Journal of Paleontology, 95(5), 2021, p. 974–993

0022-3360/21/1937-2337
doi: 10.1017/jpa.2021.24

JOURNAL OF PALEONTOLOGY
A PUBLICATION OF THE Paleontological SOCIETY

Paleoecology of naticid–molluscan prey interaction during the Late Jurassic (Oxfordian) in Kutch, India: evolutionary implications

Subhendu Bardhan,[1] Sandip Saha,[1]* Shiladri S. Das,[1] and Ranita Saha[2]

[1]Geological Studies Unit, Indian Statistical Institute, 203, B. T. Road, Kolkata 700108, India <sbardhan12@gmail.com> <sandipsaha.ju@gmail.com> <shiladri@gmail.com>
[2]Department of Geology and Geophysics, Indian Institute of Technology, Kharagpur 721302, India <ranitasahakolkata@gmail.com>

Abstract.—We document and quantify one of the oldest predator–prey interactions between naticid gastropods and molluscan prey, on the basis of drill holes in shells, from the Late Jurassic (Oxfordian) beds of Kutch, western India. Previously, many workers recorded naticid-like drill holes on prey taxa from the Triassic and the Jurassic, but in the absence of associated naticid body fossils, they remained equivocal.

The present gastropod community is dominated by turritellines (98% of the sample) that form the turritelline-dominated assemblage, and the naticid drilling predation is restricted almost entirely to turritellines among gastropods. Confamilial naticid predation takes place occasionally. Within the bivalve community, corbulids and nuculids are most abundant and are drilled more often than other taxa. These observations indicate that prey selection was opportunistic and based solely on availability. Drilling intensities at both assemblage and lower taxon levels are low. Behavioral stereotypy of naticid predation in some cases is moderately high.

Turritellines are often the preferred prey of naticid gastropods since the late Early Cretaceous. These two groups form a recurrent association reflecting prey–predator interaction. Here we suggest that both turritellines and naticids evolved during the Jurassic, and the prey–predator interaction between them was established shortly thereafter. Among bivalves, corbulids also became important prey of naticids in the same spatiotemporal framework. Corbulids are older than naticids and first appeared during the Middle Jurassic. After their first encounter with naticids, corbulids evolved conchiolin layers within the valves to resist predation.

Introduction

Predatory drill holes in marine shells provide information about ecological interaction and help make predation-related hypotheses (e.g., escalation) testable by applying detailed statistical analyses. The study of drilling predation in extant and extinct taxa, therefore, forms the focus of many research papers (Vermeij, 1977, 1987; Kelley and Hansen, 1993; Harper, 1994; Kardon, 1998; Dietl and Kelley, 2002, 2006; Kowalewski, 2002; Mondal et al., 2010, 2017, 2019a, b; Bardhan et al., 2012, 2014; Das et al., 2014; Mallick et al., 2014; Pahari et al., 2016; Sarkar et al., 2016; Anderson et al., 2017; Klompmaker et al., 2017, 2019; among others).

Drilling predation evolved in association with the rise of metazoans, and drill holes have been reported from as early as Neoproterozoic–Early Paleozoic times (Bengtson and Zhao, 1992; Morris and Bengtson, 1994; Hua et al., 2003; Huntley and Kowalewski, 2007; Porter, 2016). The Paleozoic drill holes were of various types, and some were possibly made by gastropod predators (platyceratid gastropods; Kowalewski et al., 1998; Kowalewski, 2002; Klompmaker et al., 2016) as well as by unknown taxa, including parasites (Morris and Bengtson, 1994; Klompmaker et al., 2016). Late Paleozoic and early Mesozoic drill holes were sometimes naticid-like (Klompmaker et al., 2017), but their creators remain equivocal since no naticid body fossils co-occur with the drilled taxa. There are several reports of drilled bivalve and brachiopod shells from the Mesozoic, where the shape of the drill holes resembles those made by naticid predators (i.e., circular outline, parabolic walls; resembling ichnospecies *Oichnus paraboloides* Bromley, 1981). The Late Triassic Cassian Formation of Italy contains shells of bivalves (Koken, 1892; Fürsich and Jablonski, 1984; Zardini, 1985) and brachiopods (Klompmaker et al., 2016) with the characteristic paraboloid drill holes such as those commonly made by naticids. Many workers attributed these drill holes to various gastropod genera such as *Natiria* de Koninck, 1881 or *Naticopsis* M'Coy, 1844, *Amauropsis* Mörch, 1857, and *Ampullina* Férussac, 1822, which were later found to be unrelated to true naticids (Kabat, 1991; Bandel, 1992, 1993, 1996, 1999; Bardhan et al., 2012; Hausmann and Nützel, 2015; Das et al., 2019). Kase and Ishikawa (2003) provided evidence for the herbivorous feeding habit of Recent ampullinid gastropods. Recently, Klompmaker et al. (2016) suggested that the Cassian drill holes may have been made by predatory drillers; however, they did not rule out parasitism.

The two gastropod groups (naticids and muricids), which are mainly responsible for drilling predation, were previously

*Corresponding author

believed to have evolved in the Early Cretaceous (Taylor, 1970; Adegoke and Tevesz, 1974; Vermeij and Dudley, 1982; Taylor et al., 1983; Arua and Hoque, 1989; Kelley and Hansen, 2006; Harries and Schopf, 2007; Klompmaker et al., 2016; and many others). Recently, naticids were reported from the Late Jurassic (Oxfordian) of India (Das et al., 2019).

Kowalewski et al. (1998) described three major phases of drilling history in the fossil record. In the Paleozoic phase, predation intensities were low to moderate and victims were mainly sessile benthic taxa, including brachiopods (see also Klompmaker et al., 2017). Predation intensity reached a Paleozoic peak during the Ordovician (Huntley and Kowalewski, 2007). The Mesozoic phase was marked by a lull with rare, facultative drilling events (Fürsich and Jablonski, 1984; but see Vermeij, 1977, 1987). The Cenozoic phase led to the high drilling intensities (DIs) on molluscan prey (Carriker and Yochelson, 1968; Kelley and Hansen, 1993, 1996, 2006), which continue to be observed in modern marine environments, on a variety of taxa (Dudley and Vermeij, 1978; Boucher, 1986; Vermeij, 1987; Mondal et al., 2010; Paul et al., 2013; Chattopadhyay et al., 2014; Das et al., 2014; Klompmaker et al., 2015; Pahari et al., 2016; Saha et al., 2016; Sarkar et al., 2016; Mondal et al., 2019a, b; among others).

Harper et al. (1998) and Harper and Wharton (2000) reported typical naticid-like drill holes in brachiopod shells from the Jurassic and the Early Cretaceous of the United Kingdom and Ireland. The DI sometimes attained modern values (>20%). Bardhan et al. (2012) also recorded naticid drill holes on astartids (*Neocrassina* Fischer, 1887) and other bivalves from the Upper Jurassic (Oxfordian) of Kutch, western India. At 30%, the DI was the highest ever recorded from the Mesozoic. They also found several coeval naticid-like taxa (e.g., *Ampullina* Férussac, 1822 and *Ampullospira* Harris, 1897) but could not identify a specific driller.

Against this backdrop, we herein report naticid drill holes in shells from a molluscan assemblage from the Upper Jurassic beds of Kutch, where naticid body fossils are recorded together with various other gastropods and bivalves (Das et al., 2019). The assemblage is dominated by turritellines (Das et al., 2018) and represents a turritelline-dominated assemblage (TDA) in the sense of Allmon (2007; detailed discussion follows). In the present study, we record the oldest interaction between naticid predators and turritelline prey. In addition, the naticids show a rare case of cannibalism. Bivalve diversity mimics that of gastropods, and some bivalve taxa are also found to be drilled by naticid gastropods.

Many recent and fossil prey communities show typical aspects of the naticid predation. For example, naticids are prey-selective, and the data show that they select prey taxa in a manner that is consistent with the cost–benefit model of Kitchell et al. (1981). Recent and Neogene naticids show a strong size and behavioral stereotypy while attacking their prey (Kelley, 1988; Kelley and Hansen, 1993, 1996, 2006). Prey is commonly targeted based on size (a large predator would select large prey), and drill hole sites are restricted to particular areas within the shell. Many workers suggested that prey selectivity and behavioral stereotypy of naticids developed over time (Kelley, 1988). Certain Cretaceous and Paleogene examples of naticid predation show some of the aspects mentioned, whereas others lack such evidence. For the assessment of the supposedly oldest example of naticid–molluscan prey interaction from the Late Jurassic, we have set out the following objectives: (1) to estimate predator abundance, type of prey available, and impact of predation at the beginning on molluscan prey, DI on molluscan prey is recorded; (2) to understand the process and underlying causes of prey selection during the early history of naticid predation, variations of DI at family/subfamily levels are explored, and the function of ornamentation, shell thickness, and shape of prey shells are studied; (3) to evaluate prey response to drilling predation, prey effectiveness (PE) and multiple drill holes (MULT) are analyzed (both incomplete and multiple DIs provide information about a prey's passive responses to reduce mortality due to predation); (4) to understand the predatory behavior of the early naticids, size and site selectivity of drill holes are studied (it is suggested that stereotypy offers better manipulation by predators and the least passive resistance to drilling by prey); (5) to assess whether the recurrent association of turritelline/corbulid prey and naticid predators evolved during the Jurassic, its historical development is reviewed; (6) to understand whether and how the heavily preyed taxa responded to the sudden appearance of naticid predators, we study their evolutionary history.

Materials and methods

The present collection has been made from the Dhosa Oolite Member of the Chari Formation of Kutch, western India (Mitra et al., 1979; Fürsich and Pandey, 2003). The member is well time-constrained by ammonites (Mitra and Ghosh, 1979; Roy et al., 2012) and Oxfordian in age (Das et al., 2018). The Dhosa Oolite Member is a regionally persistent unit and is characterized by typically brown-colored oolitic limestone (Fürsich et al., 1992). In the present section, the Dhosa Oolite Member consists of oolitic limestone, sandstone, and shale. Most of the studied specimens have been obtained from the shale in the upper part of the section, but several are from sandstone (for detailed stratigraphic and environmental information, see Das et al., 2018, 2019).

A total of 11 samples were collected following both bulk-sampling and random-surface-sampling protocols (Kowalewski, 2002; Mallick et al., 2013; Das et al., 2018). Most of the specimens were found loose or weakly adhered to the rocks. Specimens were separated by hand and pincer from the sediment in the laboratory. For smaller specimens (<10 mm), ASTM (American Standard Test Sieve Series) sieves (numbers 5, 10, and 20) were used to separate them from larger ones and from the matrix. Drill hole morphology, including hole outline, hole wall, and presence of a boss in incomplete drill holes, were studied under stereo microscope (Magna vision, LENSEL L104CV) and scanning electron microscope (SEM).

Gastropods and bivalves were identified on the basis of the rich taxonomic literature available for the region (Kitchin, 1903; Cox, 1940; Mitra and Ghosh, 1979; Singh and Rai, 1980; Jaitly et al., 1995; Allmon, 1996; Kanjilal, 1997; Das et al., 1999, 2005, 2018, 2019; Fürsich et al., 2000; Alberti et al., 2013a). The molluscan assemblage includes 14,012 gastropods (approximately 90% of the total molluscan fauna) and 1,380 bivalve shells (9% of the total fauna). The gastropod community consists of 19 species in 10 families and represents a TDA. An assemblage is considered a TDA when turritelline gastropods

https://doi.org/10.1017/jpa.2021.24 Published online by Cambridge University Press

make up at least 20% of the total molluscan assemblage or are two times as abundant as any other molluscan species present (Allmon, 2007). In this study, turritelline gastropods comprise 98% of the gastropod community and 89% of the total molluscan assemblage. The second-most abundant (n > 10 individuals; see Vermeij, 1987; Kelley and Hansen, 2006; Mallick et al., 2013) gastropod taxon is the Naticidae (n = 98; 0.7% of the gastropod community and 0.006% of the total molluscan assemblage). Other abundant gastropod families are Ampullinidae (n = 45; 0.32% of the gastropod community), Volutidae (n = 37; about 0.26%), Rissoidae (n = 36; about 0.26%), Cerithiopsidae (n = 30; 0.21%), and Scalidae (n = 22; 0.15%). The remaining gastropods are very rare (n < 10) and are excluded from further analysis.

Bivalves are less abundant, but equally diverse, and are represented by 19 species in 15 families. The abundant families (n > 10 shells; see Vermeij, 1987; Vermeij et al., 1989; Harper, 1994; Kelley and Hansen, 2006) in descending order are Nuculidae (n = 551 shells), Corbulidae (n = 516), Arcidae (n = 110.5), Nuculanidae (n = 93), Ostreidae (n = 43.5), Lucinidae (n = 20), and Polidevciidae (n = 14). Other ancillary taxa are bryozoans, corals, crinoids (represented by ossicles), ammonites, and belemnites, along with some unidentified broken fossils (about 1% of the total assemblage).

We recently described four turritelline species under a single genus *Turritella* sensu lato from the same assemblage (for details, see Das et al., 2018): *Turritella jadavpuriensis* Mitra and Ghosh, 1979 (75% of the turritelline shells), *Turritella amitava* Das et al., 2018 (15%), *Turritella jhuraensis* Mitra and Ghosh, 1979 (9%), and *Turritella dhosaensis* Das et al., 2018 (about 1%). Small and large turritelline shells occur together, with shells varying from 2 to 65 mm in height. Small specimens are indistinguishable from the early whorls of larger shells, indicating that they are juveniles, not a different species. The second-most abundant gastropod group comprises the naticid genera *Gyrodes* Conrad, 1860 (n = 76) and *Euspira* Agassiz in Sowerby, 1837 (n = 22) (Das et al., 2019).

The most abundant two bivalve species here are provisionally described (systematics in preparation) as *Palaeonucula* sp. (39% of the total bivalve community) and *Indocorbula* sp. (37%). Arcidae is represented by two species, *Anadara* sp. (n = 91.5) and *Arca* sp. (n = 19). Nuculanidae is also abundant and consists of one species, *Nuculana juriana* Cox, 1940 (6.7% of the total bivalve community). Three other abundant families are Ostreidae, Lucinidae, and Polidevciidae, which are represented by one species each, *Ostrea* sp. (3.2% of the total bivalve community), *Pterolucina* sp. (1.5%), and *Dacryoma lacryma* Sowerby, 1824 (1%), respectively. The remainder of the families are represented by a few specimens only (n < 10 shells) and hence are excluded from the study.

In many turritelline specimens, delicate apical parts have been preserved although protoconch are missing (Das et al., 2018). The presence of shells of varying sizes on the same bedding plane indicates that no taphonomic sorting occurred. Many bivalves (e.g., nuculids) are found articulated, and very thin-shelled bivalves (the right valves of *Ostrea* sp.) are also present. Some bivalve species occur with disarticulated valves (*Anadara* sp.); the ratio between right and left valves is close to one. These observations suggest weak taphonomic overprinting. Roy et al. (1994) demonstrated that drilled bivalve shells were weaker to "point-load compression" than undrilled shells and would thus preferentially be fragmented and disappear from the assemblage. However, Kelley (2008) from field observation on bivalves and Dyer et al. (2018) from an experimental study demonstrated that the drilled shells were not always preferentially broken due to compaction (see also Klompmaker et al., 2019). Kelley (2008) showed that the taphonomic conditions of drilled versus undrilled valves are not statistically significantly different. We thus also assume that drilled shells are not preferentially lost from the studied assemblage. Moreover, the host sediments are fine-grained sandstone and shale, indicating a relatively deep and calm environment below the storm wave base (Datta, 1992; Alberti et al., 2013b). In the following, we document several ecological parameters to understand the pattern of naticid predation during Late Jurassic time in Kutch.

Drilling intensity.—We considered only complete or near-complete gastropod shells (with only minor apertural and/or apical breakage) and intact bivalve shells (both articulated and disarticulated) to assess DI at assemblage and taxon levels (family to species). For gastropods, DI is measured as the ratio between the shells with complete drill holes and the total number of shells (cf. Allmon et al., 1990; Kowalewski, 2002; Kelley and Hansen, 2006; Mallick et al., 2014) and is expressed as a percentage. For bivalves, DI is defined as the ratio between the total number of drilled valves and the total number of bivalve individuals (Bambach and Kowalewski, 2000; Bardhan et al., 2012) and is expressed as a percentage. The total number of individuals (N) for bivalves can be calculated by the following equation: $N = (RV + LV)/2 + A$, where RV, LV, and A are the numbers of right, left, and articulated valves, respectively (Kowalewski, 2002; Harries and Schopf, 2007). Assemblage-level DI is analyzed separately for gastropods and bivalves and is calculated as the percentage of drilled individuals. Because DI may vary with prey size (Vermeij, 1987; Allmon et al., 1990; Paul et al., 2013; Sarkar et al., 2016), DI is measured for different size classes within the turritelline species. Previous workers, including Paul et al. (2013) and Sarkar et al. (2016), subdivided turritellines into two size classes with a cut-off at 4 cm shell height. The studied assemblage includes numerous small individuals (up to 2 mm). Therefore, to assess the full range of predation, we analyze DI in four size classes: (1) less than 20 mm, (2) 21 to 40 mm, (3) 41 to 60 mm, and (4) greater than 60 mm. No cut-offs were employed in bivalve species as they are mostly small.

Incomplete and multiple drilling intensities.—Incomplete drill holes indicate the failure of the predator to enter into the prey shell's interior, and multiple drill holes indicate more than one predatory attack in a prey specimen (Vermeij, 1987; Kelley et al., 2001). A single naticid may attack the same prey several times if previous attempts were unsuccessful. Likewise, a naticid may attack a prey specimen that was previously unsuccessfully attacked by another naticid. For muricids, by contrast, multiple holes in a prey specimen generally indicate simultaneous attacks by several predators (Kelley et al., 2001). The abundances of incomplete and multiple drill holes indicate the prey's passive resistance to reduce mortality due

https://doi.org/10.1017/jpa.2021.24 Published online by Cambridge University Press

to predation (Kelley and Hansen, 1993, 1996; Kelley et al., 2001). However, some workers (Ansell and Morton, 1987; Hutchings and Herbert, 2013) opposed this view. According to them, prey with incomplete drill holes may be consumed by smothering by large predators. Decreasing competition among predators may result in a decrease of incomplete drill hole intensity (Hutchings and Herbert, 2013; but for the opposite view, see Pahari et al., 2016). We consider incomplete drill holes as unsuccessful drilling attempts, irrespective of their cause (see also Visaggi et al., 2013). PE is defined as the number of incomplete drill holes divided by the total number of drill holes (Kelley and Hansen, 1993; Mallick et al., 2013, 2014) and is expressed as a percentage. MULT is defined as the ratio between the number of drill holes that occur in multiply drilled specimens and the total number of drill holes (see Kelley and Hansen, 1993; Mallick et al., 2014) and here is also expressed as a percentage. Both PE and MULT were measured separately for gastropods and bivalves at assemblage level and were also assessed at various taxon levels (family and species).

Behavioral stereotypy.—Stereotypy of drilling predation means that drill holes are concentrated in a particular site or area on a gastropod or a bivalve shell. Stereotypy of successful predation is a measure for the efficiency of the naticid predators (Kelley and Hansen, 1993, 1996, 2006). Several workers have suggested that preferred drill sites in gastropod shells represent the thinnest part of the shell, which offers the least resistance for drilling (Kitchell, 1986; Allmon et al., 1990). Therefore, we examine site selectivity in a vertical profile along the axis of coiling (following Allmon et al., 1990; Hagadorn and Boyajian, 1997) for gastropod shells. Drill holes are plotted on a two-dimensional outline of the gastropod shell, representing an axial section (see the following). The positions of drill holes are plotted by measuring the distance from the apex, scaled to prey size (Goswami et al., 2020). To depict the distribution of drill holes in the radial profile, a basal section has been constructed and divided into four quadrants where quadrants I and IV represent the apertural side, and quadrants II and III represent the abapertural side (see the following). According to Adegoke and Tevesz (1974), the radial distribution of naticid drill holes indicates whether the naticid predators attack their prey from the apertural or abapertural side. Site and size distribution of drill holes are studied for three turritelline species (*T. jadavpuriensis*, *T. jhuraensis*, and *T. amitava*) to understand the behavioral stereotypy of the Jurassic naticid predators. The other species, *T. dhosaensis*, represents fewer than 10 intact specimens and is excluded from the analysis. We plot outer drill hole diameter (ODD), which serves as a proxy for the predator size (Kitchell et al., 1981; Anderson et al., 1991) against maximum whorl height (MWH) of the prey shell to understand whether the naticids are size-selective.

For the bivalves, we draw nine-sector grids following Kelley (1988) and Bardhan et al. (2012) to evaluate whether there is any site preference of drill holes (see the following). The data have been standardized for sector size. The number of drill holes in each sector is counted and compared with other sectors to know whether the naticid predators prefer any particular sector for drilling. We consider that drill holes are randomly distributed throughout the shell as a null hypothesis to test site stereotypy. For valve selectivity, we study the occurrence of drill holes on each valve (right or left). The antero-posterior length of a bivalve shell (a proxy of the prey size) and the ODD (a proxy of the predator size) are measured and plotted in a binary diagram to evaluate the prey size preference of the predators.

Anti-predatory traits.—Morphological characters such as shell ornamentation, shell thickness, and shell slenderness of gastropods, which resulted from evolutionary adaptation, are arguably the resistant characters against predation during the Cenozoic (Vermeij et al., 1980; Signor, 1985; Paul et al., 2013; Sarkar et al., 2016). Ornamentation hinders the drilling process, and thick shells increase the drilling time; thus, more cost is involved, which makes the prey unprofitable. Slender shells having a low profile within the sediment escape notice of durophagous predators (Signor, 1985). Sarkar et al. (2016) observed lower DI in slender terebrid gastropod species than in inflated forms. Terebrids are equally high-spired like turritellines. To understand the prey's passive responses against drilling predation, shell ornamentation, degree of slenderness, and shell thickness are analyzed for the three turritelline species. All three species are highly variable with regard to shell shape; both inflated and slender variants exist. Therefore, we have recorded whether a specimen is slender or inflated and tested the role of shape in affecting drilling success. Shell slenderness in gastropods is defined as the ratio between shell diameter and shell length. In the "inflated" type, the ratio is greater than 0.35; in the "slender" variant, the ratio is less than 0.35 (see also Paul et al., 2013). Allmon et al. (1990) divided prey shells into different defensive categories on the basis of sculptures to quantify the relationship between shell ornamentation and predation intensity. Later, Paul et al. (2013) expanded and modified this ornamental scheme on the basis of the strength and number of ribs present on turritelline species. Following Paul et al. (2013), we divided the turritelline species into two categories. Category 1 has four or more strong ribs, and category 2 has fewer than four strong ribs. We measured the DI from each category data.

The thickness of the shell has been measured in two ways. In the first method, we measured the thickness near the aperture of all drilled shells. In turritelline phylogeny, shell thickness is at its minimum near the aperture (Kabat, 1991). Thus, the thickness analysis at the aperture may not give any meaningful results. Therefore, we adopted a second method. Many specimens are broken and were excluded from the DI analyses. However, some of these also have drill holes (n = 421). We used these broken but drilled specimens to measure shell thickness at the drill hole sites, thus avoiding damage to the intact but drilled shells. This analysis provides information about the general thickness of shells in different areas, making it possible to test the hypothesis that naticid gastropods drill at the thinnest part of the shell (Allmon et al., 1990). We also measured the whorl diameter of the broken shells at the drill sites.

Statistical analysis.—A two-tailed chi-square test of independence is used for comparison of DIs across taxa. A

https://doi.org/10.1017/jpa.2021.24 Published online by Cambridge University Press

two-tailed chi-square test of goodness of fit is used to understand the statistical significance of the site preference of drill holes. Prey size selectivity has been measured by using the different statistical tests (linear regression [least-square] and the correlation coefficient, Pearson's r). For all these analyses, statistical significance is measured against an α value of 0.05.

Repository and institutional abbreviation.—All specimens are archived in the Museum of Geological Studies Unit, Indian Statistical Institute, Kolkata, India. Collection numbers consist of the prefix ISI/g/Jur/ for gastropods and ISI/b/Jur/ for bivalves followed by consecutive numbers.

Results

Predator identification.—The nature of drill holes is circular in outline, with parabolic walls (ichnospecies *Oichnus paraboloides* Bromley, 1981). The drill holes are perpendicular to the shell surface and were made from the external side. They are thus recognized as naticid drill holes (Carriker and Yochelson, 1968; Dietl et al., 2004; Daley et al., 2007; Mallick et al., 2013, 2014; Fig. 1.2, 1.3, 1.9). Small drill holes, when examined under the SEM, also show the typical naticid drill hole morphologies (Fig. 2.1–2.3). In some small bivalve shells, the drill holes appear to be cylindrical with straight-sided walls. Some of them, however, have centrally located boss (Fig. 1.6, 1.7). The presence of boss indicates that the driller was naticid, and straight-walled holes were because of thin shells.

It is therefore argued that the drill holes in our samples were made by the naticid predators (see also Taylor et al., 1983; Allmon et al., 1990 for similar inference). It is pertinent to mention that the present assemblage includes naticid body fossils that belong to two species of subfamilies Gyrodiniae and Polinicinae (Das et al., 2019): *Gyrodes mahalanobisi* Das et al., 2019, and *Euspira jhuraensis* Das et al., 2019 (Fig. 3).

Molluscan prey.—We estimated DI within the gastropods and the bivalves at different taxonomic levels. The molluscan assemblage comprises 3,922 complete individuals of which 279 specimens are drilled; therefore, the assemblage level DI is 7.11.

Gastropod community.—Nineteen species are represented by 2,542 individuals of which 215 specimens are drilled (DI = 8.46). Among seven abundant gastropod families, only the species of Turritellidae are drilled (DI = 9.49). One specimen of Naticidae, *G. mahalanobisi* shows a complete drill hole (DI = 1.32; Fig. 3.6; Table 1). Turritellidae is represented only by the subfamily Turritellinae. Among turritelline species, the DI ranges from 8.93 to 11.41 (Table 1). Only *T. jadavpuriensis* contains both incomplete and multiple drill holes. PE and MULT are 4.29 and 3.06, respectively (Table 1).

The DI data for different size classes of the turritelline species are shown in Table 2. *T. jadavpuriensis*, which ranges up to 6.5 cm in height, is drilled in every size class. However, the DIs do not show significantly different values ($p > 0.05$) except for the highest size interval, which is due to the low sample size (see Table 2). Two other species are smaller (<4 cm); their DIs are also low and do not differ significantly ($p > 0.05$) from the corresponding sizes of *T. jadavpuriensis* (Table 2).

The vertical distribution of drill holes in three turritelline species is shown in Figure 4. It indicates that they are mainly restricted to the middle and lower part of the whorl height ($p << 0.05$ for all three turritelline species).

The radial distribution of drill holes is shown in Figure 5. For *T. jadavpuriensis*, the radial pattern shows significantly higher values toward the abapertural side ($p << 0.05$) whereas for other species, patterns do not show any bias toward the abapertural side (for *T. jhuraensis*, $p = 0.30$, and for *T. amitava*, $p = 0.23$).

The relationship between prey size for all turritelline species and ODD is shown in Figure 6. Overall, turritelline species show a good correlation ($r^2 = 0.63$; $p << 0.05$; Fig. 6.1). *T. jadavpuriensis* shows a significant positive correlation ($r^2 = 0.63$; $p << 0.05$; Fig. 6.2) whereas the relationship is poor in *T. jhuraensis* ($p = 0.06$; Fig. 6.3) and *T. amitava* ($p > 0.05$; Fig. 6.4).

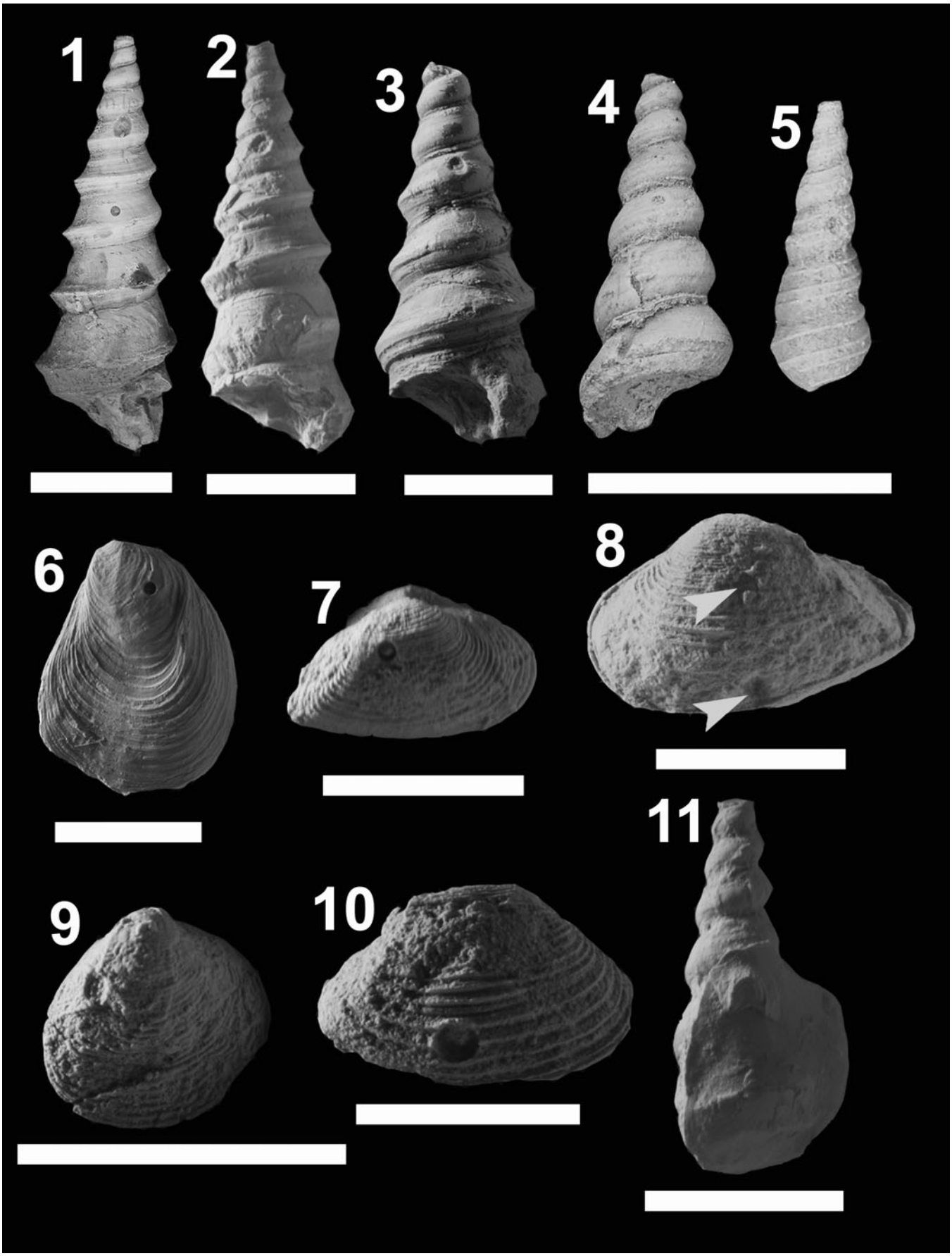
Shell shape analysis reveals that in all turritelline species, inflated variants are far more in number (Table 3). However, DI in each variant of each species is more or less the same and is not statistically significantly different (p values are > 0.5).

According to the present ornamental classification (see Materials and methods), *T. jadavpuriensis* belongs to category 1 (four or more strong ribs) whereas *T. jhuraensis* and *T. amitava* belong to category 2 (fewer than four strong ribs). *T. jadavpuriensis* has DI 8.93 and *T. jhuraensis* and *T. amitava* have DI values 11.41 and 10.45 respectively (Table 4). The differences of DIs between the strongly ornamented and the relatively weakly ornamented species, however, are not statistically significant ($p = 0.15$).

Shell thickness measured at the aperture of the drilled specimens is shown in Figure 7.1. The relation between apertural shell thickness and whorl diameter is very poor ($r^2 = 0.15$; $p << 0.05$). The alternative method that is adopted here, to measure the thickness of the shell at the drilled-hole sites, also shows equally poor correlation ($r^2 = 0.27$; $p << 0.05$; Fig. 7.2).

Bivalve community.—Out of 1,380 individual bivalve shells, only 64 shells are drilled and the DI is 4.64, which is statistically significantly different from that of the gastropod community ($p = 0.001$). Among seven abundant bivalve families, five families are drilled, of which two families (Nuculidae and Corbulidae) are relatively frequently drilled (Table 5). DIs in the two most abundant bivalve species are 6.20 (*Indocorbula* sp.) and 4.72 (*Palaeonucula* sp.) (Table 5). *Indocorbula* sp. has 32 complete drill holes. Some of them show typical shelf-like projections within the holes, which indicate the presence of conchiolin layers (Fig. 2.4, 2.5; Harper, 1994, fig. 3; Kardon, 1998, fig. 1.B). DIs of all species are shown in Table 5. Incomplete drill holes and MULT are present only in the two most abundant species (see Table 5). Incomplete drill holes in some specimens of *Indocorbul*a sp. terminate at the conchiolin layers (Fig. 2.4). One incomplete drill hole is encountered in *Ostrea* sp. (Fig. 1.6).

https://doi.org/10.1017/jpa.2021.24 Published online by Cambridge University Press



https://doi.org/10.1017/jpa.2021.24 Published online by Cambridge University Press

Figure 1. (**1–10**) Naticid drill holes in turritelline gastropods and bivalves in the present molluscan assemblage. (**1–3**) *Turritella jadavpuriensis* (specimen nos. ISI/g/Jur/T 7, 105, 109): (**1**) shows multiple drill holes; (**2, 3**) show complete drill hole. (**4**) *Turritella jhuraensis* (specimen no. ISI/g/Jur/T 201). (**5**) *Turritella amitava* (specimen no. ISI/g/Jur/T 301) bearing complete naticid drill hole. (**6**) *Ostrea* sp. (specimen no. ISI/b/Jur/O 21) having incomplete drill hole. Note parallel-sided whole morphology, (**7, 8, 10**) *Indocorbula* sp. showing naticid drill holes. Note incomplete drill hole with a centrally located boss in (**7**) and (**10**) (specimen nos. ISI/b/Jur/I 11, 13); (**8**) (specimen no. ISI/b/Jur/b 16) contains multiple drill holes (arrows). (**9**) *Palaeonucula* sp. (specimen no. ISI/b/Jur/P 21) shows a complete drill hole. (**11**) Live epizoan (Oyster) attachment on *T. jadavpuriensis* (specimen no. ISI/g/Jur/T 151) indicating its epifaunal life mode. Scale bars = 1 cm.

Naticid gastropods drill their bivalve prey on either of the two valves. In *Palaeonucula* sp. (all shells are articulated, n = 551), the numbers of drill holes on the left valve (n = 12; 2.18% of the left valves) and the right valve (n = 14; 2.54% of the right valves) are almost the same (p = 0.695). In *Indocorbula* sp., most of the shells are articulated (n = 504), and 24 valves are disarticulated, of which 17 are right and 7 are left. The number of drill holes on the right valve (n = 20; 3.84% of the right valves) and the left valve (n = 12; 2.35% of the left valves) are different, but the difference is not statistically significant (p = 0.157). Drill holes show scattered distributions on the shells of both *Indocorbula* sp. and *Palaeonucula* sp. In each case, there is no particular site preference within the nine-sector grid (p = 0.18 and 0.06, respectively; Fig. 8). Prey size and predator size show a significant positive correlation in *Palaeonucula* sp. ($r^2 = 0.61$; $p << 0.05$; Fig. 9.1); however, it is very poor in *Indocorbula* sp. ($r^2 = 0.14$; $p > 0.05$; Fig. 9.2).

Discussion

Naticid predation on the gastropod community.—This study documents one of the oldest interactions between naticid predators and molluscan prey. Our findings reveal that the present assemblage exhibits a TDA, while the overall DI in the turritelline gastropods is low (9.49). The other gastropod families are not drilled, although some of them are abundant.

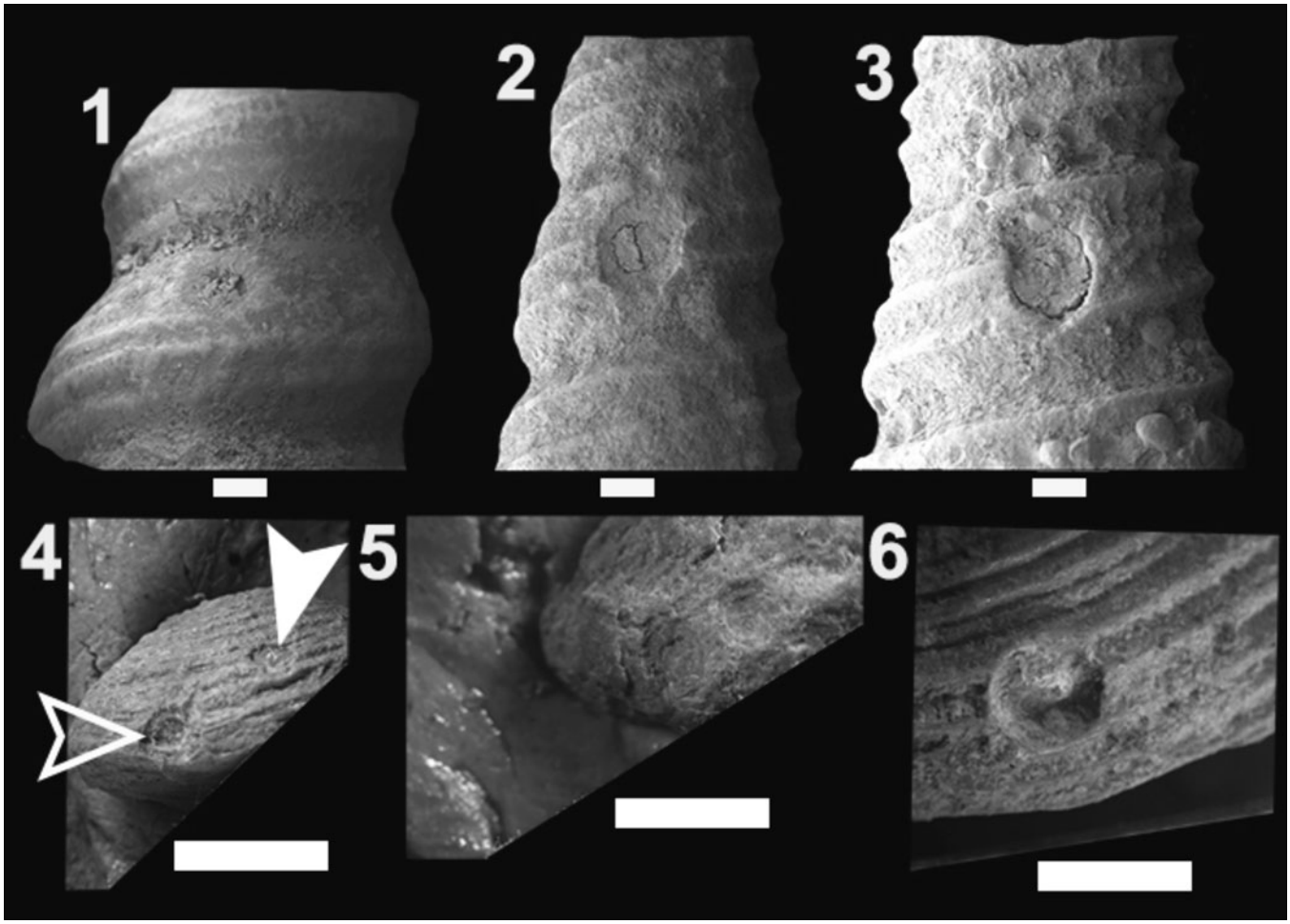


Figure 2. (**1–3**) SEM photographs of naticid drill holes on turritelline shells. (**1**) *Turritella jadavpuriensis* (specimen no. ISI/g/Jur/T 154). (**2**) *Turritella jhuraensis* (specimen no. ISI/g/Jur/T 210). (**3**) *Turritella amitava* (specimen no. ISI/g/Jur/T 321). (**4–6**) Drill holes in *Indocorbula* sp. under the microscope. (**4**) Multiple drill holes in *Indocorbula* sp. (specimen no. ISI/b/Jur/I 101). Note shelf-like development of conchiolin layer within the drill hole (hollow arrow). Incomplete drill hole terminates at conchiolin base (solid arrow). (**5**) Multiple and complete drill holes in specimen no. ISI/b/Jur/I 103 showing shelf-like projected conchiolin layer. (**6**) An incomplete drill hole with a centrally located boss (specimen no. ISI/b/Jur/I 13). Bivalve specimens were deliberately not coated with magnesium oxide to show delicate features. (**1–3**) Scale bars = 300 µm; (**4–6**) Scale bars = 2 mm.

https://doi.org/10.1017/jpa.2021.24 Published online by Cambridge University Press

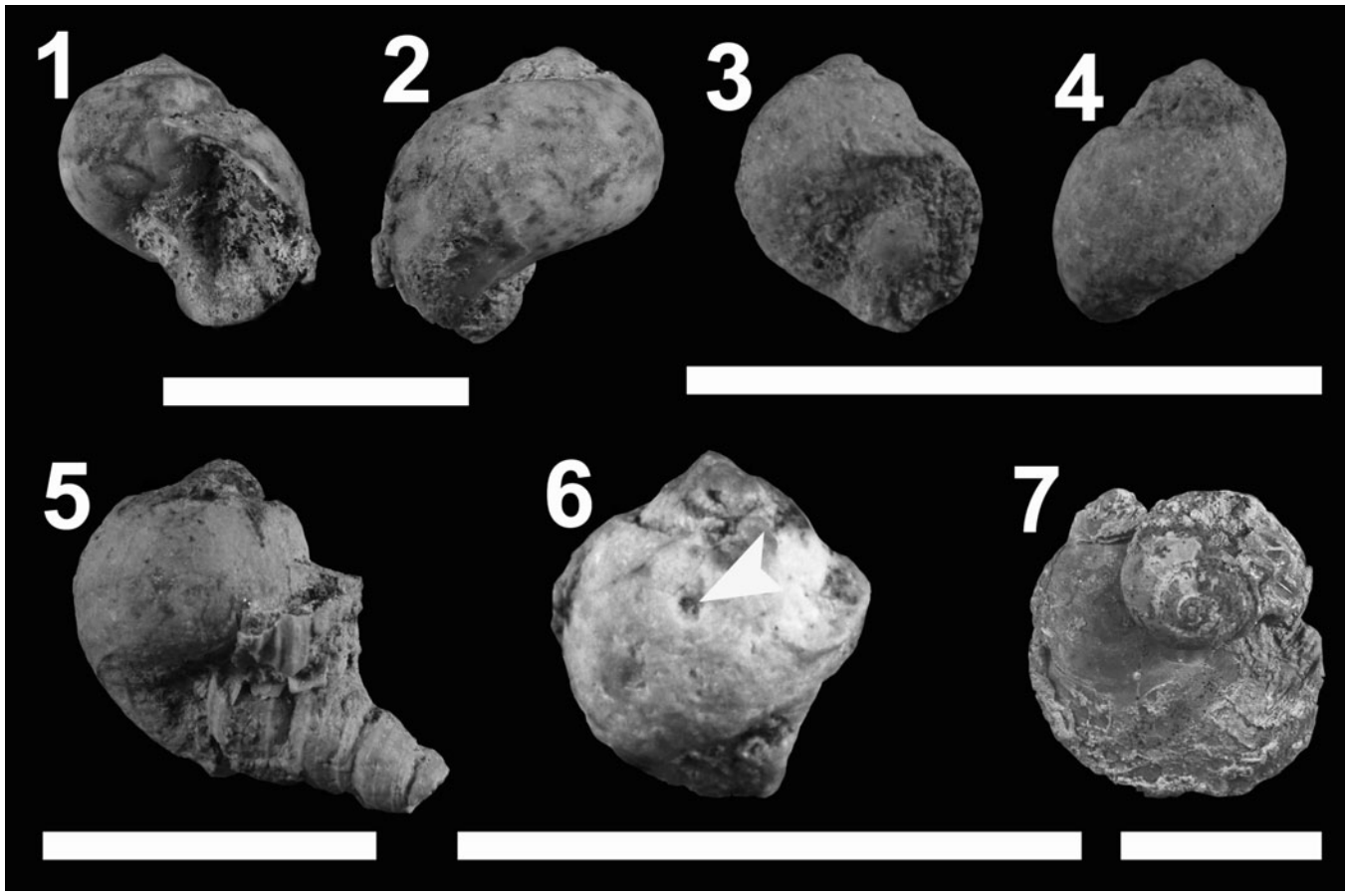


Figure 3. Predatory naticid gastropods (modified after Das et al., 2019, figs. 1, 4, 7). (**1, 2, 7**) *Euspira jhuraensis* Das et al., 2019 (specimen nos. ISI/g/Jur/N 77, 89). (**3–6**) *Gyrodes mahalanobisi* Das et al., 2019 (specimen nos. ISI/g/Jur/N 1, 13). (**5**) Co-occurrence of naticid predator and turritelline prey. (**6**) Confamilial naticid drill hole (arrow) on *G. mahalanobisi*. (**7**) Showing oyster attachment on naticid shell. Scale bars = 1 cm.

Technically, a taxon is considered to be abundant when it has at least 10 individuals in an assemblage (cf. Vermeij, 1987). However, sample size is also accounted for in our study. Abundance of other prey gastropod families ranges from 0.15% to 0.32% of the entire gastropod community. While naticids are represented by only 0.71%, turritellines make up 98% of the gastropod community. Absence of drill holes in other prey taxa is expected as well since they are ecologically and statistically close to redundancy and overall DI on turritellines is low. Only one drill hole exists on the shell of a naticid species, *Gyrodes mahalanobisi* (Fig. 3.6). Confamilial naticid cannibalism appears to be infrequent in the beginning. Prey selectivity is highly stereotyped in the naticid predation strategy and is found in both extant and fossil assemblages (Edwards, 1974; Wiltse, 1980; Kitchell et al., 1981; Kelley, 1988; and many others). In this study, turritellines were the obvious choice of naticid predators because they were practically the only available prey (Taylor et al., 1983), and the return of the maximum energy invested by the predators was satisfied (cf. Kitchell et al., 1981). Most of the drill holes in turritelline prey are confined within less than 4 cm of prey shells (91%; Table 2). *T. jadavpuriensis* is the only species whose height may range up to 6.5 cm. It shows similar DIs in different size classes ($p = 0.665$); even in the smaller group (up to 20 mm; drilled $n = 114$; DI = 9.20), DI is similar to that of the larger individuals (up to 60 mm; drilled $n = 12$; DI = 8.45). This selection for smaller shells is perhaps due to their sheer abundance.

Table 1. DIs for Turritellidae and Naticidae. PE and MULT occur only in *Turritella jadavpuriensis*. N = total number of individuals; D = total number of complete drilled specimens.

Family	Species	N	D	DI (%)	PE (%)	MULT (%)
Turritellidae		2,234	212	9.49		
	Turritella jadavpuriensis	1,601	143	8.93	4.29	3.06
	Turritella jhuraensis	298	34	11.41	0	0
	Turritella amitava	335	35	10.45	0	0
Naticidae		98	1	1.02		
	Gyrodes mahalanobisi	76	1	1.32	0	0

PE and MULT in *T. jadavpuriensis* have low values (4.29 and 3.06, respectively) compared with most of the Cenozoic values (Kelley and Hansen, 2006). In other turritelline species, PE and MULT have values of zero. Low PE and MULT might have resulted from less-abundant predators (Allmon et al., 1990) or possibly from a poorer response of the earliest turritelline prey (cf. Vermeij and Dudley, 1982). In general, high values of PE and MULT suggest a prey's passive resistance to drilling predation (Kelley and Hansen, 2006).

https://doi.org/10.1017/jpa.2021.24 Published online by Cambridge University Press

Table 2. DI in different size categories within turritelline species. Note *Turritella jadavpuriensis*, which ranges up to 6.5 cm in height, shows similar DI in different size classes. N = total number of individuals; D = total number of complete drilled individuals.

	Less than 20 mm			21 to 40 mm			41 to 60 mm			Greater than 60 mm		
Species	N	D	DI (%)	N	D	DI (%)	N	D	DI (%)	N	D	DI (%)
Turritella jadavpuriensis	1,239	114	9.20	216	16	7.41	142	12	8.45	4	1	25
Turritella jhuraensis	288	34	11.81	10								
Turritella amitava	323	34	10.53	12	1	8.33						
Total	1,850	182	9.84	238	17	7.14	142	12	8.45	4	1	25

Stereotypy of predation on the gastropod prey.—Vertical distributions of the drill holes in all three turritelline species show preference for the middle to lower part of the shell height (Fig. 4). Many workers have suggested a preference for site selectivity of drill holes on gastropod prey. According to them, this site preference relates to a predator's ability in selecting the thinnest part of the prey shell (Kitchell, 1986; Allmon et al., 1990; Hagadorn and Boyajian, 1997). Throughout their evolutionary history, the apertures of turritellines are thin-shelled, and this character thus seems phylogenetically constrained (Kabat, 1991). Moreover, apertural thickness does not change significantly during ontogeny (Fig. 7.1), and drill holes are not restricted near the apertural margin. Instead, they are restricted mainly to the two to four whorls above the aperture ($p << 0.05$ for all three turritelline species; Fig. 4). Another methodology of thickness measurement adopted here supports that the shell thickness outside the apertural region varies ontogenetically, and the presence of poor correlation suggests that predators did not target any particular site where shells are thin (Fig. 7.2). In many instances, naticids are highly stereotyped in site specificity (at the middle of the shell height) in turritelline gastropods (Kelley and Hansen, 1996; Mallick et al., 2013; Paul et al., 2013). The middle part of the shell coincides with the withdrawal limit of the soft parts of prey to avoid durophagy (Allmon et al., 1990). Site stereotypy of naticid predation has been well established in Recent and Neogene fossil assemblages (Hoffman and Martinell, 1984; Kitchell, 1986; Kelley, 1988; but see Kabat and Kohn, 1986). This selective nature of siting was developed through evolutionary time (Kelley and Hansen, 1993, 1996, 2006). However, the Late Cretaceous Ripley Formation in the USA and some Paleogene assemblages (Adegoke and Tevesz, 1974) did not show close clustering of drill holes (Kitchell, 1986; Kelley and Hansen, 2006). The present specificity of the drilled sites supports the withdrawal hypothesis and indicates that naticids achieved this selectivity right from their early history of predation. The drill hole distributions in the radial quadrant system indicate a tendency toward the abapertural side, especially for *T. jadavpuriensis* (Fig. 5.1). For turritellines, abapertural side is mostly targeted when a prey tries to escape from predators by crawling over the sediment surface (Adegoke and Tevesz, 1974; Allmon et al., 1990; Paul et al., 2013).

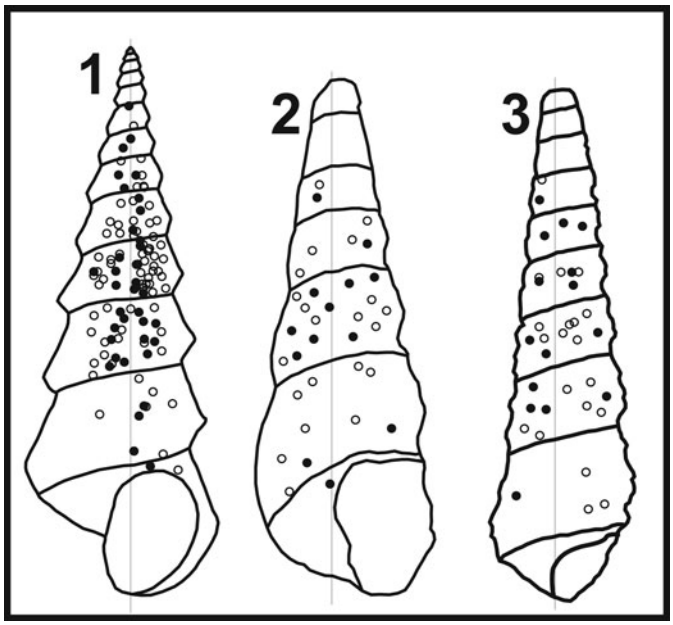


Figure 4. Schematic diagrams (not to scale) showing vertical distribution of drill holes on turritelline species. (**1**) *Turritella jadavpuriensis*. (**2**) *Turritella jhuraensis*. (**3**) *Turritella amitava*. Dots indicate drill holes at the apertural sides; circles indicate abapertural drill holes.

The overall correlation between the predator size (ODD as a proxy data) and the prey size (shell height) in turritelline gastropods is satisfactory when all species are considered (Fig. 6.1). It implies that the larger prey were consumed by the larger predators, thus satisfying the cost–benefit model of Kitchell et al. (1981). This hypothesis of maximization of energy return is especially true when we consider *T. jadavpuriensis* alone, which is drilled more than other taxa (67% of the total turritelline drill holes). The correlation between the ODD and the prey size is equally robust (Fig. 6.2). Thus, a strong size correlation between the predators and the prey indicates successful drilling in prey taxa (Kelley and Hansen, 1993, 1996). However, the other two species do not show such a good correlation (Fig. 6.3, 6.4). The size selectivity is also an evolved "non-shell character" and can be traced back to the Late Cretaceous (Kitchell, 1986; Kelley, 1988; Kelley and Hansen, 1993, 1996, 2006). We trace this aspect of naticid predation back to their early appearance, at least in some of the targeted prey (Klompmaker et al., 2017).

Ornamentation and shell shape in the turritelline prey.—The most ornamented species is *T. jadavpuriensis* (Fig. 1.1–1.3; Das et al., 2018, fig. 7). It is suggested that the ornamentation in turritelline gastropods deters drilling predation (Dudley and Vermeij, 1978; Paul et al., 2013). Although supporting this general trend, Allmon et al. (1990) observed that the resulting outcome is not consistent when the most ornamented forms are singled out and studied separately. DIs in the highly

https://doi.org/10.1017/jpa.2021.24 Published online by Cambridge University Press

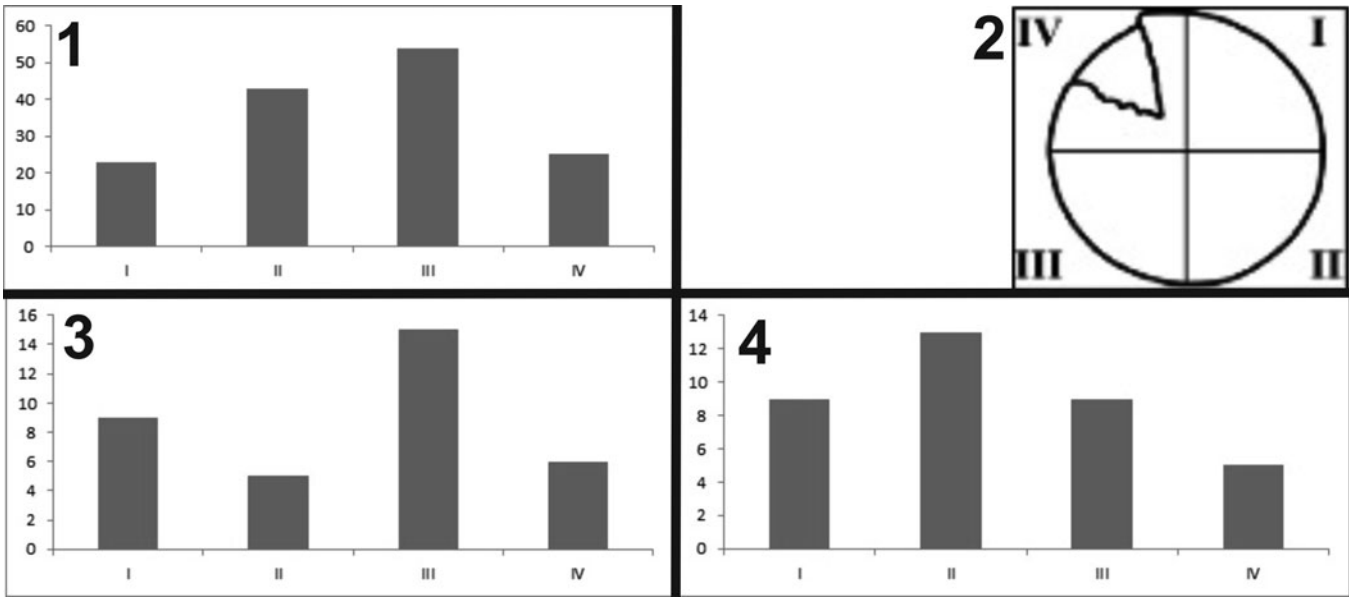


Figure 5. Radial distribution of drill holes on different turritelline species. (**1**) *Turritella jadavpuriensis*. (**2**) Distribution of different quadrants in the radial system (after Allmon et al., 1990; Mallick et al., 2013). (**3**) *Turritella jhuraensis*. (**4**) *Turritella amitava*. Note distribution of drill holes is more on abapertural side.

ornamented and the less ornamented present turritelline species are not significantly different ($p = 0.15$; Table 4). This indicates that ornamentation failed to deter naticid predation during the Oxfordian (Allmon et al., 1990; but for the opposite view, see Signor, 1985; Paul et al., 2013). Many turritelline species in their ontogeny have two distinct ecological regimes. In the early stage, they are mostly infaunal, whereas the adult individuals live mainly epifaunally (Waite and Strasser, 2011;

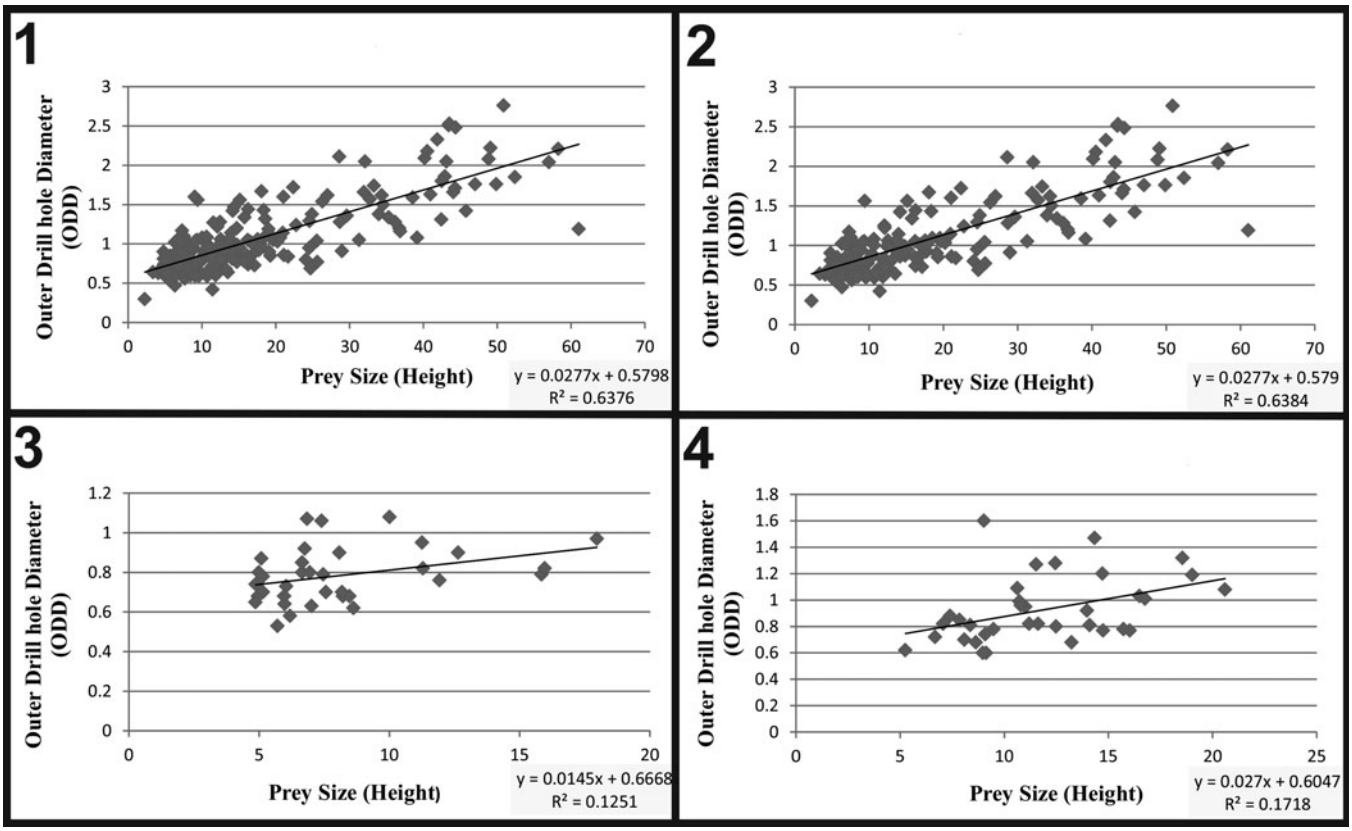


Figure 6. Bivariate plots of ODD versus turritelline prey size in: (**1**) all turritelline species; (**2**) *Turritella jadavpuriensis*; (**3**) *Turritella jhuraensis*; (**4**) *Turritella amitava*. Note strong correlation of predator size and prey size in *T. jadavpuriensis*.

https://doi.org/10.1017/jpa.2021.24 Published online by Cambridge University Press

Table 3. Relationship between DI and shell geometry (i.e., degree of slenderness in different turritelline species). N = total number of individuals; D = total number of complete drilled individuals.

	Slender variant			Inflated variant		
Species	N	D	DI (%)	N	D	DI (%)
Turritella jadavpuriensis	148	13	8.78	1,453	130	8.95
Turritella jhuraensis	13	2	15.38	285	32	11.23
Turritella amitava	119	18	15.13	216	17	7.87
Total	280	33	11.78	1,954	179	9.16

Paul et al., 2013). The strong ridge-like ornaments in the adult individuals of *T. jadavpuriensis* perhaps obstructed the easy penetration within sediments. Many larger shells of *T. jadavpuriensis* have the preferential oyster encrustation in the abapertural side (Fig. 1.11) indicating their epifaunal life mode, which facilitated the easy subjugation by the naticid predators. *T. jadavpuriensis* is robustly ornamented because it has a larger size. Strength of ornaments has a positive allometric relationship with size in the high-spired gastropod shells (Allmon et al., 1990). Such "size effects" among many large turritelline species in the Paleocene were intricately sculptured and had low DI (Dudley and Vermeij, 1978). In the current study, a similar low value of DI is observed in the larger variants of *T. jadavpuriensis* (see also Allmon et al., 1990 for other Paleocene species). Naticids usually hunt infaunally as evident from the fossil record as well as the Recent examples. However, some modern species have been reported to hunt both infaunally and epifaunally (Pahari et al., 2016). Jurassic naticids were perhaps not exclusively infaunal hunters. Moreover, one specimen of epifaunal encruster, *Ostrea* sp., bears a naticid drill hole (Fig. 1.6).

Every turritelline species has both slender and inflated variants (Allmon, 2011). Effect of naticid drilling on turritelline prey on the basis of slenderness has been studied before (Signor, 1985; Allmon et al., 1990; Paul et al., 2013). Signor (1985) found that slender species are less drilled than the robust species. Signor (1985) also argued that the evolution of slender shells helps keep a low profile of prey within sediment, thus evading detection by the predator, especially by the epifaunal calappid crabs and infaunal naticid drillers (see also Sarkar et al., 2016 for similar observations on terebrid gastropods). Nonetheless, in the present study, both slender and inflated variants are equally drilled for each species (Table 3; $p > 0.05$). This suggests that the profile of a shell did not make any difference to naticids that hunt infaunally and are not guided by vision.

Naticid predation on the bivalve community.—Low DI values in all taxonomic levels of the molluscan prey can result from two different situations. Either it may indicate an absence of enough predators (Allmon et al., 1990; Kardon, 1998; Sawyer and Zuschin, 2011) or it may indicate a lack of efficiency of the predators. Failed drilling is rare or practically absent in a gastropod prey, which may indicate their vulnerability to drilling predation. Low DI in the bivalve population may suggest that the gastropods are also targeted (Casey et al., 2015). In the present assemblage, the bivalves are less abundant than gastropods (9% of the total molluscan fauna), and their DIs range from 0.90 to 6.20. Corbulids and nuculids are the most targeted groups (DIs are 6.20 and 4.72, respectively; Table 5) because they are most abundant, but their DIs are significantly less than those of the turritelline prey ($p << 0.05$). The main reason for the overall low predation intensity in the bivalve community is perhaps the low abundance of the prey. It is already shown that the prey selection and the intensity of predation in gastropods depend on the prey abundance. In addition, the relatively high value of MULT in corbulids (see detailed discussion to follow) and moderately high value of PE in nuculids indicate that the bivalves defended well against predation. This is because corbulids have conchiolin layers and nuculids are mobile infauna. Many other bivalve species are relatively abundant but are not drilled; 67% of the specimens represent undrilled species (Supplementary Table 1). However, during the Cenozoic, they were heavily preyed upon by naticid predators (e.g., Arcidae, Lucinidae, and so on) (Kelley, 1988; Kelley and Hansen, 1993, 1996, 2006). The lack of behavioral stereotypy, especially the site specificity in drilled bivalve species (e.g., in nuculids), also suggests that the naticid predators were not efficient (cf. Kelley and Hansen, 1993, 2006) at the beginning (details follow).

We also note that in the majority of the corbulid species (including the present species), the right valves are more attacked (Kelley, 1988; Kelley and Hansen, 1993, 1996; but see Morton, 1990). This may be due to the larger surface area available to the right valve (Vermeij, 1983; Harper, 1994). The present species also has slight discordance in valve size (Fürsich et al., 2000). Thus, the preferential selection of the right valve over the left valve was established from the dawn of naticid predation.

Table 4. Relationship between DI and ornamental strength in different turritelline species. N = total number of individuals; D = total number of complete drilled individuals.

Category 1 (four or more strong ribs)				Category 2 (fewer than four strong ribs)			
Species	N	D	DI (%)	Species	N	D	DI (%)
Turritella jadavpuriensis	1,601	143	8.93	*Turritella jhuraensis*	298	34	11.41
				Turritella amitava	335	35	10.45
Total	1,601	143	8.93	Total	633	69	10.90

https://doi.org/10.1017/jpa.2021.24 Published online by Cambridge University Press

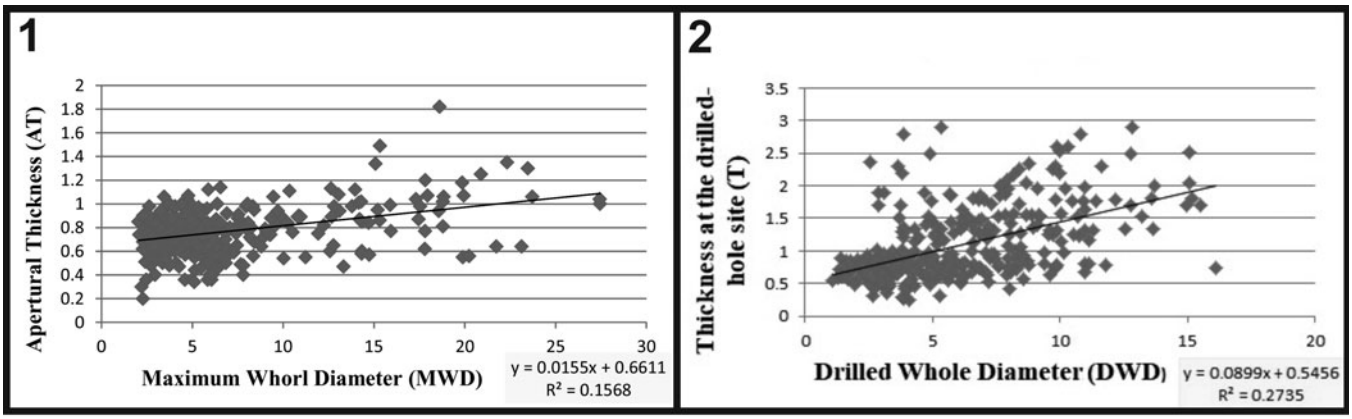


Figure 7. Bivariate distribution of whorl diameter and shell thickness in turritelline species. (**1**) Shell thickness at the apertural margin is plotted against maximum whorl diameter. (**2**) Shell thickness measured at the drill hole site is plotted against the diameter of the drilled whorl. In both cases, correlation is poor.

Stereotypy of predation on the bivalve prey.—In bivalves, the site selectivity of drill holes is very poor to absent (Fig. 8). Both experimental study (Kardon, 1998) and fossil data (Culotta, 1988; Kelley and Hansen, 1993, 1996, 2006) have revealed that naticids struggled to penetrate the conchiolin layer present in corbulid valves. They abandoned the incomplete holes many times at conchiolin layers (Fig. 2.4, solid arrow) and resumed fresh attempts, which resulted in multiple drilled shells (Fig. 2.4, 2.5) and random distribution of drill holes (Fig. 8.2). In the present corbulid species, the MULT value is as high as 21.05 (Table 5). Nonspecificity of drill holes on corbulid bivalves is almost a rule (Kelley, 1988; Harper, 1994). Nine-sector grid analysis demonstrates that the distribution of holes is random and thus supports the null hypothesis ($p > 0.05$). Therefore, it appears that the scattered pattern of drill holes on both valves of corbulids is a very ancient character of naticid predation. The lack of site selectivity in corbulids may indicate the difficulty of making complete holes for the primitive naticids; that they were inexperienced is also evident from the random distribution of drill holes in *Palaeonucula* sp. (Fig. 8.1).

In case of size selectivity, one species (*Palaeonucula* sp.) shows a good correlation between the prey size and the predator size (Fig. 9.1). In gastropods, one turritelline species (*T. jadavpuriensis*) also shows strong size selectivity (Fig. 6.2). It appears that the predators were yet to develop stereotyped behavior in prey size selection. The good size correlations in one bivalve and one gastropod species perhaps suggest that the process already began during the early stage of naticid predation.

Paleoecology of bivalves.—Among the seven abundant bivalve families in the present assemblage (Supplementary Table 1), five are infauna. Of these five infaunal bivalves, two families, Corbulidae and Nuculidae (Table 5) were mostly targeted. Such preferential selection may be attributed to their vast abundance within the bivalve community. This is in line with the observations made by Taylor et al. (1983), who noted that in the Albian (Early Cretaceous) Blackdown Greensand fauna, corbulids were most targeted because they were most abundant. Moreover, the preferential prey selection may be explained by the fact that the corbulids are very sluggish, shallow burrower to sessile infauna (Morton, 1990; Anderson, 1992; Kelley and Hansen, 1993; Harper, 1994; Fürsich et al., 2000) and therefore are very prone to being captured by the naticid predators. Corbulid DIs are always high throughout space and time (De Cauwer, 1985; Anderson, 1992; Kelley and Hansen, 2006; Supplementary Table 2). The temporal patterns of PE and MULT of naticid predation on corbulids always show high values (De Cauwer, 1985; Anderson, 1992; Kelley and Hansen, 1993; Harper, 1994; among many), even quite a high percentage of incomplete drill holes (22.22) was reported from the Early Cretaceous (Albian) Blackdown Greensand Formation (Harper, 1994). This time interval was previously thought to be the beginning of naticid evolution. In addition, the Cenozoic history of incomplete corbulid drill holes is equally high (75%–100%; Harper, 1994). Many workers have shown that the presence of a tough organic layer (i.e., conchiolin sheet) within the corbulid shell deters gastropod drilling. As a result, multiple attempts are abortive

Table 5. Naticid drilling predation on species of different bivalve families. N = total number of individuals; D = total number of complete drilled individuals.

Family	Species	N	D	DI (%)	PE (%)	MULT (%)
Corbulidae	*Indocorbula* sp.	516	32	6.20	2.63	21.05
Nuculidae	*Palaeonucula* sp.	551	26	4.72	10	6.67
Arcidae	*Arca* sp.	19	1	5.26	0	0
Lucinidae	*Pterolucina* sp.	20	1	5	0	0
Ostreidae	*Ostrea* sp.	43.5	2	4.60	33.33	0

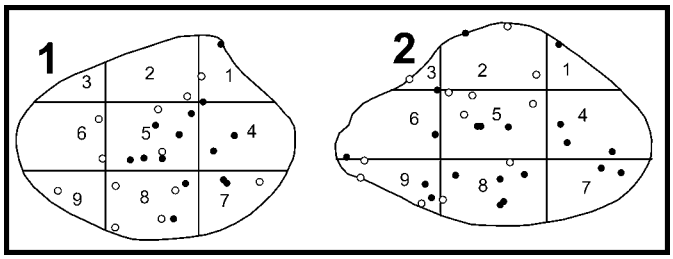


Figure 8. Schematic diagrams (not to scale) showing distribution of drill holes on bivalve species in nine-sector grids. (**1**) *Palaeonucula* sp. (**2**) *Indocorbula* sp. Note random distribution of drill holes. Dots indicate drill holes in the right valve; circles indicate drill holes in the left valve.

https://doi.org/10.1017/jpa.2021.24 Published online by Cambridge University Press

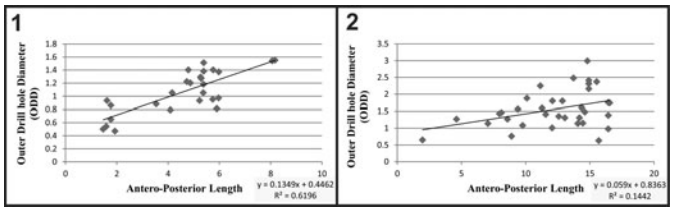


Figure 9. Size selectivity of naticid predator on two bivalve species. (**1**) *Palaeonucula* sp. (**2**) *Indocorbula* sp. Note strong correlation between ODD and prey size in *Palaeonucula* sp. whereas it is poor in *Indocorbula* sp.

(Kelley, 1988; Kelley and Hansen, 1993, 1996; Harper, 1994; but see Anderson, 1992). The percentages of incomplete drill holes in the right and the left valves of *Indocorbula* sp. are 4.76 and 0, respectively, and overall PE is 2.63. Once again, such low values may be because the species could not defend itself well from predation.

The other preferred bivalve prey is *Palaeonucula* sp., which is a deposit feeder. This species is a mobile infauna, but very small in size; antero-posterior length is less than 1 cm. Small size (but see Kelley and Hansen, 1993) facilitated easy subjugation, and they were drilled by smaller naticids (Fig. 9.1). High abundance of *Palaeonucula* sp. also made them easily available to prey. Drill holes in other abundant families, such as Nuculanidae (represented by *Nuculana juriana)* and Lucinidae (represented *Pterolucina* sp.), are either absent or very rare (Supplementary Table 1). *Nuculana juriana* is streamlined and smooth and appears to be a very rapid burrower (cf. Stanley, 1970); it used to forage sediments for labial palp feeding and could quickly reburrow (Sander and Lalli, 1982; Kelley and Hansen, 1993). *Pterolucina* sp. is perhaps a deep infaunal and slow-burrowing bivalve (Kelley, 1988; https://fossils.its.uiowa.edu/). Arcidae is also abundant and consists of two species. The most dominant species is *Andara* sp. (n = 91.5), which is large (maximum up to 4 cm), with a very thick shell and robust radial ornamentation. It is nearly circular in shell outline. All

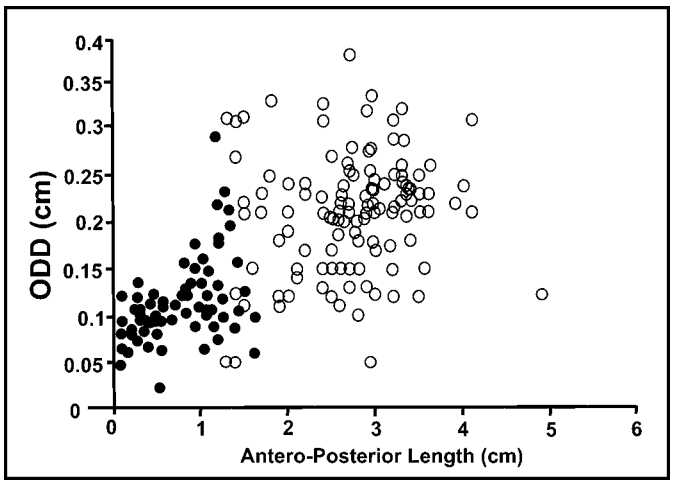


Figure 10. Comparison of the relationship between length (antero-posterior length) of two bivalve assemblages and their predator size (ODD as a proxy). Solid black circles represent drill holes on Jhura bivalves whereas open circles represent drill holes on astartid bivalves from Bhakri locality. Two distinct clusters of drill hole distribution indicate two different naticid populations.

these suggest its shallow infaunal life habit (cf. Stanley, 1970; Kelley, 1988), but its large size and thick shell perhaps prevented naticid drilling. These ecological traits help the species resist predatory drilling attacks (Mallick et al., 2014). Besides, naticids are size-specific while targeting prey (Kelley, 1988; Kelley and Hansen, 1993). One specimen of *Arca* sp. and two specimens of *Ostrea* sp. are also drilled. *Arca* sp. from its functional morphology (elongated shell with wide, flat venter) appears to be an epibyssate (cf. Stanley, 1970). Oysters are encrusted on the substrate or dead shells and therefore are very difficult to engulf by the naticid foot. For this reason, it is a rare happening, and there are very few reports of naticid drilling on oyster prey (Dietl, 2002; Chattopadhyay and Dutta, 2013; Goswami et al., 2020). Moreover, naticids live and hunt infaunally, while oysters are epifauna. They rarely meet because they are ecologically incompatible. A few attacks on epifaunal prey possibly indicate that naticids were yet to mature and specialized in choosing only infaunal prey.

Naticid evolution and infaunalization of prey.—Previously, Bardhan et al. (2012) described intense drilling predation on the astartid and other bivalves from a coeval section near Bhakri (7 km southeast of the present location; Das et al., 2018, fig. 1). Drill holes strongly resembled the paraboloid naticid holes, but Bardhan et al. (2012) failed to discover any naticid body fossils. Therefore, they refrained from commenting on the purported driller. Now, we are certain that the drillers at Bhakri were also naticids, although the absence of their body fossils is still enigmatic and may be a taphonomic artefact. The molluscan-shell-inhabiting behavior of hermit crabs already evolved during the Mesozoic (Walker, 1989; Fraaije, 2003). They use gastropod shells as a protected shelter and can transport the host shell far away from the original molluscan habitat (Walker, 1989, 1994). This may be one of the reasons for not getting the naticid body fossils in the Bhakri assemblage. However, no hermit crabs or any evidence of their presence have been reported from the area. The high DI on the Bhakri bivalves (>30) and the low DI in the present location (bivalves, 4.64; gastropods, 8.50) suggest that from the early time of naticid predation, spatial variability was the rule. The spatial variability was well documented from many subsequent geological ages (Garton and Stickle, 1980; Vermeij, 1980; Nebelsick and Kowalewski, 1999; Hoffmeister and Kowalewski, 2001; Sawyer and Zuschin, 2010, 2011; Paul et al., 2013; Chattopadhyay et al., 2014, 2015, 2016; Huntley and Scarponi, 2015; Visaggi and Kelley, 2015; Sarkar et al., 2016; Mondal et al., 2017, 2019a). At Bhakri, the main prey was one astartid bivalve species, *Neocrassina subdepressa* Blake and Hudleston, 1877, which was the most abundant. At Jhura, the two most abundant bivalve species are less drilled. In both cases, the preferred taxa were selected on the basis of availability. However, the genus *Neocrassina* was always vulnerable to drilling predation. Another species of *Neocrassina* in the Jurassic of the United Kingdom also showed a high DI value (>20; Harper et al., 1998). The variation of DI on bivalves in two adjacent localities may be due to the difference in the taxonomic composition of the prey (Hoffmeister and Kowalewski, 2001). In addition, the naticid predators may be

https://doi.org/10.1017/jpa.2021.24 Published online by Cambridge University Press

different in these two areas. The difference in drill hole sizes (Fig. 10; Klompmaker et al., 2016) and the site selectivity in Bhakri (cf. Fig. 8 and Bardhan et al., 2012, fig. 6) indicate two different naticid populations.

Many workers have suggested that drill holes in the Triassic Cassian Formation were made by naticid predators (Koken, 1892; Fürsich and Jablonski, 1984; Zardini, 1985). Klompmaker et al. (2016) reported an exceptionally high rate of multiple and incomplete drill holes from the Cassian taxa that they tentatively ascribed to the predatory origin of drill holes. The present study provides the earliest evidence of the co-occurrence of naticid genera sensu stricto (Das et al., 2019) and the naticid drill holes on prey taxa. The targeted prey (turritelline gastropods and corbulid and nuculid bivalves) are sluggish, and most of them are shallow infaunas (Kelley and Hansen, 1993, 1996; Harper, 1994). From their earlier appearance, it seems that naticids target mostly the infaunal prey. Although some modern naticids hunt epifaunally in the intertidal regions (Savazzi and Reyment, 1989; Pahari et al., 2016), this may be attributed to subsequent adaptation. The present discovery of naticids and their drill holes provides additional support for the Jurassic as the time of infaunalization of prey (Vermeij, 1977; Harper, 1994; Bardhan and Chattopadhyay, 2003). Rapid and great diversification of thick-shelled gastropods (Vermeij, 1977; Taylor et al., 1980, 1983) and bivalves (Stanley, 1968, 1977) and their increased infaunalization took place in response to the Mesozoic marine revolution (MMR of Vermeij, 1977, 1987). According to Vermeij (1977), the simultaneous and sudden increase of many durophagous predators during the Jurassic exerted tremendous predation pressure on benthic marine communities. Predators were all epifaunas and indulged in visual hunting. Prey taxa thus adapted to diverse lines of defense, including infaunalization (for details, see Bardhan and Chattopadhyay, 2003). Naticids were not initially included within these predatory groups, but perhaps evolved as a result of the MMR and became infaunal predators to get access to the new kind of prey.

Evolution of the naticid–turritelline recurrent association.—Due to their high fecundity rate (Fretter and Graham, 1962, 1981; Waite and Strasser, 2011), turritelline gastropods are found in great concentration in today's marine environment (Waite and Strasser, 2011; Paul et al., 2013). Such dense populations are also reported in the fossil records of every geological age since the Cretaceous. They are described as a TDA or a turritelline-rich assemblage (TRA; Allmon, 2007). Allmon (2007) reported 55 such TDAs through time besides many TRAs. Here we document and quantify the synecological relationship between turritelline prey and naticid predators. Our literature review revealed that many such turritelline-dominated assemblages/occurrences have prey–predator interactions with naticid gastropods in the fossil record (Supplementary Table 3). Furthermore, there are numerous cases of naticid drilling on the Recent turritellines (Paul et al., 2013, appendix 1 and references therein). Through the ages, naticids target various prey taxa, including gastropods and bivalves. However, such recurrent association between other prey and naticid predators seldom exists other than the long history of naticid–corbulid and naticid–lucinid bivalve interactions (Kelley and Hansen, 2006), which identified these three molluscan groups, especially turritellids (Allmon et al., 1990), as "heavily preyed taxa through time" (Kelley and Hansen, 1993, p. 372). Do the turritellids and naticids represent a recurrent association through space and time? One of the oldest occurrences of naticid–turritellid association speaks for some paleobiogeographic control. During the Jurassic, Kutch belonged to the southern hemisphere (Smith et al., 1994), and there are no adequate and convincing records of both taxa from the northern hemisphere except a possible Sininae naticid from the earliest Cretaceous of Spitsbergen, Svalbard (Kaim et al., 2017). Jurassic gastropod assemblages of Kutch are now well studied, especially the Late Jurassic assemblages. Although gastropods show the Tethyan affinity at the genus level (Das, 2008), species are markedly endemic (Das, 2004, 2008), which makes Kutch a distinct subprovince within the Indo-Madagascan Faunal Province (Das, 2008). All the present turritelline species are found exclusively in Kutch, and the first encounter between them and naticids took place in Kutch. However, from the Cretaceous onward, both naticids and turritellids diversified and migrated toward the north. Turritelline gastropods, as mentioned early, are slow-moving or sedentary, shallow infaunal to epifaunal animals (Allmon et al., 1990; Allmon, 2007; Waite and Strasser, 2011; Paul et al., 2013) and therefore fall easy prey to mobile naticid predators (Kelley and Hansen, 1993, 1996, 2006); the juveniles are especially very vulnerable (Mallick et al., 2013).

One of the fallouts of prey–predator interaction is the rapid evolution of both communities through "arms race" (Vermeij, 1977, 1983, 1987; DeAngelis et al., 1985; Kelley and Hansen, 1993; Thompson, 1998). For example, Stanley (1968) showed that many superfamilies of infaunal bivalves evolved in the early Mesozoic, and many gastropods underwent rapid diversification (Allmon et al., 1990; Huntley and Kowalewski, 2007). Turritelline gastropods do not show any sustained antipredatory morphological adaptation against naticid predation and maintained morphological stasis (Allmon et al., 1990; Paul et al., 2013; Das et al., 2018). Nonetheless, they show increasing prey effectiveness (i.e., the temporal increase of incomplete and multiple drill holes) over time (Kelley and Hansen, 1993, 1996, 2006). The morphological characters in the most abundant *T. jadavpuriensis* are a robust shell and strong ornamentation (Fig. 1.1, 1.2; Das et al., 2018, fig. 7), but their adult counterparts are frequently attacked (Allmon et al., 1990). Strong ornaments are found mostly in the large turritelline species and are perhaps the product of positive allometry with size. It appears that these traits have possibly evolved to avoid durophagy and could not deter the naticid drilling predation right from their early interactions (Dudley and Vermeij, 1978; Allmon et al., 1990; Paul et al., 2013). Moreover, turritellines provide ethological responses (behavioral and nonshell characters) rather than morphological adaptation against the naticid drilling (for details, see Vermeij et al., 1980; Vermeij, 1982; Allmon, 1988; Allmon et al., 1990). In addition, the high mortality, especially of young individuals, is amply compensated by the high fecundity rate ("predator saturation by very large populations" of Allmon, 1988, p. 267; "mass occurrences of turritelline gastropods" of Nebelsick et al., 2020, p. 282). For these reasons,

https://doi.org/10.1017/jpa.2021.24 Published online by Cambridge University Press

turritellines are one of the few marine gastropods that monopolized and dominated other molluscan fossil communities through ages (Price et al., 1985; Cohen, 1989; Geary and Allmon, 1990; Waite et al., 2008; Waite and Strasser, 2011) and are aptly termed as TDAs by Allmon (2007). In the present assemblage, turritellines constitute 89% of the total molluscan fauna. Vermeij (1994) described several escalated traits within prey that minimize predation intensity. Turritellines have been suffering from drilling predation through millions of years, and any heavily preyed taxon, as the hypothesis of escalation may predict, should have developed antipredatory traits (Kelley and Hansen, 1993). Some taxa even became extinct and were pushed to refugia perhaps because of the impact of predation. Interestingly, turritellines did not become extinct; they have near-global distribution (Dudley and Vermeij, 1978) and show stunning taxonomic diversity through ages (Allmon et al., 1990; Allmon, 2007; Supplementary Table 3). Our research suggests the high reproductive rate guarantees the turritellines' survival over an extended period of time. Rapid evolution, great diversity, and repeated occurrences of the TDAs in different species through ages support our assertion.

Evolution of conchiolin layers in corbulid bivalves.—Naticid predators also have another preferred prey item: corbulid bivalves. Numerous cases of interaction between them, from different geological ages since the Cretaceous, have been documented by many workers (Kelley, 1988; Harper, 1994; Kelley and Hansen, 2006). We have listed about 100 such interactions where corbulid prey are abundant ($n \geq 10$ shells; following Vermeij, 1987; Harper, 1994; Kelley and Hansen, 2006; Supplementary Table 2). The present DI on corbulid species is low, but subsequent predation history shows high DIs in many instances (De Cauwer, 1985; Anderson, 1992). However, there is no temporal trend of increasing DI (Kardon, 1998; Supplementary Table 2). Like turritellines, corbulids occur as many monospecific assemblages (Hallam, 1976; Fürsich, 1981; Harper, 1994; Fürsich et al., 2000). Many corbulid fossils and Recent species are found in the nearshore to the marginal marine environments (perhaps refugia against predation; S. Mondal, personal communication, 2019) and are extremely tolerant of environmental fluctuation (Hallam, 1976; Fürsich, 1981; Harper, 1994; Fürsich et al., 2000). Because of the stressful environment (low oxygen content and fluctuating salinity; Lewy and Samtleben, 1979; Fürsich, 1981; Anderson, 1992; Kardon, 1998; Fürsich et al., 2000), they encounter less competition and hence perhaps monopolize resources where they live.

It was previously believed that the naticids evolved during the late Early Cretaceous (Kollmann, 1982; Taylor et al., 1983; Tracey et al., 1993; Bandel, 1999; Kaim et al., 2017; but see Das et al., 2019) whereas corbulids evolved during the Late Jurassic (Kimmeridgian; Hallam, 1976; Harper, 1994; Kardon, 1998). Our present field study claims that the naticid–corbulid interaction was already established during the Jurassic and has tremendous evolutionary significance. First, they constitute a recurring benthic association since the Late Jurassic (Oxfordian). Second, naticids are also abundant in nearshore, estuary environments (Savazzi and Reyment, 1989; Subba Rao et al., 1991, 1992; Sawyer and Zuschin, 2011; Pahari et al., 2016) where many corbulids thrive. Like turritellines, corbulids are very sluggish or sessile, shallow infaunal animals (Lewy and Samtleben, 1979; Kelley and Hansen, 1993; Harper, 1994; Kardon, 1998). Therefore, they are very vulnerable to naticid predation.

Corbulids have been experiencing predation pressure since the Jurassic, and they have evolved no effective external morphological traits that could minimize the predation intensity. *Indocorbula* sp. of the present study is ornamented (comarginal ridges; Fig. 1.10), but still shows many successful naticid drill holes (DI = 6.20). Many other species of corbulids were strongly ornamented and were highly drilled (De Cauwer. 1985; Anderson, 1992). Valve discordance in corbulids perhaps evolved to resist durophagous or peeling predators (Vermeij, 1977, 1987; Mondal et al., 2014; Mondal and Harries, 2015), although tight valve closure could prevent the escape of chemical cues (P. Kelley, personal communication, 2020). Shells with unequal valves are ineffective against drilling. Many high DIs on corbulid bivalves have been reported from different regions and geological ages (Supplementary Table 2). One internal morphological character considered as functional to deter naticid predation is the presence of conchiolin layers in the microstructure of corbulid valves (Vermeij, 1987; Kelley, 1988; Kelley and Hansen, 1993; Harper, 1994; Kardon, 1998). Conchiolin layer is an organic-rich layer found in many families of bivalves (Wilbur, 1964). It is distributed throughout the valve as a single layer or numerous layers, but less as continuous layers. It is a constructional morphological character (sensu Seilacher, 1984), and the thickening of conchiolin layers in the corbulid microstructure is a classic example of a long-term evolutionary trend. Hence, it is consistent with the escalation hypothesis of Vermeij (1987, 1994).

Some workers have suggested that these conchiolin layers act as anti-naticid drilling characters either as adaptation (Harper, 1994) or as exaptation (Kardon, 1998). Harper (1994) hypothesized that conchiolin layers in corbulids evolved only during the Cretaceous when naticid predation first took place. She claimed, therefore, that the evolution of conchiolin layers in corbulids was due to the adaptation against naticid drilling. It is difficult to accept her suggestions. First, the conchiolin layers already appeared during the Jurassic (Kardon, 1998, and the present study). Second, our analysis demonstrates that naticid–corbulid interaction already began at least during the Late Jurassic (Oxfordian). Kardon (1998), however, suggested that the presence of conchiolin layers in corbulids is an exaptation (cf. Gould and Vrba, 1982) and acts as deterrence against the naticid drilling predation since the Cretaceous. She argued that the corbulids evolved in the Late Jurassic (Kimmeridgian) and the conchiolin layers were already present since their evolution. The conchiolin layers serve many functions right from the beginning, such as anticorrosion of the shell, enhancement of physical strength against durophagy, usefulness for hermetic sealing (tight closure of the valves), and others (Lewy and Samtleben, 1979; Anderson, 1992; Harper, 1994). Their role as an antidrilling device has been exapted later, when the naticid came to target them during the late Early Cretaceous.

Our present argument about the already established existence of the interaction between Jurassic naticids and corbulids does not allow us to accept Kardon's hypothesis, either. In

https://doi.org/10.1017/jpa.2021.24 Published online by Cambridge University Press

Kutch, the Jurassic corbulid species are diverse and abundant. They are represented by two genera, *Corbulomima* Vokes, 1945 and *Indocorbula* Fürsich et al., 2000, and range in age from the Bajocian to Callovian (Middle Jurassic) (Sowerby, 1840; Cox, 1940; Singh and Rai, 1980; Kanjilal, 1997; Fürsich et al., 2000); we have now extended their range up to the Upper Jurassic (Oxfordian). The majority of the older species formed the monospecific assemblages and lived in the nearshore environment with highly reduced salinity (Fürsich et al., 2000). None of them has a ventral furrow inside the right valve, which proxies for the presence of the conchiolin layer (Harper, 1994). Most of the present specimens are articulated. Therefore, the study of the presence of a comarginal ventral furrow in the right valve could not be successfully ascertained. However, the presence of successful naticid drill holes with the internal shelf-like morphology as well as incomplete drill hole with the flat base indicate the presence of a conchiolin layer in the present species (Fig. 2.4 [hollow arrow], 2.5; Harper, 1994, fig. 3; Kardon, 1998, fig. 1). The question is how did the older corbulids adapt in a very hostile brachyhaline condition without the presence of the organic layer? Fürsich et al. (2000) observed some evolutionary features that appeared before the development of conchiolin layers to adapt in such a stressful environment. For example, *Indocorbula lyrata* Sowerby, 1840 (Bajocian to Callovian) shows high intraspecific variability with respect to shape and ornamentation. This dynamic morphological character state is a reflection of an "opportunistic lifestyle" in a very unstable environment. Besides, the tight closure of the valves is an essential prerequisite to stay in a hostile environmental condition. Here, the pre-Late Jurassic corbulids show a remarkable morphological innovation. Fürsich et al. (2000) noted the "crenulated ventral margin of the left valve together with the transverse crenulations on the inside of the right valve served to tightly lock the valves, clearly an advantage during phases of adverse environment conditions" (p. 140). Tight closure of the valves (hermetic sealing; Lewy and Samtleben, 1979) was accomplished during the Oxfordian by the development of conchiolin layers in the ventral furrow by the present *Indocorbula* species, which perhaps evolved from *I. lyrata* (personal observation). We are not aware of any younger corbulid species that has ventral crenulation for adduction in both valves.

It appears that the oldest history of corbulids comes from Kutch (since Bajocian), and no attempts so far have been done to study the drilling predation on them. No workers have mentioned this interaction, but some of the published photographs are interesting. *I. lyrata* was described by both Singh and Rai (1980) and Fürsich et al. (2000). Some of the specimens, especially those of the Callovian, appear to bear characteristic naticid (paraboloides) drill holes (Singh and Rai, 1980, pl. 1, figs. 5, 9, 11b; Fürsich et al., 2000, pl. 17, figs.7a, 14a). One specimen even shows an incomplete drill hole with a centrally located boss (Singh and Rai, 1980, pl. 1, fig. 3b). However, all these observations require physical verification of the types and other specimens and, furthermore, must include fresh collection from the field. If the Callovian drill holes are truly naticids in nature, then our claim of naticid appearance may be further pushed back down to the Callovian. In short, we suggest that conchiolin layers in corbulid shells only appeared during the Oxfordian in response to the evolution of predatory naticid gastropods. It is an example of adaptation. Conchiolin layers were later exapted for tight adduction of the valves and other uses.

There are many reports of naticid-like drill holes from other Mesozoic records of the world, but the presence of naticid body fossils is yet to be recorded from the Triassic to Middle Jurassic. Our study gives an account of naticid drill holes in corbulids from the Middle Jurassic of Kutch based on literature survey. Circumstantial evidence (e.g., the beveled drill holes and the infaunalization of prey) are ubiquitous in many Mesozoic fossil assemblages, and these suggest that the naticid radiation perhaps already took place as a part of the Mesozoic marine revolution. Allmon et al. (1990) long ago predicted the appearance of ornaments in turritellines in response to predation pressure during the Mesozoic revolution and anticipated the time of possible turritelline origin in the late Jurassic or Early Cretaceous (see also Merriam, 1941). Here we work on the interaction between turritellines and naticid gastropods from the Late Jurassic (see also Das et al., 2018). A future planned search may yield more evidence of drilling predation and naticid body fossils from the older fossil record.

Conclusions

Naticid gastropods, right from their early appearance, started predation on mollusks, especially on turritelline gastropods and corbulid bivalves. The Oxfordian fossil assemblage presented here is so far the oldest record of the paleoecological relationship between naticid gastropod predators and molluscan prey, where naticid body fossils and their typical paraboloid drill holes on prey shells occur side by side.

DI is relatively low, and the prey selection is opportunistic and based only on availability. The presence of size stereotypy of predation in some prey species suggests that the naticids evolved to maximize energy from the larger prey. Well-developed behavioral stereotypy with regard to the drill site on turritelline shells suggests that naticids were efficient in hunting.

Naticid cannibalism already started during the Late Jurassic but was occasional.

The selectivity of the two most abundant prey puts considerable predation pressure on them. This set the development of the longest (since the Late Jurassic) predator–prey recurrent association, which continues even today.

The two main prey taxa (turritelline gastropods and corbulid bivalves) evolved long-term escalated features for survival. Turritellines responded by developing a high fecundity rate. The TDA appeared as soon as the naticid–turritellines interaction began. This reproductive strategy is an example of a non-shell adaptation against predation. High mortality is compensated by the high birth rate. No other gastropod clade in the marine environment was capable of producing such a dominant pair in the geological record.

Evolution of conchiolin layers in corbulids helped to deter drilling predators. The concomitant appearance of the naticid predators and the development of conchiolin layers in the corbulids provide a good example of adaptation.

https://doi.org/10.1017/jpa.2021.24 Published online by Cambridge University Press

Acknowledgments

We acknowledge the Indian Statistical Institute, Kolkata, for financial and infrastructural facilities. S.S. thanks DST-INSPIRE (reference no.: DST/INSPIRE fellowship/IF160434) for providing funds to pursue the field and laboratory work. We all are very much thankful to S. Mukherjee, Department of Geological Sciences, Jadavpur University, for logistic support. We are also thankful to our lab mates S. Mallick, R. Dutta, and K. Bose for their help during the field and laboratory work. Two reviewers, P. Kelley and A. Kaim, and associate editor, S. Schneider, critically reviewed the manuscript and provided many valuable suggestions. S. Mondal, S. Paul, P. Goswami, S. Saha, and N. Ganguly read the manuscript. B. Chattopadhyay, a native English speaker and the daughter of K.C. Mitra, who first discovered the present turritelline assemblage, and N. Hughes, University of California, Riverside, critically read the grammatical aspects of the manuscript and vastly improved the quality of the language.

Data Availability Statement

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.nzs7h44qv.

Supplementary Table 1. List of all species of the present molluscan (gastropods and bivalves) assemblages and their state of preservation and drilling intensity.

Supplementary Table 2. Spatiotemporal data of naticid drilling predation on corbulid bivalves ($n \geq 20$ valves) from all over the world.

Supplementary Table 3. Spatiotemporal data on abundant turritelline assemblages and naticid predation on them (if any) from the fossil record of the world.

References

Adegoke, O.S., and Tevesz, M.J.S., 1974, Gastropod predation patterns in the Eocene of Nigeria: Lethaia, v. 7, p. 17–24.

Alberti, M., Nützel, A., Fürsich, F.T., and Pandey, D.K., 2013a, Oxfordian (Late Jurassic) gastropods from the Kachchh Basin, western India: Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen, v. 270, p. 275–300.

Alberti, M., Fürsich, F.T., and Pandey, D.K., 2013b, Deciphering condensed sequences: a case study from the Oxfordian (Upper Jurassic) Dhosa Oolite member of the Kachchh Basin, western India: Sedimentology, v. 60, p. 574–598.

Allmon, W.D., 1988, Ecology of Recent turritelline gastropods (Prosobranchia, Turritellidae): current knowledge and paleontological implications: Palaios, v. 3, p. 259–284.

Allmon, W.D., 1996, Systematics and evolution of Cenozoic American Turritellidae (Mollusca: Gastropoda) I: Paleocene and Eocene coastal plain species related to "*Turrritella mortoni* Conrad" and "*Turritella humerosa* Conrad": Palaeontographica Americana, v. 59, 134 p.

Allmon, W.D., 2007, Cretaceous marine nutrients, greenhouse carbonates, and the abundance of turritelline gastropods: The Journal of Geology, v. 115, p. 509–523.

Allmon, W.D., 2011, Natural history of turritelline gastropods (Cerithiodea: Turritellidae): a status report: Malacologia, v. 54, p. 159–202.

Allmon, W.D., Nieh, J.C., and Norris, R.D., 1990, Drilling and peeling of turritelline gastropods since the Late Cretaceous: Palaeontology, v. 33, p. 595–611.

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

Anderson, L.C., Geary, D.H., Nehm, R.H., and Allmon, W.D., 1991, A comparative study of naticid gastropod predation on *Varicorbula caloosae* and *Chione cancellata*, Plio–Pliestocene of Florida, USA: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 85, p. 29–46.

Anderson, B.M., Hendy, A., Johnson, E.H., and Allmon, W.D., 2017, Paleoecology and paleoenvironmental implications of turritelline gastropod-dominated assemblages from the Gatun Formation (upper Miocene) of Panama: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 470, p. 132–146.

Ansell, A.D., and Morton, B., 1987, Alternative predation tactics of a tropical naticid gastropod: Journal of Experimental Marine Biology and Ecology, v. 111, p. 109–119.

Arua, I., and Hoque, M., 1989, Fossil predaceous gastropod borings from Nigeria: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 73, p. 175–183.

Bambach, R.K., and Kowalewski, M., 2000, How to count fossils: Geological Society of America Abstracts with Programs, v. 32, p. 332.

Bandel, K., 1992, Über Caenogastropoda der Cassianer Schichten (Obertrias) der Dolomiten (Italien) und ihre taxonomische Bewertung: Mitteilungen aus dem Geologisch-Paläontologischen Institut der Universität Hamburg, v. 73, 379 p.

Bandel, K., 1993, Caenogastropoda during Mesozoic times: Scripta Geologica, special issue 2, p. 7–56.

Bandel, K., 1996, Some heterostrophic gastropods from Triassic St. Cassian Formation with a discussion on the classification of the Allogastropoda: Paläontologische Zeitschrift, v. 70, p. 325–365.

Bandel, K., 1999, On the origin of the carnivorous gastropod group Naticoidea (Mollusca) in the Cretaceous with description of some convergent but unrelated groups: Greifswalder Geowissen schaftliche Beiträge, v. 6, p. 143–175.

Bardhan, S., and Chattopadhyay, D., 2003, The Mesozoic marine revolution: an overview of a biological 'arms race': Indian Journal of Earth Sciences, v. 30, p. 1–28.

Bardhan, S., Chattopadhyay, D., Mondal, S., Das, S.S., Mallick, S., Chanda, P., and Roy, A. 2012, Record of intense predatory drilling from Upper Jurassic fauna of Kutch, India: implications for the history of biotic interaction: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 317–318, p. 153–161.

Bardhan, S., Mallick, S., and Das, S.S., 2014, Palaeobiogeographic constraints on drilling gastropod predation: a case study from the Miocene Khari Nadi Formation in Kutch, Gujarat: Special publication of the Palaeontological Society of India, v. 5, p. 205–213.

Bengtson, S., and Zhao, Y., 1992, Predatorial borings in late Precambrian mineralized exoskeletons: Science, v. 257, p. 367–369.

Blake, J.D., and Huddleston, W.H., 1877, The Corallian rocks of England: The Quarterly Journal of the Geological Society of London, v. 13, p. 260–405.

Boucher, L.M., 1986, Coral predation by muricid gastropods of the genus Drupella at Enewetak, Marshall Islands: Bulletin of Marine Science, v. 38, p. 9–11.

Bromley, R.G., 1981, Concepts in ichnotaxonomy illustrated by small round holes in shells: Acta Geologica Hispanica, v. 16, p. 55–64.

Carriker, M.R., and Yochelson, E.L., 1968, Recent gastropod boreholes and Ordovician cylindrical borings: US Geological Survey Professional Paper 593B, 26 p.

Casey, M.M., Farrell, Ú.C., Dietl, G.P., and Veilleux, D.J., 2015, Mixed assemblages of drilling predators and the problem of identity in the fossil record: a case study using the muricid gastropod Ecphora: Paleobiology, v. 41, p. 680–696.

Chattopadhyay, D., and Dutta, S., 2013, Prey selection by drilling predators: a case study from Miocene of Kutch, India: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 374, p. 187–196.

Chattopadhyay, D., Zuschin, M., and Tomašových, A., 2014, Effects of a high-risk environment on edge-drilling behavior: inference from Recent bivalves from the Red Sea: Paleobiology, v. 40, p. 34–49.

Chattopadhyay, D., Zuschin, M., and Tomašových, A., 2015, How effective are ecological traits against drilling predation? Insights from recent bivalve assemblages of the northern Red Sea: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 440, p. 659–670.

Chattopadhyay, D., Zuschin, M., Dominici, S., and Sawyer, J.A., 2016, Patterns of drilling predation in relation to stratigraphy, locality and sieve size: insights from the Eocene molluscan fauna of the Paris Basin: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 459, p. 86–98.

Cohen, A.S., 1989, The taphonomy of gastropod shell accumulations in large lakes: an example from Lake Tanganyika, Africa: Paleobiology, v. 15, p. 26–45.

Conrad, T.A., 1860, Descriptions of new species of Cretaceous and Eocene fossils of Mississippi and Alabama: Academy of Natural Sciences of Philadelphia, v. 2, p. 275–297.

Cox, L.R., 1940, The Jurassic Lamellibranchiata fauna of Kachh (Cutch): Palaeontologia Indica, v. 9, 157 p.

Culotta, E., 1988, Predators and available prey; naticid predation during a Neogene molluscan extinction event [M.S. thesis]: Ann Arbor, University of Michigan, 136 p.

Daley, G.M., Ostrowski, S., and Geary, D.H., 2007, Paleoenvironmentally correlated differences in a classic predator–prey system: the bivalve *Chione elevata* and its gastropod predators: Palaios, v. 22, p. 166–173.

Das, A., Mondal, S., and Bardhan, S., 2014, A note on exceptionally high confamilial naticid drilling frequency on *Natica gualteriana* from the Indian subcontinent: Historical Biology, v. 26, p. 758–764.

Das, S.S., 2004, New assemblage of the Mesozoic gastropod faunas of Kutch, western India—a study of systematics, palaeobiogeography and evolution [Ph.D. thesis]: Kolkata, India, Jadavpur University, 161 p.
Das, S.S., 2008, Gastropod diversity patterns and evolutionary tempo during the early rifting phase (Jurassic) of the Kutch Basin: Journal of the Palaeontological Society of India, v. 53, p. 9–18.
Das, S.S., Bardhan, S., and Lahiri, T.C., 1999, The late Bathonian gastropod fauna of Kutch, western India—a new assemblage: Paleontological Research, v. 3, p. 268–286.
Das, S.S., Bardhan, S., and Kase, T., 2005, A new pleurotomariid gastropod assemblage from the Jurassic sequence of Kutch, western India: Paleontological Research, v. 9, p. 329–346.
Das, S.S., Saha, S., Bardhan, S., Mallick, S., and Allmon, W.D., 2018, The oldest turritelline gastropods: from the Oxfordian (Upper Jurassic) of Kutch, India: Journal of Paleontology, v. 92, p. 373–387.
Das, S.S., Mondal, S., Saha, S., Bardhan, S., and Saha, R., 2019, Family Naticidae (Gastropoda) from the Upper Jurassic of Kutch, India and a critical reappraisal of taxonomy and time of origination of the family: Journal of Paleontology, v. 93, p. 673–684.
Datta, K., 1992, Facies, fauna and sequence: an integrated approach in the Jurassic Patcham and Chari Formations, Kutch, India [Ph.D. thesis]: Kolkata, India, Jadavpur University, 167 p.
DeAngelis, D.L., Kitchell, J.A., and Post, W.M., 1985, The influence of naticid predation on evolutionary strategies of bivalve prey: conclusions from a model: The American Naturalist, v. 126, p. 817–842.
De Cauwer, G., 1985, Gastropod predation on corbulid bivalves. Palaeoecology or taphonomy?: Annales de la Société royale zoologique de Belgique, v. 115, p. 183–196.
De Koninck, L.L., 1881, Neue Reaction auf Kali: Zeitschrift für analytische Chemie, v. 20, p. 390–391.
Dietl, G.P., 2002, Traces of naticid predation on the gryphaeid oyster *Pycnodonte dissimilaris*: epifaunal drilling of prey in the Paleocene: Historical Biology, v. 16, p. 13–19.
Dietl, G.P., and Kelley, P.H., 2002, The fossil record of predator–prey arms races: coevolution and escalation hypotheses: The Paleontological Society Papers, v. 8, p. 353–374.
Dietl, G.P., and Kelley, P.H., 2006, Can naticid gastropod predators be identified by the holes they drill?: Ichnos, v. 13, p. 103–108.
Dietl, G.P., Herbert, G.S., and Vermeij, G.J., 2004, Reduced competition and altered feeding behavior among marine snails after a mass extinction: Science, v. 306, p. 2229–2231.
Dudley, E.C., and Vermeij, G.J., 1978, Predation in time and space: drilling in the gastropod turritella: Paleobiology, v. 4, p. 436–441.
Dyer, A.D., Ellis, E.R., Molinaro, D.J., and Leighton, L.R., 2018, Experimental fragmentation of gastropod shells by sediment compaction: implications for interpreting drilling predation intensities in the fossil record: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 511, p. 332–340.
Edwards, H.M., 1974, Rieman's Zeta Function. Pure and Applied Mathematics, v. 58: New York, Academic Press, 314 p.
Férussac, A.E. de, 1822, Tableaux systematic ques des Animaux Mollusques classes en familles naturelles, dans lesquels on aétabli la concordance de tous les systèmes; suivis d'un prodrome général pour tous les mollusques terrestres ou fluviatiles, vivants ou fossiles: Paris, Bertrand, 110 p.
Fischer, P., 1887, Manual of Conchyliology and Conchyliological Palaeontology or Natural History of Live or Fossil Molluscs, Volume 1: Paris, Savy, 23 pl., 1369 p.
Fraaije, R.H., 2003, The oldest in situ hermit crab from the Lower Cretaceous of Speeton, UK: Palaeontology, v. 46, p. 53–57.
Fretter, V., and Graham, A., 1962, British Prosobranch Molluscs: London, Ray Society, 755 p.
Fretter, V., and Graham, A., 1981, The prosobranch molluscs of Britain and Denmark. Part 6: Cerithiacea, Strombacea, Hipponacea, Calyptracea, Lamellariacea, Cypraeacea, Naticacea, Tonnacea, Heteropoda: Journal of Molluscan Studies, v. 9, p. 285–363.
Fürsich, F.T., 1981, Salinity controlled benthic associations from the Upper Jurassic of Portugal: Lethaia, v. 14, p. 203–223.
Fürsich, F.T., and Jablonski, D., 1984, Late Triassic naticid drillholes: carnivorous gastropods gain a major adaptation but fail to radiate: Science, v. 224, p. 78–80.
Fürsich, F.T., and Pandey, D.K., 2003, Sequence stratigraphic significance of sedimentary cycles and shell concentrations in the Upper Jurassic–Lower Cretaceous of Kutch, Western India: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 193, p. 285–309.
Fürsich, F.T., Oschmann, W., Singh, I.B., and Jaitly, A.K., 1992, Hardgrounds, reworked concretion levels and condensed horizons in the Jurassic of Western India: their significance for basin analysis: Journal of the Geological Society, v. 149, p. 313–331.
Fürsich, F.T., Heinze, M., and Jaitly, A.K., 2000, Contributions to the Jurassic of Kachchh, western India. VIII. The bivalve fauna; part IV, subclass Heterodonta: Beringeria, v. 27, p. 63–146.
Garton, D., and Stickle, W.B., 1980, Effects of salinity and temperature on the predation rate of *Thais haemastoma* on *Crassostrea virginica* Spat: The Biological Bulletin, v. 158, p. 49–57.
Geary, D.H., and Allmon, W.D., 1990, Biological and physical contributions to the accumulation of strombid gastropods in a Pliocene shell bed: Palaios, v. 5, p. 259–272.
Goswami, P., Das, S.S., Bardhan, S., and Paul, S., 2020, Drilling gastropod predation on the lower Miocene gastropod assemblages from Kutch, western India: spatiotemporal implications: Historical Biology, https://doi.org/10.1080/08912963.2020.1716343.
Gould, S.J., and Vrba, E.S., 1982, Exaptation—a missing term in the science of form: Paleobiology, v. 8, p. 4–15.
Hagadorn, J.W., and Boyajian, G.E., 1997, Subtle changes in mature predator–prey systems: an example from Neogene Turritella (Gastropoda): Palaios, v. 12, p. 372–379.
Hallam, A., 1976, Stratigraphic distribution and ecology of European Jurassic bivalves: Lethaia, v. 9, p. 245–259.
Harper, E.M., 1994, Are conchiolin sheets in corbulid bivalves primarily defensive? Palaeontology, v. 37, p. 551–578.
Harper, E.M., and Wharton, D.S., 2000, Boring predation and Mesozoic articulate brachiopods: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 158, p. 15–24.
Harper, E.M., Forsythe, G.T.W., and Palmer, T., 1998, Taphonomy and the Mesozoic marine revolution: preservation state masks the importance of boring predators: Palaios, v. 13, p. 352–360.
Harries, P.J., and Schopf, K.M., 2007, Late Cretaceous gastropod drilling intensities: data from the Maastrichtian Fox Hills Formation, Western Interior Seaway, USA: Palaios, v. 22, p. 35–46.
Harris, G.F., 1897, Catalogue of Tertiary Mollusca in the Department of Geology, British Museum (Natural History). Part 1: The Australasian Tertiary Mollusca: London, British Museum, 404 p., 8 pl.
Hausmann, I.M., and Nützel, A., 2015, Diversity and palaeoecology of a highly diverse Late Triassic marine biota from the Cassian Formation of north Italy: Lethaia, v. 48, p. 235–255.
Hoffman, A. and Martinell, J., 1984, Prey selection by naticid gastropods in the Pliocene of Emporda (northeast Spain): Neues Jahrbuch für Geologie und Paläontologie, Monatshefte, v. 7, p. 393–399.
Hoffmeister, A.P., and Kowalewski, M., 2001, Spatial and environmental variation in the fossil record of drilling predation: a case study from the Miocene of central Europe: Palaios, v. 16, p. 566–579.
Hua, H., Pratt, B.R., and Zhang, L.Y., 2003, Borings in Cloudina shells: complex predator–prey dynamics in the terminal Neoproterozoic: Palaios, v. 18, p. 454–459.
Huntley, J.W., and Kowalewski, M., 2007, Strong coupling of predation intensity and diversity in the Phanerozoic fossil record: Proceedings of the National Academy of Sciences USA, v. 104, p. 15006–15010.
Huntley, J.W., and Scarponi, D., 2015, Geographic variation of parasitic and predatory traces on mollusks in the northern Adriatic Sea, Italy: implications for the stratigraphic paleobiology of biotic interactions: Paleobiology, v. 41, p. 134–153.
Hutchings, J.A., and Herbert, G.S., 2013, No honor among snails: conspecific competition leads to incomplete drill holes by a naticid gastropod: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 379, p. 32–38.
Jaitly, A.K., Fürsich, F.T., and Heinze, M., 1995, Contributions to the Jurassic of Kachchh, western India. IV. The bivalve fauna. Part I. Subclasses Palaeotaxodonta, Pteriomorphia, and Isofilibranchia: Beringeria, v. 16, p. 147–257.
Kabat, A.R., 1991, The classification of the Naticidae (Mollusca: Gastropoda): review and analysis of the supraspecific taxa: Bulletin of the Museum of Comparative Zoology, v. 152, p. 417–449.
Kabat, A.R., and Kohn, A.J., 1986, Predation on early Pleistocene naticid gastropods in Fiji: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 53, p. 255–269.
Kaim, A., Hryniewicz, K., Little, C.T., and Nakrem, H.A., 2017, Gastropods from the Late Jurassic–Early Cretaceous seep deposits in Spitsbergen, Svalbard: Zootaxa, v. 4329, p. 351–374.
Kanjilal, S., 1997, *Corbula* (*Corbula*) *haboensis* n. sp. (Bivalvia) from the Callovian (middle Callovian) sediments of the Habo Hills, Kachchh, western India: its functional morphology and inferred habit and habitat: Indian Journal of Geology, v. 69, p. 294–299.
Kardon, G., 1998, Evidence from the fossil record of an antipredatory exaptation: conchiolin layers in corbulid bivalves: Evolution, v. 52, p. 68–79.
Kase, T., and Ishikawa, M., 2003, Mystery of naticid predation history solved: evidence from a "living fossil" species: Geology, v. 31, p. 403–406.
Kelley, P.H., 1988, Predation by Miocene gastropods of the Chesapeake group: stereotyped and predictable: Palaios, v. 3, p. 436–448.
Kelley, P.H., 2008, Role of bioerosion in taphonomy: effect of predatory drill holes on preservation of mollusc shells, *in* Wisshak, M., and Tapanila, L., eds., Current Developments in Bioerosion: Berlin, Springer, p. 451–470.

https://doi.org/10.1017/jpa.2021.24 Published online by Cambridge University Press

Kelley, P.H., and Hansen, T.A., 1993, Evolution of the naticid gastropod predator–prey system: an evaluation of the hypothesis of escalation: Palaios, v. 8, p. 358–375.
Kelley, P.H., and Hansen, T.A., 1996, Naticid gastropod prey selectivity through time and the hypothesis of escalation: Palaios, v. 11, p. 437–445.
Kelley, P.H., and Hansen, T.A., 2006, Comparisons of class and lower taxon-level patterns in naticid gastropod predation, Cretaceous to Pleistocene of the US Coastal Plain: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 236, p. 302–320.
Kelley, P.H., Hansen, T.A., Graham, S.E., and 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, v. 166, p. 165–176.
Kitchell, J.A., 1986, The evolution of predator–prey behavior: naticid gastropods and their molluscan prey, *in* Nitecki, M., and Kitchell, J. A., eds., Evolution of Animal Behavior: Paleontological and Field Approaches: Oxford, Oxford University Press, p. 88–110.
Kitchell, J.A., Boggs, C.H., Kitchell, J.F., and Rice, J.A., 1981, Prey selection by naticid gastropods: experimental tests and application to the fossil record: Paleobiology, v. 7, p. 533–552.
Kitchin, F.L., 1903, The Jurassic fauna of Cutch, the Lamellibranchiata, genus *Trigonia*: Memoirs of the Geological Survey of India, Palaeontologia Indica, ser. 9, v. 3, 122 p.
Klompmaker, A.A., Portell, R.W., Lad, S.E., and Kowalewski, M., 2015, The fossil record of drilling predation on barnacles: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 426, p. 95–111.
Klompmaker, A.A., Nützel, A., and Kaim, A., 2016, Drill hole convergence and a quantitative analysis of drill holes in mollusks and brachiopods from the Triassic of Italy and Poland: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 457, p. 342–359.
Klompmaker, A.A., Kowalewski, M., Huntley, J.W., and Finnegan, S., 2017, Increase in predator–prey size ratios throughout the Phanerozoic history of marine ecosystems: Science, v. 356, p. 1178–1180.
Klompmaker, A.A., Kelley, P.H., Chattopadhyay, D., Clements, J.C., Huntley, J.W., and Kowalewski, M., 2019, Predation in the marine fossil record: studies, data, recognition, environmental factors, and behavior: Earth-Science Reviews, v. 194, p. 472–520.
Koken, E., 1892, Ueber die Gastropoden der rothen Schlernschichten nebst Bemerkungen über Verbreitung und Herkunft einiger triassischer Gattungen: Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, v. 2, p. 25–36.
Kollmann, H.A., 1982, Gastropoden-Faunen aus der höheren Unterkreide nordwest deutschlands: Geologische Jahrbücher (A), v. 65, p. 517–551.
Kowalewski, M., 2002, The fossil record of predation: an overview of analytical methods, *in* Kowalewski, M., and Kelley, P. H., eds., The Fossil Record of Predation: Paleontological Society Special Papers, v. 8, p. 3–42.
Kowalewski, M., Dulai, A., and Fürsich, F.T., 1998, A fossil record full of holes: the Phaneorozoic history of drilling predation: Geology, v. 26, p. 1091–1094.
Lewy, Z., and Samtleben, C., 1979, Functional morphology and palaeontological significance of the conchiolin layers in corbulid pelecypods: Lethaia, v. 12, p. 341–351.
Mallick, S., Bardhan, S., Paul, S., Mukherjee, S., and Das, S.S., 2013, Intense naticid drilling predation on turritelline gastropods from below the K–T boundary at Rajahmundry, India: Palaios, v. 28, p. 683–696.
Mallick, S., Bardhan, S., Das, S.S., Paul, S., and Goswami, P., 2014, Naticid drilling predation on gastropod assemblages across the K–T boundary in Rajahmundry, India: new evidence for escalation hypothesis: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 411, p. 216–228.
M'Coy, F., 1844, A Synopsis of the Characters of the Carboniferous Limestone Fossils of Ireland: Dublin, M.H. Gill, 207 p.
Merriam, C.W., 1941, Fossil turritellas from the Pacific coast region of North America: University of California Publications in Geological Sciences, v. 26, 214 p.
Mitra, K.C., and Ghosh, D.N., 1979, Jurassic turritellas from Kutch, Gujarat: Quarterly Journal of the Geological Mining and Metallurgical Society of India, v. 51, p. 119–122.
Mitra, K.C., Bardhan, S., and Bhattacharya, D., 1979, A study of Mesozoic stratigraphy of Kutch, Gujarat, with special reference to rock-stratigraphy and biostratigraphy of Keera dome: Bulletin of the Indian Geological Association, v. 12, p. 129–143.
Mondal, S., and Harries, P.J., 2015, Temporal patterns in successful and unsuccessful shell-breaking predatory attack strategies on Varicorbula in the Plio-Pleistocene of Florida: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 428, p. 31–38.
Mondal, S., Bardan, S., and Sarkar, D., 2010, Testability of the Energy Maximization Model (Kitchell et al., 1981) of naticid predation on two bivalve prey from the eastern coast of India: Nautilus, v. 124, p. 137–150.
Mondal, S., Harries, P.J., Paul, S., and Herbert, G.S., 2014, Paleoecological significance of coupling metrics of successful and unsuccessful shell-breaking predation: examples using Neogene bivalve prey: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 399, p. 89–97.
Mondal, S., Goswami, P., and Bardhan, S., 2017, Naticid confamilial drilling predation through time: Palaios, v. 32, p. 278–287.
Mondal, S., Chakraborty, H., and Paul, S., 2019a, Latitudinal patterns of gastropod drilling predation intensity through time: Palaios, v. 34, p. 261–270.
Mondal, S., Maitra, A., Bose, K., Goswami, P., Bardhan, S., and Mallick, S., 2019b, Substrate-controlled naticid gastropod drilling predation on recent barnacles from Chandipur, India and its palaeontological implications: Historical Biology, https://doi.org/10.1080/08912963.2019.1677639.
Mörch, O.A.L., 1857, Fortegnelse over Grønlands Bløddyr, *in* Rink, H. ed., Grønland, geographisk ogstatistisk beskrevet: Copenhagen, L. Kleins, p. 74–100.
Morris, S.C., and Bengtson, S., 1994, Cambrian predators: possible evidence from boreholes: Journal of Paleontology, v. 68, p. 1–23.
Morton, B., 1990, The biology and functional morphology of *Corbula crassa* (Bivalvia: Corbulidae) with special reference to shell structure and formation: The Marine Flora and Fauna of Hong Kong and Southern China II, v. 3, p. 1055–1073.
Nebelsick, J.H., and Kowalewski, M., 1999, Drilling predation on recent clypeasteroid echinoids from the Red Sea: Palaios, v. 14, p. 127–144.
Nebelsick, J.H., Rasser, M., Höltke, O., Thompson, J.R., and Bieg, U., 2020, Turritelline mass accumulations from the lower Miocene of southern Germany: implications for tidal currents and nutrient transport within the North Alpine Foreland Basin: Lethaia, v. 53, p. 280–293.
Pahari, A., Mondal, S., Bardhan, S., Sarkar, D., Saha, S., and Buragohain, D., 2016, Subaerial naticid gastropod drilling predation by *Natica tigrina* on the intertidal molluscan community of Chandipur, eastern coast of India: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 451, p. 110–123.
Paul, G., Das, A., Bardhan, S., and Mondal, S., 2013, Predation on Recent turritelline gastropods from the Indian subcontinent and comparison with a revised global database: Malacologia, v. 56, p. 193–213.
Porter, S.M., 2016, Tiny vampires in ancient seas: evidence for predation via perforation in fossils from the 780–740 million-year-old Chuar Group, Grand Canyon, USA: Proceedings of the Royal Society B: Biological Sciences, v. 283, https://doi.org/10.1098/rspb.2016.0221.
Price, B.A., Killingley, J.S., and Berger, W.H., 1985, On the pteropod pavement of the eastern Rio Grande Rise: Marine Geology, v. 64, p. 217–235.
Roy, K., Miller, D.J., and LaBarbera, M., 1994, Taphonomic bias in analyses of drilling predation: effects of gastropod drill holes on bivalve shell strength: Palaios, v. 9, p. 413–421.
Roy, A., Bardhan, S., Das, S., Mondal, S., and Mallick, S., 2012, Systematic revision and palaeobiogeography of *Perisphinctes* Waagen (Ammonoidea) from the Oxfordian of Kutch, India: stratigraphic and evolutionary implications: Palaeoworld, v. 2, p. 167–192.
Saha, S., Mondal, S., Bardhan, S., Mallick, S., Pahari, A., Sarkar, D., Buragohain, D., Das, A., Goswami, P., and Dutta, R., 2016, Predator–prey interaction on the Molluscan assemblage from Chandipur-on-Sea, Odisha: The National Geo-Research Scholars Meet 2016 (NGEOSM-2016), Wadia Institute of Himalayan Geology, Dehradun, India, p. 80.
Sander, F., and Lalli, C.M., 1982, A comparative study of mollusk communities on the shelf–slope margin of Barbados, West Indies: Veliger, v. 24, p. 309–318.
Sarkar, D., Bardhan, S., Mondal, S., Das, A., Pahari, A., Buragohain, D., and Saha, S., 2016, Predation on Recent terebrid gastropods from the Indian subcontinent and a spatiotemporal reappraisal based on a revised global database: Malacologia, v. 59, p. 271–303.
Savazzi, E., and Reyment, R.A., 1989, Subaerial hunting behavior in *Natica gualteriana* (naticid gastropod): Palaeogeography, Palaeoclimatology, Palaeoecology. v. 74, p. 355–364.
Sawyer, J.A., and Zuschin, M., 2010, Intensities of drilling predation of molluscan assemblages along a transect through the northern Gulf of Trieste (Adriatic Sea): Palaeogeography, Palaeoclimatology, Palaeoecology, v. 285, p. 152–173.
Sawyer, J.A., and Zuschin, M., 2011, Drilling predation in mollusks from the lower and middle Miocene of the Central Paratethys: Palaios, v. 26, p. 284–297.
Seilacher, A., 1984, Constructional morphology of bivalves: evolutionary pathways in primary versus secondary soft-bottom dwellers: Palaeontology, v. 27, p. 207–237.
Signor, P.W., III, 1985, The role of shell geometry as a deterrent to predation in terebrid gastropods: Veliger, v. 28, p. 179–185.
Singh, C.S.P., and Rai, J.N., 1980, Bathonian-Callovian fauna of western Bela Island (Kutch). Part 1. Bivalve families Cardiidae, Neomiodontidae and Corbulidae: Journal of the Palaeontological Society of India, v. 23, p. 71–80.
Smith, A.G., Smith, D.G., and Funnell, B.M., 1994, Atlas of Mesozoic and Cenozoic Coastlines: Cambridge, Cambridge University Press, 99 p.

Sowerby, J.D., 1837, Mineral-Conchologie Grossbrittaniens, von James Sowerby; deutsche Bearbeitung, herausgegeben von Hercules Nicolet, durchgesehen von Dr. Agassiz: Neuchâtel, H. Nicolet, 52 p.
Sowerby, J. de C., 1823–1824, The Mineral Conchology of Great Britain, Volume 5: London, Richard Taylor, 171 p.
Sowerby, J. de C., 1840, Description of fossils from the Upper Secondary Formation of Cutch collected by C.W. Grant: Transactions of the Geological Society of London, v. 2, no. 5, pl. 21–23.
Stanley, S.M., 1968, Post-Paleozoic adaptive radiation of infaunal bivalve molluscs: a consequence of mantle fusion and siphon formation: Journal of Paleontology, v. 42, p. 214–229.
Stanley, S.M., 1970, Relation of Shell Form to Life Habitats in the Bivalvia (Mollusca): Geological Society of America Memoir 125, 296 p.
Stanley, S.M., 1977, Trends, rates, and patterns of evolution in the Bivalvia, *in* Hallam, A., ed., Patterns of Evolution, as Illustrated by the Fossil Record. Developments in Palaeontology and Stratigraphy, v. 5: Amsterdam, Elsevier, p. 209–250.
Subba Rao, N.V., Surya Rao, K.V., and Maitra, S., 1991, Marine molluscs of Orissa, *in* Director, Zoological Survey of India, ed., Fauna of Orissa, Part 3. State Fauna Series 1: Calcutta, Zoological Survey of India, p. 1–175.
Subba Rao, N.V., Dey, A., and Barua, S., 1992, Estuarine and marine molluscs of West Bengal, *in* Director, Zoological Survey of India, ed., Fauna of West Bengal, Part 9. State Fauna Series 3: Calcutta, Zoological Survey of India, p. 129–268.
Taylor, J.D., 1970, Feeding habitats of predator gastropods in Tertiary (Eocene) molluscan assemblages from the Paris Basin: Palaeontology, v. 13, p. 254–260.
Taylor, J.D., Morris, N.J., and Taylor, C.N., 1980, Food specialization and the evolution of predatory prosobranch gastropods: Palaeontology, v. 23, p. 375–409.
Taylor, J.D., Cleevely, R.D., and Morris, N.J., 1983, Predatory gastropods and their activities in the Blackdown Greensand (Albian) of England: Palaeontology, v. 26, p. 521–553.
Thompson, J.N., 1998, Rapid evolution as an ecological process: Trends in Ecology & Evolution, v. 13, p. 329–332.
Tracey, S., Todd, J.A., and Erwin, D.H., 1993, Mollusca: Gastropoda, *in* Benton, M.J., ed., The Fossil Record 2: London, Chapman and Hall, p. 137–167.
Vermeij, G.J., 1977, The Mesozoic marine revolution: evidence from snails, predators, and grazers: Paleobiology, v. 3, p. 245–258.
Vermeij, G.J., 1980, Drilling predation of bivalves in Guam—some paleoecological implications: Malacologia, v. 19, p. 329–334.
Vermeij, G.J., 1982, Unsuccessful predation and evolution: The American Naturalist, v. 120, p. 701–720.
Vermeij, G.J., 1983, Traces and trends of predation, with special reference to bivalved animals: Palaeontology, v. 26, p. 455–465.
Vermeij, G.J., 1987, Evolution and Escalation: An Ecological History of Life: Princeton, Princeton University Press, 527 p.
Vermeij, G.J., 1994, The evolutionary interaction among species: selection, escalation, and coevolution: Annual Review of Ecology and Systematics, v. 25, p. 219–236.
Vermeij, G.J., and Dudley, E.C., 1982, Shell repair and drilling in some gastropods from the Ripley Formation (Upper Cretaceous) of the south-eastern USA: Cretaceous Research, v. 3, p. 397–403.
Vermeij, G.J., Zipser, E., and Dudley, E.C., 1980, Predation in time and space: peeling and drilling in terebrid gastropods: Paleobiology, v. 6, p. 352–364.
Vermeij, G.J., Dudley, E.C., and Zipser, E., 1989, Successful and unsuccessful drilling predation in recent pelecypods: Veliger, v. 32, p. 266–273.
Visaggi, C.C., and Kelley, P.H., 2015, Equatorward increase in naticid gastropod drilling predation on infaunal bivalves from Brazil with paleontological implications: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 438, p. 285–299.
Visaggi, C.C., Dietl, G.P., and Kelley, P.H., 2013, Testing the influence of sediment depth on drilling behaviour of *Neverita duplicata* (Gastropoda: Naticidae), with a review of alternative modes of predation by naticids: Journal of Molluscan Studies, v. 79, p. 310–322.
Vokes, H.E., 1945, Supraspecific groups of the pelecypod family Corbulidae: Bulletin of the American Museum of Natural History, v. 86, p. 1–32.
Waite, R., and Strasser, A., 2011, A comparison of recent and fossil large, high-spired gastropods and their environments. The Nopparat Thara tidal flat in Krabi, South Thailand versus the Swiss Kimmeridgian carbonate platform: Facies, v. 57, p. 223–248.
Waite, R., Wetzel, A., Meyer, C.A., and Strasser, A., 2008, The paleoecological significance of nerineoid mass accumulations from the Kimmeridgian of the Swiss Jura Mountains: Palaios, v. 23, p. 548–558.
Walker, S.E., 1989, Hermit crabs as taphonomic agents: Palaios, v. 4, p. 439–452.
Walker, S.E., 1994, Biological remanie: gastropod fossils used by the living terrestrial hermit crab, *Coenobita clypeatus*, on Bermuda: Palaios, v. 9, p. 403–412.
Wilbur, K.M., 1964, Shell formation and regeneration, *in* Wilbur, K.M., and Yonge, C.M., eds., Physiology of Mollusca, Volume 1: New York, Academic Press, p. 243–282.
Wiltse, W.I., 1980, Predation by juvenile *Polinices duplicatus* (Say) on *Gemma gemma* (Totten): Journal of Experimental Marine Biology and Ecology, v. 42, p. 187–199.
Zardini, R., 1985, Fossili Cassiani (Trias Medio-Superiore). Primo aggiornamento all'Atlante dei Bivalvi e secondo aggiornamento all'Atlante Gasteropodi della formazione di S. Cassiano raccolti nella regione Dolomitica attorno a Cortina d'Ampezzo: Cortina d'Ampezzo, Edizione Ghedina, 17 p.

Accepted: 14 February 2021