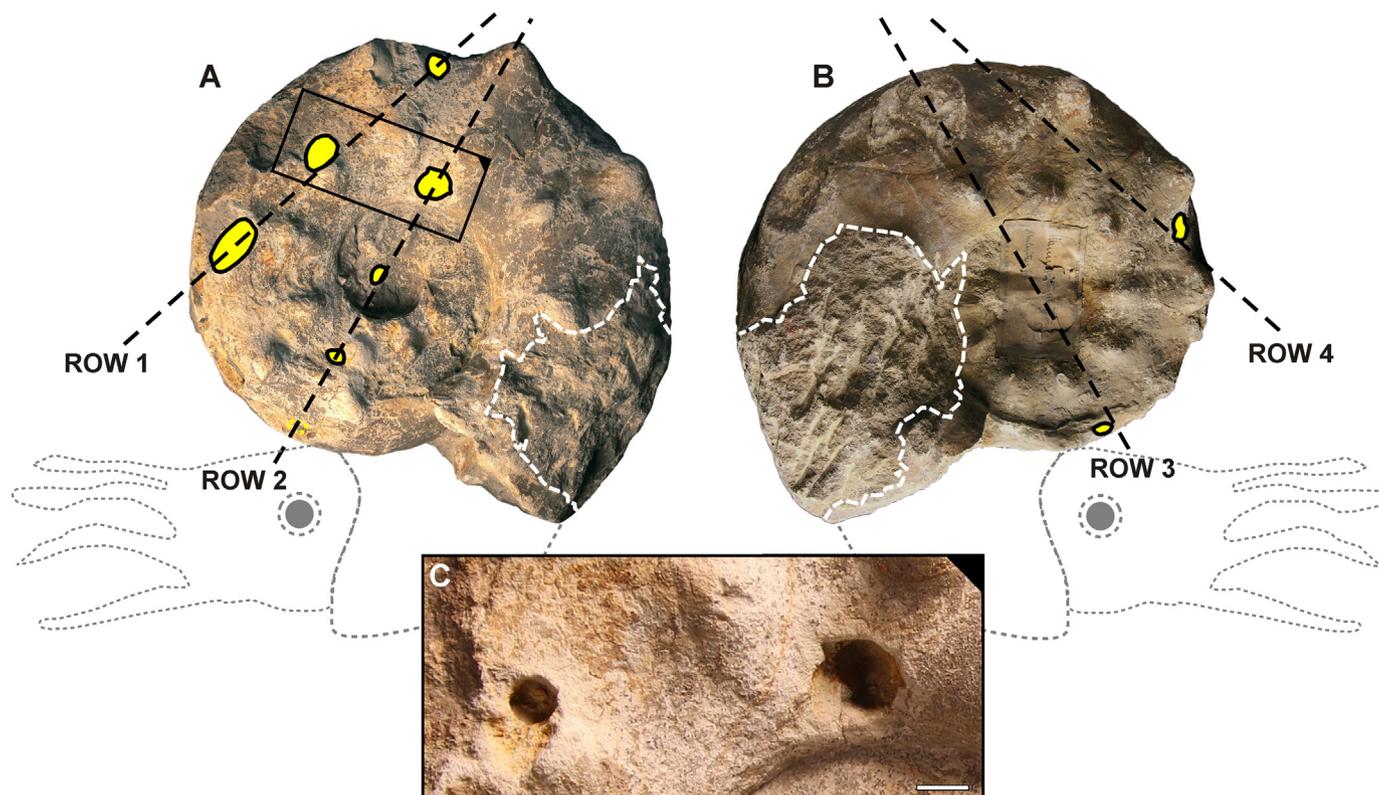


Fig. 3. *Mammites nodosoides* (Schlüter, 1871) (specimen CHMHZ-Mch0001). A–B: Tooth imprints (yellow), arranged in rows 1, 2, 3 and 4 (black dashed lines). The area of the additional attack on the body chamber is marked by a white dashed line. C: Enlarged part of the left side of the box (A, black rectangle), showing oval and square bite marks. Scale bar equals 10 mm.

4. Systematic part

4.1. Ammonite taxonomy

Class Cephalopoda Cuvier, 1798

Subclass Ammonoidea von Zittel, 1884

Order Ammonitida von Zittel, 1884

Suborder Ammonitina Hyatt, 1889

Superfamily Acanthoceratoidea de Grossouvre, 1894

Family Acanthoceratidae de Grossouvre, 1894

Subfamily Mammitinae Hyatt, 1900

Genus *Mammites* Laube and Bruder, 1887

***Mammites nodosoides* (Schlüter, 1871)**

Figs. 2–3

For synonymy, see Wright and Kennedy (1981).

Short description. The present, only slightly compacted specimen is a typical representative of this species, fully comparable to common specimens recorded in the literature (see Wright and Kennedy, 1981 and references therein). Its diameter exceeds 290 mm, the body chamber width reaches 95 mm. There are 10 ribs per whorl, with well-developed ventrolateral and umbilical tubercles. From the inner whorl onwards, the umbilical tubercles are slightly shifted towards the flanks. The left side of the shell is damaged and shows six holes oriented in two slightly converging rows (Figs. 2, 3), while the right side has two holes situated at the shell margin. Furthermore, a considerable (approximately 120 × 150 mm) part of the body chamber is fractured; this injury is distinct from the oriented bite marks.

Remarks. *Mammites nodosoides* ranks amongst the commoner ammonite taxa in upper lower Turonian strata in the study area. Almost all specimens are preserved exclusively as internal moulds. In general, lower Turonian ammonites lack shell material and only occasionally do they show suture lines (Košťák et al., 2020). The preservation of the present specimen, however, reveals a rather unusual, smooth layer of different colour that covers a larger surface of the conch and is here considered to document shell remains possessing also suture lines preserved (Fig. 4).

4.2. Ichnology

Biting traces on bones, although well known to palaeobiologists in the nineteenth and the first half of the twentieth century (Abel, 1935), have been considered in systematic ichnology not earlier than the start of the twenty-first century (Mikuláš et al., 2006). From that moment onwards, several important contributions have appeared (e.g., Pirrone et al., 2014). However, it may be assumed that published papers on the systematics of biting traces represent only a small fraction of instances in the fossil record, not documenting the true significance of this phenomenon.

For the specimen described herein, we consider that it was probably repeatedly attacked and bitten by a mosasaurid reptile. As a first step in our interpretation, we shall assess the entire jaw first or, more precisely, each side of both jaws.

Ichnogenus *Nihilichnus* Mikuláš, Kadlecová, Fejfar and Dvořák, 2006

Diagnosis (Mikuláš et al., 2006). Roughly triangular, circular or ovoid holes or external pits, occurring solitarily or in groups, which may show recurring patterns. Outer part of the margin of the cavity shows minute, irregular jags, resulting from a brittle deformation. **Type ichnospecies.** *Nihilichnus nihilicus* Mikuláš, Kadlecová, Fejfar and Dvořák, 2006.

Nihilichnus quadripertitus Mikuláš, isp. nov.

Etymology. Latin *quadripertitus*, meaning fourfold.

Diagnosis. Roughly circular openings occurring on a fourfold of nearly parallel, slightly divergent rows. The rows form an angle of 20° at most, while the openings maintain a regular distance and are situated more or less opposite each other along the length axis; the distance between the holes is approximately an order of magnitude greater than their diameter.

Holotype. Specimen (i.e., a fourfolds of rows preserved in ammonite described herein; CHMHZ-Mch0001).

Type horizon. *Mammites nodosoides* ammonite Zone, spongilitic calcareous, silty marlstones to limestones, Bílá Hora Formation (lower to middle Turonian), lower Turonian 'Malnice Beds'.

Type locality. Měcholupy (Czech Republic).

Material. Holotype only.

Description. Four rows (two of these merely indicated) of predominantly circular to oval perforations in ammonite shell of a maximum diameter of 290 mm. The rows occur both on the left and right shell halves. The rows on both sides form an angle of 18–20°. Row 1 (see Fig. 3) consists of three perforations. The distance from the edge of the shell (from apertural side) to the centre of the first perforation is 30 mm, the distance from the centre of the first to that of the second perforation is 80 mm, the distance from the



Fig. 4. Suture lines are well preserved in some parts of the shell, documenting a relatively good type of preservation.

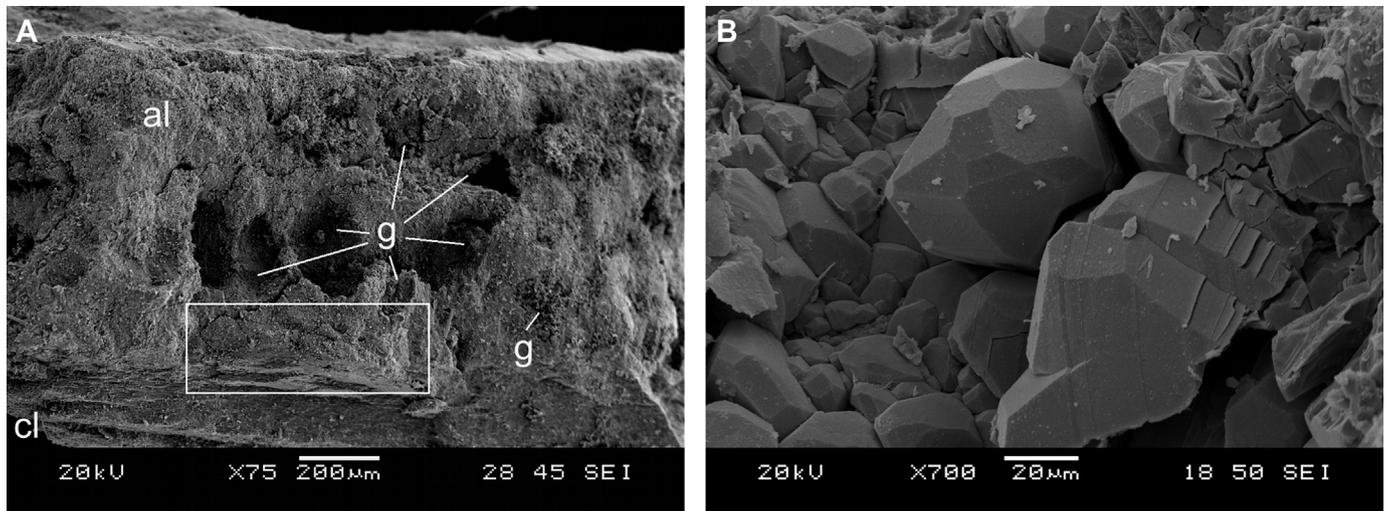


Fig. 5. A: Cross section of a piece of altered shell remains, showing original layer arrangement (calcified, bottom of sample – inner part of shell). Abbreviations: cl – inner calcium carbonate layers (calcitic replacement/permineralisation); al – altered calcium carbonate layers, g – gypsum crystals. Cavities inside the altered (calcium carbonate) shell are fully or partly infilled by gypsum; the outer surface is replaced/coated by gypsum. Square: area of calcium carbonate layer degradation (continuous); B: detail of gypsum crystals.

centre of the second to that of the third perforation is 92 mm, while the distance from the centre of the third perforation to the edge of the shell (in the direction of the row) is 4.0 mm. The dimensions of the perforations are (in the direction of the row) 26 × 14 mm, 15 × 9 mm and 9 × 10 mm. The 1st hole in row 1 is significantly larger because it is on the rounded edges of the shell and thus had a larger contact area between tooth and shell. Rows 2 to 4 are preserved fragmentarily, but the basic data (distance of perforations around 80 mm) and apertural dimensions of the hole (roughly 10–15 × 8–14 mm) are comparable to the first, more complete row. *Remarks.* For bite traces of vertebrates, which are characterised most often by those inflicted by jaws containing numerous

discernible teeth, two basic approaches can be specified. Firstly, traces of individual teeth may be assessed, and secondly, the bite of the whole jaw (if the result is repetitive) may be interpreted as a single trace fossil (compare Mikuláš et al., 2006, fig. 4-5 for both positions). We anticipate that these two approaches will compete in certain specific situations and that different „guiding principles“ will be proposed in the future. In the end, practice will decide between the first or second interpretation for specific traces and substrates. In anticipation of such a development, the sentence “... pits, occurring solitary or in groups, which may show recurring patterns” has here been inserted into the original diagnosis of the ichnogenus *Nihilichnus* (Mikuláš et al., 2006). In the ichnological

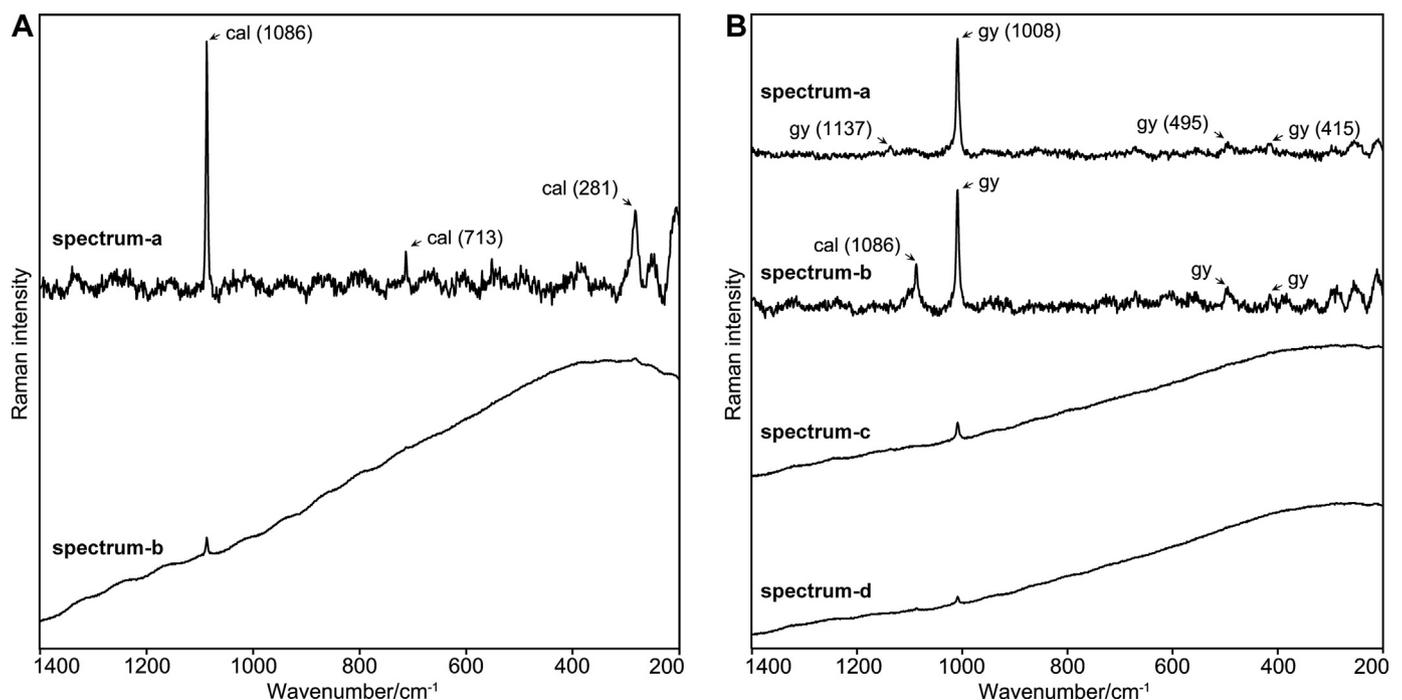


Fig. 6. A: Raman spectrum of calcite, the material of the light-coloured shell remains. The spectrum-a shows baseline corrected original spectrum-b. B: Raman spectrum of gypsum, dominant phase within the dark-coloured material. The top pair (spectrum-a and spectrum-b) shows baseline corrected spectrum-c and spectrum-d, respectively.

literature, there are no indications as to whether any recurring shapes are ichnotaxobases at the ichnospecies level or not. The use of repetitive shapes is an option that any ichnologist can rely on whenever adequate material is available. However, in those cases where limited bone material is richly supplemented by ichnological information, the shape of individually preserved perforations can be taken into account. A comparison of the configuration of the holes in the shell of the present ammonite and a mosasauroid jaw reveals a high degree of similarity. From this we conclude that a mosasaur likely was the tracemaker. We hope that this preliminary conclusion will soon be supported by the documentation of other examples, because, as has happened on several occasions in the history of ichnological studies, ichnologically “damaged” material was removed from collections during amassing material for systematic processing.

5. Results

5.1. SEM

Our SEM investigation has revealed that shell remains have a diagenetically strongly affected original composition (Fig. 5A), the original matter having been partly substituted by gypsum (Fig. 5B).

5.2. Raman spectroscopy

The light-coloured surface material was identified as calcite by its bands located at 1086, 713 and 281 cm^{-1} . The darker-coloured material is composed predominantly of gypsum (1008, 495, 415 cm^{-1}), occasionally accompanied by a weak signal of calcite. The shoulder at 1015 cm^{-1} of the main gypsum Raman band of 1008 cm^{-1} can be attributed to the presence of anhydrite in some spots. Moreover, the signal at around 960 cm^{-1} is missing, which means that apatite is not present in significant amounts. Therefore, secondary phosphatisation of the shell may be excluded. The presence of organics could not be confirmed, mainly due to the presence of broad spectral instrumental artefacts caused by the processing of the very high fluorescence background signal (Fig. 6).

6. Discussion

6.1. Taphonomic implications

Generally, Cenomanian–Coniacian ammonites from the BCB are preserved mainly as internal moulds. Only in few places and in narrow stratigraphical intervals (e.g., upper Turonian, lower/middle Coniacian) have ammonites with preserved shells (in part possessing original aragonite; MK, pers. obs.) been recovered. Lower Turonian ammonites are preserved exclusively as internal moulds. Based on SEM and Raman spectroscopy results (see above), we conclude that shell remains, albeit strongly altered, are still preserved in our specimen. The SEM investigation has documented remains of diagenetically strongly affected shell, but this retains the layer arrangement (Fig. 5A) and a secondary crystal structure (gypsum) inside the altered calcium carbonate (Fig. 5A) and at its surface (Fig. 5B). The thickness of these remains ranges between 60 and 80 μm . However, there are no signs of original aragonite, meaning that aragonite was replaced by calcite and later by gypsum during diagenesis.

Diagenetic (post-depositional) geochemical alterations of aragonitic shells are frequent due to the relative instability of that mineral over time, resulting in secondary mineralisation and calcite replacement in particular. These processes, i.e., when biogenic aragonite is rapidly replaced by calcite, are well documented also in the same type of sedimentary rocks, e.g., porous limestones

(“opoka” facies) from Poland (Janiszewska et al., 2018). The layer arrangement (Fig. 5A, abbreviation *cl*) may reflect gradual replacement of aragonite by calcite and/or permineralisation (*sensu* Janiszewska et al., 2018, fig. 6). Towards the shell surface – outer layers are much more altered (Fig. 5A), resulting in a gypsum cover (see below).

In diagenetically strongly affected shells, replacement and overgrowth also by secondary gypsum crystals has been recorded previously for Upper Cretaceous ammonites (Buchardt and Weiner, 1981) and is documented here as well (Fig. 5A). Inside the altered

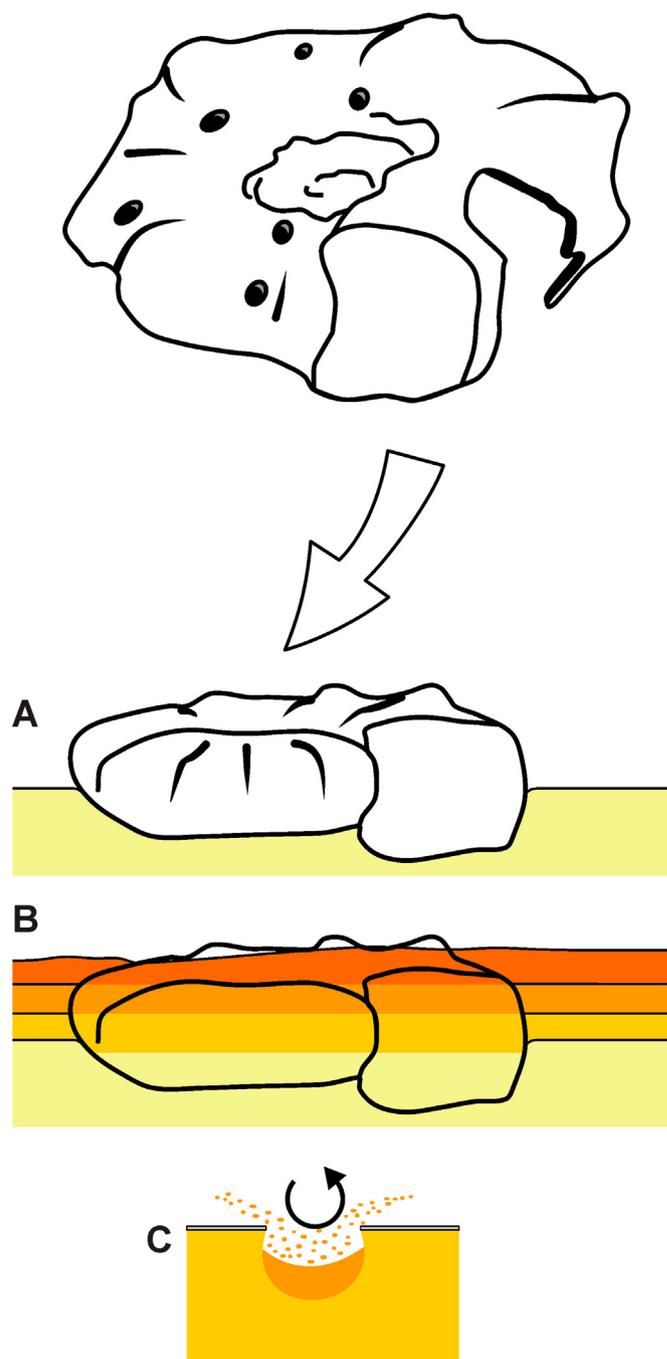


Fig. 7. Scenario of ammonite shell burial process (A–C), implying rather rapid burial (supported by absence of any episkeletozoans on the surface), infilling of the shell (B) and erosion of the internal sediment (C). The black dots mark the holes resulting from a bite.

calcite carbonate, the gypsum crystals form “nest-like” structures and gypsum also covers and forms the outer surface of the shell.

The Raman spectroscopy has clearly identified gypsum (Fig. 6) as the prominent component to have replaced the originally aragonitic shell. The internal mould reveals a marked CaCO₃ content, expressed by calcite in the Raman spectra (Fig. 6 and Supplementary Figs. A–C).

The presence of original shell, at the time of the predatory attack, is also well supported by the character of the direct vicinity of the bite marks, e.g., angular crushed zones (Fig. 3C). Similar or even identical crushing effects have been recorded earlier as mosasaur-like predation on ammonites and nautiloids by Kauffman (2004, fig. 1D) and Gale et al. (2017, fig. 1), as well as in experimental simulations („mosasaur robot”) on Recent *Nautilus* shells (Kase et al., 1998, fig. 3B, D). These fracture patterns clearly document not only rounded (circular), but also angular and fractured bite marks, also seen in the present ammonite.

An extensively damaged area is seen on the body chamber. Notably, this is not linked to the rows of holes in the shell. The large fracture on both sides of the body chamber shows angular crushing (Fig. 3C), similar to results of crushing experiments on extant *Nautilus* (Kase et al., 1998, fig. 2B). For this reason, we assume an additional attack on the body chamber (Fig. 3A, B) to have caused a lethal injury to the ammonite (see below). Following burial on the sea floor, the shell was filled in by fine-grained sediment which was partly eroded later (Fig. 7).

6.2. Possible agent

Within the BCB, several possible predators, representing various vertebrate groups, may be considered to have inflicted these bite marks (Ekrt et al., 2001; Kear et al., 2014; Fig. 8 here). The main features observe in the present ammonite are the shape of the holes (circular to oval), their spacing and distribution, including their arrangement (converging lines; approximately at 18–20°). The overall size of the ammonite shell also suggests an attack of a larger-toothed vertebrate with jaws of at least 40 cm in length.

We here exclude elasmobranchs on account of their distinct type of tooth shapes and arrangement within the jaws, i.e., teeth are arranged in semicircle-like or parabolic lines. Most sharks recorded from the Cretaceous of the BCB possess flat or semi-circular teeth with a flattened labial side (e.g., lamniforms and squaliforms) or small and narrowly pointed teeth (e.g., orectolobiforms or scyliorhiniforms) (Fig. 8C, D). Bite marks inflicted by such types of teeth are well seen, for example, in a dinosaur bone from the BCB (Fejfar et al., 2005). Another type of elasmobranch found in BCB is that of durophagous specialists (*Ptychodus*) with crushing teeth; these would have been unable to create circular to oval bite marks, because their hunting tactics revolved around the destruction of the entire shell by pressure.

The holes in the present ammonite indicate that the bite marks are those produced by conical teeth with a circular or oval cross section in the horizontal plane. This kind of dentition is well known

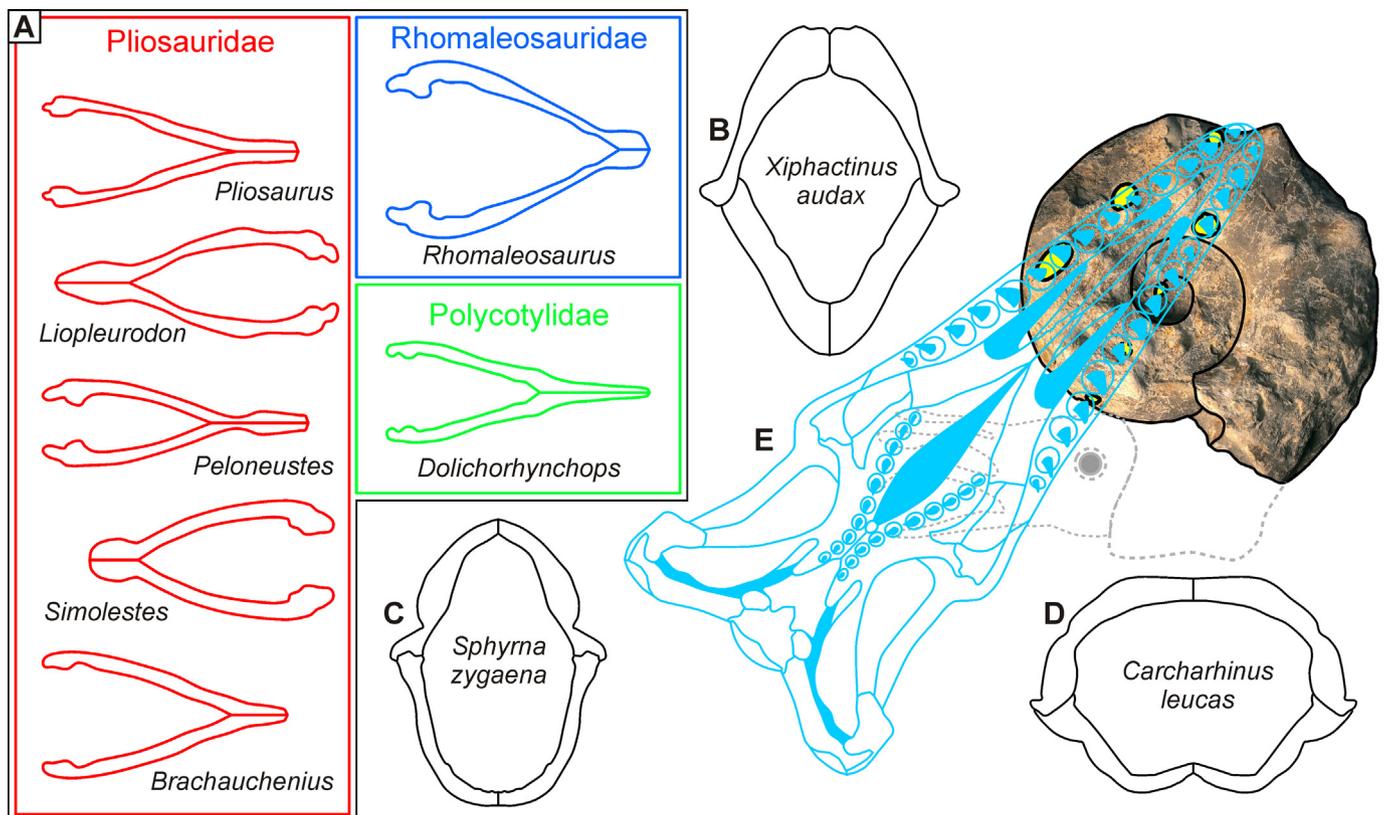


Fig. 8. Possible large-sized vertebrate agents recorded from the BCB, as potential attackers. A: examples of lower jaw shapes in sauropterygians (after Angst and Bardet, 2016); B: the bony fish *Xiphactinus audax* with a broad angle between the lateral (maxillary) teeth (after mounted cast at Tellus Science Museum, Cartersville, Georgia, USA); C–D: sharks of the extant genera *Sphyrna* and *Carcharhinus*; the line of teeth is curved in elasmobranchs (after Berkovitz and Shellis, 2017); E: projection of a mosasaur attack on the present ammonite (ventral view of mosasaur skull after Lingham-Soliar, 1995). The position of the bite suggests that the attack was from bottom up and was primarily directed at those parts holding the soft tissues (tentacles and head of the ammonite). As a secondarily inflicted injury resulted in perforation of the shell from above.

in bony fishes. Amongst these, a representative of the giant genus *Xiphactinus* is known in the BCB (Ekrt and Matějka, 2004); this has long conical teeth, set in large jaws. Although this genus could attain jaw lengths of up to 40 cm in the largest individuals (estimated total body lengths of up to 6 m), the arrangement of its teeth in a parabola-like shape does not fit the pattern of the present bite marks. The lateral branches of the dental arch are straight, but form an angle of around 60° (see Fig. 8B, from a mounted cast in the Tellus Science Museum, Cartersville, Georgia, USA). Crossopterygian fishes (represented by the genus *Macropoma* in the BCB) are significantly smaller and can be ruled out as agents of these traces.

Representatives of aquatic amniotes such as turtles, sauropterygians and squamates (Mosasauroidae) have also been recorded from the BCB (Ekrt et al., 2001; Kear et al., 2014) and wider vicinity (Palci et al., 2013; Sachs et al., 2018). Turtles do not leave imprints of a row of teeth, due to their absence. Therefore, only representatives of the Sauropterygia (mainly Polycotylidae) and Mosasauroidae (mainly represented by the Tethysaurinae) seem to be relevant candidates. In these taxa, the main distinguishing feature is the course of the lateral row of teeth, which is straight in the horizontal plane by mosasauroids and curved (concave-convex) in plesiosaurs represented in the BCB (Fig. 8A, E). Based on these characters, we assume a mosasauroid to have been the agent of these traces.

Of mosasauroids, several taxa were represented in the western Tethys (North and South America, Africa and Europe). Narrowing this down to the Turonian, members of the subfamilies Mosasaurinae (*Dallasaurus turneri*), Plioplatecarpinae (*Angolasaurus bocagei*), Yaguarasaurinae (*Romeosaurus fumanensis*, *Russellosaurus coheni*, *Yaguarasaurus columbianus*) and Tethysaurinae (*Tethysaurus nopcsai*) are on record (Lingham-Soliar, 1994; Bardet et al., 2003; Bell and Polcyn, 2005; Polcyn and Bell, 2005; Bardet et al., 2008; Konishi and Caldwell 2011; Palci et al., 2013; Kear et al., 2014; Madzia and Cau, 2017; Sachs et al., 2018). Members of the genus *Dallasaurus* are comparatively small and reach only a third of jaw length (approximately 150 mm) needed to create such large bite marks. Members of the genera *Angolasaurus* and *Yaguarasaurus* are exclusively known from Africa and both Americas to date, although *Angolasaurus* would have had the possibility to reach Europe as a trans-Atlantic representative. The most likely taxa involved in the current example thus are representatives of the genera *Romeosaurus* and *Russellosaurus*, which have a suitable temporal and geographical distribution and a sufficiently large overall body size. However, an as yet unknown taxon cannot be ruled out.

6.3. Biting attack strategy

The uneven number of preserved tooth impressions on opposite sides of the ammonite shell is interesting. The greater number of tooth impressions on the left side of the shell might be explained by the better “adhesion” of the lower jaw to the surface of the shell due to the intramandibular joint, while on the right side only the posterior maxillary teeth captured the shell, while the anterior teeth of the upper jaw were beyond the shell surface due to that jaw's inflexibility. Consequently, holes formed only closest to the jaw joint. Based on biting marks preserved, we have not recognised any traces of pterygoid teeth; such would be smaller, differently arranged and located much deeper in the mouth (see Fig. 8E).

Although we have observed a prominent attack to the head part, we cannot exclude that the primary target strategy of mosasauroids was the chambered part of the phragmocone. Bites into the gas chambers might limit the buoyancy of an ammonite and the final attack probably tore out the soft parts from the body chamber. In

our specimen, we assume all identified injuries were lethal. Due to the rarity of biting trace records, we would not dare to generalise the attack strategy just yet, and consider that both (and possibly other) variants are possible.

7. Conclusions

We here report the first record of mosasaur-like predation in the northernmost Peri-Tethyan shelf margin – e.g., in the central European Bohemian Cretaceous Basin. The present bite marks in the lower Turonian ammonite shell from this basin probably represent the first European record.

Based on a morphological analysis of the shell injury, we have identified a “possible agent” of the rank of the mosasauroid subfamily Yaguarasaurinae, particularly of representatives of the genera *Romeosaurus* and *Russellosaurus*, which have a suitable temporal and geographical distribution and a sufficiently large overall body size. However, an as yet unknown taxon cannot be ruled out.

Based on this unusually preserved ammonite phragmocone, we interpreted it also an attack strategy of the reptile, linked to jaw flexibility. The crushed body chamber of the ammonite shell suggests also a repetitive attack.

The arrangement of bite marks in four rows has also been analysed from an ichnological point of view, resulting in the establishment of a new ichnospecies, *Nihilichnus quadripertitus* Mikuláš, n. isp.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.cretres.2023.105714>.