



# Predatory drill holes in the oldest thyasirid bivalve, from the Lower Jurassic of South Germany

BARAN KARAPUNAR , WINFRIED WERNER, FRANZ T. FÜRSICH AND ALEXANDER NÜTZEL 



## LETHAIA



Karapunar, B., Werner, W., Fürsich, F. T., & Nützel, A. 2020: Predatory drill holes in the oldest thyasirid bivalve, from the Lower Jurassic of South Germany. *Lethaia*, <https://doi.org/10.1111/let.12399>.

### Abstract

Drill holes provide valuable information about palaeoecological interactions in fossil ecosystems, but the Jurassic drill-hole record is scarce. We report circular drill holes in the infaunal bivalve *Eothyasira antiqua* (Münster in Goldfuss) from the Pliensbachian grey shales of the Amaltheenton Formation of Franconia, southern Germany. The outcrop of the Amaltheenton Formation at Buttenheim yields a rich bivalve fauna (57 species), which represents a typical soft-bottom community. *Eothyasira antiqua*, the yet oldest known member of the family Thyasiridae, represents only 1% of the total bivalve specimens from Buttenheim, but shows an exceptionally high frequency of drill holes. With a drilling rate of 81% of the well-preserved articulated specimens, this occurrence is unique compared with other drilled bivalve records from the Mesozoic and even from Recent assemblages. The drill holes resemble those of modern naticids with a larger outer opening and are assigned to the ichnospecies *Oichnus paraboloides* Bromley. Statistical methods show a non-random distribution of the drill holes over the shell surface with a concentration on the central flank. The drill-hole producer was highly efficient in drilling and exhibited a remarkable prey and site-selective behaviour. The drill holes on the moderately deep infaunal *Eothyasira* suggest that the predator was also infaunal for at least parts of its life and could cope with poorly oxygenated substrate conditions occurring temporarily in the Amaltheenton environment. Drill-hole characteristics point to a gastropod as producer. None of the about 50 gastropod taxa of the Amaltheenton Formation can be associated with the drill holes with certainty, but *Hayamia reticulata* (Münster) seems to be the most likely candidate. The results of this study support the opinion that drill holes are generally a scarce phenomenon in the Early Jurassic generated by rare, probably highly specialised predators. Preservation biases are considered to have been less important. □ *Early Jurassic, Pliensbachian, drill hole, predation, infaunal bivalve, Thyasiridae.*

Baran Karapunar  [baran.karapunar@campus.lmu.de], and Alexander Nützel Department für Geo- und Umweltwissenschaften, Ludwig-Maximilians-Universität München, Paläontologie und Geobiologie, Richard-Wagner-Strasse 10 München 80333, Germany; Baran Karapunar  [baran.karapunar@campus.lmu.de], Winfried Werner [werner@snsb.de], and Alexander Nützel Bayerische Staatssammlung für Paläontologie und Geologie, Richard-Wagner-Strasse 10 München 80333, Germany; Winfried Werner [werner@snsb.de], Alexander Nützel GeoBio-Center LMU, Richard-Wagner-Strasse 10 München 80333, Germany; Franz T. Fürsich [franz.fuersich@fau.de], Fachgruppe Paläoumwelt, GeoZentrum Nordbayern der Universität Erlangen-Nürnberg, Loewenichstrasse 28 Erlangen 91054, Germany; manuscript received on 8/04/2020; manuscript accepted on 26/07/2020.

## Introduction

Drill holes provide direct and valuable information about palaeoecological interactions in fossil communities. Predatory drill holes are a very reliable source to demonstrate predatory behaviour in the fossil record and help palaeontologists to test evolutionary hypotheses about predation such as the Mesozoic marine revolution (Vermeij 1977). Although drill holes have been frequently recorded from the Cretaceous onwards, they are rare in the Palaeozoic and Early Mesozoic (Kowalewski *et al.* 1998; Huntley & Kowalewski 2007; Klompmaker *et al.* 2016; Tackett &

Tintori 2019). Based on a literature survey, Kowalewski *et al.* (1998) proposed three phases in the Phanerozoic history of drilling predation. The phase from the Permian to the Early Cretaceous is the time span with the lowest drill-hole record in the Phanerozoic (Kowalewski *et al.* 1998; Huntley & Kowalewski 2007). It is a matter of discussion whether predators were so rare during this period (Kowalewski *et al.* 1998) or whether taphonomic and diagenetic features masked their occurrence (Harper *et al.* 1998).

In Recent marine communities, drill holes are produced by gastropods, octopods, nematodes and flatworms (Kabat 1990; Kowalewski 2002; Klompmaker *et al.* 2019). Flatworms are known to make irregular

minute holes (up to 0.2 mm) on Recent juvenile oysters (Bromley 1981; Kabat 1990). Nematodes prey on foraminifera and produce very small drill holes (diameter up to 0.1 mm) (Kabat 1990). Among gastropods, the members of the family Capulidae live on molluscs and echinoderms as parasites and produce straight-sided drill holes. The parasitic drill holes made by capulids can be recognized by the attachment scar around the drill hole (Matsukuma 1978). Most of the predatory drill holes in Recent marine molluscs are produced by members of the families Naticidae and Muricidae, which are unique among gastropods in having an accessory boring organ (ABO) (e.g. Carriker 1981; Harper & Kelley 2012). Circular holes bored into calcareous skeletal substrates are named as *Oichnus* Bromley, 1981 (Wishak *et al.* 2015; Donovan 2017; but see Zonneveld & Gingras 2014). The circular outline of naticid and muricid drill holes distinguishes them from the ovate to tear-drop-shaped drill holes produced by octopods and attributed to the ichnotaxon *Oichnus ovalis* (Bromley 1981, 1993; Klompmaker *et al.* 2013; Hiemstra 2015). Muricid and naticid drill holes can be distinguished from each other according to the shape of the drill hole and the life habit of their preferred prey. Muricids produce straight-sided drill holes (*Oichnus simplex*) and prey mainly on epifaunal taxa, while naticids produce parabolic drill holes (*Oichnus paraboloides*) where the outer diameter is larger than the inner one and their prey consists mainly of infaunal taxa (e.g. Carriker & Yochelson 1968; Bromley 1981; Kelley & Hansen 2003). Both gastropod groups drill shells by combining chemical and mechanical actions. They secrete enzymes and acids to weaken the prey's shell and use the radula for rasping it off (Carriker 1981).

Although muricid and naticid types of drill holes are found in Palaeozoic and Early Mesozoic fossils, the fossil record of naticids and muricids does not go back further than the Cretaceous (Kabat 1990; Kase & Ishikawa, 2003). The Triassic and Jurassic gastropods previously assigned to Naticidae (Sohl 1969; Kabat 1991) are considered to be doubtful and need revision (Klompmaker *et al.* 2016). Recently, Das *et al.* (2019) reported naticids from the Oxfordian of Kachchh, India, which would be the earliest occurrence of naticids although the preservation of the specimens seems insufficient for a safe attribution to Naticidae. The identity of the drilling predator(s) before the Late Jurassic is still unknown (Harper *et al.* 1998; Klompmaker *et al.* 2016).

From Triassic strata, drill holes have been reported in infaunal and epifaunal molluscs and brachiopods from the Carnian Cassian Formation, Italy (Fürsich & Jablonski 1984; Klompmaker *et al.* 2016), in one

brachiopod from the Anisian of Poland (Klompmaker *et al.* 2016), in an infaunal nuculoid bivalve from the Norian Riva di Solto Formation, Italy (Tackett & Tintori 2019), in an epifaunal bivalve from the Norian Wallowa Terrane of Hell's Canyon, USA (Newton *et al.* 1987), and in the infaunal bivalve *Septocardia* from the Norian of the Farewell Terrane, Alaska (McRoberts & Blodgett 2000).

From Jurassic strata, drill holes have been described in brachiopods from the Sinemurian Hierlatz Limestone of Hungary (Kowalewski *et al.* 1998), from the Lower and Upper Jurassic of the United Kingdom and France (Harper & Wharton 2000) and from the Lower Jurassic of Spain (Sohl 1969), in the infaunal bivalve *Palaeonucula cuneiformis* (J. de C. Sowerby, 1840) from the Callovian of the Kachchh Basin, India (Kowalewski *et al.* 1998), in infaunal and epifaunal bivalves from the Jurassic of the United Kingdom and Ireland (Bromley 1981; Harper *et al.* 1998), in infaunal bivalves from the Pliensbachian Amaltheenton Formation in northern Germany (Aberhan *et al.* 2011), and in infaunal and epifaunal bivalves from the Oxfordian of Kachchh, India (Bardhan *et al.* 2012).

Here, we report circular naticid-like drill holes in the infaunal bivalve *Eothisira antiqua* (Münster in Goldfuss, 1841) from the Pliensbachian Amaltheenton Formation of Franconia, southern Germany. In the clay pit of Buttenheim, this species is part of a diverse bivalve fauna of altogether 57 species (Karapunar *et al.* 2020). It is interpreted as one of the oldest representatives of the family Thyasiridae that is known for a chemosymbiotic life habit (e.g. Allen 1958; Kauffmann 1969). *Eothisira antiqua* differs from all other species at this locality by its high proportion of drilled specimens. Only a single specimen of another infaunal species at Buttenheim, *Neocrassina gueuxii* (d'Orbigny, 1850), also exhibits a drill hole (Fig. 8B). In addition, a single specimen of the gastropod species *Levipleura blainvillei* (Münster in Goldfuss, 1844) exhibits a drill hole which is, however, much smaller in diameter (0.35 mm) (Figs 8A1–A2).

The aim of this paper is to document this remarkable Early Jurassic occurrence and to discuss it in the context of prey selection, site selectivity and size selectivity of the producer in the Pliensbachian (Early Jurassic). In addition, the scarcity of drill holes in the Early Jurassic is discussed with respect to two hypotheses: (1) generally low drilling predation at this time *versus*; (2) taphonomic and diagenetic masking of an actually more frequent occurrence.

### *Material and methods*

*Material.* – The material is from the Upper Pliensbachian Amaltheenton Formation exposed in a clay

pit near Buttenheim, Franconia (southern Germany) (49°47'42.2"N 11°02'41.7"E). There, the Amaltheenton Formation consists of poorly lithified silty clay deposits that contain nodular, calcareous concretions, occasionally pyritic concretions, thin shell beds, shell pavements and condensation horizons at certain levels. The material studied was collected from the surface or extracted mechanically from the argillaceous sediments over many years. The collection was quantitative, and the collector did not prefer certain taxa or drilled specimens. The bivalve collection studied comprises approximately 7,000 bivalve specimens from the clay pit near Buttenheim (Karapınar *et al.* 2020). Of them, 77 specimens have been assigned to the species *Eothyasira antiqua* (Münster in Goldfuss, 1841) (Karapınar *et al.* 2020). Eight *Eothyasira* specimens represent fragments or single valves and are therefore not included in the statistical analyses of the present study. Nearly all *Eothyasira* specimens are preserved with articulated valves. In contrast to the argillaceous sediment, from which the specimens generally come, the fill of the specimens consists of a strongly lithified limestone. In few cases, *Eothyasira* specimens are embedded nearly completely within concretions. Apart from the specimens in the Buttenheim collection, the type material of Münster in Goldfuss (1841) and the specimen figured by Kuhn (1936), both from Pliensbachian strata of northern Bavaria and deposited in the Bayerische Staatssammlung für Paläontologie und Geologie, have been examined. One of the seven syntypes of Münster and the specimen figured by Kuhn (1936) also exhibit a drill hole. However, these specimens are not included in the statistical analyses of the present study, since they come from other localities.

The material studied (approximately 7,000 specimens) has been deposited in the Bayerische Staatssammlung für Paläontologie und Geologie under the main inventory number SNSB-BSPG 2011 XI.

The shell and the sediment fill of *Eothyasira antiqua* have been examined by X-ray analysis to clarify the mineralogy and a possible diagenetic overprint. X-ray powder diffraction data were obtained using a PHILIPS Xpert X-ray diffractometer operating at 40 kV and 30 mA. Diffraction data were collected with CuK $\alpha$  X-radiation between  $2\Theta = 5$  and  $60^\circ$ . Data processing was done with the ADM software package from Wassermann, Kempten (unpubl.) (all data pers. comm. R. Hochleitner).

*Statistical methods.* – In order to evaluate possible site selectivity of the predator, the shells have been divided into six sectors (Kelley 1988; Kowalewski 2002) and the drill holes within each sector have

been counted. In order to define the sectors, the valve has been divided into upper and lower regions with a commarginal line representing the mid-height between the umbo and ventral margin. The anterior and posterior ends of this imaginary commarginal line are situated dorsally to the anterior and posterior muscle scars, respectively. The valve is further divided into three regions by two radial lines, dividing the mid-commarginal line at a ratio of 2:3:2 and the ventral margin at a ratio of 3:5:3 in lateral view (Fig. 1). The middle region represents the region with maximum valve convexity, anterior and posterior regions cover the area where the anterior and posterior muscle scars are situated. The three imaginary lines (one mid-commarginal line and two radial lines) together divide the valve into six sectors that are not equal in area. The observed numbers of drill holes in each sector (for both right and left valves) have been tested against the null hypothesis that the total number of drill holes in each sector is distributed proportionally to the area of each sector by using the chi-square goodness-of-fit test (Kelley 1988). Since the sectors are not equal in area, expected numbers of drill holes in the chi-square test have been calculated according to the area of each sector. The chi-square test is used herein because the drill holes are not normally distributed and the variables are mutually exclusive.

A difference in the frequency distribution of drill holes in different size classes may indicate a change in site selectivity of the predator during its life time. In order to assess a possible difference, the drill holes have been divided into two size categories. Drill holes with diameters smaller than the mean diameter of 1.4 mm have been defined as small and those with diameters larger than, or equal to, 1.4 mm have been defined as large. The difference in the frequency distribution of drill holes between the two size classes has been tested against the null hypothesis that the frequency distribution of drill holes in the small and large size classes among the sectors is the same by using the chi-square test.

To assess size selectivity, the equality of the median lengths of the drilled and non-drilled specimens has been tested by using the Mann–Whitney U-test. The Mann–Whitney U-test is used herein because the size data are not normally distributed. The size-frequency distributions (SFD) of the drilled specimens were tested against the SFD of the non-drilled specimens by using the Kolmogorov–Smirnov test. This statistical test is used to test whether the drilled and non-drilled specimens show equal size distributions (Kowalewski 2002, p. 46) and used here because the size distributions of the drilled and non-drilled shells are not normal. The drill-hole size is a good

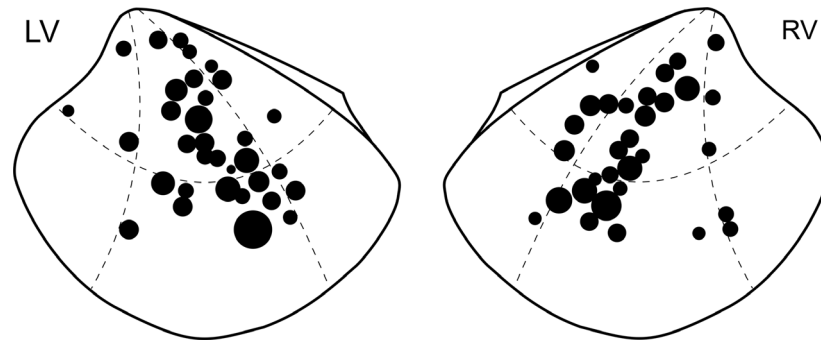


Fig. 1. The position of the drill holes. The drill-hole sizes are scaled with respect to each other, but not scaled to the specimen.

indicator of the size of the predator (Kitchell *et al.* 1981; Kelley 1988; Kelley & Hansen 2003; Klomp-maker *et al.* 2017). Therefore, the drill-hole size is used as a proxy for predator size. In order to understand whether larger predators prefer larger prey, the rank correlation between drill-hole size and prey size (shell height or shell length) has been measured using the Spearman rank correlation method. Spearman rank correlation is used here as the shell height/length is not normally distributed (Kowalewski 2002, p. 26–27). Ordinary least squares method is used to draw the linear regression line in Figures 5 and 6.

## Results

A total of 7,000 bivalve specimens belonging to 57 taxa have been examined for drill holes. Apart from the specimens assigned to *Eothisira antiqua* (Münster in Goldfuss, 1841), only a single specimen belonging to the infaunal bivalve species *Neocrassina gueuxii* (d'Orbigny, 1850) exhibits a drill hole (Fig. 8 B).

The specimens of the infaunal bivalve *Eothisira antiqua* (Münster in Goldfuss, 1841) from Büttenheim show a high frequency of drill holes. Of the well-preserved articulated specimens, 81% (56 out of 69) have been drilled. Although most of the drilled specimens exhibit only a single drill hole, eight specimens have two drill holes either on the same valve (six specimens) or on both valves (two specimens). In total, 33 drill holes were counted on 29 left valves and 31 on 29 right valves (Fig. 1). All drill holes are complete, that is the valve is entirely perforated. Unsuccessful drilling attempts were not encountered. The shape of the drill holes is circular, and the outer opening is slightly larger than the inner one (Fig. 7 A2,E,H); thus, it is of naticid type and can be assigned to the ichnospecies *Oichnus paraboloides* Bromley, 1981. The outer diameters range from 0.7 to 2.9 mm with an arithmetic mean and median of 1.4 mm. Five specimens (SNSB-BSPG 2011 XI 518,

549, 963, 970 and 976) display numerous small pits (ca. 0.04 mm in diameter) on the outer shell surface surrounding the drill hole (Fig. 7F–G).

The distribution of drill holes among the six shell sectors is non-random ( $\chi^2 = 38.94$ ,  $df = 5$ ,  $p < 0.01$ ), most drill holes being concentrated on the central part of the shell (sectors 2 and 5; Fig. 2). The mean size of the drill holes differs among the sectors and is higher in the sectors 2 and 5 (Fig. 3). The distribution of small (<1.4 mm in diameter) and large ( $\geq 1.4$  mm in diameter) drill holes on the shell sectors is given in Table 1. Although the larger drill holes are more frequently found in shell sectors 2 and 5, the chi-square test shows no significant difference in the frequency distribution of the drill holes between the two size classes ( $\chi^2 = 7.91$ ,  $df = 5$ ,  $p = 0.16$ ).

The mean and median size of the drilled specimens are higher than the mean and median size of non-drilled specimens (Fig. 4); however, the difference in the medians between the drilled and non-drilled specimens is not statistically significant (Mann–Whitney U-test, for median shell lengths,  $U = 226.5$ ,  $p = 0.079$ ; for median shell heights,  $U = 191.5$ ,  $p = 0.057$ ). The Kolmogorov–Smirnov test suggests that there is no significant difference in the size-frequency distributions between the drilled and non-drilled specimens (K-S for height,  $D = 0.29$ ,  $p = 0.36$ ; for length  $D = 0.34$ ,  $p = 0.16$ ). There is a weak positive association between the size of the drill holes and the size of the drilled specimens (Figs 5–6). However, the size of the drill holes does not show a statistically significant correlation with the size of the drilled specimens (Spearman rank correlation: drill-hole size vs. shell height,  $r_s = 0.14$ ,  $p = 0.31$ ; drill-hole size vs. shell length,  $r_s = 0.14$ ,  $p = 0.37$ ).

X-ray analyses show that the shells of *Eothisira antiqua* from Büttenheim are composed of about 60% calcite and about 40% aragonite (R. Hochleitner, pers. comm.). It is difficult to decide whether this proportion reflects the original composition of the

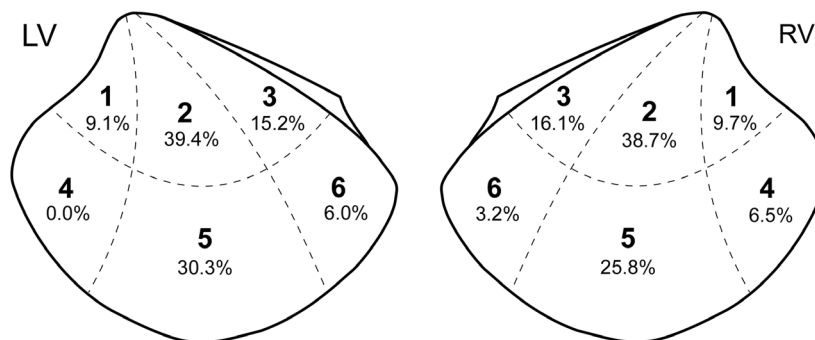


Fig. 2. Shell sectors and percentage of the drill holes in each sector.

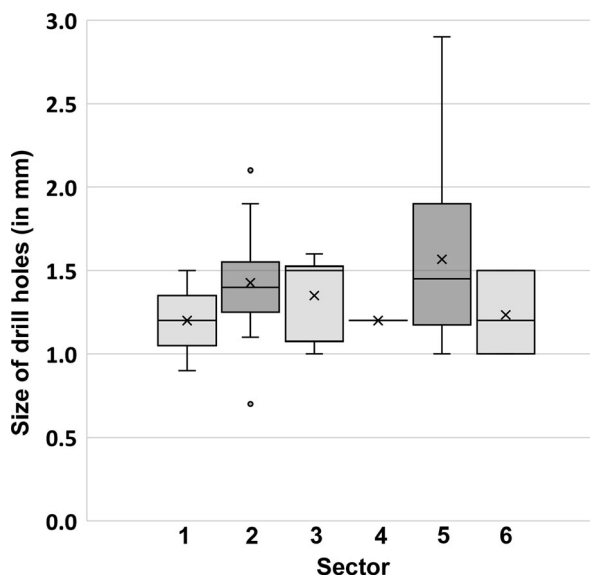


Fig. 3. Box plots showing the distribution of drill-hole size (diameters) within each sector. Horizontal line within the box represents the median, x represents the mean, box represents central 50% of the data, and whiskers represent the observed range except the whiskers of Sector 2, which exclude two data points (outliers) denoted by circle.

shell or an uncomplete diagenetic recrystallisation of a former completely aragonitic shell as it is typical of lucinid bivalves (Taylor *et al.* 1973). In any case, the presence of aragonite points to a relatively low-to-moderate diagenetic overprint. The fill of the shell consists nearly completely of calcite with traces of quartz. Neither pyrite nor apatite could be detected in the examined specimens, even though pyrite is an important constituent of some concretions at Buttenheim (Keupp 2015).

### Discussion

*Parasitic versus predatory origin.* – Drill holes can be caused by predators, by parasites or by domicile-seeking organisms (domichnia). Domichnia can be excluded as producer based on the pronounced selectivity alone (almost only *Eothyasira antiqua*) and the fact that we cannot identify any possible species present in the Buttenheim clay pit potentially having this lifestyle. In the fossil record, it is difficult to distinguish predatory drill holes from parasitic ones. Kelley & Hansen (2003, p. 115) and Klompmaker *et al.* (2016, table 4; 2019, p. 482–484) summarised criteria to differentiate predatory drill holes from parasitic and other kind of drill holes. Accordingly, the drill holes in *Eothyasira* shells from Buttenheim are most likely predatory in origin. This is supported by the shape of the drill holes, which is parabolic in cross section and has a circular outline, the absence of drill holes passing through both valves, a non-random distribution of drill holes on the shell surface and the perpendicular penetration of the shell surface. Additionally, according to Klompmaker *et al.* (2016, 2019) the absence of healing blisters and the scarcity of multiple drill holes on single specimens argue against a parasitic origin of the drill holes. Klompmaker *et al.* (2019) suggested that the drill holes located on soft tissue are more likely to be predatory in origin and that drill holes in animals with more soft tissue (e.g. molluscs compared with echinoderms or brachiopods) are more likely to be predatory in origin. The list of criteria for predatory drill holes (e.g. Klompmaker *et al.* 2019) includes also the absence of circular scars around the hole on

Table 1. Distribution of the drill holes among the sectors according to their size

Drill-hole size	Sector 1	Sector 2	Sector 3	Sector 4	Sector 5	Sector 6
Large ( $\geq 1.4$ mm)	1	15	6	0	12	1
Small ( $< 1.4$ mm)	5	10	4	2	6	2

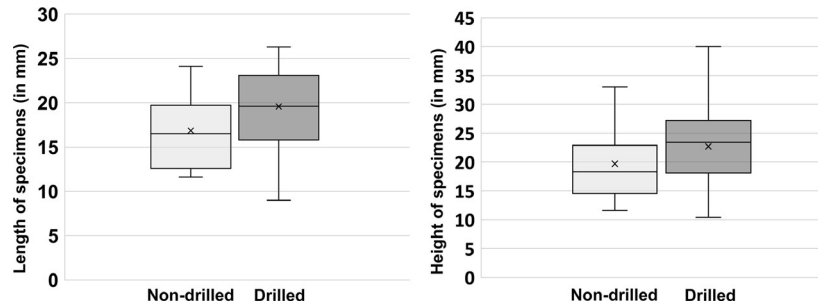


Fig. 4. Box plots showing length (on the left) and height (on the right) distributions of the drilled and non-drilled specimens. Horizontal line within the box represents the median, x represents the mean, box represents central 50% of the data, and whiskers represent the observed range.

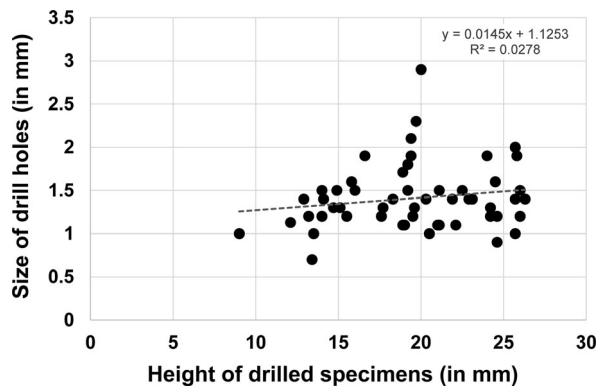


Fig. 5. Size of drill holes vs. height of the drilled specimens. The dashed line represents the linear regression line.

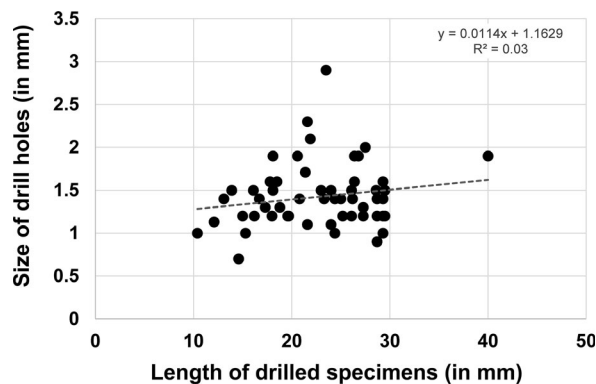


Fig. 6. Size of drill holes vs. length of the drilled specimens. The dashed line represents the linear regression line.

the shell of the prey, because such scars are more characteristic of parasite activities, for instance the holes produced by certain eulimid gastropods on the coronas of sea urchins (Neumann & Wisshak 2009). Such scars are not present in the Buttenheim material. It is, however, remarkable that five *Eothisyris* specimens exhibit small pits around the drill holes. Only in one specimen (SNSB-BSPG 2011 XI 534), similar, but slightly larger, pits are located also in

other parts of the shell (Fig. 7A). In this specimen, the left valve exhibits two drill holes and the small pits. In the other specimens, the small pits are restricted to the area around the drill holes. This suggests a direct relationship between the pits and the drill hole. Most likely, the small pits were produced by acid secreted by the predator. An alternative, less likely explanation would be that they are attachment scars of a parasite.

The fact that all *Eothisyris* specimens exhibiting drill holes are preserved with articulated valves could suggest that the holes were made by a parasite. One would expect that a bivalve dies after a successful attack by a predator, and thus, the two valves gape because the ligament opens the valves once the adductor muscles have been weakened and deactivated. A parasitic attack does not generally cause the death of the host. In the case of the specimens from Buttenheim, the infaunal bivalves were clearly attacked within the sediment, when the bivalves were still alive. All palaeoecological data (e.g. co-occurrence and diversity of infaunal and epifaunal taxa, ichnofauna) point to a soft, but not soupy substrate (Karapunar *et al.* 2020). Thus, the lateral pressure of the sediment on the shell was obviously sufficient enough to prevent the gaping of the valves after death of the bivalve. Therefore, the preservation as articulated valves is insufficient as an argument against a predatory origin of the drill holes.

In conclusion, a parasitic origin of the studied drill holes cannot be excluded but is clearly less likely than a predatory origin.

*Drilling efficiency.* – Eight specimens possess two drill holes, seven of which consist of one small and one relatively large drill hole, which suggests that in most cases, the holes were produced by different individuals. It is hard to say whether the boreholes were produced simultaneously or subsequently. It is possible that after successful drilling, the first predator was disturbed and replaced by another, larger

predator (see Kelley & Hansen 2003, p. 120 for other explanations of this phenomenon). In the case of the specimen with two equally sized drill holes, these might have been produced one after the other by the same individual. It is known that modern drill-hole producers (e.g. naticids; Kitchell *et al.* 1981, p. 539) are unable to re-occupy their own previous drill holes. Nevertheless, the absence of incomplete drill holes suggests that the drill-hole producer of Büttenheim was highly efficient.

*Site selectivity.* – The drill holes in *Eothyasira* show a non-random distribution and are concentrated on the central part of the shell (sectors 2 and 5 in Fig. 2), suggesting a site selectivity. The shell thickness of *Eothyasira antiqua* shows little variation across the shell except for a slight thickening at the umbo. Therefore, the observed site selectivity cannot be explained by preferred drilling of thin regions to lower the cost of drilling. The central shell region of *Eothyasira antiqua* represents the region where the inflation of the shell is highest and the bulk of the soft tissue can be expected. In Recent *Mytilus edulis*, the region with the digestive gland, representing the richest source of glycogen and thus the highest energy content, is the shell part most affected by drill holes (Hughes & Dunkin 1984, p. 63). Possibly the predator on *Eothyasira* was also able to trace the soft parts richest in nutrients as some Recent muricids do (Hughes & Dunkin 1984). Naticid gastropods produce drill holes preferably in the umbonal or central shell regions of their bivalve prey and are thought to be site-selective (Harper & Kelley 2012; see also Calvet 1992 for an alternative view). The drill holes *O. simplex* and *O. paraboloides* in the astartid *Neocrassina subdepressa* from the Oxfordian of Kachchh, India, occur also in the central shell part (Bardhan *et al.* 2012), which is very similar to the site selectivity observed in *Eothyasira*.

One might expect that site selectivity improves and changes with increasing age of the predator (e.g. Hughes & Dunkin 1984, table 2). Consequently, the distribution of drill holes among the sectors should change with respect to their size and frequency. Consistent with this assumption, the distribution of the two drill-hole size classes differs slightly among the six sectors and the drill-hole frequency of the larger size class increases in sectors 2 and 5 (Table 1). The difference of the frequency distribution of drill holes between the two drill-hole size classes is not statistically significant. If there is an improvement in site selection with age, the mean size of drill holes can be expected to be larger in the sectors favoured by the predator. As expected, the mean drill-hole size is larger in sectors 2 and 5 (Fig. 3). Observations on site

selectivity of naticid drill holes show a variability, which is not in accordance with a hypothetical site optimum concerning cost vs. benefit calculation for the predator (Kitchell 1986). According to Kitchell (1986), the variance of sites among the individuals remains low and the energetic return for the predator is, nevertheless, substantially higher than a generally random siting behaviour.

What is here called ‘improvement in site selectivity’ based on the concentration of larger drill holes on certain sectors might be related to the anatomy of the predator rather than a learning behaviour. The Recent naticid gastropod *Naticarius hebraeus* grabs its bivalve prey from its ventral margin with its mesopodium, so its boring organ is mostly positioned near the umbonal region (Calvet 1992). Therefore, the position of the drill hole changes with regard to the size of the predator or/and prey. Such grabbing behaviour of the predator might also explain why the dorsal flank part of the *Eothyasira* shells studied (sectors 1, 2, 3) shows a higher frequency of drill holes than the lower (ventral) part (sectors 4, 5, 6) (64% vs. 36%, Fig. 2), although the dorsal part has a smaller shell area. An alternative explanation would be that the predator was living at a shallower depth within the sediment than its prey and started the attack on the prey from above. Therefore, the upper (dorsal) shell sectors of the prey might be concerned more often than the lower (ventral) ones. This would be consistent with the likely life position of *Eothyasira antiqua*, if this is interpreted similar to that of modern and Cretaceous Thyasiridae (e.g. Kauffmann 1969), that is with the umbo facing upwards and the sagittal plane perpendicular to the substrate surface. On the other side, the drilling of holes by naticid and muricid gastropods is known to be time-consuming requiring up to a few days (Kitchell 1986) and a strong fixation of the predator on its prey. In bivalves, this is provided on the flank centres rather than on the umbonal part of the shell.

The concentration of the drill holes in more central parts of the shell clearly points to a gastropod producer rather than to a member of another drilling group. For instance, octopods and flatworms use the strategy to inject a poison through the drill hole to relax the muscles of the bivalve and to open its valves (Nixon & Maconnachie 1988; Kabat 1990). Consequently, the drill holes made by octopods are concentrated on the region of the adductor muscles (Cortez *et al.* 1998), which in *Eothyasira* shows the lowest number of attacks (sectors 4 and 6 in Fig. 2). The predator of *Eothyasira* has obviously not drilled the shell to open the valves but to digest the soft tissues through the drill hole, while the prey was still within

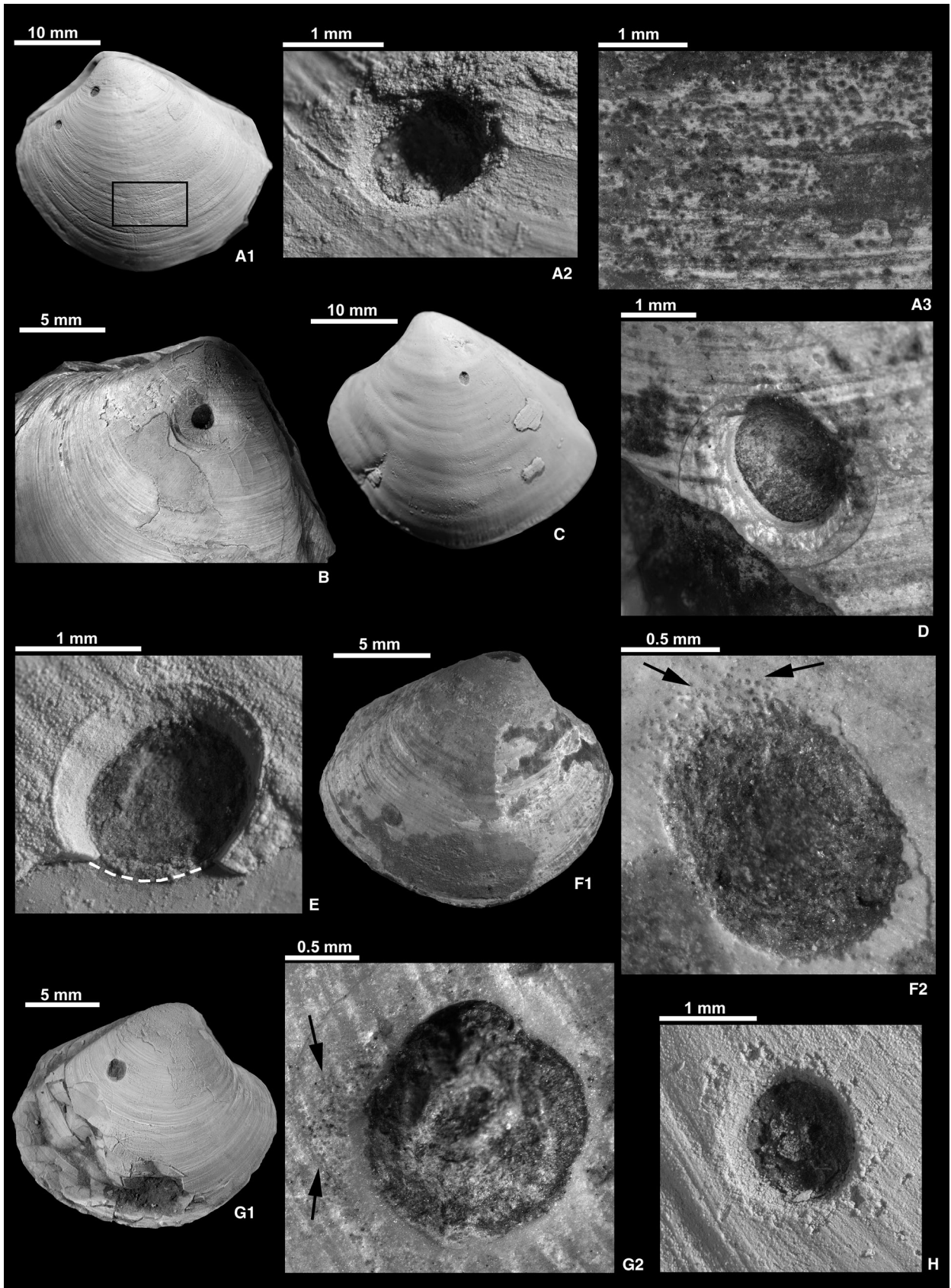




Fig. 7. *Eothisyris antiqua* (Münster in Goldfuss, 1841) specimens from the Upper Pliensbachian (Spinatum Zone), Buttenheim. Specimens coated with ammonium chloride unless stated otherwise. A1–3, articulated specimen SNSB-BSPG 2011 XI 534. A1, left valve view; framed area: see A3. A2, detail of A1 showing upper drill hole. A3, detail of A1 showing small pits on the flank (not coated with ammonium chloride). B, articulated specimen SNSB-BSPG 2011 XI 264, left valve view; note that the periphery of the drill hole is crushed. C, internal mould SNSB-BSPG 2011 XI 626 possessing a hole corresponding to the position of a drill hole; left valve view. D, articulated specimen SNSB-BSPG 2011 XI 265 (not coated with ammonium chloride), detail of right valve showing a circular drill hole; the dark-coloured thin ring around the drill hole is a sediment-filled micro-crack formed by compaction. E, articulated specimen SNSB-BSPG 2011 XI 975, right valve view; dashed line indicates the border between drill hole and internal mould. F1–2, articulated specimen SNSB-BSPG 2011 XI 970, right valve view. F2, detail of F1, arrows pointing small pits near drill hole. G1–2, articulated specimen SNSB-BSPG 2011 XI 963, right valve view. G2, detail of G1, arrows pointing small pits near drill hole. H, articulated specimen SNSB-BSPG 2011 XI 976, detail of left valve view showing a drill hole.

the sediment. Such a behaviour has been so far observed only in naticids (Carriker 1981; Kabat 1990).

**Prey selection.** – The focus of the drilling activity on a single taxon from the Buttenheim clay pit (among 57 bivalve taxa and ca. 7,000 examined specimens) and the absence of drill holes in other taxa except in a single specimen of *Neocrassina gueuxii* (d'Orbigny, 1850) (Fig. 8B) point to a pronounced prey-selective behaviour of the predator. A single drill hole was found on a shell of the small gastropod *Levipleura blainvillei* (Münster in Goldfuss, 1844). However, having a diameter of 0.35 mm (Fig. 8A1,A2) it is clearly not the product of the same predator that drilled *Eothisyris* (with drill-hole diameter of 0.7–2.9 mm).

The absence of incomplete drill holes in *Eothisyris* suggests that the predator was very successful and experienced unlike the predator in the Late Triassic Cassian Formation, where multiple unsuccessful attempts (incomplete drillings) are not uncommon (Klomp maker *et al.* 2016). Drill holes in one of the paralectotypes of *Eothisyris antiqua* from Altdorf (SNSB-BSPG AS VII 2035) and in the figured specimen of Kuhn (1936) from Neumarkt (SNSB-BSPG 1935 I 518) show that drilled specimens of this species are not restricted to Buttenheim. Drill holes

in *E. antiqua* seem to be a general phenomenon in the Amaltheenton Formation of Franconia. Such a focus of drilling activity on a single taxon has not yet been recorded in the Early Mesozoic, and such a high drilling frequency within a single species (81% of the well-preserved *Eothisyris* specimens) is even rare among Recent bivalve communities (e.g. Vermeij *et al.* 1989). In a study on Upper Jurassic bivalves from Kachchh (India), Bardhan *et al.* (2012) could show prey selection by probable gastropod predators. In their example, the shallow infaunal astartid *Neocrassina* is the most drilled taxon of the fauna. However, the within-species frequency of drilled *Neocrassina* specimens is about 30% and thus significantly lower than the frequency of drilled *Eothisyris* specimens (81%). It is interesting to note that none of the articulated *Neocrassina* specimens from Kachchh exhibit drill holes (Bardhan *et al.* 2012), which is in contrast to the *Eothisyris* specimens of our study.

The drilling frequency might be overestimated, if a study is based on articulated specimens and if non-drilled preys were removed by durophagous predators ('durophagy bias', Smith *et al.* 2019). However, durophagy bias is absent or did play only a minor role because *Eothisyris* was living moderately deep within the sediment (probably up to 10 cm below the sediment-water interface). *Eothisyris* specimens

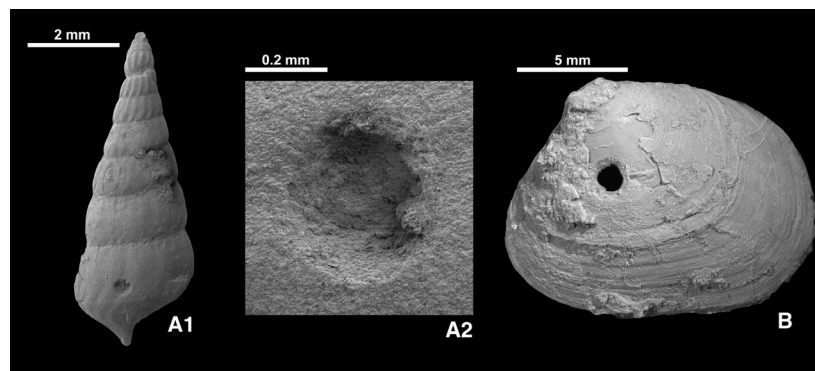


Fig. 8. Drill holes found in taxa other than *Eothisyris* from the Upper Pliensbachian (Spinatum Zone) of Buttenheim. A1–2, *Levipleura blainvillei* (Münster in Goldfuss, 1844) SNSB-BSPG 2011 XI 1051, SEM picture. A2, detail of A1. B, *Neocrassina gueuxii* (d'Orbigny, 1850), left valve SNSB-BSPG 2011 XI 260, external view.

have only been found in the uppermost 5–6 m of the Amaltheenton Formation exposed in the Buttenheim clay pit (below and in the echinid–pectinid horizon; Karapunar *et al.* 2020, text-fig. 2). The studied *Eothisira* specimens and hence the observed drilling frequency (81%) are time-averaged. Time-averaging affects drilling frequency only if the non-drilled shells are removed from the assemblage either by durophagous predators (durophagy bias) or by differential preservation (if the non-drilled ones are not preserved). As mentioned above, durophagy bias can be excluded and there is no hint for a differential preservation of *Eothisira* specimens; therefore, the drilling frequency is not considered overestimated due to time-averaging. In contrast, the observed drill-hole frequency regarding the overall assemblage (56 drilled out of altogether 7,000 bivalve specimens, ca. 0.8%) is rather underestimated due to the fact that the studied bivalves have been collected not only from the uppermost 5–6 m of the section where *Eothisira* has yet been found but throughout the whole 35-m-thick section (Karapunar *et al.* 2020).

Harper *et al.* (1998) reported drill holes in different taxa from the Early Jurassic of the United Kingdom and Ireland. Of these, the epifaunal bivalve *Harpax spinosus* and the infaunal bivalves *Palaeonucula hammeri* and *Neocrassina gueuxii* are also present in Buttenheim. We have only one complete specimen of *Palaeonucula hammeri* from the Buttenheim clay pit, albeit without a drill hole. Not a single drilled specimen of *Harpax spinosus* has been found at Buttenheim, although it is the most abundant species in this clay pit. All the drill holes reported by Harper *et al.* (1998) belong to the ichnospecies *Oichnus simplex*, which is characterised by straight-sided, non-parabolic holes. In contrast, the drill holes in *Eothisira antiqua* are of the naticid type and can be attributed to *Oichnus paraboloides*. The absence of drill holes in *Harpax spinosus*, the most abundant taxon in the clay pit, and the differences in the shape of the drill holes suggest that the predator(s) producing the drill holes in the Pliensbachian of the United Kingdom and the predator in Franconia belong to different taxa.

Aberhan *et al.* (2011) mentioned drill holes in infaunal bivalves from the Pliensbachian Amaltheenton Formation of northern Germany without, however, indicating the exact shape of the drill holes. The drill holes are found in a specimen of the shallow infaunal *Neocrassina gueuxii* and in specimens of the deep infaunal *Pholadomya ambigua* and *Pleuromya costata*. These three taxa occur also at Buttenheim, but are represented by a single (*P. ambigua*) or only very few specimens (*N. gueuxii*, *P. costata*). Only one of eleven specimens of *Neocrassina gueuxii* exhibits a

naticid-like drill hole, the specimens of other taxa lack drill holes. It is not clear whether the producers of the drill holes from the Pliensbachian of northern Germany and southern Germany belong to the same taxon. It is noteworthy that the drilled taxa reported by Aberhan *et al.* (2011) and *Eothisira antiqua* are relatively large infaunal species among the Amaltheenton bivalves – generally, most of these species are small. If the drill holes were produced by the same predator, it might point to a size selectivity. Even the smallest drilled *E. antiqua* specimen (9 mm in height) is larger than most of the other infaunal species from the Buttenheim clay pit (mostly nuculanids, nuculids and small astartids). However, the Kolmogorov–Smirnov test suggests no significant difference in the size-frequency distribution between non-drilled and drilled *Eothisira* specimens, and thus no intraspecific size selectivity among *Eothisira* specimens. There is a weak positive association between the size of the drilled specimens and the size of the drill holes (Figs 5–6), which suggests that the large predators preferred larger prey. However, the Spearman rank correlation test does not show a significant correlation between the drilled prey and drill-hole size (predator size). Therefore, it cannot be assumed with certainty that a larger predator prefers a larger prey.

It is interesting to note that one relatively large infaunal taxon from Buttenheim, the lucinid *Mactromya cardioideum*, does not exhibit drill holes. On the one hand, this species is distinctly larger than most of the *Eothisira* specimens but has a much more inflated shell and thus more voluminous soft parts than most of the *Eothisira* specimens. On the other hand, the shell of *Mactromya* is distinctly thicker than that of *Eothisira*. The costs of drilling through a *Mactromya* shell were obviously higher for the predator, which may explain the lack of drill holes in this taxon. It is also possible that the drill holes are not detected due to the rare occurrence of *Mactromya* in Buttenheim (only five specimens out of approximately 7,000 bivalve specimens have been reported; Karapunar *et al.* 2020). As the strength of the commarginal ornamentation of the drilled specimen of *Neocrassina* is similar to that of *Mactromya*, the ornamentation style cannot explain the lack of drilling attacks in *Mactromya* (see also below).

Some of our results are in contrast with the results of studies of younger faunas. For instance, Leonard-Pingel & Jackson (2013) documented a significantly higher drilling frequency in smaller, shallow infaunal specimens than in larger, deeper burrowing specimens. Additionally, bivalves with a stronger ornamentation seem to have been attacked more frequently than smooth or weakly ornamented ones

(see also, e.g., Robba & Ostinelli 1975; Vermeij 1980). The reason for that phenomenon is not clear, but ornamentation might provide better fixation for grabbing the prey. The peculiar record of drill holes from the Buttenheim clay pit (e.g. lack of drill holes in very shallow infaunal species and in the epifauna, restriction to a single deeper burrowing species, and a relatively large prey taxon) points, again, to a unique predator–prey relationship and to a very specialised predator.

Recent and Cretaceous representatives of the genus *Thyasira* preferably occur in dark clays/claystones, occasionally in mud/shaly mudstones. These bivalves live(d) deeply buried, up to ten times their shell length below the sediment–water interface, connected by a particle-coated inhalant tube with the seawater (Kauffmann 1969). Adaptations in the soft part organisation allow these bivalves a life in oxygen-poor, hydrogen sulphide-rich environments not accessible for many other molluscan species (for details, see Allen 1958; Kauffmann 1969). Similar parameters are assumed to have at least periodically prevailed in the Amaltheenton environment at Buttenheim, especially in fine-grained sediments few millimetres below the sediment–water interface (Nützel & Gründel 2015; Karapınar *et al.* 2020). The scarcity of other deep infaunal species at Buttenheim, such as the genera *Pholadomya*, *Pleuromya*, *Gresslya*, supports such restricted, limiting conditions. Apart from the shell size, it is therefore possible that *Eothyasira antiqua* may have been the exclusive food source for a predator occupying a relatively deep infaunal tier where food in the form of infaunal shelly taxa was limited. This may also explain the lack of drill holes in other species.

The drill-hole record of Recent and fossil thyasirids is, to our knowledge, relatively poor. Houart & Sellanes (2006) reported drill holes in *Thyasira methanophila* from a chemosymbiotic cold seep community off Chile. This species exhibits a relatively high rate of attacks (about 27% of the individuals show drill holes), whereas one other bivalve (*Calyptogena gallardoii*) shows only few drill holes (2% of individuals with sign of attack, of which only half of them were with complete drill holes), all other bivalve species at this site (other vesicomyid species) do not show signs of attacks. The authors assumed trophonin gastropods (family Muricidae) as producer of these drill holes. These gastropods are vagrants and occur at such cold seep sites and in other deep water environments. The prey selection and the high drill-hole rate in *Thyasira methanophila* are explained by the thin shell of the thyasirid. All other bivalves at this site exhibit thicker shells. This may in part coincide with the situation in the

Buttenheim clay pit, where the predator selected its prey according to the shell size and to the shell thickness, both strategies to optimise the cost/benefit ratio.

It remains unclear how the predator of *Eothyasira* selected its favoured prey. Prey selection is a common feature in Recent gastropods and may be innate or acquired relatively fast by experience (e.g. Croll 1983 and references therein). For the localization of the potential food, the gastropods use mainly chemical cues, but also taste and smell (Croll 1983). *Eothyasira* had a moderately deep to deep infaunal life habit, which can be assumed also for the predator. The location of the prey within the sediment was certainly detected mainly using a chemosensor. One can speculate whether the localisation of *Eothyasira* and the differentiation from other potential prey were enhanced by the chemosymbiotic life style of the lucinid. In Recent communities, lucinids are known to be more commonly attacked than venerids of similar size and ornamentation. This has, however, been interpreted as being mainly the result of differences in the life habit and sediment type (e.g. Leonard-Pingel & Jackson 2013).

*Producer of the Eothyasira drill holes.* – The producer of the drill holes in *Eothyasira antiqua* made naticid-like holes, preferred the central parts of the shell flanks and a relatively large infaunal prey. These characteristics point to a gastropod as culprit, particularly a member of the family Naticidae. As mentioned above, this family had been known only from the Cretaceous onwards. Recently, Das *et al.* (2019) documented the occurrence of naticid gastropods together with naticid-type drill holes from the Oxfordian of Kachchh and suggested naticids as the culprit for the drill holes in gastropod and bivalve shells found there. This would extend the record of naticids back to the Upper Jurassic. However, the preservation of this gastropod material does not allow for a certain assignment to this family, especially given the fact that the bulbous, smooth shells typical of modern naticids repeatedly occur in unrelated gastropod groups (this is by the way reflected by the extensive use of the genus name *Natica* in the historical literature for shells as old as Palaeozoic). The strong recrystallization of the alleged Upper Jurassic naticid material does not show the larval shell morphology and ontogenetic boundaries in sufficient detail. Anyhow, the alleged first appearance date of Naticidae from the Upper Jurassic is still long after the present Pliensbachian drill-hole occurrences reported herein. The Lower Jurassic gastropod fauna from Franconia does not yield gastropod taxa of the family Naticidae nor taxa with a naticid morphology (Nützel &

Gründel 2015), maybe with the exception of *Hayamia reticulata* (Münster in Goldfuss, 1844) (see below). A further argument against a naticid culprit in Buttenheim may be also the fact that naticids do not live in soft silty substrates, as assumed for the Amaltheenton Formation at Buttenheim, but in slightly coarser, more stable sediments (Yochelson *et al.* 1983, p. 12; Maxwell 1988, p. 31). It is probable that the naticid-type drilling behaviour (i.e. using a radula and acids to create a circular hole, while the prey was in the sediment and to digest the soft parts through the drill hole) evolved independently within different extinct gastropod lineages (see also Fürsich & Jablonski 1984) and did not become widespread until the expansion of the family Naticidae.

It remains questionable whether one of the about fifty gastropod taxa described from the Amaltheenton Formation of Franconia was the producer of the drill holes in *Eothisyris*. To delimit the number of possible gastropod taxa, the positive correlation of the size of the drill hole with the predator size can be used as an indicator (Klompemaker *et al.* 2017), as already tested in naticids (Kitchell *et al.* 1981; Kitchell 1986) and muricids (Carriker & Gruber 1999). The outer diameter of the drill holes in *Eothisyris* changes between 0.7 and 2.9 mm with an arithmetic mean and median of 1.4 mm. An estimation of the size of the culprit by using the drill-hole diameter based on data from Recent gastropods (Kitchell *et al.* 1981) points to a shell size of about 2–3 cm of the drill-hole producer in question – this excludes most of the gastropod species from Buttenheim because their adult size is considerably smaller, commonly smaller than 10 mm (Nützel & Gründel 2015). Two gastropod species at Buttenheim fall into this size range: the ptychomphalid gastropod *Angulomphalus expansus* (J. Sowerby, 1821) and the neritopsid gastropod *Hayamia reticulata* (Münster in Goldfuss, 1844). Ptychomphalids are an extinct group, their closest Recent relatives are the members of the family Pleurotomariidae, which are feeding on sponges, tunicates and corals (Hickman 1984). *Pleurotomaria amalthei* Quenstedt, 1858 is present in Buttenheim (Nützel & Gründel 2015), but none of the Recent members of this group have ever been reported as active predators. Ptychomphaloid gastropods are generally interpreted as epifaunal algal grazers (e.g. *Rhaphistomella radians* in Fürsich & Wendt 1977). About 600 *Angulomphalus expansus* specimens (out of ca. 7,100 gastropod specimens) have been reported from Buttenheim clay pit by Nützel & Gründel (2015), which seems to be a large number for a potential predator compared with the abundance of the prey *Eothisyris* (78 out of ca. 7,000 bivalve specimens; Karapunar *et al.* 2020). To our knowledge, there are no Pleurotomariida or Vetigastropoda that show

drilling behaviour, and therefore, *Angulomphalus expansus* and *Pleurotomaria amalthei* can be excluded. Also, unlike *Eothisyris* these species are not restricted to the upper metres of the section exposed in Buttenheim. In gastropods, drilling seems to be restricted to caenogastropods except for the Palaeozoic platyceratids. *Hayamia reticulata*, in contrast, is very rare and represented by only a few specimens. On the one hand, the high whorl expansion rate of *Hayamia reticulata* might imply a high metabolic rate (Vermeij 2002), which suggests an active life style. On the other hand, its umbilicus does not bear a callus, which is expected to be present in gastropods with an infaunal mode of life (Vermeij 2017). However, in this species (also known as *Nerita alternans* Tate, 1876 from the Lias of England), aperture and base of fully grown specimens are insufficiently known. *Hayamia reticulata* was preliminarily classified as Neritimorpha but could also belong to Caenogastropoda (Nützel & Gründel 2015). It co-occurs with *Eothisyris* in the uppermost 5–6 m of the Amaltheenton Formation exposed in the Buttenheim clay pit (J. Schobert, pers. comm. 2020), and its overall low-spined shape resembles that of Naticidae. Schubert *et al.* (2008) reported its presence also in the Amaltheenton of the Bielefeld area, where drilled bivalves has been mentioned by Aberhan *et al.* (2011).

One conspicuous gastropod species from the Buttenheim clay pit is the high-spined *Pseudokatosira undulata* (Benz in Zieten, 1830) representing 1% (70 specimens) of the gastropods analysed in Nützel & Gründel (2015). This species has an aperture about 2 cm across and reaches up to 10 cm in height and is the largest gastropod in this assemblage. It has a stream-lined shell sculpture and a siphon, which indicates that it was able to detect the direction of chemical signals (Vermeij 2007). If this species had an infaunal mode of life, it may have been able to burrow to a depth of around ten centimetres, the maximum depth that an adult *Eothisyris* may have reached (see interpretation above). Another interesting point is that this species is present in other European Lower Jurassic localities from which drill holes have been reported, such as Austria (Hierlatz Limestone; Szabo 2008) and England (Lower Lias of the Dorset coast; Todd & Munt 2010). However, this species has not been found in the uppermost 5–6 m of the Amaltheenton Formation exposed in the Buttenheim clay pit (J. Schobert, pers. comm. 2020), which suggests that it did not coexist with *Eothisyris* at this locality.

*Taphonomy of the drill holes.* – The drill holes from Buttenheim show a remarkable preservational feature: the drill holes are not only recognisable on the

shell but are also visible, at least in some specimens by a depression in the sediment filling of the shell (Fig. 7C, E). This shallow depression has the same diameter as the hole in the shell. Such a depression in the internal mould allows the recognition of a drilling attack even if the shell is no longer present, either due to early dissolution or, more likely, due to loss of the shell after recovering the specimen from the outcrop. The drill holes on 19 specimens (out of 56 drilled specimens) are recognized by the presence of the shallow depression on the sediment fill. These depressions are, of course, diagenetic in origin because the predator certainly did not drill a dead, sediment-filled bivalve. The area immediately beneath the drill hole remained obviously unlithified during the very early diagenetic lithification of the sediment fill that also prevented compaction of the articulated shell. This may be explained by differences in chemical conditions between the shell interior and the surrounding matrix, which today consists of only weakly lithified sediment. It seems that the formation of the internal mould started from the internal surface of the shell and continued to the innermost parts. This also explains why the innermost part of some specimens (e.g. specimen SNSB-BSPG 2011 XI 519) remained unlithified. The formation of the internal mould facilitated preservation of the drill holes and of the very thin-shelled *Eothyasira* specimens (shell thickness about 0.3 mm), which might have been otherwise destroyed by compactional fracturing. In few specimens, the area immediately around the drill hole exhibits a thin dark-coloured ring (Fig. 7B,D,G2). This is a secondary infill into a micro-crack formed by crushing of the weakened shell after the drilling process, most probably during very early diagenesis.

*Comparison with Triassic drill holes.* – The present drill holes differ from the drill holes reported from the Cassian Formation (Klompaker *et al.* 2016) in that there are no more than two drill holes in any specimen. Moreover, no incomplete drill holes with a central boss were found in the material from Buttenheim studied by us. Such drill holes are made by naticids (Kabat 1990) but have also been reported from Devonian strata (Smith *et al.* 1985). By contrast, multiple drillings are common in fine-grained siliciclastics from the Cassian Formation – there are up to eight drill holes in a single gastropod shell. Both the drill holes in *Eothyasira* and the Cassian taxa were made by an infaunal predator (Fürsich & Jablonski 1984; see also Klompaker *et al.* 2016). If the Triassic drill-hole producer and the Pliensbachian predator are relatives, this suggests a significant increase in the success of making complete drill

holes. It is highly likely that the highly specialised Pliensbachian predator belonged to a group that evolved a drilling behaviour earlier than the Late Pliensbachian. However, there are no indications of any relationship between the Triassic and Early Jurassic drill-hole producers.

*Scarcity of drill holes in the Early Jurassic.* – The general scarcity and patchy occurrence of the drill-hole record in the Triassic and Jurassic has been repeatedly emphasized (e.g. Klompaker *et al.* 2016 with references therein). Some attempts have been made to explain this feature: in terms of a general low abundance of drilling predators at this time (Kowalewski *et al.* 1998), a competition by concurrent durophagous vertebrates (Tackett & Tintori 2019) or by taphonomic processes that masked an actually higher percentage of drilling (Harper *et al.* 1998). The presence of a considerable amount of aragonite (about 40–50%), besides calcite (50–60%), in the shells of *Eothyasira* from Buttenheim might at a first glance support the argument of a diagenetic background for the preservation of drill holes as suggested by Harper *et al.* (1998). However, such favourable diagenetic conditions are present throughout the section exposed in the Buttenheim clay pit. Bivalve shells are commonly very well preserved and can be extracted easily from the poorly lithified sediments. Thus, the Amaltheenton at Buttenheim and other places qualifies as a Liberation Fossilagerstätte sensu Roden *et al.* (2020). If drill holes were present in considerable numbers, they would be easy to detect. The rarity of drill holes among the 7,000 bivalve specimens studied shows that predation pressure by drillers was generally low in the Amaltheenton environment at Buttenheim as was also proposed for the Early Jurassic in general. The nearly exclusive occurrence and the concomitantly high frequency of drill holes in *Eothyasira* clearly show that drilling was executed by a highly specialised predator. This predator obviously focused on an infaunal bivalve prey of a considerable size when compared to other infaunal bivalves from this occurrence. The predator was probably not living at the sediment–water interface but in slightly deeper parts of the fine-grained substrate. *Eothyasira* is considered to represent one of the oldest, if not the oldest known representative of the family Thyasiridae (Karapınar *et al.* 2020). If so, it can be assumed that *Eothyasira* was adapted to environments with oxygen-poor and hydrogen sulphide-rich sediments, which is strongly supported by the dark fine-grained, partly pyrite-rich sediment. The drilling predator could obviously cope with such adverse conditions. Otherwise, it would not

have drilled so successfully its favoured prey (about 81% of the well-preserved *Eothisira* specimens are drilled).

Similar naticid-like drill holes produced probably by an infaunal gastropod have been reported from the Amaltheenton Formation of northern Germany (Aberhan et al. 2011). This occurrence is similar to Buttenheim in that the prey consists exclusively of infaunal bivalves. However, *Eothisira* has not been documented from that region and it is not sure whether the same predator was responsible for both occurrences although *Hayamia reticulata* was reported from there (Schubert et al. 2008). Harper et al. (1998) reported drill holes from sediments of a similar stratigraphicage from England in a variety of infaunal and epifaunal taxa which they identified as *Oichnus simplex*. The producers of the drill holes in Buttenheim and England were obviously not identical. Moreover, none of the many hundred specimens of *Harpax spinosus* from Buttenheim exhibit a drill hole, whereas this species belongs to the attacked species in the Lower Jurassic strata of England (Harper et al. 1998). Obviously, different drilling predators existed within the Early Jurassic benthic faunas, which were, however, partly highly specialised as the Buttenheim example demonstrates. This may in part explain the scarcity of drill holes at that time. Differences exist also to the drilling records from the Carnian Cassian Formation and the Norian Riva di Solto Formation concerning the diversity of infaunal and epifaunal prey and the strategy of the predator (for details, see Fürsich & Jablonski 1984; Klompmaker et al. 2016; Tackett & Tintori 2019). It seems plausible that several gastropod taxa or lineages with drilling ability existed in the Early Mesozoic (drill-hole convergence; Klompmaker et al. 2016). Drilling is, however, not the only way of predation in gastropods. Recent naticids are known to feed also on prey without drilling, for instance by grabbing bivalves and forcing the valves open (Kabat 1990, p. 173). Such predator activity is difficult to demonstrate in the fossil record but may have been a common behaviour in the past.

## Conclusions

- 1 Naticid-like drill holes on the infaunal bivalve *Eothisira antiqua* from the Pliensbachian Amaltheenton Formation are assigned to the ichnospecies *Oichnus paraboloides* Bromley, 1981 and are interpreted as predatory drill holes although a parasitic producer cannot be excluded entirely.
- 2 The distribution of drill holes on the shell is non-random, most being concentrated on the central

region of the shell flank, suggesting that the predator was site-selective.

- 3 The drilling frequency on a single species (81% of the well-preserved articulated *Eothisira antiqua* specimens) and the lack of drill holes in all other bivalve taxa from Buttenheim (with the exception of one *Neocrassina* specimen) show that the predator was highly prey-selective preferring infaunal and relatively large prey.
- 4 Because of the moderately deep infaunal life habit of *Eothisira*, it is suggested that the predator itself lived at least temporarily within the sediment and could cope with the temporarily poorly oxygenated Amaltheenton environment.
- 5 The producer of the naticid-like drill holes was probably a gastropod. None of the about 50 known gastropod taxa of the Amaltheenton Formation can be associated with the drill holes with certainty. Size and the co-occurrence in the uppermost 5–6 m of the Amaltheenton Formation exposed at Buttenheim suggest that the low-spined *Hayamia reticulata* (Münster in Goldfuss, 1844) with *Natica*-like shape, also known from England under the name *Nerita alternans* Tate, 1876, could represent the drill-hole producer. *Pseudokatosira undulata* (Benz in Zieten, 1830) is another possible candidate regarding its size but does not co-occur with *Eothisira* in Buttenheim.
- 6 The occurrence at Buttenheim, where thousands of well-preserved bivalve shells have been examined, supports the opinion that the drill-hole records from the Early Jurassic are generally scarce and the drill-hole production was restricted to rare, highly specialised predators. Preservation biases are considered of only minor importance.

*Acknowledgements.* – We are grateful to the private collector Johann Schobert (Hirschaid) for his untiring efforts in collecting a large amount of fossil specimens including the studied material from Buttenheim and donating them to the BSPG. We thank Rupert Hochleitner, Munich, for X-ray analyses and their interpretation. Gregory Dietl and an anonymous reviewer are acknowledged for their constructive comments, which improved the text.

## References

- Aberhan, M., Scholz, A. & Schubert, S. 2011: Das Ober-Pliensbachium (Domerium) der Herforder Liasmulde-Teil 3-Taxonomie und Paläoökologie der Bivalvia aus der Amaltheenton-Formation (Unterjura) der Herforder Liasmulde. *Geologie und Paläontologie in Westfalen* 80, 61–109.
- Allen, J.A. 1958: On the basic form and adaptations to habitat in the Lucinacea (Eulamellibranchia). *Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences* 241, 421–484.

- Bardhan, S., Chattopadhyay, D., Mondal, S., Das, S.S., Mallick, S., Roy, A. & Chanda, P. 2012: Record of intense predatory drilling from Upper Jurassic bivalves of Kutch, India: Implications for the history of biotic interaction. *Palaeogeography, Palaeoclimatology, Palaeoecology* 317–318, 153–161.
- Bromley, R.G. 1981: Concepts in ichnotaxonomy illustrated by small round holes in shells. *Acta Geologica Hispanica* 16, 55–64.
- Bromley, R.G. 1993: Predation habits of octopus past and present and a new ichnospecies, *Oichnus ovalis*. *Bulletin of the Geological Society of Denmark* 40, 167–173.
- Calvet, C. 1992: Borehole site-selection in *Naticarius hebraeus* (Chemnitz in Karsten, 1789) (Naticidae: Gastropoda)? *Orsis: organismes i sistemes* 7, 57–64.
- Carriker, M.R. 1981: Shell penetration and feeding by naticacean and muricacean predatory gastropods: a synthesis. *Malacologia* 20, 403–422.
- Carriker, M.R. & Gruber, G.L. 1999: Uniqueness of the gastropod accessory boring organ (ABO): Comparative biology, an update. *Journal of Shellfish Research* 18, 579–595.
- Carriker, M.R. & Yochelson, E.L. 1968: Recent gastropod boreholes and Ordovician cylindrical borings. *U.S. Geological Survey Professional Paper* 593B, B1–26.
- Cortez, T., Castro, B.G. & Guerra, A. 1998: Drilling behaviour of *Octopus mimus* Gould. *Journal of Experimental Marine Biology and Ecology* 224, 193–203.
- Croll, R.P. 1983: Gastropod chemoreception. *Biological Reviews* 58, 293–319.
- Das, S.S., Mondal, S., Saha, S., Bardhan, S. & Saha, R. 2019: Family Naticidae (Gastropoda) from the Upper Jurassic of Kutch, India and a critical reappraisal of taxonomy and time of origination of the family. *Journal of Paleontology* 93, 673–684.
- Donovan, S.K. 2017: A plea not to ignore ichnotaxonomy: recognizing and recording *Oichnus* Bromley. *Swiss Journal of Palaeontology* 136, 369–372.
- D'Orbigny, A. 1850: *Prodrome de paléontologie stratigraphique universelle des animaux mollusques & rayonnés* 1, 1–394; 2, 1–428. Masson, Paris.
- Fürsich, F.T. & Jablonski, D. 1984: Late Triassic naticid drillholes: carnivorous gastropods gain a major adaptation but fail to radiate. *Science* 224, 78–80.
- Fürsich, F.T. & Wendt, J. 1977: Biostratigraphy and palaeoecology of the Cassian Formation (Triassic) of the Southern Alps. *Palaeogeography, Palaeoclimatology, Palaeoecology* 22, 257–323.
- Goldfuss, G.A. 1826–1844: *Petrefacta Germaniae*. I (1): I–VIII, 1–76, 1826, I(2), 77–164, 1829; I (3): 165–240, 1831; I (4): 241–252, 1833; II (1): 1–68, 1833; II (2): 69–140, 1835; II (3): 141–224, 1837; II (4): I–III, 225–312, 1841; III 1: 1–20, 166–171, 1841; III (2): 21–28, 1844; III (3): I–IV, 29–128, 1844. Arnz, Düsseldorf.
- Harper, E.M., Forsythe, G.T.W. & Palmer, T. 1998: Taphonomy and the Mesozoic marine revolution; preservation state masks the importance of boring predators. *Palaaios* 13, 352–360.
- Harper, E.M. & Kelley, P.H. 2012: *Treatise on Invertebrate Paleontology*, Part N, Revised, Volume 1, Chapter 22: Predation of bivalves. *Treatise Online* (44), 1–21.
- Harper, E.M. & Wharton, D. 2000: Boring predation and Mesozoic articulate brachiopods. *Palaeogeography, Palaeoclimatology, Palaeoecology* 158, 15–24.
- Hiemstra, A.F. 2015: Recognizing cephalopod boreholes in shells and the northward spread of *Octopus vulgaris* Cuvier, 1797 (Cephalopoda, Octopodoidea). *Vita Malacologica* 13, 53–56.
- Houart, R. & Sellanes, J. 2006: New data on recently described Chilean trophonines (Gastropoda: Muricidae), description of a new species and notes of their occurrence at a cold seep site. *Zootaxa* 1222, 53–68.
- Hughes, R.N. & de Dunkin, S. de B., 1984: Behavioural components of prey selection by dogwhelks, *Nucella lapillus* (L.), feeding on mussels, *Mytilus edulis* L., in the laboratory. *Journal of Experimental Marine Biology and Ecology* 77, 45–68.
- Huntley, J.W. & Kowalewski, M. 2007: Strong coupling of predation intensity and diversity in the Phanerozoic fossil record. *Proceedings of the National Academy of Sciences* 104, 15006–15010.
- Kabat, A.R. 1990: Predatory ecology of naticid gastropods with a review of shell boring predation. *Malacologia: International Journal of Malacology* 32, 155–193.
- Kabat, A.R. 1991: The classification of the Naticidae (Mollusca: Gastropoda): review and analysis of the supraspecific taxa. *Bulletin of the Museum of Comparative Zoology* 152, 417–449.
- Kase, T. & Ishikawa, M. 2003: Mystery of naticid predation history solved: evidence from a 'living fossil' species. *Geology* 31, 403–406.
- Karapınar, B., Werner, W., Fürsich, F.T. & Nützel, A. 2020: Taxonomy and palaeoecology of the Early Jurassic (Pliensbachian) bivalves from Buttenheim, Franconia (Southern Germany). *Palaeontographica Abteilung A* 318, 1–127.
- Kauffmann, E.G. 1969: Form, function, and evolution. N129–N205. In Moore, R. C. (ed): *Treatise on Invertebrate Paleontology*, Part N, Mollusca 6. Bivalvia, Geological Society of America and University of Kansas, Boulder, Colorado, and Lawrence, Kansas.
- Kelley, P.H. 1988: Predation by Miocene gastropods of the Chesapeake Group: stereotyped and predictable. *Palaaios* 3, 436–448.
- Kelley, P.H. & Hansen, T.A. 2003: The fossil record of drilling predation on bivalves and gastropods. In Kelley, P.H., Kowalewski, M. & Hansen, T.A. (eds): *Predator-prey Interactions in the Fossil Record*. Kluwer Academic/Plenum Publishers, New York.
- Kitchell, J.A. 1986: The evolution of predator-prey behavior: naticid gastropods and their molluscan prey. 88–110. In Nitecki, M.H. & Kitchell, J.A. (eds): *Evolution of Animal Behavior: Paleontological and Field Approaches*. Oxford University Press, New York.
- Kitchell, J.A., Boggs, C.H., Kitchell, J.F. & Rice, J.A. 1981: Prey selection by naticid gastropods: experimental tests and application to the fossil record. *Paleobiology* 7, 533–552.
- Klompaker, A.A., Karasawa, H., Portell, R.W., Fraaije, R.H. & Ando, Y. 2013: An overview of predation evidence found on fossil decapod crustaceans with new examples of drill holes attributed to gastropods and octopods. *Palaaios* 28, 599–613.
- Klompaker, A.A., Nützel, A. & Kaim, A. 2016: Drill hole convergence and a quantitative analysis of drill holes in mollusks and brachiopods from the Triassic of Italy and Poland. *Palaeogeography, Palaeoclimatology, Palaeoecology* 457, 342–359.
- Klompaker, A.A., Kowalewski, M., Huntley, J.W. & Finnegan, S. 2017: Increase in predator-prey size ratios throughout the Phanerozoic history of marine ecosystems. *Science* 356, 1178–1180.
- Klompaker, A.A., Kelley, P.H., Chattopadhyay, D., Clements, J.C., Huntley, J.W. & Kowalewski, M. 2019: Predation in the marine fossil record: studies, data, recognition, environmental factors, and behavior. *Earth-Science Reviews* 194, 472–520.
- Kowalewski, M. 2002: The fossil record of predation: an overview of analytical methods. *The Paleontological Society Papers* 8, 3–42.
- Kowalewski, M., Dulai, A.D. & Fürsich, F.T. 1998: A fossil record full of holes: the Phanerozoic history of drilling predation. *Geology* 26, 1091–1094.
- Kuhn, O. 1936: Die Fauna des Amaltheentons (Lias delta) in Franken. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, Abteilung B* 75, 231–311.
- Leonard-Pingel, J.S. & Jackson, J.B. 2013: Drilling intensity varies among Neogene tropical American Bivalvia in relation to shell form and life habit. *Bulletin of Marine Science* 89, 905–919.
- Matsukuma, A. 1978: Fossil boreholes made by shell-boring predators or commensals, part I: boreholes of capulid gastropods. *Venus* 37, 29–45.
- Maxwell, P.A. 1988: Late Miocene deep-water Mollusca from the Stillwater Mudstone at Greymouth, Westland, New Zealand: paleoecology and systematics. *New Zealand Geological Survey Bulletin* 55, 1–120.
- McRoberts, C.A. & Blodgett, R.B. 2000: Late Triassic (Norian) mollusks from the Taylor Mountains Quadrangle,

- southwestern Alaska. *US Geological Survey Professional Paper* 1662, 55–67.
- Neumann, C. & Wisshak, M. 2009: Gastropod parasitism on Late Cretaceous to Early Paleocene holasteroid echinoids – Evidence from *Oichnus halo* sp. n. *Palaeogeography, Palaeoclimatology, Palaeoecology* 284, 115–119.
- Newton, C.R., Whalen, M.T., Thompson, J.B., Prins, N. & Delalla, D. 1987: Systematics and paleoecology of Norian (Late Triassic) bivalves from a tropical island arc: Wallowa Terrane, Oregon. *Journal of Paleontology* 61, 1–83.
- Nixon, M. & Macconnachie, E. 1988: Drilling by *Octopus vulgaris* (Mollusca: Cephalopoda) in the Mediterranean. *Journal of Zoology* 216, 687–716.
- Nützel, A. & Gründel, J. 2015: Early Jurassic (Pliensbachian) gastropods from Franconia, Southern Germany. *Palaeontographica Abteilung A* 305, 1–89.
- Robba, E.O.F. 1975: Studi paleoecologici sul Pliocene Ligure I. Testimonianze di predazione sui molluschi Pliocenici di Albenga. *Rivista Italiana di Paleontologia* 81, 309–371.
- Roden, V.J., Hausmann, I.M., Nützel, A., Seuss, B., Reich, M., Urlichs, M., Hagdorn, H. & Kiessling, W. 2020: Fossil liberation: a model to explain high biodiversity in the Triassic Caspian Formation. *Palaeontology* 63, 85–102.
- Schubert, S., Gründel, J. & Nützel, A. 2008: Early Jurassic (Upper Pliensbachian) gastropods from the Herforder Liasmulde (Bielefeld, Northwest Germany). *Paläontologische Zeitschrift* 82, 17–30.
- Smith, S.A., Thayer, C.W. & Brett, C.E. 1985: Predation in the Paleozoic: Gastropod-like drillholes in Devonian brachiopods. *Science* 230, 1033–1035.
- Smith, J.A., Dietl, G.P. & Handley, J.C. 2019: Durophagy bias: the effect of shell destruction by crushing predators on drilling frequency. *Palaeogeography, Palaeoclimatology, Palaeoecology* 514, 690–694.
- Sohl, N.F. 1969: The fossil record of shell boring by snails. *American Zoologist* 9, 725–734.
- Sowerby, J. 1812–1822: *The Mineral Conchology of Great Britain*, volume 1–4, pls 1–383 Meredith, London.
- Sowerby, J. de C. 1823–1846: *The Mineral Conchology of Great Britain*, volume 5–7, pls 384–648. Meredith, London.
- Szabo, J. 2008: Gastropods of the Early Jurassic Hierlatz Limestone Formation; part 1: a revision of the type collections from Austrian and Hungarian localities. *Fragmenta Palaeontologica Hungarica* 26, 1–108.
- Tackett, L.S. & Tintori, A. 2019: Low drilling frequency in Norian benthic assemblages from the southern Italian Alps and the role of specialized durophages during the Late Triassic. *Palaeogeography, Palaeoclimatology, Palaeoecology* 513, 25–34.
- Tate, R. 1876: Class Gasteropoda 331–356. In Tate, R. & Blake, J.F. (eds): *The Yorkshire Lias*. John Van Voorst, London.
- Taylor, J.D., Kennedy, W.J. & Hall, A. 1973: The shell structure and mineralogy of the Bivalvia. II. Lucinacea-Clavagellacea, Conclusions. *The Bulletin of the British Museum (Natural History)* 22, 253–294.
- Todd, J.A. & Munt, M.C. 2010: 10. Mollusca - Gastropods. 147–168. In Lord, A.R. & Davis, P.G. (eds): *Fossils from the Lower Lias of the Dorset Coast. Field Guide to Fossils*. The Palaeontological Association, London.
- Vermeij, G.J. 1977: The Mesozoic marine revolution: evidence from snails, predators and grazers. *Paleobiology* 3, 245–258.
- Vermeij, G.J. 1980: Drilling predation of bivalves in Guam: Some paleoecological implications. *Malacologia* 19, 329–334.
- Vermeij, G.J. 2002: Characters in context: molluscan shells and the forces that mold them. *Paleobiology* 28, 41–54.
- Vermeij, G.J. 2007: The ecology of invasion: acquisition and loss of the siphonal canal in gastropods. *Paleobiology* 33, 469–493.
- Vermeij, G.J. 2017: Shell features associated with the sand-burying habit in gastropods. *Journal of Molluscan Studies* 83, 153–160.
- Vermeij, G.J., Dudley, E. & Zipser, E. 1989: Successful and unsuccessful drilling predation in Recent pelecypods. *The Veliger* 32, 266–273.
- Wisshak, M., Kroh, A., Bertling, M., Knaust, D., Nielsen, J.K., Jagt, J.W., Neumann, C. & Nielsen, K.S. 2015: In defence of an iconic ichnogenus—*Oichnus Bromley*, 1981. *Annales Societatis Geologorum Poloniae* 85, 445–451.
- Yochelson, E.L., Dockery, D. & Wolf, H. 1983: Predation on Sub-Holocene Scaphopod Mollusks from Southern Louisiana. *Geological Survey Professional Paper* 1282, 1–13.
- von Zieten, C.H. 1830–1833: Die Versteinerungen Württembergs. i–viii + 1–16, pls 11–12 (1830); 17–32, pls 13–24 (1831); 33–64, pls 25–48 (1832); 65–102, pls 49–72 (1833). Schweizerbart, Stuttgart.
- Zonneveld, J.P. & Gingras, M.K. 2014: Sedilichnus, Oichnus, Fos-sichnus, and Tremichnus: ‘small round holes in shells’ revisited. *Journal of Paleontology* 88, 895–905.

## Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Size measurements of *Eothisyris* specimens and the drill holes.