

Octopodiform drill holes on the larger foraminifera *Nummulites obtusus* (Sowerby, 1840) from the Harudi Formation (middle Eocene) of Kutch, Gujarat, India

Evidence of fossil predators enables us to infer the importance and evolution of predation, predator ethology and prey defence mechanisms in deep time¹. Foraminifera, an ubiquitous component of the marine seafloor community with a high preservation potential, are often subjected to predation². However, bioerosion traces do not necessarily reflect predation traces because live foraminiferans may bear parasite feeding traces, and dead foraminiferal tests may be subjected to boring by protoplasm-scavenging taxa or endoliths³. Here, we report octopodiform (terminology after Villegas-Martin *et al.*⁴) drill holes on the middle Eocene larger foraminiferan *Nummulites obtusus* (Sowerby⁵) from Kutch, western India. We have collected 35 *N. obtusus* Form B specimens bearing the octopodiform drill holes (Figure 1). These drilled foraminiferans were collected from the ‘obtusus bed’ of the Harudi Formation (middle Eocene) exposed along the flanks of the Rato river, north of the Harudi ($23^{\circ}30'30''$, $68^{\circ}41'10''$) village in Kutch, Gujarat^{6,7}. Collected specimens are housed in the Micropalaeontology Laboratory of Calcutta University under the collective number CU/RR/35.

The octopodiform drill holes are of moderate depth, penetrating the spiral laminae and alar prolongation of the foraminifera (Figure 1). The drilling axis is perpendicular to the foraminiferal test surface. The drill holes have an elliptical outer diameter and a comparatively small elliptical inner diameter. The cavity wall is smooth and parabolic in cross-section (Figure 1f). The drill holes occur between the pole and the periphery of the foraminiferal tests but never at the test periphery/edge. The presence of multiple drill holes on one or both sides of the foraminiferal test was observed in three *N. obtusus* specimens (Figure 1d). The minor axis and major axis of the outer diameter of the trace fossil range from 0.9 to 1.56 mm and 1.89 to 3.30 mm respectively. Figure 2 is a bivariate plot of *N. obtusus* test size and the octopodiform drill hole size. On the basis of a millimetre-size countersunk excavation with an elliptical outer diameter, the drill holes have been identified as *Oichnus ovalis* Bromley, 1993 (refs 8–13). Zonneveld and Gingras¹⁴

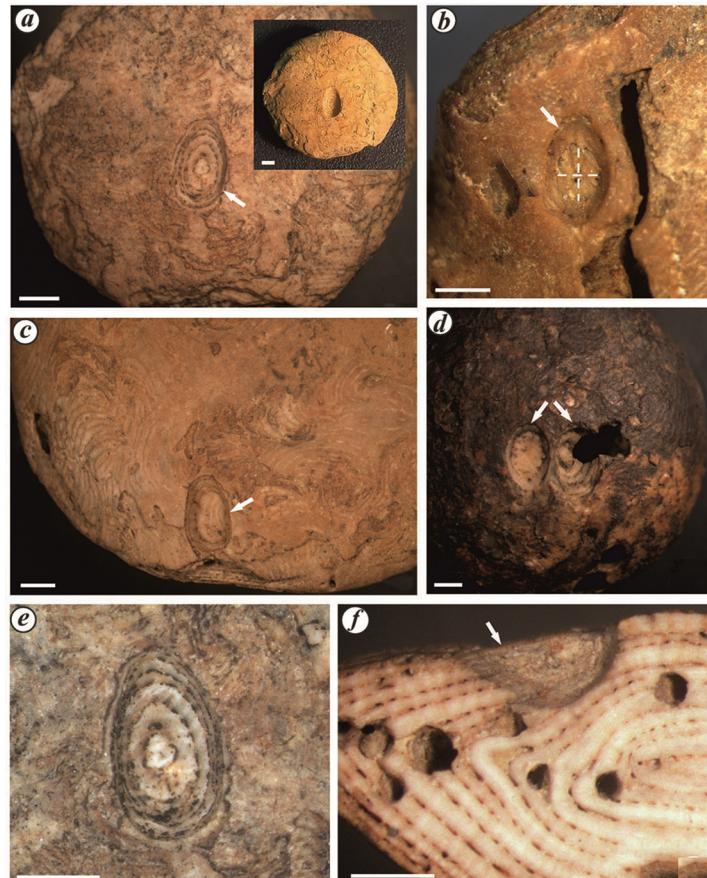


Figure 1 a–f. Octopodiform drill holes identified as *Oichnus ovalis* Bromley, 1993 (marked by arrows) on the larger foraminifera *Nummulites obtusus* (Sowerby, 1840) Form B from the Rato river section, middle Eocene, Kutch, Gujarat, India. (a) Presence of *O. ovalis* across successive whorls of *N. obtusus*. (Inset) Polar view of the foraminiferal specimen. (a, d) *O. ovalis* near the test pole. (b, c) *O. ovalis* near the test periphery. (b) Inner end of *O. ovalis* marked by broken lines. (d) Two examples of *O. ovalis* on the same test. (e) Enlarged view of the drill hole shown in (a). (f) Longitudinal section of *O. ovalis*. (e, f) *O. ovalis* penetrating the spiral laminae (light colour) and alar prolongation (dark colour) of *N. obtusus*. All scale bars are 1.0 mm. *O. ovalis* specimen numbers. (a) CU/RR/35/7. (b) CU/RR/35/17. (c) CU/RR/35/9. (d) CU/RR/35/5 (left drill hole) and CU/RR/35/6 (right drill hole) and (f) CU/RR/35/VS2.

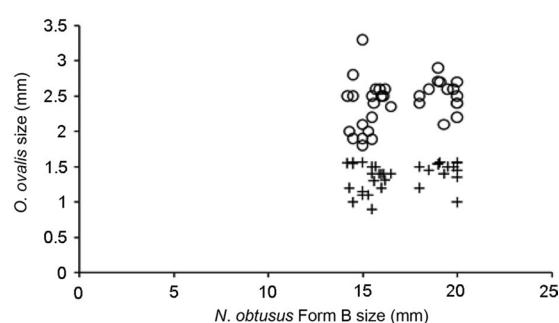


Figure 2. Bivariate plot of *N. obtusus* Form B test size versus outer diameter of *O. ovalis* (see Appendix 1). Note narrow size range of the drilled *N. obtusus* tests. Minor (+) and major (o) axes of the outer drill hole diameter of *O. ovalis* are shown separately. There is no strong relationship between test size and drill hole size.

Appendix 1. *Oichnus ovalis* data

<i>O. ovalis</i> sample no.	<i>O. ovalis</i> museum no.	<i>Nummulites</i> <i>obtusus</i> Form B test diameter (mm)	<i>O. ovalis</i> outer diameter size	
			Major axis (mm)	Minor axis (mm)
1	CU/RR/35/1	15	3.3	1.56
2	CU/RR/35/2	20	2.4	1.45
3	CU/RR/35/3	20	2.2	1
4	CU/RR/35/4	15.6	2.4	1.3
5	CU/RR/35/5	14.5	2.5	1.54
6	CU/RR/35/6	14.5	2.8	1.56
7	CU/RR/35/7	15.5	2.2	1.4
8	CU/RR/35/8	20	2.5	1.55
9	CU/RR/35/9	16.5	2.35	1.4
10	CU/RR/35/10	20	2.7	1.56
11	CU/RR/35/11	19.5	2.6	1.5
12	CU/RR/35/12	19	2.71	1.53
13	CU/RR/35/13	15.5	2.5	1.5
14	CU/RR/35/14	15.5	1.89	0.9
15	CU/RR/35/15	16	2.5	1.4
16	CU/RR/35/16	19	2.9	1.54
17	CU/RR/35/17	15	2.1	1.15
18	CU/RR/35/18	14.5	1.9	1
19	CU/RR/35/19	15	1.89	1.1
20	CU/RR/35/20	18	2.4	1.2
21	CU/RR/35/21	16	2.5	1.2
22	CU/RR/35/22	15.3	2	1.1
23	CU/RR/35/23	19.1	2.7	1.56
24	CU/RR/35/24	15.7	2.6	1.5
25	CU/RR/35/25	18.5	2.6	1.45
26	CU/RR/35/26	15	1.9	1.1
27	CU/RR/35/27	16.2	2.6	1.31
28	CU/RR/35/28	18	2.5	1.5
29	CU/RR/35/29	15.9	2.6	1.4
30	CU/RR/35/30	19.8	2.6	1.5
31	CU/RR/35/31	14.2	2.5	1.55
32	CU/RR/35/32	19.3	2.1	1.4
33	CU/RR/35/33	20	2.4	1.35
34	CU/RR/35/34	16.1	2.5	1.4
35	CU/RR/35/VS2	14.3	2.0	1.2

have argued that *Oichnus* Bromley is a junior synonym of *Sedilichnus* Müller, 1977, and revised the binomen *Oichnus ovalis* to *Sedilichnus ovalis*. Subsequently, Pokorný and Štofík¹⁵ have followed the nomenclature of Zonneveld and Gingras¹⁴. However, *Sedilichnus* is unavailable on account of it being an atelonym (conditionally proposed)¹⁶. In this study, the identification of the drill holes as *O. ovalis* follows the works of Bromley⁸ and Wissak et al.¹⁶. The presently recorded *O. ovalis* superficially resembles *Oichnus asperus* Nielsen and Nielsen¹⁷ and *Oichnus paraboloides* Bromley¹⁸. The ichnospecies *Oichnus asperus* has an elliptical outer outline and a straight side, while *O. ovalis* has an elliptical outer outline and a curved side. Both *O. paraboloides* and *O. ovalis* have curved sides, but the former has a circular outer outline as opposed to the oval outer outline of the latter.

The *obtusus* bed in Harudi Formation is studded with *Nummulites* species comprising *N. obtusus*, *N. vredenburgi* Prever, 1908 (ref. 19) and *N. spectabilis* Samanta et al.²⁰. The occurrence of *O. ovalis* has been observed on 35 moderately sized (specimen size range 7.4–26.2 mm), smooth, inflated, ellipsoidal Form B specimens of *N. obtusus*. Examination of 50 specimens of small-sized (specimen size range 2.6–5.0 mm) and inflated *N. obtusus* Form A, 60 dimorphic forms of compressed ellipsoidal and granulated *N. vredenburgi* (Form B specimen size range 9.2–20.0 mm; Form A specimen size range 2.8–5.5 mm) and five-minute specimens of *N. spectabilis* Form B (specimen size range 1.75–2.20 mm) revealed no samples of *O. ovalis*. In Kutch, previously documented sclerobionts that thrived upon live and dead Paleogene larger foraminifera include acrothoracican cirriped, Annelida, bivalves, gastropods, green algae,

scleractinian corals, bryozoans, parrotfishes (Scaridae) and other undiagnosed foraminiferans^{21–28}. Trace fossils we recorded from *N. obtusus* include *Oichnus simplex* Bromley¹⁸; *O. ovalis* Bromley, 1993 (the present study); *Gastrochaenolites* Leymerie²⁹; cf. *Trypanites* Mägdefrau³⁰; cf. *Ichnoteticulina* Radtke and Golubic³¹ and *Sulcichnus meandriformis* Martinell and Domènec³². We additionally recorded undiagnosed, funnel-shaped, open and plugged (injury-healing) predation drill holes in *N. obtusus*²⁴. Attached taxa that thrived upon *N. obtusus* included the bivalve *Flamingostrea* Vredenburg³³, the scleractinian solitary coral *Trochocyathus* Edwards and Haime³⁴; undiagnosed annelids, the bryozoan *Therenia* David and Pouyet³⁵, *Stomatopora* Bronn³⁶ (in Guha and Gopikrishna³⁷) and *Proboscina* Audouin³⁸ (in Guha and Gopikrishna³⁷). This wide spectrum of the benthic biota that subsisted upon *N. obtusus* highlights the crucial palaeoecological role of the protist.

The ichnospecies *O. ovalis* has been widely recognized as an octopodoid (Cephalopoda) feeding trace^{8,17,39,40}. Fossil octopodoids have a shallow preservation potential (taphonomic loser⁸) due to the absence of hard parts. Their frugal preservation includes body impressions and detached chitino-protein jaw elements⁴¹. However, feeding traces of octopods in the form of small holes in prey exoskeletons to inject venom are more prevalent in the fossil records^{8,42}. Based on molecular phylogeny and fossil data, it has been estimated that the early octopods evolved in the Late Carboniferous^{43,44} and crown-group octopods appeared in the Late Cretaceous^{44–47}. Some of the oldest octopod holes include the doubtful micron-sized *O. ovalis* drillings in the middle Eocene larger foraminifera of Jamaica (original authors did not interpret the holes as octopodoid feeding traces)¹², the millimetre-sized *O. simplex* borings (resembling the drilling of extant Chilean *Octopus mimus*) in the Early Eocene (Ypresian) bivalves of southern England⁴⁷ and Late Cretaceous (Campanian) *O. ovalis* borings in lucinid bivalves of South Dakota, USA⁴². Although the present documentation of *O. ovalis* from the middle Eocene of Kutch is within the known stratigraphic range of crown-group octopods, the identity of the trace maker is kept open due to the absence of reliable records of octopodoid predation on extant larger foraminifera. Moreover, octopodiform drillings in several organisms have been ascribed to Gastropoda^{48,49} and soft-bodied

organisms of unknown affinity⁴. In this context, it may be mentioned that *N. obtusus* was not associated with gastropod body fossils in the sampled area of Kutch. The micron-sized, narrow, lenticular, predatory drilling of a soft-bodied flatworm is morphologically different from *O. ovalis* reported here⁵⁰. Further studies are required to understand the biological affinity of the *O. ovalis* trace maker in Kutch.

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