

Record of intense predatory drilling from Upper Jurassic bivalves of Kutch, India: Implications for the history of biotic interaction

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ARTICLE INFO

Article history:

Received 30 August 2011

Received in revised form 15 December 2011

Accepted 2 January 2012

Available online 8 January 2012

Keywords:

Drilling predation

Bivalve prey

Jurassic

Mesozoic marine revolution

ABSTRACT

The study of past biotic interactions is important not only to understand the paleoecological history of a community, but also to test the evolutionary role of such interactions. Drill holes in invertebrate exoskeletons provide one of the very few scenarios where biotic interaction could be studied directly and the related hypotheses could be tested with statistical rigor. Hence, the documentation and interpretation of the spatio-temporal patterns of drill hole frequencies has been the subject of extensive paleontological research. The two main gastropod groups responsible for the drilling predation in modern marine environment arose in Cretaceous as supported by their body fossil. However, the drill holes have been reported from the fossils of as far back as Precambrian age. The trend shows an overall low but variable intensity in Paleozoic and Mesozoic and a significant increase in Cenozoic. There are few reported cases of drilled bivalves from the Mesozoic, although in those instances, frequencies are fairly low. Most of the previous records of drilling predation during Paleozoic and Mesozoic come from North America and Western Europe. Here we report 148 drilled bivalve specimens of a single species from the Upper Jurassic horizon in western India. This is highest in number for any taxon ever recorded since Precambrian to Cretaceous. The frequency of drilling constitutes 30% of shells of the same species examined. This drilling frequency is highest when compared to all the reported Mesozoic drilling frequencies in Bivalves. The shapes of the drill holes are indicative of gastropod predation. The drilling gastropods responsible for these lethal attacks are also similar to their modern counterparts in terms of their highly selective prey choice and site-specificity. These results suggest that (1) Mesozoic bivalves were preyed upon by drilling gastropods, often with high intensities, and (2) the specialized characters of modern drilling predators were also present in Mesozoic. This largely unexplored record of bivalve drill holes from the Middle Mesozoic contradicts the general trend of “Mesozoic quiescence” as claimed by most researchers.

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1. Introduction

Biotic interaction, especially predation, is one of the important driving forces of natural selection in modern marine environments (Carriker and Yochelson, 1968; Vermeij, 1987; Stanley, 2008). To understand the nature of evolutionary trends through deep time, it is essential to have a detailed understanding of the history of biotic interaction. Unfortunately, in most of the cases of predation, the victim is either consumed as a whole or crushed beyond recognition

leaving no preservable record. Drill holes in shells of invertebrates represent one of the few cases of predatory or parasitic behavior that can be readily studied in fossil organisms. Additionally, since the drilling predatory behavior still persists today in marine molluscs, it also serves as a model system to conduct neontological experiments and compare similar findings in the fossil record. Not surprisingly, they have been used extensively for evaluating hypotheses that stress the evolutionary importance of biotic interactions, such as, coevolution (e.g., DeAngelis et al., 1985; Kitchell, 1986, 1990) and escalation (e.g., Vermeij, 1987; Kelley and Hansen, 1993, 1996; Dietl and Alexander, 2000). In this context, molluscs have been the primary focus of researchers, possibly because of the facts that they were the favorite target of drilling predators in the Cenozoic and the identity of their predators was easy to ascertain (Kowalewski et al., 1998) and for their exceptionally good fossil record.

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Kowalewski et al. (1998, 1999) presented an overview of Phanerozoic drilling predation generated from a literature survey. They proposed three distinct intervals in the history of drilling predation and suggested that this predatory strategy was present throughout much of the Paleozoic but at a much lower rate than that seen in the Late Mesozoic and Cenozoic. Of particular interest is the “Mesozoic Phase” (Permian–Early Cretaceous) characterized by very low drilling frequencies attributed by Kowalewski et al. (1998) to either a period of “background drillers which possessed a latent drilling adaptation (exaptation) which for some reason never became successful and widespread” (see also Fursich and Jablonski, 1984) or a time when the predators were facultative and only drilled rarely (Kowalewski et al., 2005; Chattopadhyay, 2011). There are, very few reported data points from this interval to contradict this observation (Taylor et al., 1983; Fursich et al., 1994; Harper et al., 1998). To date the majority of research on drilling predation on molluscs has focused on the Late Mesozoic and Cenozoic after unquestionable appearance of modern drilling gastropod families (Sohl, 1969).

It is within the context of this apparent temporal trend in drilling predation history that we report on the drilling frequencies in bivalves from the Upper Jurassic of Kutch, western India. Our data show that drilling frequencies can be very high locally, as high as reported values for Cenozoic molluscs. We have also found that drilling is most probably done by gastropods and that at localities with high frequencies a discernible ecological signal can be detected, for example, with regard to taxonomic selectivity by the drillers. Results indicate that the pattern seen in this locality is unlike the drilling patterns for other Mesozoic intervals characterized by an exceptionally low frequencies

drilling predation. When placed in a spatio-temporal framework, it is definitely an exception to the general trend of “Mesozoic quiescence” in drilling predation history as claimed by previous studies (Kowalewski et al., 1998).

2. Materials and methods

2.1. Geologic and paleontologic settings

The samples examined in this study were collected from one locality near Bhakri village in Kutch region of western India. Bhakri is situated within Jhura dome which is one of many of the anticlinal highs where Jurassic rocks are exposed. Jhura dome is 50 km north–west of Bhuj, the district town of Kutch (Fig. 1). All specimens come from the Upper Jurassic (Oxfordian) Dhosa Oolite Member of the Chari Formation. It is a distinct marker bed (Pandey et al., 2009) occurring throughout the mainland of Kutch. It is an oolitic fossiliferous limestone and can be easily recognized in the field because of its brown to yellow color. The bed is at places intercalated with shale, mostly massive and conglomeratic toward the top. The thickness of the bed is highly variable, ranging from less than 40 cm to maximum of 5 m. Dhosa Oolite represents a condensed deposit which resulted from a relative sea level high stand (Singh, 1989; Fursich et al., 1992, 2001). Presence of features like hard ground, intraformational conglomerate, ferruginous crust etc. gives evidence of reworking and strongly reduced sedimentation (Fursich et al., 1992). Generally an offshore setting well below fair weather base often punctuated by storms is believed to have prevailed (Dutta, 1992; Fursich et al.,

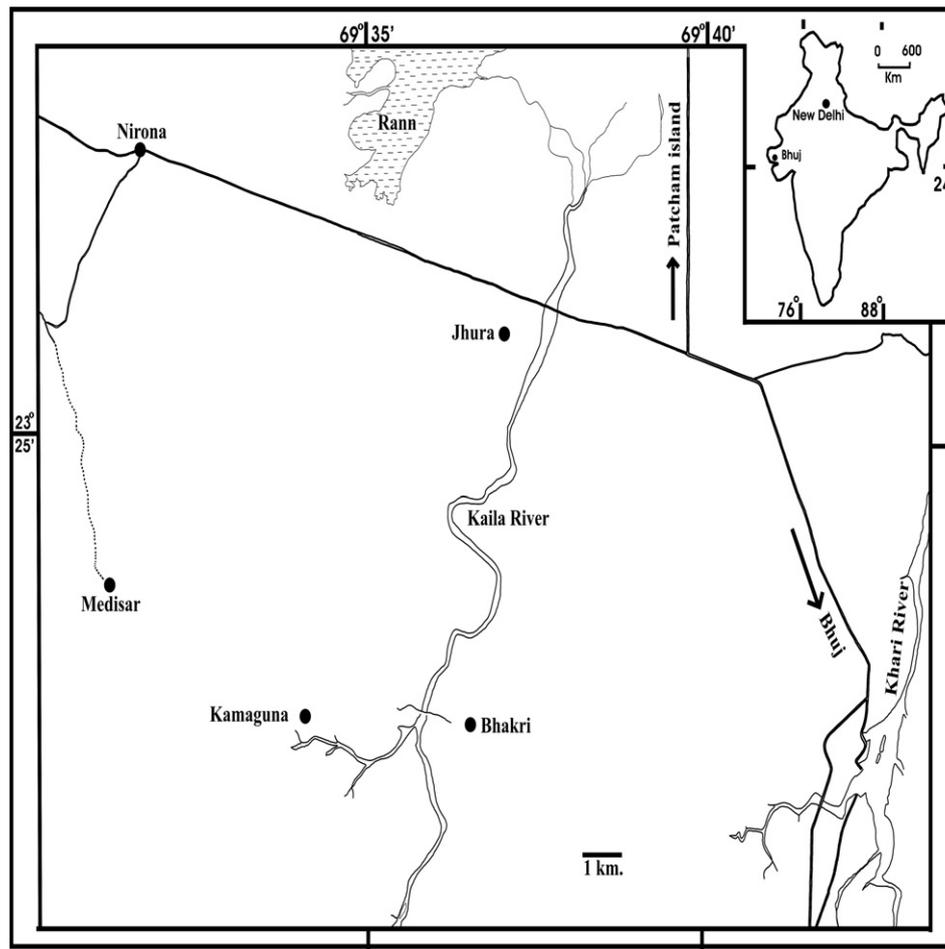


Fig. 1. Geographic locations (solid circle) of the Dhosa Oolite Member. Present fossil collection has been made near Bhakri.

1992). The Early to Middle Oxfordian age of the area has been established based on time diagnostic ammonite assemblage (Fursich et al., 2001; Alberti et al., 2011).

The faunal assemblage includes various ammonite genera such as *Perisphinctes* Waagen, *Mayaites* Spath, *Peltoceras* Waagen, *Taramiliceras* Del Campana, *Peltoceratoides* Spath (Spath, 1927–1933; Alberti et al., 2011; Roy, 2011). Among other molluscan classes, this locality is rich in gastropods e.g., *Leptomaria* E. Eudes-Deslongchamps; *Indomaria* Das (Das et al., 2005) and *Ampullina* sp. (personal observation). Bivalve includes *Neocrassina subdepressa* Blake and Hudleston; *Pinna mitis* Phillips; *Trigonia dhosaensis*, Kitchin; *Grammatodon virgatus* J. DE C. Sowerby; *Actinostreon marshi*, J. Sowerby (Jaitly et al., 1995; Fursich et al., 2000).

2.2. Collection protocol and specimens

There were two consecutive field trips, organized in 2009 and 2010, to collect samples. In both of the field trips we carried out similar sampling protocol to recover comparable samples. The bed yielding the drilled specimens is a hardground and very resistant. It is exposed in some discrete patches due to erosion of younger beds by local streams. Where the exposure is continuous we have been able to collect specimens through grid samples. In 2010 we have made 5 grids of 1.7 m × 1.7 m each. There are some patches where fossils are abundant but grid sampling is not possible. In these areas we have made random sampling, collecting all the specimens we encountered including *Neocrassina subdepressa* as well as other rarely drilled species. The grids are photographed and analyzed to count the number of species present. In the second phase we identified the drilled specimens and collected them. The hardness of the rock was very high, which made it impossible to collect all the samples from the grid, as well as collecting intact specimens most of the time. Therefore, we have decided to collect only the drilled specimens and thoroughly documented the rest of the specimens by taking detailed photographs.

It is seen that species other than *Neocrassina subdepressa* show a very low drilling frequency inside as well as outside the grids. This perhaps suggests that *N. subdepressa* was the preferred prey item. For this reason we have only provided systematic drilling frequency for the most frequently encountered species (i.e. *N. subdepressa*) while assemblage level drilling frequency has not been measured since it may not be much informative (see Kowalewski, 2002; Vermeij, 2002, and Kelley and Hansen, 2006 for discussion concerning the use of lower taxon frequency vs. assemblage frequency). In addition to the gridded samples, we have also collected specimens outside the grid to have a representation of a much larger area. In these random samples we have collected an unbiased assemblage of the most dominant bivalve (i.e. *N. subdepressa*) from outside the gridded region irrespective of whether they were drilled or not. We have also searched for drilled shells of the other taxa that show a very low drilling frequency inside the grids. For this reason we have only provided systematic drilling frequency for the most frequently encountered species (i.e. *N. subdepressa*) while assemblage level drilling frequency has not been measured since it is not much informative (Kowalewski, 2002, and Kelley and Hansen, 2006).

Although the original shell material is totally replaced (i.e. neomorphosed), our samples seem to suffer the least taphonomic alteration (for details see Discussion). We have encountered several articulated valves. Fractures on few valves are present haphazardly, sometimes passing through the existing drill hole and sometimes not.

Our study focuses mainly on the frequently drilled species *Neocrassina subdepressa*. All the specimens were visually examined for evidence of drill holes in the field. Specimens with drill holes were brought to the laboratory and photographed including SEM. The photographs are later analyzed for maximum size, shape and size of the drill holes using digitization software (ImageJ). Anterior–posterior length and height of the shells have been measured with

digital calipers nearest to the 0.1 mm. The material is housed in the collections of Department of Geological Sciences, Jadavpur University, India.

2.3. Data analysis

Frequency of drilling predation is calculated by dividing number of bored to total individuals in the collection (equation one of Bambach and Kowalewski, 2000). Although it is likely that all the valves came from the separate individuals (Gilinsky and Bennington, 1994), we need a correction for disarticulated valves (Bambach and Kowalewski, 2000). Since majority of our samples are disarticulated valves, we have used the formulae recommended by Kowalewski (2002) that is dividing the number of valves with drill holes by half the total number of valves. The ratio of total number of drill holes to the total number of individuals is generally not equivalent to the drilling frequency. As only one specimen has multiple holes, in our analysis both of them are synonymous. Another important aspect of calculating drilling frequency is to consider articulated specimens with disarticulated ones. To solve this we have used the following equation to calculate total number of individuals (N) in the sample:

$$N = [(RV + LV)/2] + A$$

where RV, LV and A are number of left, right and articulated valves.

So the drilling frequency (DF) is:

$$DF = DV/N$$

where DV is the number of drilled valves.

To understand any preferential selection for drill site we have made nine sector grids on *Neocrassina* shell, following Kelley (1988). The data is standardized by the sector size to normalize for different sizes of the sectors. The number of drill holes in each sector was counted and divided by the sectors area to run chi-squared test. We considered that drill holes are distributed all over the shell as our null hypothesis to test site stereotypy.

3. Results

In our two consecutive fieldworks at several sections near Bhakri village, we have collected drilled shells from the Oxfordian Dhosa Oolite bed. The sample size is sufficient enough to run different types of analyses on drilling patterns and compare these results with comparable reports from other parts of the world.

3.1. Drilling frequencies

Frequency of drilling is important in understanding the intensity of predation (e.g., Vermeij, 1987; Allmon et al., 1990; Kelley and Hansen, 1993). We have examined 921 specimens of *Neocrassina subdepressa*, the most frequently drilled bivalve species from Bhakri and found that 148 were drilled (Fig. 2, Table 1).

The lower taxon drilling frequency (LTF, as per Kowalewski, 2002) calculated for *Neocrassina subdepressa* is about 29.36% (2009) and 29.97% (2010) (Table 1). The overall drilling frequency combining data from grid and random sample is 30.53%. We found only 2 unsuccessful drill holes and one case of multiple drill holes from *N. subdepressa*. None of the articulated valves is drilled. Other available prey taxa are rarely attacked. In Bhakri, the other bivalves which have been drilled are *Pinna mitis* Phillips, 1829 and *Grammatodon virgatus* Sowerby, 1840. Only two drilled *Pinna* specimens have been collected of which one has unsuccessful drill hole (Fig. 3). We have recovered two *Grammatodon* specimens with complete drill holes (Fig. 4).



Fig. 2. *Neocrassina subdepressa* with a complete drill hole. An undrilled pleurotomarid gastropod is found right next to the bivalve.

3.2. Taxon selectivity

Drilling predation appears to be prey-specific. Among the diverse bivalve species present in the Dhosa Oolite (Jaitly et al., 1995; Fürsich et al., 2000) drilling has been found mostly on *Neocrassina subdepressa*. In the gridded sample of 2010, we encountered 278 *Neocrassina* samples and 184 other bivalves that are undrilled (Table 2). In that collection out of 86 completely drilled samples, only 3 are from taxa other than *Neocrassina*. *Neocrassina* was facultatively mobile, shallow infaunal suspension feeder. Table 2 clearly demonstrates *N. subdepressa* as most abundant group (62.1%). However, other species contributes 37.9% of the population and only 3 drill holes are found from *Pinna mitis* and *Grammatodon virgatus*. *Trigonia dhosaensis* is the second most abundant (16.66%) and infauna, but does not bear a single drill hole.

3.3. Valve selectivity

Drill holes can be found on the left or the right valve. For *Neocrassina*, the number of drill holes on the left valve is 76 (52%) and on the right valve is 69 (47%) (see Table 1). This difference is not statistically significant: the null hypothesis that there is no valve selectivity cannot be rejected at $p < 0.05$ using the chi-squared test. Our dataset is only restricted for *Neocrassina*, we cannot provide any this kind of data for *Pinna* or *Grammatodon* as they are rarely drilled.

3.4. Size selectivity

To identify whether the predator is size selective or not we have plotted outer bore hole diameter (OBD) against length of drilled prey specimens (Fig. 5). The correlation is not significant ($p \gg 0.05$).

3.5. Site selectivity

All valves of *Neocrassina* have been drilled from outside the shell. It is also true for drilled *Pinna* and *Grammatodon*. It appears that drill



Fig. 3. Unsuccessful drilling in *Pinna mitis*.

holes are highly site-stereotyped and concentrated near sector five ($p < 0.001$) which is situated at the center of the near circular shells (Fig. 6A and B). Of all these drill holes none has been identified as edge drilling.

3.6. Drill hole shape

All the drill holes that are studied here are circular and none of them are oval (Figs. 2, 3, and 4). Although these drill holes show some degree of variation in shape, size and internal structures, majority of them are cylindrical, straight-sided (*Oichnus simplex* Bromely), some are beveled boreholes which taper downward and in some cases the walls are parabolic (*Oichnus Paraboloides* Bromely) (Fig. 7). The holes, in most of the cases, penetrate the prey valve at right angle and outer bore hole diameter (OBD) is always greater than inner borehole diameter (IBD). Due to the presence of sediments it is often impossible to measure IBD, but it often appears smaller compared to OBD.

4. Discussion

4.1. Nature of drilling

Drill holes reported from the modern and paleo-ecosystem are generally interpreted as result of two biologic activities; namely, 1) substrate penetration and 2) predatory or parasitic interaction. The morphological characteristics of the drill holes, such as circular outline, size, axis perpendicular to shell surface, and the almost absence of multiple holes described in this study meet the criteria of having been produced by predatory or parasitic organisms rather than by a substrate penetrator (see Leighton, 2001; Kelley and Hansen, 2003). In particular, they are features characteristic of drill holes made by extant gastropods in modern invertebrate shells, including bivalves (Kitchell et al., 1981; Kowalewski, 2002; Chattopadhyay and Baumiller, 2007). Prey specificity is typical of biotic origin of drill holes (see Kowalewski, 2002). If these traces are abiotic in origin, then traces should be random, depending upon mineralogy, microstructure and physical durability of skeletons (Leighton, 2001). Our study shows that drill holes are prey specific, only present in a specific infaunal prey species. The high incidence of drill holes in *Neocrassina subdepressa* can't be explained just by its abundance, rather it is preferred as a prey taxon. There are many examples of such highly evolved gastropod predatory preferences from Recent and

Table 1
Neocrassina subdepressa prey collected in the present study.

	Total number of undrilled specimen		Total number of drilled specimen				Drilling frequency
	Disarticulated	Articulated	L	R	Unsuccessful	Multiple	
Grid collection (2009)	83	5	7	9	0	0	29.36%
Grid collection (2010)	278	0	22	27	0	0	29.97%
Random collection (2009)	203	17	29	17	2	0	32.51%
Random collection (2010)	179	9	18	16	0	1	29.44%

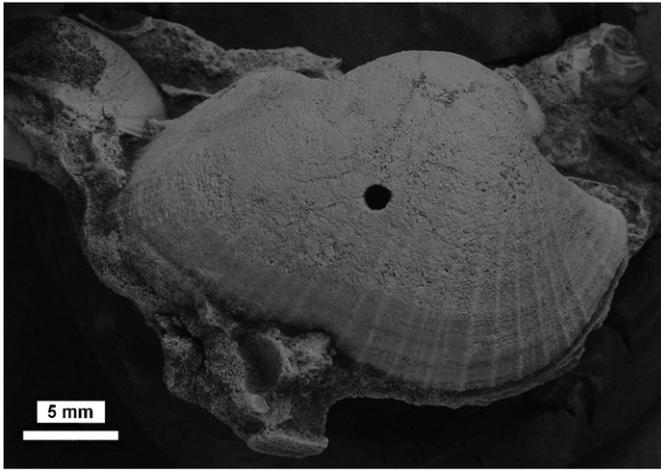


Fig. 4. A *Grammatodon* with a complete drill hole.

fossil record (Carriker, 1955; Carriker and Yochelson, 1968; Kitchell et al., 1981; Croll, 1983).

Drill holes are always almost circular (i.e. geometric in shape) and none of them deviated significantly from this shape. This character is useful to rule out substrate boring as an origin of drill holes (Leighton, 2001; Kowalewski, 2002). If drill holes are predatory/parasitic, their sizes are generally narrowly distributed (Kowalewski, 1993), compared to abiotic one which tend to be more variable. Our drill holes show a narrow range in outer bore hole diameter (OBD), which is indicative of its predatory/parasitic origin. The lack of correlation between prey size and OBD is not enough to reject the predatory origin since the experimental studies have often demonstrated such patterns in Recent predatory drillings (Kowalewski, 2004; Chattopadhyay and Baumiller, 2007). Such pattern is also comparable with what have been reported by Harper et al. (1998) from the astartid specimens of Europe, where they have also found poor correlation between predator and prey size.

Predatory/parasitic holes are site-stereotyped (Reyment, 1971; Kelley, 1988; Leighton, 2001) whereas the substrate borings are not. Reported drill holes are site stereotyped, mostly occur at the central position of the shell, indicating a possible predatory/parasitic origin.

From ecological point of view, interactions could be considered to be positive (+), negative (–) and neutral (0). In the case of two interacting organisms, one of the six possible interactions is exploitation (+, –) where one group at the expense of the other (Clarke, 1954). Two types of exploitive behavior are recognized: predation and parasitism. The difference between parasitism and predation is one of degree rather than kind and that makes it an extremely challenging problem to identify them uniquely in the fossil records. One basic difference between these two interaction is that while predators typically kill their prey, parasites might kill their hosts, but not without first making use of their living victims for an extended period. Therefore, one feature of the host that may be affected by the presence of a parasite, and that is readily quantifiable, is size. It is expected that the infested host would be smaller than an uninfested individual.

Table 2

The diversity of bivalves observed in 2010 in the grids of the present study. These numbers include both drilled and undrilled samples. IB = infaunal bivalve, SIB = semi-infaunal bivalve, EB = epifaunal bivalve.

Grid	<i>Neocrassina subdepressa</i> (family – Astartidae) (IB)	<i>Pinna mitis</i> (family – Pinnidae) (SIB)	<i>Trigonia dhosaensis</i> (family – Trigonidae) (IB)	<i>Grammatodon virgatus</i> (family – Parallelodontidae) (IB)	<i>Actinostreon marshi</i> (family – Palaeolophidae) (EB)
1	88	4	7	7	16
2	70	8	9	12	0
3	71	1	28	14	7
4	47	2	35	10	3
5	52	12	8	1	0

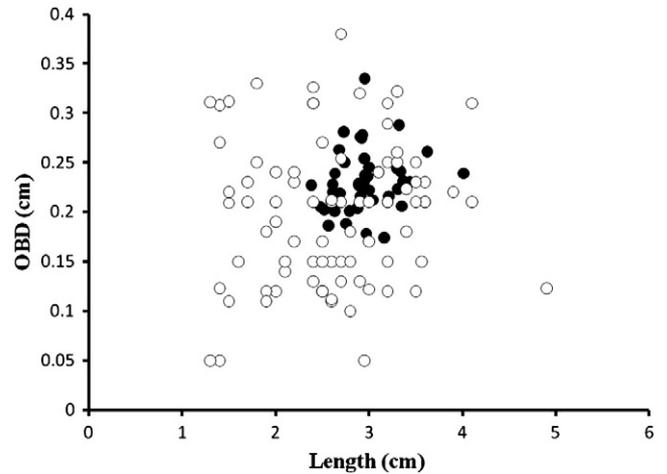


Fig. 5. Plot showing the relationship between the length of *Neocrassina subdepressa* and the OBD of the drill holes present on the shells. The solid black circles represent the subsamples of the collection of 2009 and the open circles represent the subsamples of the collection of 2010.

Using this criterion parasitism has been established for fossil crinoids and platiceratid gastropod where the later served as the parasite (Rollins and Brezinski, 1988; Baumiller and Gahn, 2002). In our study we do not see any significant size difference between shells with and without drill holes which does not support the parasitic origin of the drill holes. Additionally, attachment scars on the host organism are one of the significant features of long term parasitic relationship between two animals (Matsukuma, 1978). We have not found any parasitic attachments in any of the shells we studied. Considering the absence of these two vital indicators, this is quite unlikely to be a case of parasitic drilling. We can also try to address this problem by studying the nature of the drill hole. Leighton (2001) has listed several identifying features which can be effectively used to distinguish predatory drill holes from parasitic ones (for other examples see Carriker and Yochelson, 1968; Miller and Sundberg, 1984; Chatterton and Whitehead, 1987).

Although, there are instances of multiple predatory drill holes in one shell (Bromley, 1993; Dietl, 2000; Dietl and Alexander, 2000; Kelley et al., 2001; Chattopadhyay and Baumiller, 2007), majority of the predatory drill holes are singular in nature (Kelley and Hansen, 2003). On the other hand parasitic drill holes tend to be multiple in a single shell (Waren et al., 1994; Nebelsick and Kowalewski, 1999). Sometimes multiple predatory drill holes may be found in a single shell due to group foraging done by muricid gastropods (Brown and Alexander, 1994), but envelop prey within their foot.

Predatory drill holes are always initiated from outside the shell whereas the parasitic drill holes often show the opposite pattern (Richards and Shabica, 1969; Kaplan and Baumiller, 2000). All of our samples contain drill holes that have been initiated from outside resembling a predatory drill hole.

After considering all of the above facts we can rule out the possibility of substrate boring or parasitic activity as a possible cause of

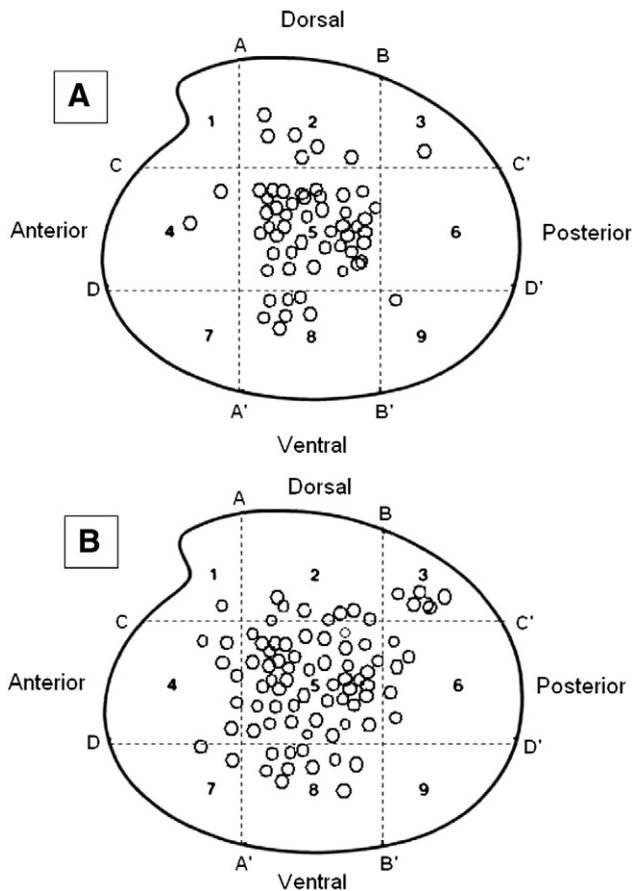


Fig. 6. The distribution of drill holes on prey taxa *Neocrassina subdepressa* (site selectivity), showing prominent size stereotypy at location 5 for samples collected during 2009 (A) and 2010 (B).

the drill holes recovered from Bhakri. That leaves us with the last option of predatory attack as the possible origin of these drill holes.

4.2. Identity of the predator

After the discussion above, we can at least assign the nature of the drill holes to be predatory in origin. Among extant predatory groups, two gastropod families (Naticidae and Muricidae) and octopus are mainly responsible for drilling predation. Since the produced drill holes differ morphologically (circular for gastropods and oval for octopod), it is possible to identify the driller by studying the drill holes (Bromley, 1981). While the exact identity of the driller cannot be established unequivocally, the cylindrical holes resemble those made by extant muricids, while the conical holes are similar to holes made by naticids. We did not find any drill hole that has an oval shape, characteristic of octopod drilling (see Bromley, 1993). Moreover, if we compare drill holes produced by gastropods versus octopod drilling, gastropod drill holes are always larger (Kowalewski, 1993). The drill holes reported here are morphologically and morphometrically comparable with drill holes reported by Fürsich and Jablonski (1984) from Triassic Cassian formation and Harper et al. (1998, 1999), Harper and Wharton (2000), and Harper (2003) from Jurassic of Europe. Our data suggest a predatory gastropod origin, as majority of the drill holes are greater than 1 mm in diameter.

Although morphologically the drill holes resemble those produced by naticids or muricids, we cannot undoubtedly assign them to be the culprit since we are reporting the drill holes from the Upper Jurassic bed. Both muricids and naticids body fossils first appeared in Cretaceous (Sohl, 1969; Taylor et al., 1983). Consequently all the drill holes produced before that suffers from the ambiguity regarding the

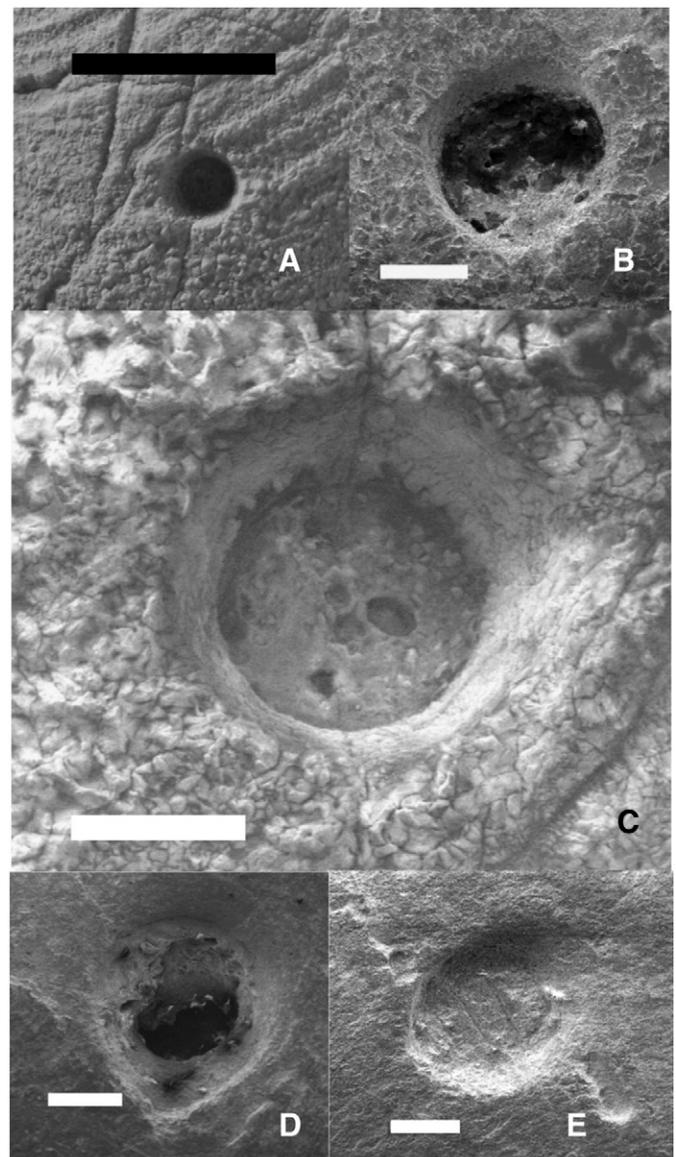


Fig. 7. Studied naticid like drill holes on *Neocrassina subdepressa* collected from Kutch, India. (A) Digital photographs, cylindrical, straight-sided complete drill hole, scale bar = 1 cm.; (B–E) SEM photographs, (B) cylindrical complete bore hole; (C) beveled bore hole; (D) bore hole showing parabolic wall; (E) incomplete bore hole on bivalve shell, scale bar = 1 mm.

identity of the predator (e.g., Ausich and Gurrola, 1979). Moreover, true naticids have not been found in the rocks near Bhakri. Given the intense sampling of all size fractions at this site, it is highly unlikely that these gastropods would have been missed, even if they were exceedingly rare. A plausible scenario is that their absence is a taphonomic artifact – given the compositional differences between the tests of bivalves and gastropods, the former may have been preserved while the latter preferentially dissolved at Bhakri. An analogous situation has been described by Ceranka and Zlotnik (2003). They found small drill holes in the tests of Middle Miocene echinoids which they interpreted as having been made by juvenile cassids. The absence of juvenile cassids in the investigated area was inferred to be the result of non-preservation. However *Neocrassina* belong to the family Astertidae and Recent astertids are made up of aragonite and therefore gastropods would not be expected to be less preservable. Moreover, there is significant presence of pleurotomarid gastropods (Jaitly et al., 2000; Das et al., 2005) and ammonites (Roy, 2011 and personal observation) with shell (both were originally aragonitic)

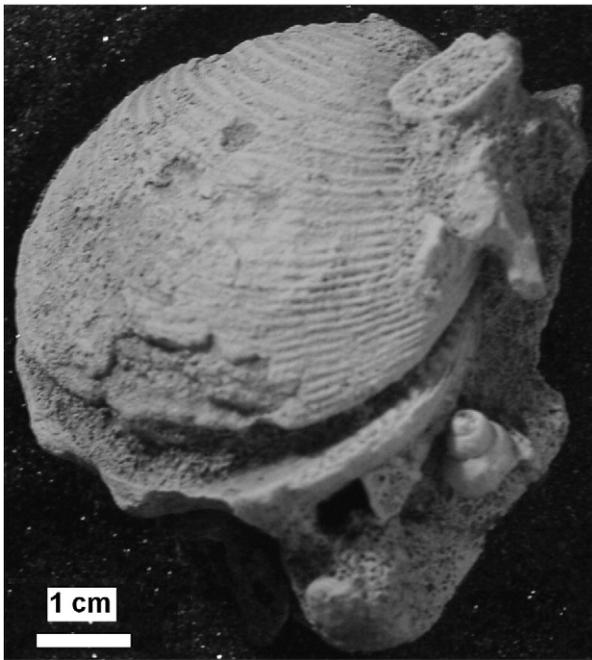


Fig. 8. *Neocrassina subdepressa* with a complete drill hole. An undrilled gastropod (*Ampullina* sp.) is found right next to the bivalve.

preserved in the locality, which does not really support this explanation of preferential non-preservation.

We have found (personal observation) two new gastropod species, *Ampullina* sp. (Fig. 8) and *Globularia* sp. from Bhakri and Jumara respectively within the Dhosa Oolite. These two species have many naticid – like morphological characters. The taxonomic affinities of these genera are still uncertain. Many workers considered *Globularia* (Wenz, 1941; Sohl, 1965; Kase, 1984; Fischer and Weber, 1997; Das et al., 1999) and *Ampullina* (Fursich and Jablonski, 1984) as Naticidae. But others (Kase, 1990; Bandel, 1993 and Szabo and Jaitly, 2004) considered them as belonging to entirely different families like Ampullospiridae (see Kase, 1990), Ampullinidae (see Szabo and Jaitly, 2004). Recently Kase and Ihsikawa, 2003 found extant ampullinids as herbivorous gastropod and not related to naticid. We therefore here refrain from considering *Globularia* and *Ampullina* as true naticids. The fact that all the drilled taxa are infaunal supports potential naticid predation since among extant predatory gastropods; naticid gastropods mostly drill infaunal prey (Carriker and Yochelson, 1968).

However, some authors have questioned this method of assigning predatory habit by the virtue of morphological resemblance to an extant predatory group (Kowalewski et al., 1998). Predators have often been identified as any species related to extant drillers that occur with drilled prey in the same or coeval units. However, none of the species found in the studied area is related to predatory clades that are known to drill (see Vermeij, 1987; Kabat, 1990; Kowalewski, 1993). According to Kowalewski et al. (1998) this approach is debatable because drilling is a highly convergent trait, and phylogenetically distant drillers such as gastropods and flatworms may coexist in the same habitats. Thus, the Jurassic holes may record early prosobranchs that failed to radiate (as suggested for Triassic holes by Fursich and Jablonski (1984)), but they may also record dwindling descendants of Paleozoic drillers (e.g., Sheehan and Lesperance, 1978; Smith et al., 1985; Chatterton and Whitehead, 1987), octopods (Bromley, 1993), or some unknown Jurassic predators.

Therefore the identity of the Bhakri driller or drillers still remains elusive – gastropods appear to be likely culprits, but without catching the drilling organism “in the act” (Baumiller, 1990), we cannot unambiguously assign these holes to a specific drilling organism (Bromley, 1981).

4.3. Predation intensity and taphonomic artifact

We have argued above that the drill holes described herein represent the activities of a predatory or a parasitic organism, most likely a gastropod. Frequency of drill holes has often been used to estimate predation intensity (Taylor, 1970; Stanton and Nelson, 1980; Vermeij et al., 1980; Vermeij and Dudley, 1982; Kabat and Kohn, 1986) while the consistency of drill hole placement on prey shells (drill-hole stereotypy) has been used to infer important information about predator behavior in the fossil record (Kelley and Hansen, 2003 and references therein). The tacit assumption of these studies, however, is that patterns of drilling are not altered by taphonomic processes, which might not be always true (Kowalewski, 2002; Kelley, 2008). For example, physical and biotic factors that affect either drilled or undrilled bivalves unequally bias the measured frequencies, regardless of the frequency metric used. Differences between drilled and undrilled specimens may include hydrodynamic properties (Lever et al., 1961; Kaplan and Baumiller, 2000; Chattopadhyay and Baumiller, 2007), leading to sorting by water currents, or resistance to loading, leading to differential crushing of specimens (Roy et al., 1994; Kaplan and Baumiller, 2000; Zuschin and Stanton, 2001). However, in the present case, differential transport can be discounted because a substantial part of the bivalve shells are assorted and many are articulated thus indicating minimal current energies. Moreover, the ratio of left and right valve is close to 1 indicating to the fact that the shells were not preferentially transported. Associated ammonites show delicate ornamentation and often peristome preserved suggesting no long distance transport. Differential resistance to loading of drilled and undrilled tests has also been shown to operate on disarticulated, not on articulated tests, and so it is not applicable to this data. It is often advocated that, preferential chemical dissolution might lead to elevated drilling frequency in one prey taxon (Harper and Wharton, 2000; Harper, 2003). The astarid specimens as we have stated early are neomorphosed and were originally aragonitic. So, what appears as a taxon selectivity might be simply due to preservation. However, the fact that other taxa (Pleurotomarid gastropods and ammonites, who were originally aragonitic) in the study show similar degree of preservation that enables us to reject taphonomic bias as a causal factor for observed taxon selectivity.

While abiotic factors are unlikely to have biased the drill hole frequency data, shell-crushing predators preferentially ingesting undrilled, live bivalves could introduce a bias. We have no direct evidence for crushing predation on bivalves at Bhakri, but the small proportion of fragmented bivalve shells relative to complete specimens argues that unless such material was removed from this locality by the predator (swallowed whole, see Fouke and LaBarbara, 1986) or crushed beyond recognition, it could not have been important. It has been demonstrated that with increasing durophagous activity the number of incomplete drill holes increases in the laboratory experiments (Chattopadhyay and Baumiller, 2007) and in the fossil assemblages (Chattopadhyay and Baumiller, 2010). The presence of durophagous predators poses a risk for the driller and thereby increasing the occurrence of failed drilling attacks. The relative absence of incomplete drill hole and repair scars are also indicative of the fact that this community was not severely affected by the shell crushing and peeling predation. Therefore we can conclude that the resultant taphonomic effect is not that significant to obscure the biotic signal documented by the drilling frequency.

4.4. Implications

Although, the drill holes are reported as far back as Proterozoic (Bengtson and Zhao, 1992), the high frequency of drilling is not reported until Cenozoic. Kowalewski et al. (1998, 1999) described a three-phase pattern of drilling predation throughout the Phanerozoic, where drilling levels were high between the Late Pre-Cambrian and Carboniferous and again during the Late Mesozoic and Cenozoic, with an intervening phase (Permian to Late Cretaceous) where drilling was

neither intense nor common. During the Mesozoic Phase (Permian–Early Cretaceous), drilling predators were so rare (<0.1 occurrences per million years and drilling frequencies below 1%) that they typically are documented by single or few holes. They interpreted this phase as an interval of “background” drillers that possessed a “latent” drilling adaptation (exaptation), which, for some reason (see Fürsich and Jablonski, 1984; Smith et al., 1985), never became successful and widespread. Kowalewski et al. (1998) based their conclusion primarily on the lack of literature data from this period and the low drilling frequency of recovered samples from Hungary and India. The lone Indian drilled shell was found from the Middle Jurassic of the Kutch basin, Gujarat, western India (Fürsich and Oschmann, 1993). The fauna is dominated by infaunal bivalves. Lithology and fauna indicate a shallow-marine environment, but below storm wave base. Interestingly our samples were collected from a locality quite close to that of Fürsich and Oschmann, 1993 with similar depositional environment show a 30 fold increase in drilling frequency. This present find records the highest number of predatory drill holes in any species during the entire Mesozoic (see Harper, 2003; Appendix-1). We know only one example from Paleozoic where drilling frequency exceeds 30% (Hoffmeister et al., 2003). Although we are not sure about the identity of the drilling, this study shows that the general trend of “Mesozoic quiescence” could very well be an artifact of the lack of studies. Interestingly, Harper has reported similar level of predation intensity, taxon and site selectivity from Jurassic bivalves of UK (Harper et al., 1998). This observation has always been considered as a local phenomenon and different from the global trend. But with our data, it becomes unlikely to be a very restricted local happening. Most of the fossil records of drilling predation come from North America and Western Europe (Huntley and Kowalewski, 2007). Our present find extends it up to the subtropic of the southern hemisphere where India was positioned during Oxfordian (Smith et al., 1994). Historically it has been seen that with increasing interest and sampling, overall trends in many paleobiologic issues has been corrected, modified and sometimes even reverted. In a recent analysis of refined data which are statistically valid, Harper (2003) shows no significant change in drilling frequency during Paleozoic and Mesozoic. For predation history itself, the classical case of apparent immunity of Cenozoic brachiopods from drilling predation has been reevaluated. As a result researchers could establish that Cenozoic brachiopods were not immune from drilling (e.g., Taddei Ruggiero, 1991, 1999; Bitner, 1996, 2000; Taddei Ruggiero and Annunziata, 2002; Baumiller and Bitner, 2004; Harper et al., 2011). Hopefully, in future with more rigorous sampling we can fill up the apparent gap in the Mesozoic drilling predation history and understand the true biotic trend in drilling predation history.

Acknowledgment

S.B acknowledges partial funding from CAS and PURSE - DST of Department of Geological Sciences, Jadavpur University. D.C acknowledges the financial and infrastructural support provided by Indian Institute of Science Education and Research, Kolkata. Arpita Roy has made valuable contribution in image processing. S.M acknowledges the fund provided by UGC. S.S.D is grateful to the Indian Statistical Institute, Kolkata, for providing financial support and infrastructural facilities. The authors are thankful for the comments from G. Vermeij and E. Harper on earlier drafts of this manuscript. We would also like to thank two reviewers, P. Kelley and G. P. Dietl, for their constructive comments.

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