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Predatory drilling in Tertiary larger foraminifera from India

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Evidence of predatory drilling in the microspheric tests of Middle Eocene larger foraminifera *Nummulites obtusus* (Sowerby) from western Kutch is reported in this communication from the Indian Tertiary sequences. Evidence in the form of repair structures present in the foraminiferal wall and indicative of post-attack healing, has been described and illustrated. While biological identity of the predator remains enigmatic at the present stage of investigation, this report is likely to throw light on similar instances of predator–prey interaction in previously accounted Tertiary larger foraminiferal assemblages of India.

Keywords: Kutch, larger foraminifera, Middle Eocene, *Nummulites obtusus* (Sowerby), predation.

PREDATION plays a major role in shaping the shallow marine benthonic fauna[1]. Benthic foraminifera, a common constituent of the shallow marine bottom community with high preservation potential, are often subjected to bioerosion[2]. All bioeroded foraminifera, however, do not necessarily reflect predatory action, as dead tests are subjected to boring by endoliths or protoplasm scavenging taxa[3]. As such, the prey–predator interaction involving foraminifera as the prey may not be easy to infer, especially in the fossil record. In this backdrop, unequivocal evidence of predatory drilling can be gathered from the study of foraminiferal specimens surviving one or more sub-lethal attacks to live long enough to heal their damaged tests[4]. Thus, documentation of repair structure in the foraminiferal test wall confirms the prey–predator interaction in either present or fossil foraminiferal assemblages. In this communication, we report the occurrence of repair structures in the microspheric tests of the Middle Eocene larger foraminifera *Nummulites obtusus* (Sowerby) from western Kutch. Perhaps constrained by the limited scope of publication, authors of a previous report[5] on the predation of Eocene larger foraminifera from Kutch, did not include the detailed account of predation. To our knowledge, there is no other publication on the predation of Tertiary larger foraminifera from India.

So far, interaction among shallow marine benthic biota from the Tertiary basin of Kutch has been sporadically explored. Such studies include the Miocene benthic community in general[6] and the Miocene mollusks in particular[7], the Middle Eocene ostracods[8] and the

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Eocene–Oligocene larger foraminifera[9–12]. Bioerosion recorded in the tests of Palaeogene larger foraminifera includes *Oichnus simplex* Bromley, *Sulcicnus meandriformis* Martinell and Domènech, cf. *Zapfella* Saint-Seine and cf. *Ichnoreticulina* Radtke and Golubic[9–11]. Interestingly, no repair structure was observed in the aforementioned bioerosional cavities in the larger foraminifera.

In the course of the present work, *N. obtusus* was identified on the basis of the systematic account of the species provided by Samanta[13], Samanta *et al.*[14] and Saraswati *et al.*[15]. Specimens of *N. obtusus* were collected from a narrow (0.3–0.4 m), yellowish brown marl foraminiferal shell-bed occurring in the upper part of the Middle Eocene Harudi Formation, exposed in the type locality of the formation near Harudi village in western Kutch[16] (Figure 1). The sampled foraminiferal shell-bed, characterized by the occurrence of *Nummulites* taxa in rock-forming abundance, extends from NE to SW Kutch and has been informally referred to as the '*obtusus* band'[16] or the '*obtusus* bed'[10], after the most abundantly occurring

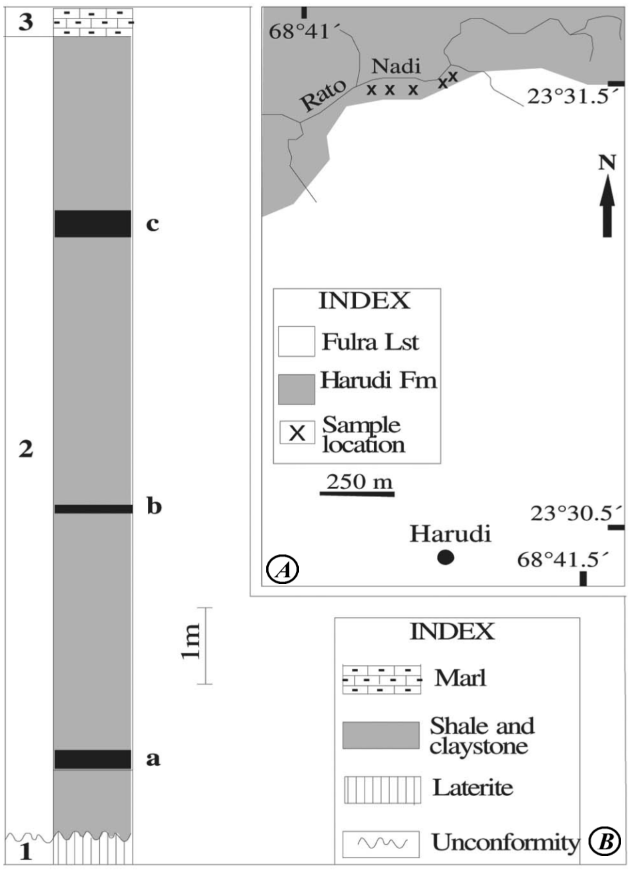

Figure 1. *A*, Geological map of the area around Harudi village showing location of samples collected from the '*obtusus* bed'. ***B***, Stratigraphic section of Harudi Formation from the type locality. Beds a, b and c represent major shell beds; beds a and b represent macroinvertebrate shell beds; bed c represents the '*obtusus* bed'. Stratigraphic intervals 1, 2 and 3 represent upper part of Naredi Formation, Harudi Formation and lower part of Fulra Limestone respectively.

foraminifera *N. obtusus*. The '*obtusus* bed' lacks sorting and orientation of the bioclasts. Primary sedimentary structures were not recorded in the shell-bed. Repair structures in the foraminiferal tests were examined using the light microscope and scanning electron microscope (SEM). Additionally, polar plug of the megalospheric form of *N. obtusus* was examined under SEM to record the ultrastructure of the imperforate wall. Presently, 14 repair structures have been externally examined under the stereo microscope; 10 tests had 1 repair structure per test, while 2 repair structures per test was recorded in 2 tests. Internal examination of the repair structures was based on the study of polished transverse sections of four plugged cavities under the stereo microscope. SEM examination was extended to the exterior of three repair structures and the polar plug of three megalospheric tests of *N. obtusus*. All illustrated specimens have been reposited in the Geology Department of Calcutta University.

Repair structures were found to be associated with the shallow funnel-like cavities oriented perpendicular to the test surface. The cavities show nearly circular outline (maximum dimension ranging from 0.8 to 4.6 mm) on the test surface and irregularly *Y*-shaped outline in transverse section (Figure 2 *a–e*). Cavities penetrate the spiral lamellae and the alar prolongation of successive whorls. These cavities are morphologically distinct from the shallow cylindrical borings of *O. simplex* reported earlier[10,11]. The development of imperforate test material within and outside the cavities forms the blister-like repair structures. The imperforate material may copiously plug the cavities to form dome-like structure on the test surface, covering the cavity outline completely (Figure 2 *a*). Where cavity plugging is less intense, the imperforate material occurs close to the cavity margin, revealing the cavity outline (Figure 2 *b–e*).

Extension of the imperforate layer on the test surface beyond the cavity margin covers the outer openings of the spiral lamellae pores (Figure 2 *g*). This considerably alters the original porous structure of the foraminiferal wall, which is rather significant because pores are known to facilitate gas exchange, especially when the protoplasm remains retracted within the test[17–19]. Again, the relief of the cavity plug is quite different from the smoothly curved foraminiferal wall. The above observations are in line with the injury healing of the test wall exhibited by the extant Globigerinid foraminifera *Globigerinoides sacculifer*[20] and the fossil Fusulinid foraminifera *Triticites ventricosus*[21]. These globigerinid and fusilinid foraminifera reveal that the curvature and pore character of the repaired wall may not conform to the original test architecture. Prevalence of imperforate repaired wall has been reported in the perforate taxon *G. sacculifer*[20].

Although bioerosion of the '*obtusus* bed' foraminifera by suspected green alga and polychaete worms has been recorded[11], biological affinity of the present predator remains enigmatic at this stage of study. *Nummulites* maintains free connection among the chambers and also between the chambers and the alar prolongation by virtue of test interconnectivity. In this respect, it is more likely for the predator to access the foraminiferal protoplasm upon successful penetration of only the outermost wall. However, the observed repair structures reveal that the predatory drilling extends across several whorls. Following the notion of predator avoidance strategy of Arnold *et al.*[4], it may be envisaged that individuals of *N. obtusus* were perhaps able to withdraw their protoplasm from the outer whorls at the time of attack. The predator in turn had to drill deeper at the expense of more energy to gain access to the elusive protoplasm. This may have acted as a deterrent, prompting the predator to abort its feeding activity and to let off the live prey. Alternatively, it may be envisaged that by sheer chance, a few foraminifera were dissociated from the predator and escaped alive. Instances of two repair structures per test may reflect either recurrence of the predator attack over a period of time or simultaneous multiple attacks.

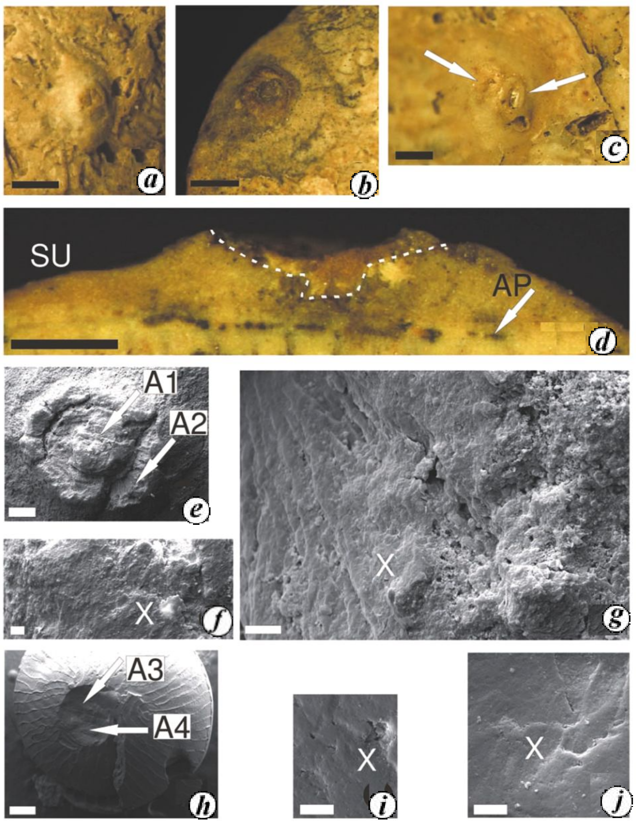

Figure 2. Repair structures in microspheric tests of *Nummulites obtusus* (Sowerby) and ultrastructure of polar plug in megalospheric tests of *N. obtusus*, Harudi Formation, '*obtusus* bed', Harudi area, western Kutch. ***a–g***, Microspheric tests; ***h–j***, Megalospheric test. ***a–d***, Light microscope images; ***e–j***, SEM images. ***a–c***, ***e***, Repair structures on test surface; ***c***, Occurrence of two repair structures (arrows); ***d***, Repair structure in transverse section, funnel-like cavity outline is marked by broken line; ***e***, Parts of repair structure marked by arrows and labelled as A1 and A2; ***f–g***, Enlarged portions of repair structure marked as A1 and A2 respectively in (e); ***g***, Imperforate layer (left-hand side) covering part of the porous test surface (right-hand side); ***h***, Polar view showing inner parts of polar plug marked by arrows and labelled as A3 and A4; ***i–j***, Enlarged portions of polar plug marked as A3 and A4 respectively in (h). Layered appearance of test material at locations marked X in (***f***), (***g***), (***i***) and (***j***); layering is also noticeable in other locations. SU, Test surface, AP, In-filled alar prolongation. Bar scales: 1 mm for (***a***, ***b***); 0.5 mm for (***c***, ***d***); 10 μm for (***f***, ***g***, ***i***, ***j***); 200 μm for ***e*** and 400 μm for ***h***.

The funnel-like bioerosional cavities present in *N. obtusus* and the blister-like plugging of the same are essentially different from several other unplugged bioerosional cavities recorded in the larger foraminifera from the '*obtusus* bed'[10,11]. Unplugged bioerosional cavities may reflect bioeroder activity following the natural death of the foraminifera or intense predatory activity resulting in the premature death of the foraminifera. Plugged cavities provide robust evidence of injury healing by the foraminifera following truncated attack of the predator. The ontogeny of *Nummulites* involves thickening of the outer whorl wall due to accretion of the test material during each episode of chamber addition[22]. Such accreted layers are discernible in the imperforate portion of the test such as the polar plug present in the megalospheric tests of *N. obtusus* (Figure 2 *h–j*). The layered appearance of the polar plug is similar to the layered nature of the imperforate test material used in the plugging of the predator-induced cavities (Figure 2 *e–g*). This ultrastructural similarity indicates that cavity plugging was accomplished in a manner similar to the accretion of the test wall during post-injury growth of the test.

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Functional morphology of *Melonis barleeanum* and *Hoeglundina elegans*: a proxy for water-mass characteristics

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Morphometric study of *Melonis barleeanum* and *Hoeglundina elegans* was carried out on 15 core top samples from the Indian Ocean. Length to breadth ratios and wall and septal thicknesses of the largest tests of both the species from each sample, along with $\delta^{13}C$ and $\delta^{18}O$ values of *Cibicides wuellerstorfi* were measured. Both the species show equal growth rates of the test in their normal habitat. However, the high organic carbon preference species *M. barleeanum* shows more elongation of the test during food scarcity. This effect is not evident in *H. elegans*, which varies in its wall and septal thicknesses with bottom-water oxygen levels of the deep water mass up to 2000 m, probably to maintain the required rate of osmosis for the intake of dissolved O_2. Below this depth both parameters show parallel relationship with deviation indicating that oxygenation may play some role in the variation of wall and septal thicknesses. Thinning or thickening of the wall and septa in *M. barleeanum* and *H. elegans* has no relation with the water depth, indicating no relation with either the overlying pressure effect or nutrients as each deep water mass has a different nutrient budget. Depletion in $\delta^{13}C$ and enrichment in $\delta^{18}O$ below 2000 m water depth suggests that up to 2000 m depth, the Indian Ocean is bathed by the well-oxygenated, low-nutrient North Atlantic Deep Water (NADW), whereas below 3000 m cold, nutrient-rich Antarctic Bottom Water (AABW) is dominant. Between 2000 and 3000 m water depths, the water mass in the Indian Ocean is a mixture of NADW and AABW.

Keywords: Benthic foraminifera, *Hoeglundina elegans*, *Melonis barleeanum*, osmosis, septal thickness.

THE distribution of benthic foraminifera on the ocean floor is mainly controlled by the bottom-water oxygenation, and input and quality of organic carbon on the sea floor[1–4]. The epifaunal and shallow infaunal benthic

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