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Prey selection by drilling predators: A case study from Miocene of Kutch, India

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ABSTRACT

The fossil record of predatory drill holes in shelled invertebrates provides valuable evidence to understand the evolutionary role of biotic interactions in deep time. It is hypothesized from modern studies that predatory gastropods do not randomly attack molluscan prey; rather they select their prey in order to maximize the energy gain. We have tested this hypothesis using bivalves from Miocene marine deposits of Kutch, India. The prey group consists of *Chlamys* sp., *Placuna lamellata* and four species of oyster bivalve namely *Ostrea latimarginata*, *Ostrea angulata*, *Crassostrea gigensis*, and *Hyotissa hyotis*. The overall drilling frequency is 20% and the species level frequency is as high as 35%. There is quite a high incidence of incomplete drill holes; while the assemblage level frequency is 41%, the species level frequency is as high as 57%. Our assemblage demonstrates preferred selection of prey in terms of taxonomy, size, site and valve by the predatory gastropod. Such selections are guided by the energy maximization strategy of the predator. Moreover, the high incidence of incomplete drill hole makes the dynamics even more intriguing since it shows a different pattern of selectivity compared to that of successful attacks. The success rate of an attack differs with size of the predators, hence indicative of an ontogenetic improvement in predatory skills. The overall predation intensity, although comparable to a few reports from other continents, is largely different from the global average of drilling frequency of Miocene.

1. Introduction

Predation plays a major role in natural selection. It has contributed significantly in shaping the global biodiversity of the marine fauna (Carriker and Yochelson, 1968; Vermeij, 1987; Huntley and Kowalewski, 2007; Stanley, 2008). Although the importance of predation has been recognized, it is often difficult to study the effect in deep time due to the lack of preservable traces of such interactions. Predation by drilling gastropods creates a unique scenario where it produces a readily preservable signature of the predatory event in the victim itself. Drilling predation, therefore, has been extensively studied to evaluate hypotheses on evolutionary significance of biotic interaction, such as coevolution (e.g., De Angelis et al., 1985; Kitchell, 1986, 1990) and escalation (e.g., Vermeij, 1987; Kelley and Hansen, 1993, 1996; Dietl and Alexander, 2000). The borehole produced by a muricid or naticid gastropod on prey provides evidence of the success or failure of predation, a measure of the size of the predator and a simultaneous measure of relevant characteristics of the prey (Kitchell et al., 1981; Chattopadhyay and Baumiller, 2007). Moreover, the presence of drilling behavior in Recent molluscan assemblages allows us to conduct actualistic studies and use the results to decipher the biotic interaction in deep time.

Extensive studies have been conducted worldwide to understand the details of drilling predation on bivalves in Recent (reviewed by Kitchell et al., 1981; Kelley and Hansen, 2003; Sawyer and Zuschin, 2010) and ancient ecosystems (reviewed by Kelley and Hansen, 2003; Harper 2003, 2006; Huntley and Kowalewski, 2007). Most of such studies have been conducted on Cenozoic assemblages. There have been reports on Miocene bivalves showing predatory drill holes from all over the globe (Hoffman et al., 1974; Dudley and Dudley, 1980; Colbath, 1985; Kelley, 1988; Kowalewski, 1990; Anderson, 1992; Hoffmeister and Kowalewski, 2001; Zlotnik, 2001; Amano, 2003, 2006; Kelley and Hansen, 2006; Sawyer and Zuschin, 2011) except from the Indian subcontinent. The only study on drilling predation from this area focuses on Mesozoic assemblage (Bardhan et al., 2012).

In the global reports on Cenozoic drilling predation on molluscs, only a very few studies established the nature and cause of selectivity of such attacks. Some approaches tried to explain the selectivity from ecological preference (Hoffmeister and Kowalewski, 2001; Sawyer and Zuschin, 2010) by showing difference in predation intensity in different ecological guilds. Others studied it using energy maximization model to demonstrate the difference in net energy gain by selecting a specific prey (Kitchell et al., 1981; Kelley, 1988).

This study presents the first report of extensive drilling predation from Miocene strata of Kutch, India. We have further investigated the nature of drilling behavior from ecological as well as energy-maximization strategy.

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2. Materials and methods

2.1. Geologic and paleontological settings

All the samples used for the study were collected from an exposure near Rampar village (N 23°20.110′, E 68°48.735′) located in Kutch region of Western India (Fig. 1) during a field trip in December, 2011. The beds belong to the lower Chhasra Formation of Early Miocene age. The thickness of the beds varied from 30 cm to 200 cm in this region. Chhasra Formation is comprised of two members: lower Claystone and upper Siltstone member (Kumar et al., 2009). The specimens belong to the biostromal composite concentration (also known as community shell concentration, Norris, 1986; Meldahl, 1993; Cantalamessa et al., 2005) of the lower claystone member of the Chhasra Formation, mainly characterized by matrix-supported fabric, randomly oriented shells, low to moderate fragmentation and dissolution of shells (Fig. 2).

Molluscan specimens were collected from the vertical face of the exposure by surface sampling; the heavy rainfall during 2011 considerably loosened the claystone yielding intact fossil specimens. Where the hard rock prohibited the safe recovery of the specimen, we took detailed field photographs for documentation. The Cenozoic molluscan assemblages from Kutch region have been studied and described in detail (Kachhara et al., 2012; Borkar et al., 2004; Chattopadhyay, 2004; Kulkarni et al., 2007, 2009). The present locality represents many of the typical taxa. The faunal assemblage of this locality consists of bivalves (dominantly oysters), gastropods, echinoids and bryozoans.

2.2. Data collection and analysis

Specimens were brought back to the laboratory for detailed study. All the specimens were photographed and examined for evidence of drill holes. The photographs were later analyzed for maximum size, shape and size of the drill holes using digitization software (ImageJ). Dimensions of some fragmented specimens were reconstructed using the relationship between anterior-posterior and dorsal-ventral length of intact specimens of the same species. The size of a drill hole was measured by measuring the maximum outer diameter of the hole (outer borehole diameter or OBD). The valves were recognized as right or left in order to check selectivity of valve by the predator. The collected samples were housed in the paleontology laboratory of Department of Earth Sciences, IISER Kolkata (IISER-K/Ku/Mio/1-319).

All the specimens in our collection were disarticulated valves. Hence, the frequency of drilling predation was calculated by dividing the number of bored valves by the half of total number of valves in the collection (Kowalewski, 2002).

$$\text{Drilling Frequency(DF)} = N_D/(N * 0.5)$$

where

N_D	Number of valves with complete drill hole
N	Total number of valves.

The incomplete drilling frequency however was calculated by dividing the total number of incompletely drilled valves by the total number of drilled valves present in the collection.

$$\text{Incomplete Drilling Frequency (IDF)} = N_{ID}/(N_{ID} + N_D)$$

where

N_{ID}	Number of valves with incomplete drill hole
N_D	Number of valves with complete drill hole.

Previous workers have used a similar index called "prey effectiveness (PE)," defined by Vermeij as the number of incomplete drill holes divided by the total number of attempted drillholes (complete and incomplete). Our metric would be comparable to PE if there is no incidence of multiple drill holes. Both DF and IDF were calculated for assemblage level as well as for species level. Assemblage Frequency

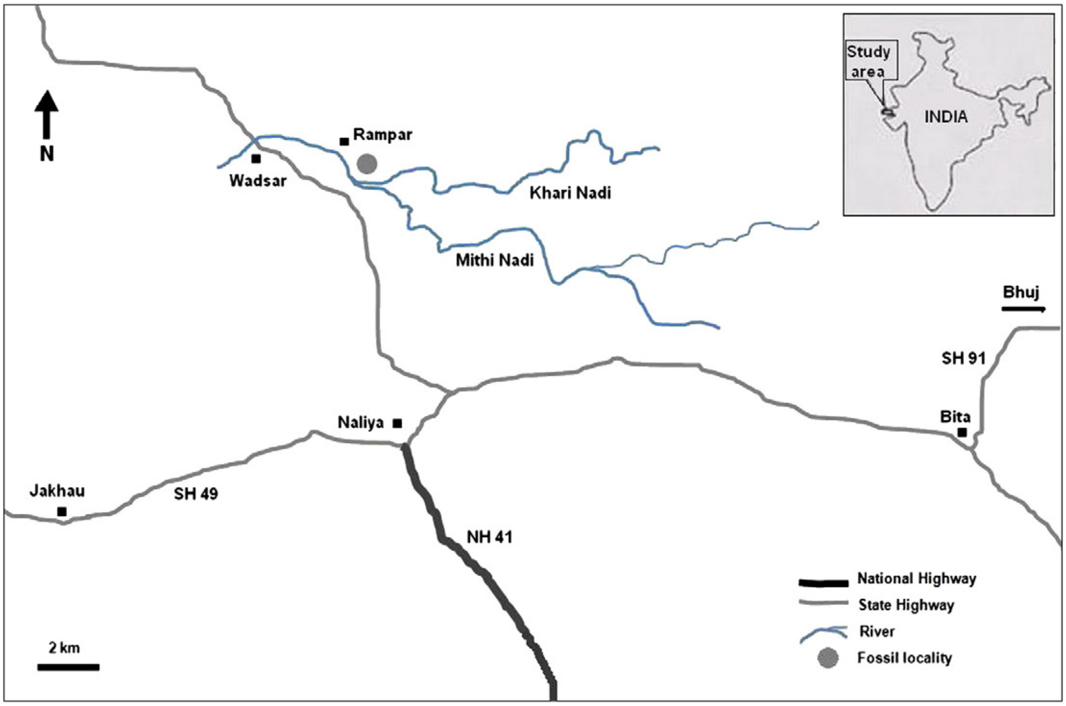

Fig. 1. Detailed map of the locality.

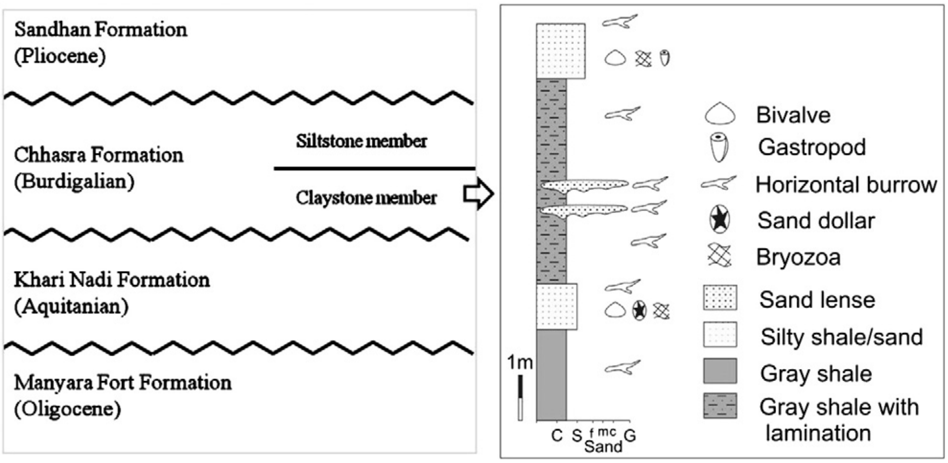

Fig. 2. Lithostratigraphic classification of Miocene rocks of Kutch (after Biswas, 1992) with the detailed litholog of the Claystone member of Chhasra Formation.

metric (AF) and Lower Taxon Frequency metric (LTF) were calculated using the protocol described by Kowalewski (2002).

Size preference was evaluated by two methods: 1) comparing the size of drilled valves with undrilled valves of the same species and 2) evaluating the relationship between OBD and corresponding prey size for a drill hole. In order to check for site stereotypy, it is been a standard practice to use nine sector grids following Kelley (1988). However, it was difficult to implement the protocol on the oysters because of their irregular shape. Therefore, we adopted another protocol similar to what is been frequently used for testing stereotypy on gastropod prey (Berg and Nishenko, 1975). Once all the specimens were photographed and digitized using ImageJ, the umbo was identified. We measured the angle between the tangents drawn on the outline of the shell in two opposite sides near umbo. The angle was then divided in five equal parts and incidence of drill holes was studied in each of the segments. We compared the incidence of drill holes in different sectors after normalizing for their difference in area. It is worth noting that this method, however, has the disadvantage of dividing the prey's shell into dorso-ventrally elongated sectors. This might permit a considerable degree of variation in placement of the drill holes along the long axis of the sector to count as a non-random distribution in placement. This method was exercised only on two species of *Ostrea*. Others had too few drill holes to run any meaningful statistical analysis. All the statistical analyses were performed in PAST 2.16 (Hammer et al., 2001).

3. Results

3.1. Basic structure of the studied assemblage

A total of 275 valves of bivalve molluscs were collected, identified to species level and studied for drill holes. These shells represent four species of Oysters (*Ostrea latimarginata*, *Ostrea angulata*, *Hyotissa hyotis*, *Crassostrea gigensis*), *Placuna lamellata* and *Chlamys* sp. (Fig. 3, Table 1). The two most abundant bivalve species are *Ostrea latimarginata* and *Ostrea angulata.*

3.2. Drilling frequency

We found 27 of the valves with complete drill holes in our collection (Fig. 3, Table 1). The Assemblage Frequency metric, AF, is 20%. The LTF metric showed that the 2nd most common species, *Ostrea angulata*, exhibits the highest frequency of drill holes (35.4%) followed by *Ostrea latimarginata* (15%) and *Chlamys* sp. (13%) (Table 1).

The overall incidence of incomplete drill hole is quite high (41%). Out of a total of 19 incomplete drill holes, *Ostrea latimarginata* alone has 12 while *Ostrea angulata* has 5 (Fig. 5a, Table 1). *Hyotissa hyotis* does not have any complete or incomplete drill holes. There is no incidence of multiple drill holes in any of the specimens.

3.3. Taxa selectivity

Among the diverse bivalve species present, the predator successfully preyed upon predominantly one species, *Ostrea angulata. O. angulata* has a higher drilling frequency compared to any other species. This difference is statistically significant for *Ostrea latimarginata* (χ^2 test, $p<0.05$) (Fig. 3). *O. latimarginata* has a higher incomplete drill hole frequency compared to any other species. This difference is statistically significant for *O. angulata* (χ^2 test, $p<0.05$) (Fig. 4).

3.4. Size selectivity

We compared the size of drilled (complete and incomplete) individuals with the undrilled valves in each species that has drill holes (Fig. 5). For *Ostrea angulata* the average size of individuals with drill holes is significantly higher than the undrilled individual ($t=4.58$, $p<<0.05$). The specimens of *O. angulata* with incomplete drill holes are significantly larger than those with complete drill holes ($t=2.78$, $p<<0.05$) (Fig. 5a). For *O. latimarginata*, the trend remains the same (Fig. 5b). For *Chlamys* sp. too the specimens with incomplete drill holes are larger than those with complete drill holes (Fig. 5c). However, the completely drilled specimen of *Crassostrea gigensis* is larger than the incompletely drilled one (Fig. 5d). No statistical analysis could be performed on these species because of the small sample size.

There is no significant correlation between prey size and OBD for *Ostrea angulata*. However, the average OBD for complete drill holes is significantly higher compared to the incomplete drill holes ($t=3.29$, $p<<0.05$) (Fig. 6a). The same is true for *Ostrea latimarginata* ($t=2.27$, $p<<0.05$) (Fig. 6b). For combined data on *O. latimarginata* and *O. angulata* we compared the success rate (relative proportion of complete and incomplete drill holes) of small ($OBD<0.15$ cm) and large ($OBD>=0.15$ cm) predators. We found that the larger predators have a significantly higher success rate (χ^2 test, $p<0.05$). For *Chlamys* sp. and *Crassostrea gigensis*, the sample size is too small for such statistical evaluation. However, for both the groups, the OBD size for completely drilled specimens is higher than those with incomplete drill holes (Fig. 7).

3.5. Site selectivity

All the drilled valves have been drilled from outside confirming their predatory origin. The drill hole positions vary within and between species (Figs. 8, 9). For both *Ostrea latimarginata* and *Ostrea angulata* all the drill holes are concentrated in sector 2, 3 and 4. For

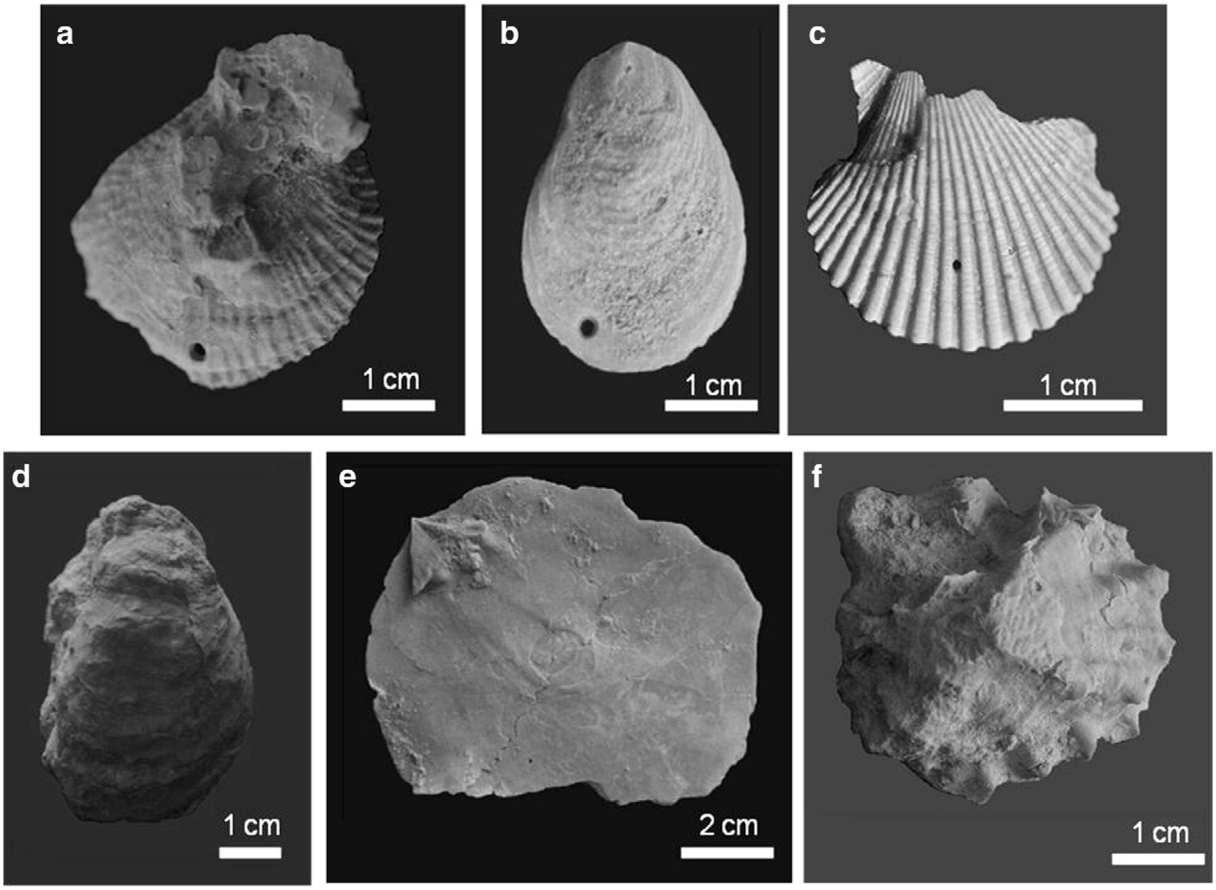

Fig. 3. Complete drillhole on specimens of *Ostrea angulata* (a), *Ostrea latimarginata* (b), *Chlamys* sp.(c). Complete specimens of *Crassostrea gigensis* (d), *Placuna lamellata* (e) and *Hyotisa hyotis* (f).

O. angulata, sector 3 has the highest concentration of drill holes and this concentration is statistically significantly higher than other sectors (χ^2 test, $p<0.05$). For *O. latimarginata*, sector 3 has the highest concentration of drill holes and this concentration is statistically significantly higher than all other sectors (χ^2 test, $p<0.05$) except 2 where it is marginally significant (χ^2 test, $p=0.05$) (Fig. 8). For the rest of the species, the position of the drill holes varies quite a lot. We did not find any edge drilling in any of the specimens.

3.6. Valve selectivity

Drill holes are observed to be found on both of the left and the right valve. Careful study of the valve selectivity pattern reveals that for *Ostrea angulata* the left valve was chosen 9 times out of 14, and *Ostrea latimarginata* had 8 out of 9 drill holes on its left valve. This difference of incidence of drill hole between right and left valve is statistically significant (χ^2 test, $p<0.05$).

Table 1
Taxonomic summary of drill hole data.

Group	Valves	Complete drills	Incomplete drills	DF	IDF
Ostrea latimarginata	120	9	12	0.15	0.57
Ostrea angulata	79	14	5	0.35	0.26
Chlamys sp.	30	2	1	0.13	0.33
Crassostrea gigensis	22	1	1	0.09	0.5
Placuna lamellata	17	1	0	0.12	0
Hyotissa hyotis	7	0	0	0	0
Total	275	27	19	0.2	0.41

4. Discussion

An event of drilling gets captured in its entirety in a drilled shell providing a wealth of information about the event such as the identity of the predator. The beveled, parabolic holes of naticids are easily distinguished from relatively smaller and more cylindrical muricid holes. Apart from the identity of the predator, the drill holes are also indicative of size of the individual predator since OBD is correlated with the size of the predator for both naticid (Kitchell et al., 1981) and muricid (Carriker and Gruber, 1999; Chattopadhyay and Baumiller, 2009) as revealed by neontological experiments. The detailed study of the drill hole itself reveals whether or not the attack was successful. Incomplete or multiple drill holes are often indicative of failed drilling attempt. The position of the drill hole on the shell provides information on prey-handling behaviors of the predator. Combination of the above techniques of inference could produce a detailed picture of past biotic interaction which otherwise is extremely difficult to achieve.

4.1. Nature of drilling

The drill holes in our collection are confirmed to be of predatory origin as we find distinctive traces of predatory activities such as circular outline, axis perpendicular to shell surface, sizes being narrowly distributed and narrow range of outer borehole diameter (Leighton, 2001; Kelley and Hansen, 2003). Moreover, the parabolic shape of the drill hole cross-section and a raised central area in incomplete drill holes suggest the predator to be a Naticidae. The presence of naticid-like form *Globularia carlei* from the same locality is also reported by previous researchers (Harzhauser et al., 2009; Kulkarni

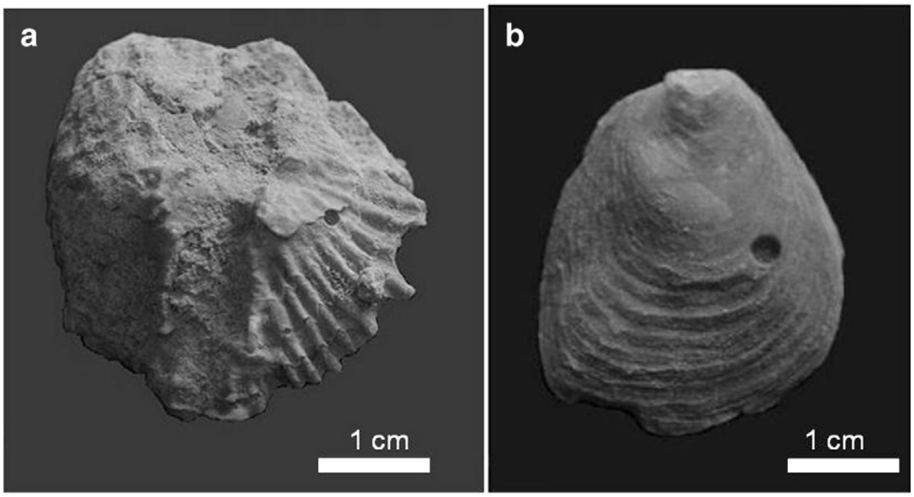

Fig. 4. Incomplete drillhole on *Ostrea angulata* (a), *Ostrea latimarginata* (b).

et al., 2010). Many workers considered *Globularia* (Sohl, 1965; Kase, 1984; Fischer and Weber, 1997; Das et al., 1999) to be a Naticidae. However, it is worth noting that sometimes it is quite impossible to differentiate between the drill holes made by muricid and naticid gastropods (Herbert and Dietl, 2002). A few additional taxa have been discovered to drill holes that resemble those made by naticids (Harper et al., 1998) such as Marginellidae, Nassariidae (Ponder and Taylor, 1992; Morton and Chan, 1997). It is also quite rare to find naticid attacks on oysters and scallops which are more frequently preyed upon by muricids. However, the absence of any muricid gastropod from the studied locality inhibits us from concluding muricids as the true identity of the predators.

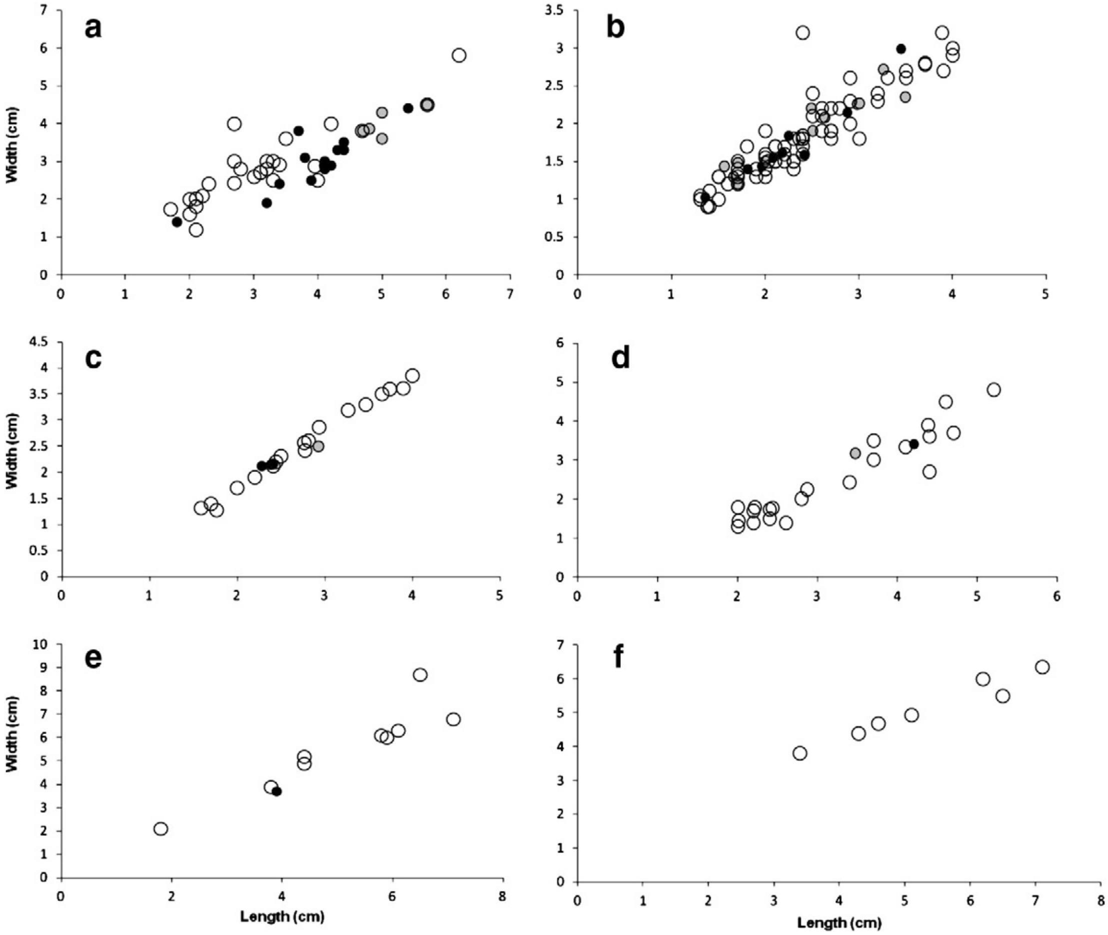

Fig. 5. Plot showing the relationship between length and width of specimens of *Ostrea angulata* (a), *Ostrea latimarginata* (b), *Chlamys* sp. (c), *Crassostrea gigensis* (d), *Placuna lamellata* (e), and *Hyotissa hyotis* (f). Solid black circles represent completely drilled specimens and grey solid circles represent incomplete drillholes. Open circles represent undrilled specimens. Fragmented specimens have not been plotted.

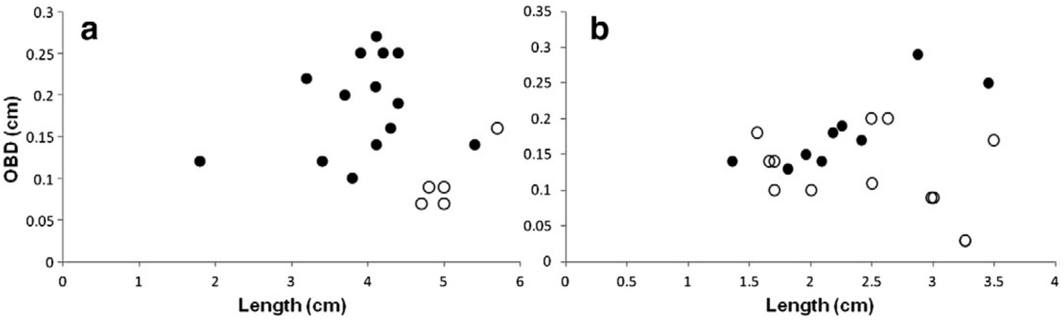

Fig. 6. Plot showing the relationship between prey length and outer borehole diameter (OBD) for *Ostrea angulata* (a), and *Ostrea latimarginata* (b). Solid circles represent completely drilled specimens and open circles represent incomplete drill holes.

4.2. Prey selectivity

Our study shows that the frequency of drill holes are taxon specific, as the highest drilling frequency in *Ostrea angulata* is significantly higher compared to all other groups. The other species of *Ostrea*, although attacked the most (represented by total number of complete and incomplete drill holes), yields a much lower complete drilling frequency. Abundance does not explain the high incidence of complete drill holes in *O. angulata* as *Ostrea latimarginata* is more abundant but records a high incomplete drilling frequency. The other species show a much lower drilling frequency that might be linked to their morphological or behavioral adaptation. *Chlamys* sp. are known for their swimming adaptations that often makes it difficult for the gastropod drillers to drill them. *Crassostrea gigensis* has extremely thick shells besides having a large size. Therefore, it is not surprising to find only 50% success rate of drilling attack for this species. *Placuna lamellata*, although not a thick-shelled bivalve, has a very large size. Therefore, it is particularly difficult to tackle for the naticid predators that trap the prey in their mesopodium and drag it under the sediment. In such circumstances, it is not unusual to find the drill hole to be concentrated near the margin. The only drilled specimen of *Placuna lamellata* in our collection has a drill hole that is very close the margin (Fig. 9c). *Hyotissa hyotis* has an extremely thick and corrugated shell of considerable size that might have made it an undesirable prey item. Examples of such highly specific prey preferences in predatory gastropods are observed in the Recent and are also available in the fossil record (Carriker, 1955; Carriker and Yochelson, 1968; Kitchell et al., 1981; Croll, 1983; Kelley, 1988, 1991; Dietl and Alexander, 1995).

Size seems to be another extremely important contributing factor in prey selection. For all the groups the average size of undrilled specimens is smaller than the drilled specimens. This result contradicts the claim of a size refuge where attaining a particular larger size makes a prey resistant to predatory attack (Vermeij, 1987). The predator–prey dynamics seems to be much more complex. Kitchell et al. (1981) have argued that the naticid predator selects its prey in order to maximize net energy gain. They have demonstrated the phenomena using the data from live and fossil assemblages of naticid predation. The same has also been demonstrated for extant muricid drillers (Chattopadhyay and Baumiller, 2009). Both studies have demonstrated that for a specific size class of a predator, there exists an optimal prey size. If the predator attacks a prey smaller than that optimal size, the net energy gain would be lower than the optimal value. Likewise, if the predator attacks a prey larger than the optimal size, it might not be able to finish the attack because of its own physiological constraints. The net energy gain, therefore, would be zero because of a failed attack. Kitchell et al. (1981) have also demonstrated the existence of a “handling limit” for a specific size of naticid predator beyond which the attacks are more likely to fail. Moreover, if the size ratio of a prey to its predator is too large, the predator could be overpowered the prey; the outcome of the attack might be fatal for the predator (Casey and Chattopadhyay, 2008) and therefore yielding a negative energy gain. Such specific prey size selection by predatory gastropods is also documented by other neontological studies. Vignali and Galleni (1986) argued that bivalve predation mortality initially increases with prey size up to a maximum that represents the preferred size, beyond which mortality progressively decreases towards the maximum prey size attained. Naticid predation therefore appears to be most intense on medium-sized bivalves (Edwards and Huebner, 1977; Franz, 1977), a similar finding to the present study. The lack of strict correlation between OBD and prey size does not negate the existence of size selection by the predator in their prey choice. The

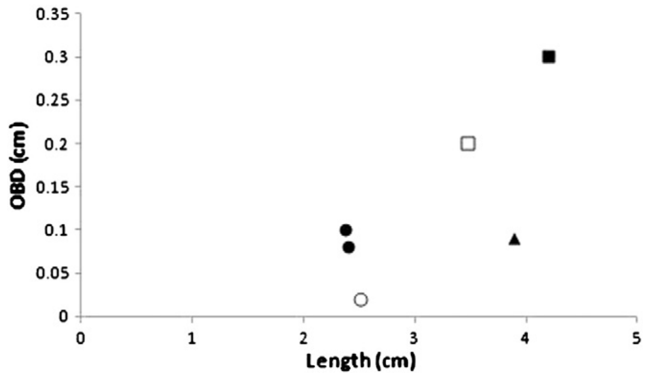

Fig. 7. Plot showing relationship between prey length and outer borehole diameter (OBD) for three species. Circles represent *Chlamys* sp., squares represent *Crassostrea gigensis* and the triangle represents *Placuna lamellata*. Solid symbols represent complete drill holes and the open symbols represent incomplete drillings.

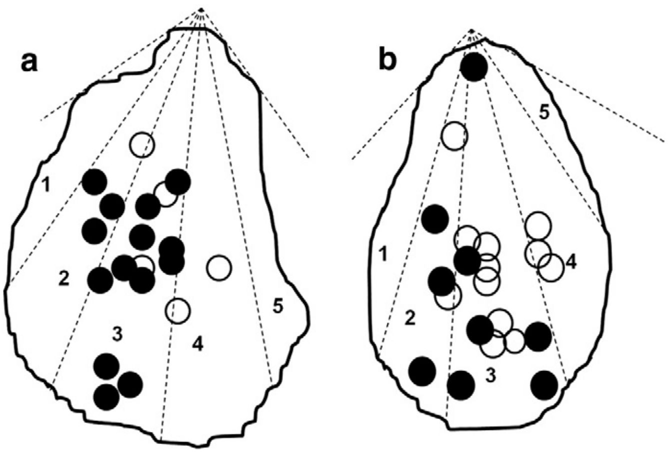

Fig. 8. Diagram showing the position of drill holes in *Ostrea angulata* (a) and *Ostrea latimarginata* (b). The dotted lines represent the boundary of the sector grids. The solid circles represent complete drill holes and the open circles represent incomplete drill holes.

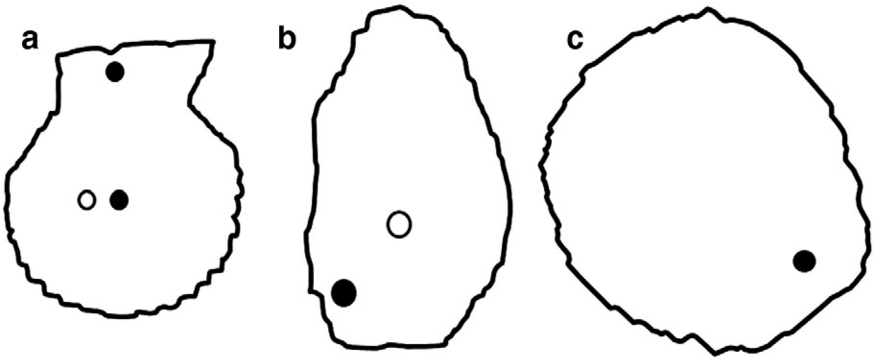

Fig. 9. Diagram showing the position of drill holes in *Chlamys* sp. (a), *Crassostrea gigensis* (b) and *Placuna lamellata* (c). The solid circles represent complete drill holes and the open circles represent incomplete drill holes.

experimental studies have demonstrated that even energetically viable attacks are often associated with an insignificant correlation between OBD and prey size (Chattopadhyay and Baumiller, 2007, 2009).

Stereotypic behavior of selecting a specific site for drilling is quite common among drilling predators, especially naticids. The stereotypy of drilling behavior frequently results in the clustered distribution of drill holes on the prey shell. Indeed, non-random siting of drill holes by the Naticidae is widely reported (Taylor, 1970; Berg and Porter, 1974; Berg and Nishenko, 1975; Rosewater, 1980; Kitchell et al., 1981). For naticids, the position of the drill hole is largely affected by prey handling (Ziegelmeier, 1954), which may be influenced by size and shape of the prey (Ansell, 1960; Kitchell, 1986; Roopnarine and Willard, 2001). Stereotypy in drill hole position is exhibited by naticids immediately upon metamorphosis (Berg, 1976). Researchers have observed ontogenetic change in prey-handling skills among naticids (Vignali and Galleni, 1986) and muricids (Urrutia and Navarro, 2001). It has been argued that selectivity of drill hole site increases the overall energy gain and placing it in the thinnest area of the shell could considerably increase the profitability and success rate (Hughes and de Dunkin, 1984; Kitchell, 1986; Kelley, 1988). Our study shows a considerable degree of site stereotypy for two dominant prey species, *O. angulata* and *O. latimarginata*. For the two dominant prey groups, the central segment with the highest incidence of complete drill holes is not the thinnest part of the shell either. However, that is the spot where the adductor muscle of these monomyarian bivalves is situated and attacking the muscle, therefore, ensures the immediate opening of the valves. Such behavior has been observed in drillers preying upon oysters (Chattopadhyay, 2011) and abalone (Hughes and de Dunkin, 1984; Thomas and Day, 1995). We did not find any significant difference between the complete and incomplete drill holes in terms of their stereotypy. It is worth noting that the site stereotypy of the incomplete drill holes are often complicated to asses since the prey continues to grow after the attack and hence alter the relative position of an incomplete drill hole with respect to morphological landmarks such as umbo and margin.

It is not expected to find valve preference by the predator for prey with symmetric valves. For asymmetric valves, however, such preference could be expected due to a greater ease of manipulation, or due to differences associated with the cost of drilling (Fretter and Graham, 1994). The periostracum of the left valve of corbulid bivalves prevents it from getting drilled and producing a right-valve heavy distribution of drill holes in corbulids (Lewy and Samtleben, 1979). Conversely, the naticid *Neverita didyma* preferentially drills the left valve of *Ruditapes philippinarum* (Rodrigues et al., 1987). A higher degree of drilling in a specific valve may also be caused by the orientation of the bivalve in the sediment that results in a greater accessibility for the predator to a specific valve over the other. We have observed a higher proportion of drilled left valves compared to the right valves for the two species of *Ostrea*. Right valves of oysters are always attached to the substrate and therefore it might be difficult to drill (Harper, 1991). This could explain the high proportion of drilled left valves in the population. However, for the same reason, valve selectivity could be related to the biased preservation potential of *Ostrea* valves if only the left valve gets dislodged and therefore preserved individually. In fact, our specimens of the undrilled valves of *Ostrea* species show a higher proportion of left valves compared to the right valves. Transportation could also result in such biased assemblage of valves due to variation in hydrodynamic properties of valves as demonstrated in the laboratory experiments with Recent shells (Chattopadhyay et al., in press).

4.3. Success of predator

Success of drilling attempts is inferred from the frequency of complete drill holes. Incomplete drill holes are used as proxy for failure of the predator. Although it represents a failed attack in majority of the cases, there are instances where prey was suffocated after such failed attack (Kowalewski, 2002; but see Visaggi et al., 2012). Incomplete drill holes might be a result of predator inefficiency, mechanical limits to drilling thick shells or interruption of drilling. Such interruption could be mediated by biological factors such as the escape of the prey. Larger, therefore thicker, prey are susceptible to sustain incomplete holes because the greater time required to penetrate a thick shell increases the likelihood of interruption of drilling by physical factors or prey escape behaviors. A change in the frequency of incomplete drill holes thus indicates change in the prey's defensive ability relative to the capacity of the predator through physiological changes such as changes in shell thickness, size or mobility. Kelley (1988) found a positive relationship between degree of selectivity of prey size and percentage of predation attempts that were successful. Incomplete drilling frequency is thus conventionally interpreted as a proxy for prey-effectiveness (Kelley and Hansen, 2003). However, there are instances where the incomplete drill holes are created by reasons unrelated to prey's morphological or behavioral characteristics. In the presence of a secondary predator a driller is prone to abandon a drilling attempt and leave an incomplete drill hole on the prey (Chattopadhyay and Baumiller, 2007). In those scenarios, incomplete drill holes would not be concentrated in larger shells since the decision of abandoning a drilling attempt is dictated by the invested drilling time. A change in incomplete drilling frequency in deep time, therefore, could also be linked to the risk of the driller (Chattopadhyay and Baumiller, 2010). These two entirely different causes of incomplete drill holes, one linked to the intrinsic properties of the prey and the other to the ambient ecosystem, brings a simple interpretation of incomplete drilling frequency as “prey-effectiveness” into question. Although there is no direct way to ascertain which of the causal mechanism is true for a particular assemblage, we can use an indirect method of drill hole depth to conclude. Chattopadhyay and Baumiller (2007) have demonstrated that when under threat, the drillers are prone to preferentially abandon the prey on which they have invested less time. Consequently, such “time-dependent” behavior would produce incomplete drill holes that are quite shallow. On the contrary, we would expect to have a broader distribution of incomplete drill hole depths if the interaction is guided by the prey size (and shell thickness).We can use this relative difference in incomplete drill hole depth to establish the causal nature of failure.

In our observed specimens, the incomplete drilling frequency is significantly different between *O. angulata* and *O. latimarginata* where the last has the highest incomplete drilling frequency. Comparing the size of the individuals with incomplete vs complete drill holes reveals that the specimens with incomplete drill holes are larger than those with complete ones. This pattern could suggest a causal mechanism of such failure that is linked to the morphological/behavioral attributes of larger prey. As Kitchell et al. (1981) suggested the existence of a “handling limit” in prey size for specific predator size beyond which the predator does not succeed. Therefore, the larger prey might have posed the handling limit due to their size resulting in higher incidences of incomplete drill holes. However, this explanation hold true only if the size of the prey did not increase after the attack. Since incomplete drill holes are nonlethal, the prey is likely to grow after the failed attack. Hence the observed size does not represent the size during the attack. On the contrary, the size of a completely drilled shell represents the true size during the lethal attack. Such intrinsic difference in captured size of shells with complete and incomplete drill holes could produce the observed pattern. It is not possible to differentiate between these two possibilities with our existing data.

Predator success could also be a function of predator size. It has been demonstrated that larger predators could handle both small as well as large prey (Kingsley-Smith et al., 2003). Hughes and de Dunkin (1984) have showed that *Nucella lapillus* modified its drilling behavior through learning that resulted in a higher success. For both naticid and muricid, the drilling behavior changes with experience (Calvet, 1992; Gosselin and Chia, 1996; Gordillo and Amuchastegui, 1998; Dietl, 2000). In our study we found that the rate of success depends on the size of the predator. The OBD size for complete drill holes is significantly larger than those for incomplete drill holes for each of the five prey species. This might be indicative of an increasing success rate in drilling with ontogeny. Such ontogenetic change in success rate in predatory attack has rarely been documented in palaeoecosystems.

5. Implication

Predatory drilling traces are among the most widely studied evidence of biotic interactions in the fossil record (Vermeij, 1982, 1987; Vermeij and Dudley, 1982; Kelley and Hansen, 2003 and reference there in). In order to test evolutionary hypotheses such as coevolution and escalation, temporal trend of drilling predation data has widely been used (Kelley, 1992; Kelley and Hansen, 1993). For such studies, assemblage-level patterns of drilling predation data are essential. One such compilation comes from the Cenozoic deposits along the Atlantic Coast of the United States (Kelley and Hansen, 1993, 1996, 2007; Kelley et al., 2001). The other detailed studies of various Cenozoic time period are focused on Central Europe (Hoffmeister and Kowalewski, 2001; Sawyer and Zuschin, 2011). It is well established that both in Recent and paleoecosystems, nature of ecological interactions dramatically change geographically (Kelley and Hansen, 2007). We, therefore, need to bring more data from other continents to fill the gap. Our present find fills it up to the subtropics of the northern Hemisphere where India was positioned during Miocene. In contrast to the North American Atlantic Coastal Plain or Europe, the Cenozoic of India has a complex geologic history where it travelled a considerable distance before reaching to its current position. Due to its history of long journey and fluctuating environments, one would expect the ecological history of India, including that of drilling predation, to differ from the ecological history of both North American Atlantic Coastal Plain and Central Europe. This is the first study to evaluate the Cenozoic drilling predation on molluscs from this area. When we compare our result with the global picture, we find patterns that are quite intriguing. The assemblage level drilling frequency of 20% reported in the present study is comparable to data reported from Miocene basins of Central Paratethys and Southeastern North Atlantic. However, it is quite different from comparable units of US Atlantic Coast, Boreal, Paratethys and Del Norte Country, California, US (Table 2). Such spatial variation in drilling frequency places temporal average into question unless we incorporate enough data from various parts of the world.

Table 2

Statistical comparison of the drill frequencies of the present study with published data from other Miocene basins. Only the bivalve data has been considered.

Locality	Undrilled	Drilled	DF (%)	χ^2	p	Source
Kutch, India	229	27	20	–	–	Present study
Central Paratethys	7747	726	8.6	1.23	0.266	Sawyer and Zuschin, 2011
Boreal	461	102	18.1	7.6	<<**0.05**	Hoffmeister and Kowalewski, 2001
Paratethys	353	72	16.9	5.25	<**0.05**	Hoffmeister and Kowalewski, 2001
Southeastern North Atlantic	43	5	10.4	0.0007	0.9	Hoffmeister and Kowalewski, 2001
US Atlantic Coast	14372	7435	34.1	62.68	<<**0.05**	Kelley and Hansen, 2006
Del Norte Country, California, US	2185	52	2.3	50.61	<<**0.05**	Watkins, 1974

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References

Amano, K., 2003. Predatory gastropod drill holes in upper Miocene cold seep bivalves, Hokkaido, Japan. Veliger 46, 90–96.

Amano, K., 2006. Temporal pattern of naticid predation on *Glycymeris yessoensis* (Sowerby) during the Late Cenozoic in Japan. Palaios 21, 369–375.

Anderson, L.C., 1992. Naticid gastropod predation on corbulid bivalves: effects of physical factors, morphological features, and statistical artifacts. Palaios 7, 602–620.

Ansell, A.D., 1960. Observations on predation of *Venus striatula* (Da Costa) by *Natica alderi* (Forbes). Proceedings of the Malacological Society of London 34, 157–164.

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.

Berg, C.J., 1976. Ontogeny of predatory behavior in marine snails (Prosobranchia: Naticidae). Nautilus 90, 1–4.

Berg Jr., C.J., Nishenko, S., 1975. Stereotypy of predatory boring behavior of Pleistocene naticid gastropods. Paleobiology 1, 258–260.

Berg, C.J., Porter, M.E., 1974. A comparison of predatory behaviour among the naticid gastropods *Lunatia heros*, *Lunatia triseriata* and *Polinices duplicatus*. Biological Bulletin 147, 469–470.

Biswas, S.K., 1992. Tertiary stratigraphy of Kutch. Journal of Palaeontological Society of India 37, 1–29.

Borkar, V.D., Kulkarni, K.G., Bhattacharjee, S., 2004. Studies of molluscan of the Miocene sediments of Kachchh, Gujarat, India – Part 1. Oysters. Geophytology 34, 1–7.

Calvet, C., 1992. Borehole site-selection in *Naticarius hebraeus* (Chemnitz in Karsten, 1769) (Naticidae: Gastropoda)? Orsis 7, 57–64.

Cantalamessa, G., Di Celma, C., Ragaini, L., 2005. Sequence stratigraphy of the Punta Ballena Member of the Jama Formation (Early Pleistocene, Equador): insights from integrated sedimentologic, taphonomic and paleoecologic analysis of molluscan shell concentrations. Palaeogeography, Palaeoclimatology, Palaeoecology 216, 1–5.

Carriker, M.R., 1955. Critical Review of Biology and Control of Oyster Drills *Urosalpinx* and *Eupleura*. U.S. Fish & Wildlife Service. Spec. Scientific Rep., 148, p. 150.

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. United States Geological Survey Professional Paper 593, 1–26.

Casey, M., Chattopadhyay, D., 2008. Clumping behavior: an antipredatory strategy against drilling predation. Journal of Experimental Marine Biology and Ecology 367, 174–179.

Chattopadhyay, D., 2004. New record of a coral-mollusca reefal community from the Early Tertiary of Kutch, Gujarat. Indian Minerals 58, 169–182.

Chattopadhyay, D., 2011. First evidence of predatory drilling from Upper Cretaceous Eutaw Formation (Santonian), Georgia. Southeastern Geology 48, 37–44.

Chattopadhyay, D., Baumiller, T.K., 2007. Drilling under threat: an experimental assessment of the drilling behavior of *Nucella lamellosa* in the presence of a predator. Journal of Experimental Marine Biology and Ecology 352, 257–266.

Chattopadhyay, D., Baumiller, T.K., 2009. An experimental assessment of penetration, excavation and consumption rates of the muricid gastropod, *Nucella lamellosa*. Journal of Shellfish Research 28, 1–7.

Chattopadhyay, D., Baumiller, T.K., 2010. Effect of durophagy on drilling predation: a case study of Cenozoic molluscs from North America. Historical Biology 22, 367–379.

Chattopadhyay, D., Rathie A., Das A., in press. The effect of morphology on post-mortem transportation of bivalve and its taphonomic implications. Palaios.

Colbath, S.L., 1985. Gastropod predation and depositional environments of two molluscan communities from the Miocene Astoria formation at Beverly Beach State Park, Oregon. Journal of Paleontology 59, 849–869.

Croll, R.P., 1983. Gastropod chemoreception. Biological Reviews of the Cambridge Philosophical Society 58, 293–319.

Das, S.S., Bardhan, S., Lahiri, T.C., 1999. The Late Bathonian gastropod fauna of Kutch, western India — a new assemblage. Paleontological Research 3, 268–286.

De Angelis, D.L., Kitchell, J.A., Post, D.M., 1985. The influence of naticid predation on evolutionary strategies of bivalve prey: conclusions from a model. American Naturalist 126, 817–842.

Dietl, G.P., 2000. Successful and unsuccessful predation of the gastropod *Nucella lapillus* (Muricidae) on the mussel *Mytilus edulis* from Maine. Veliger 43, 319–329.

Dietl, G.P., Alexander, R.R., 1995. Borehole site and prey size stereotypy in naticid predation on *Euspira (Lunatia)* heros Say and *Neverita (Polinices) duplicata* Say from the southern New Jersey coast. Journal of Shellfish Research 14, 307–314.

Dietl, G.P., Alexander, R.R., 2000. Post-Miocene shift in stereotypic naticid predation on confamilial prey from the Mid-Atlantic shelf: coevolution with dangerous prey. Palaios 4, 414–429.

Dudley, E.C., Dudley, E.C., 1980. Drilling predation on some Miocene marine mollusks. Nautilus 94, 63–66.

Edwards, D.C., Huebner, J.D., 1977. Feeding and growth rates of *Polinices duplicatus* preying on *Mya arenaria* at Barnstable Harbor, Massachusetts. Ecology 58, 1218–1236.

Fischer, J.C., Weber, C., 1997. Revision critique de la Paleontologie francaise. Gastropodes jurassiques, Masson, Paris, 2, pp. 1–300.

Franz, D.R., 1977. Size and age-specific predation by *Lunatia heros* (Say, 1822) on the surf clam *Spisula solidissima* (Dillwyn, 1817) off western Long Island, New York. Veliger 20, 144–150.

Fretter, V., Graham, A., 1994. British Prosobranch Molluscs: their functional anatomy and ecology. Royal Soc. London.

Gordillo, S., Amuchastegui, S., 1998. Predation strategies of *Trophon geversianus* (Pallas) (Muricoidea: Trophonidae). Malacologia 39, 83–91.

Gosselin, L.A., Chia, F.S., 1996. Prey selection by inexperienced predators: do juvenile snails maximize net energy gains on their first attack? Journal of Experimental Marine Biology and Ecology 199, 45–58.

Hammer, Ø., Harper, D.A.T., Ryan, P.D., 2001. PAST: Paleontological Statistics Software Package for education and data analysis. Palaeontologia Electronica 4 (178 kb, http://palaeo-electronica.org/2001_1/past/ issue1_01.htm).

Harper, E.M., 1991. The role of predation in the evolution of the cemented habit in bivalves. Palaeontology 34, 455–460.

Harper, E.M., 2003. Assessing the importance of drilling predation over the Palaeozoic and Mesozoic. Palaeogeography, Palaeoclimatology, Palaeoecology 201, 185–198.

Harper, E.M., 2006. Dissecting post-Palaeozoic arms races. Palaeogeography, Palaeoclimatology, Palaeoecology 232, 322–343.

Harper, E.M., Forsythe, G.T.W., Palmer, T., 1998. Taphonomy and the Mesozoic Marine Revolution: Preservation state masks the importance of boring predators. Palaios 13, 352–360.

Harzhauser, M., Reuter, M., Piller, W.E., Berning, B., Kroh, A., Mandic, O., 2009. Oligocene and Early Miocene Gastropods from Kutch (NW-India) document an early biogeographic switch from Western Tethys to Indo-Pacific. Paläontologische Zeitschrift 83, 333–372.

Herbert, G.S., Dietl, G.P., 2002. Tests of the escalation hypothesis: the role of multiple predators. Geological Society of America Abstracts with Programs 34, 538–539.

Hoffman, A., Pisera, A., Ryszkiewicz, M., 1974. Predation by muricid and naticid gastropods on the Lower Tortonian molluscs from the Korytnica clays. Acta Geologica Polonica 24, 249–260.

Hoffmeister, A.P., Kowalewski, M., 2001. Spatial and environmental variation in the fossil record of drilling predation: a case study from the Miocene of Central Europe. Palaios 16, 566–579.

Hughes, R.N., de Dunkin, S.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 of the United States of America 104, 15006–15010.

Kachhara, R.P., Jodhawat, R.L., Bigyapati Devi, K., 2012. Lower Oligocene bivalves of Ramanian Stage from Kachchh, Gujarat, India. Journal of Earth System Science 121, 405–438.

Kase, T., 1984. Early Cretaceous Marine and Brackish-water Gastropoda from Japan. Nat. Sc. Mus. Tokyo. (199 pp. + 31 pls).

Kelley, P.H., 1988. Predation by Miocene gastropods of the Chesapeake Group: stereotyped and predictable. Palaios 3, 436–448.

Kelley, P.H., 1991. Cannibalism by Chesapeake group naticid gastropods: a predictable result of stereotyped predation. Journal of Paleontology 65, 75–79.

Kelley, P.H., 1992. Evolutionary patterns of naticid gastropods of Chesapeake Group: an example of co-evolution. Journal of Paleontology 66, 794–800.

Kelley, P.H., Hansen, T.A., 1993. Evolution of the naticid gastropod predator–prey system: an evaluation of the hypothesis of escalation. Palaios 8, 358–375.

Kelley, P.H., Hansen, T.A., 1996. Naticid gastropod prey selectivity through time and the hypothesis of escalation. Palaios 11, 437–445.

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 Press, pp. 113–139.

Kelley, P.H., Hansen, T.A., 2006. Comparisons of class- and lower taxon-level patterns in naticid gastropod predation, Cretaceous to Pleistocene of the U.S. Coastal Plain. Palaeogeography, Palaeoclimatology, Palaeoecology 236, 302–320.

Kelley, P.H., Hansen, T.A., 2007. Latitudinal patterns in naticid gastropod predation along the East coast of the United States:A modern baseline for interpreting temporal patterns in the fossil record. SEPM Sp. Publ., Tulsa, 88, pp. 287–299.

Kelley, P.H., Hansen, T.A., Graham, S.E., Huntoon, A.G., 2001. Temporal patterns in the efficiency of naticid gastropod predators during the Cretaceous and Cenozoic of the United States Coastal Plain. Palaeogeography, Palaeoclimatology, Palaeoecology 166, 165–176.

Kingsley-Smith, P.R., Richardson, C.A., Seed, R., 2003. Stereotypic and size-selective predation in *Polinices pulchellus* (Gastropoda: Naticidae) Risso 1826. Journal of Experimental Marine Biology and Ecology 295, 173–190.

Kitchell, J.A., 1986. The evolution of predator–prey behavior: naticid gastropods and their molluscan prey. In: Nitecki, M., Kitchell, J.A. (Eds.), Evolution of Animal Behavior: Paleontological and Field Approaches. Oxford University Press, Oxford, pp. 88–110.

Kitchell, J.A., 1990. The reciprocal interaction of organism and effective environment: learning more about "and". In: Ross, R.M., Allmon, W.D. (Eds.), Causes of Evolution: A Paleontological Perspective. The University of Chicago Press, Chicago, pp. 151–169.

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.

Kowalewski, M., 1990. A hermeneutic analysis of the shell-drilling predation on molluscs in the Korytnica Clays (Middle Miocene; Holy Cross Mountains, Central Poland). Acta Geologica Polonica 40, 183–214.

Kowalewski, M., 2002. The fossil record of predation: an overview of analytical methods. Paleontological Society Special Paper 8, 3–42.

Kulkarni, K.G., Bhattacharjee, S., Borkar, V.D., 2007. Entobian Bioerosion of Miocene Oysters, Kachchh, Gujarat. Journal of the Geological Society of India 69, 827–833.

Kulkarni, K.G., Bhattacharjee, S., Borkar, V.D., 2009. Molluscan Fauna from the Miocene Sediments of Kachchh – Part 2. Bivalve subgenus *Indoplacuna*. Cainozoic Research 6, 71–81.

Kulkarni, K.G., Bhattacharjee, K.S., Borkar, V.D., 2010. Molluscan fauna from the Miocene sediments of Kachchh, Gujarat, India – Part 3. Gastropods. Journal of Earth System Science 119, 307–341.

Kumar, P., Saraswati, P.K., Banerjee, S., 2009. Early Miocene shell concentration in the mixed carbonate-siliciclastic system of Kutch and their distribution in sequence stratigraphic framework. Journal of the Geological Society of India 74, 432–444.

Leighton, L.R., 2001. New example of Devonian predatory boreholes and the influence of brachiopod spines on predator success. Palaeogeography, Palaeoclimatology, Palaeoecology 165, 53–69.

Lewy, Z., Samtleben, C., 1979. Functional morphology and palaeontological significance of the conchiolin layers in corbulid pelecypods. Lethaia 12, 341–351.

Meldahl, K.H., 1993. Geographic gradients in the formation of shell concentrations: Plio-Pleistocene marine deposits, Gulf of California. Palaeogeography, Palaeoclimatology, Palaeoecology 101, 1–25.

Morton, B., Chan, K., 1997. The first report of shell-boring predation by a representative of the Nassariidae (Gastropoda). Journal of Molluscan Studies 63, 476–478.

Norris, R.D., 1986. Taphonomic gradients in shelf fossil assemblages: Pliocene Purisima Formation, California. Palaios 1, 256–270.

Ponder, W.F., Taylor, J.D., 1992. Predatory shell drilling by two species of *Austroginella* (Gastropoda: Marginellidae). Journal of Zoology 228, 317–328.

Rodrigues, C.L., Nojima, S., Kikuchi, T., 1987. Mechanics of prey size preference in the gastropod *Neverita didyma* preying on the bivalve *Ruditapes philippinarum*. Marine Ecology Progress Series 40, 87–93.

Roopnarine, P.D., Willard, S., 2001. Bivalve prey morphology as a guide to drilling stereotypy of naticid and muricid gastropods: venerids, naticids and muricids in Tropical America. PaleoBios 21, 109–110.

Rosewater, J., 1980. Predator boreholes in *Periploma margaritaceum*, with a brief survey of other Periplomatidae. Veliger 22, 248–251.

Sawyer, J.A., Zuschin, M., 2010. Intensities of drilling predation of molluscan assemblages along a transect through the northern Gulf of Trieste (Adriatic Sea). Palaeogeography, Palaeoclimatology, Palaeoecology 285, 152–173.

Sawyer, J.A., Zuschin, M., 2011. Drilling predation in mollusks from the lower and middle Miocene of the central Paratethys. Palaios 26, 284–297.

Sohl, N.F., 1965. Marine Jurassic gastropods, central and southern Utah. United States Geological Survey Professional Paper 503D, 1–29.

Stanley, S.M., 2008. Predation defeats competition on the seafloor. Paleobiology 34, 1–21.

Taylor, J.D., 1970. Feeding habits of predatory gastropods in a Tertiary (Eocene) Molluscan assemblage from the Paris basin. Palaeontology 13, 254–260.

Thomas, M., Day, R.W., 1995. Site selection by a small drilling predator: why does the gastropod *Haustrum baileyanum* drill over muscle tissue of the abalone *Haliotis rubra*? Marine and Freshwater Research 46, 647–655.

Urrutia, G., Navarro, J.M., 2001. Patterns of shell penetration by *Chorus giganteus* juveniles (Gastropoda, Muricidae) on the mussel *Semimytilus algosus*. Journal of Experimental Marine Biology and Ecology 258, 141–153.

Vermeij, G.J., 1982. Unsuccessful predation and evolution. American Naturalist 120, 701–720.

Vermeij, G.J., 1987. Evolution and escalation. An Ecological History of Life. Princeton University Press, New Jersey (527 pp.).

Vermeij, G.J., Dudley, E.C., 1982. Shell repair and drilling in some gastropods from the Ripley Formation (Upper Cretaceous) of the southeastern U.S.A. Cretaceous Research 3, 397–403.

Vignali, R., Galleni, L., 1986. Naticid predation on soft bottom bivalves: a study on a beach assemblage. Oebalia 13, 157–177.

Visaggi, C.C., Dietl, G.P., Kelley, P.H., 2012. Alternate modes of naticid predation: an experimental test of the influence of substrate depth on drilling behaviors. Geological Society of America Abstracts with Programs 149, 15.

Watkins, R., 1974. Molluscan paleobiology of the Miocene Wimer formation, Del Norte County, California. Journal of Paleontology 48, 1264–1282.

Ziegelmeier, E., 1954. Beobachtungen fiber den Nahrungserwerb bei der Naticide *Lunatia nitida* Donovan (Gastropoda, Prosobranchaia). Helgoländer Wissenschaftliche Meeresuntersuchungen 5, 1–33.

Zlotnik, M., 2001. Size-related changes in predatory behaviour of naticid gastropods from Middle Miocene Korytnica Clays, Poland. Acta Palaeontologica Polonica 46, 87–97.