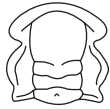


High frequency of drill holes in brachiopods from the Pliocene of Algeria and its ecological implications

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The fossil record holds a wealth of ecological data, including data on biotic interactions. For example, holes in the skeletons of invertebrates produced by drilling activities of their enemies are widely used for exploring the intensity of such interactions through time because they are common and easily distinguished from non-biotic holes or holes produced by other types of interactions. Such drill holes have been described in numerous studies of Palaeozoic brachiopods but rarely in those focusing on brachiopods of the post-Palaeozoic, a striking pattern given that in the late Mesozoic and Cenozoic drilling gastropods diversified and frequencies of drilled molluscs increased dramatically. During the past several years, however, drilled brachiopods were reported in several studies of the Mesozoic and Cenozoic, suggesting that this phenomenon may be more common than has been previously assumed. Here we report on drilled brachiopods from a Pliocene locality in Algeria where 90 of 261 (34.5%) specimens of *Megerlia truncata* show evidence of predatory drilling. These data confirm that Cenozoic drilling frequencies of brachiopods may be locally high and, when taken together with other published data, that drilling frequencies are highly heterogeneous in space and time.

□ *Algeria, brachiopods, drill holes, Pliocene, predation.*

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The role of biotic interactions in evolution continues to be an important, though controversial, theme of evolutionary biology (Knoll & Bambach 2000; Allmon & Bottjer 2001). Vermeij, who has written extensively on the subject (Vermeij 1977, 1982, 1987, 1994, 1999), has argued that such interactions ('interactions among metabolizing entities', Vermeij 1999, p. 243) have predictable consequences producing trends that give a directionality to the history of life. In this context, the role of predators has been claimed to have special importance (Vermeij 1987). Because palaeontological data are critical for reconstructing evolutionary histories and because fossils often provide direct evidence of predator-prey interactions (see Kowalewski & Kelley 2002; Kelley *et al.* 2003), palaeontology is central to testing claims about the evolutionary role of biotic interaction in general, and predation in particular.

For brachiopods, a group with a rich fossil record and a long history, the evolutionary role of predation has often been considered. For example, the first-order trend in the evolutionary history of brachiopods characterized by a dramatic drop in diversity between the Palaeozoic and post-Palaeozoic, was explained by Stanley (1974, p. 966) as a consequence of brachiopods'

failure to re-radiate following the Permo-Triassic biotic crisis because of their 'inability to cope with advanced predators'. Donovan & Gale (1990) considered predation pressure by asteroids to be causally connected to the large-scale patterns in brachiopod evolutionary history (but see Blake & Guensburg 1990). Links between morphological trends and predation have also been explored (Signor & Brett 1984; Alexander 1990; Dietl & Kelley 2001; Leighton 2001, 2003a). To test such evolutionary hypotheses, direct evidence of predation has often been sought. The most common evidence consists of trace fossils, such as repair marks, representing failed attacks by predators, or drill holes, representing lethal traces of predation. Because drill holes are one of the most easily interpretable, quantifiable, and least subject to bias traces of lethal predation, recently much attention has been devoted to the study of drill holes in brachiopods (see Leighton 2003b for review).

Kowalewski *et al.* (1998) used the published record of drill holes to extract data on drilling frequencies through time. One of the striking features of the pattern that emerged was that virtually all of the reported data on drilled brachiopods came from the Palaeozoic; no Tertiary drilled brachiopods were reported. If this

pattern were accurate, it would be interesting in the context of the high frequencies of drilled molluscs and the high diversities of their drillers, the muricid and naticid gastropods, in the Tertiary. However, in the years since Kowalewski *et al.* conducted their literature survey, it has become clear that the published data for drilled brachiopods available in 1998 presented an incomplete, and in some instances a misleading temporal pattern of drilling frequencies for brachiopods. Data gathered since then have not only allowed a refinement of the Palaeozoic record (Kowalewski *et al.* 2005), but have shown that during the Cenozoic (Baumiller & Bitner 2004; Harper 2005) brachiopods were subject to drilling predation, that was occasionally intense. In this study, we provide yet another example of intense drilling predation on Tertiary brachiopods from Algeria.

Materials and methods

The specimens of the terebratulide brachiopod, *Megerlia truncata*, examined in this study come from a collection made by M. Dalloni at the beginning of the 20th century. The material was collected at the locality of Sidi Youcef in the central part of the Chelif Basin, northern Algeria, from the sandy marls of the uppermost Lower Pliocene (Zanclean) (Fig. 1).

The marine Pliocene deposits in Algeria are found as outcrops along the Mediterranean coast and in two major basins, the Chelif Basin in the western part of the country (Dalloni 1915; Perrodon 1957), and one near Algiers (Dalloni 1932; Perrodon 1957; Yassini 1973, 1979; Saoudi 1989; Hamdane & Moissette 1997). The

Lower Pliocene sedimentary record in Algeria overlies uppermost Miocene gypsum and is represented by deep-water marls, the so-called blue marls, which are rich in microfossils. In their upper part, the marls gradually turn sandy and macrofauna appears. The Middle and Upper Pliocene is characterized by shallow-water deposits, such as sands, conglomerates, calcareous sandstones and limestones with abundant macrofauna of molluscs, bryozoans, brachiopods and echinoids.

All brachiopods examined in this study are excellently preserved (Fig. 2), and all 261 specimens were articulated. Specimens were examined by eye for evidence of drill holes. The diameter of drill holes and specimen size were measured using a binocular microscope accurate to 0.1 mm. Drill holes were categorized qualitatively according to shape as conical, with tapered sides, or cylindrical, with straight sides.

To assess site selectivity of the borer, the spatial pattern of drill holes was tested against the expected pattern using a Monte Carlo simulation (Baumiller & Rome 1998). The positions of all cylindrical drill holes on ventral valves ($n = 43$) were projected onto an image of the ventral valve of standardized size (Fig. 3B) and their x-y coordinates were obtained using Scion Image © software (release 4.0.3.2). The nearest neighbour (NN) distances were computed for each drill hole, and the mean NN distance (μ_{observed}) was calculated. Each randomization consisted of 43 points randomly chosen to lie within the area of the standardized ventral valve shown in Fig. 3B. The mean of the NN distances were calculated for the 43 random points (μ_{random}). This procedure was iterated 1000 times. The expectations of a clustered distribution of drill holes correspond to the

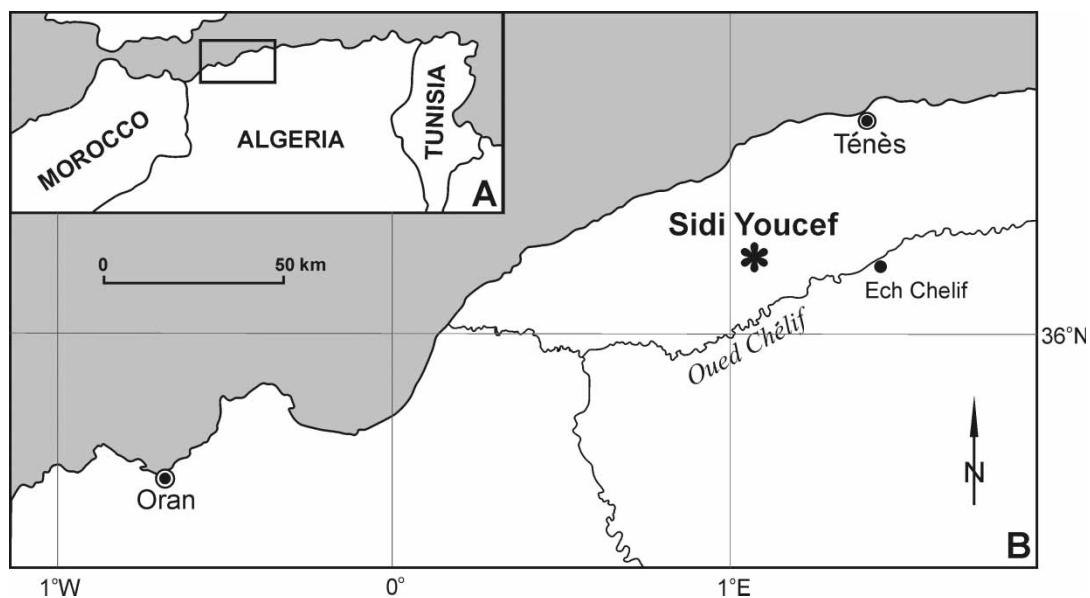


Fig. 1. Geographical location of the study area. □ A. Map of North Africa. The area in the box is shown in B; □ B. Locality from which brachiopods were collected (after Dalloni 1915 and Perrodon 1957, modified and simplified).

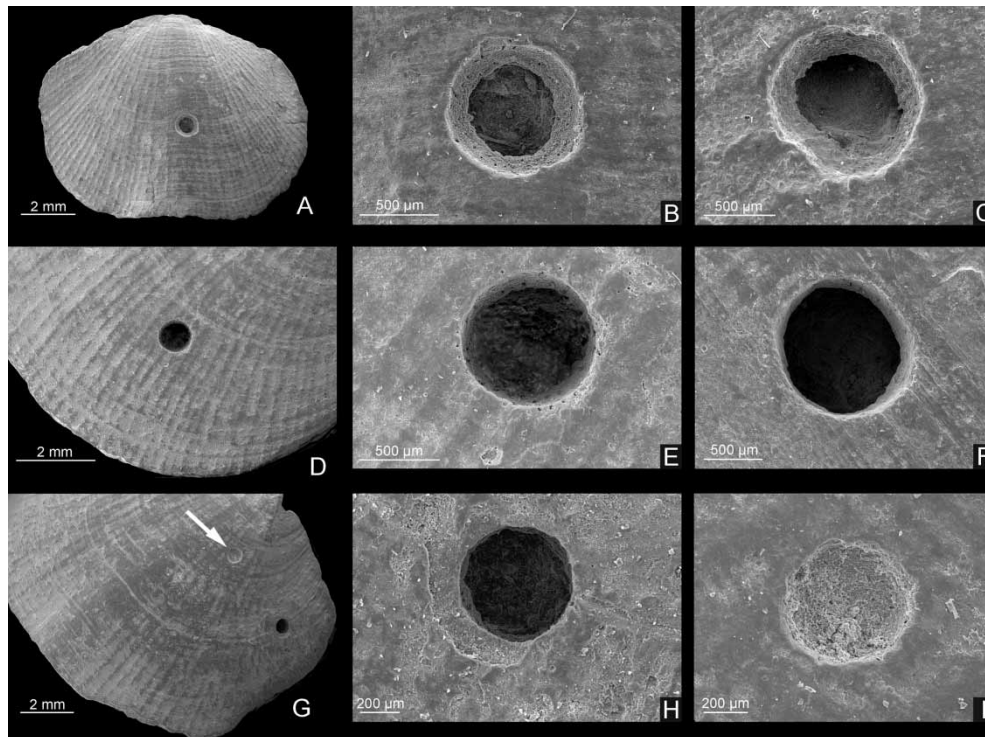


Fig. 2. Drilled specimens of *Megerlia truncata* (Linnaeus) from the Lower Pliocene of Sidi Youcef, northern Algeria. □ A–B. ZPAL Bp.55/153, ventral view of complete specimen and a close-up image of drill hole. □ C. ZPAL Bp.55/162, ventral valve. □ D–E. ZPAL Bp.55/150, ventral view and a close-up of the drill hole. □ F. ZPAL Bp.55/124, dorsal valve. □ G–I. ZPAL Bp.55/157, ventral view showing a complete and a failed drill hole (arrow), and close-up of the drill hole and the failed drill hole.

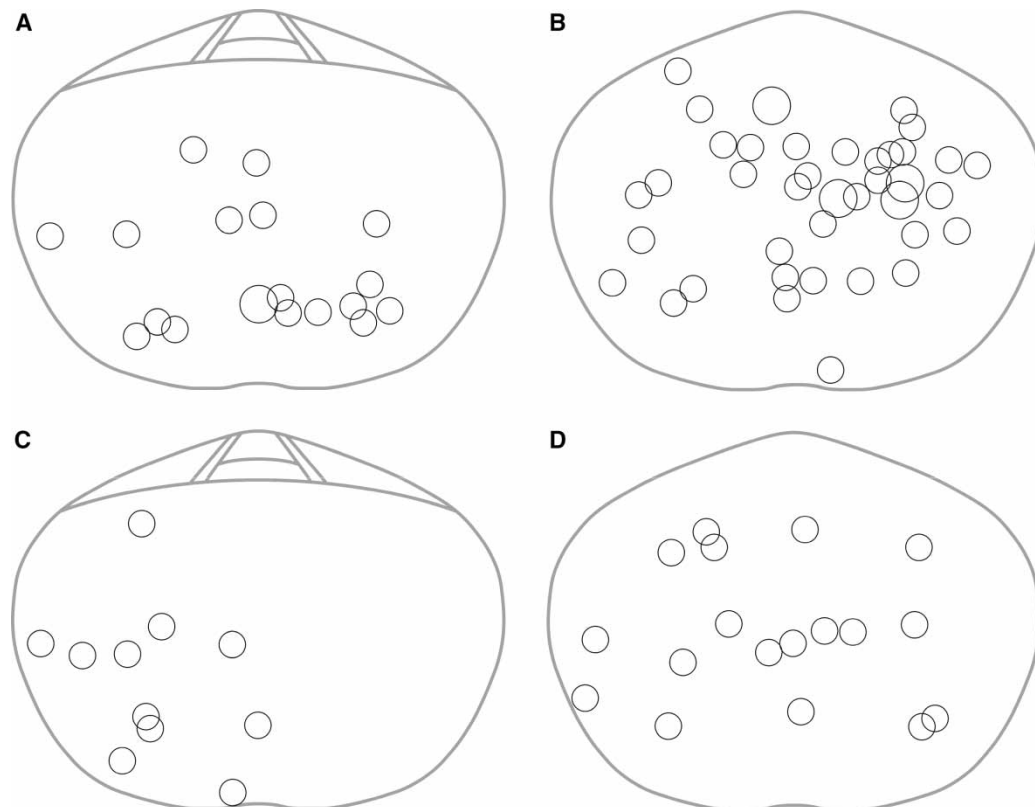


Fig. 3. The distribution of drill holes on *Megerlia truncata* from Sidi Youcef. The small circles correspond to 1 drillhole, the larger circles to 2 drill holes. □ A. Dorsal cylindrical ($n=19$), □ B. Ventral cylindrical ($n=43$), □ C. Dorsal conical ($n=11$), □ D. Ventral conical ($n=18$).

observed mean NN distance smaller than the mean NN distance of a random distribution while an expectation of an overdispersed distribution corresponds to the observed mean NN distance greater than the mean NN distance of a random distribution. A comparison of the observed mean NN distance to each of the 1000 randomized mean NN distances allows one to use a criterion of $\alpha = 0.05$ to determine whether the observed distribution is significantly clustered ($\mu_{\text{observed}} < \mu_{\text{randomized}}$ in 950 or more simulations), significantly overdispersed ($\mu_{\text{observed}} > \mu_{\text{randomized}}$ in 950 or more simulations), or indistinguishable from random. This approach was repeated for cylindrical holes on the dorsal valves ($n = 19$; Fig. 3A), conical holes on the dorsal valves ($n = 11$; Fig. 3C), conical holes on the ventral valves ($n = 18$; Fig. 3D), and combined conical and cylindrical holes on the ventral ($n = 61$) and dorsal ($n = 30$) valves.

The material is housed in the collections of the Institute of Paleobiology (Polish Academy of Sciences, Warsaw) under the number ZPAL Bp.55.

Results

Drill-hole frequencies

We examined 261 specimens of *Megerlia truncata* and found that 90 were drilled (Fig. 2; Table 1). The total number of drilled specimens divided by the total number of specimens expressed as a percentage is thus 34.5%, and represents the Assemblage Frequency metric, AF, of Kowalewski (2002).

Size selectivity

To determine whether the sizes of drilled and undrilled individuals differ, the mean lengths of the two using a two-tail t-test were compared. The length of drilled specimens (12.0 mm, SD = 1.9) was marginally smaller than that of undrilled specimens (12.5 mm, SD = 2.0) (Fig. 4).

Drill-hole shape

While all of the drill holes in the sample are circular in outline, and can be categorized as *Oichnus* Bromley, in cross section two end-member morphologies can be distinguished by eye: cylindrical and conical. It is

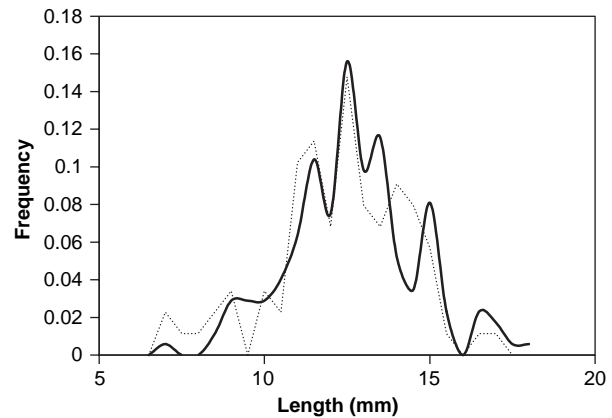


Fig. 4. The size frequency distribution of drilled (dotted; $n = 90$) and undrilled (solid; $n = 171$) individuals.

important to note, however, that the conical holes lack beveling. Without quantifying their shapes, drilled individuals were categorized as having either a cylindrical or a conical drill hole and the outer diameters of the holes were measured; for conical holes, the inner diameter was also measured. The outer diameter of the conical holes ($n = 29$; mean = 0.96 mm; SD = 0.13 mm) is significantly (two tailed *t*-test; $p < 0.05$) larger than the cylindrical holes ($n = 62$; mean = 0.89; SD = 0.13 mm). The ratio of outer to inner diameter for the conical holes averages 1.44 (SD = 0.13).

Valve selectivity

Drill holes occur on the ventral (61) and the dorsal valves (30); in one case, the drill hole occurs on both valves (Table 1). This apparent preference for the slightly larger ventral valve (area of ventral valve: area of dorsal valve = 1.06) is statistically significant: the null hypothesis that there is no valve selectivity can be rejected at $p < 0.01$ using the binomial test when probability of drill hole on dorsal and ventral valve is equal ($p = q = 0.5$) or when the probability is set proportional to relative area of each valve ($p = 0.51$, $q = 0.49$). The same significant preference for the ventral valve characterizes the cylindrical drill holes, but the difference between the two valves is not significant for the conical drill holes (Table 2).

Site selectivity

The comparisons of observed NN means to the expected NN means derived from Monte Carlo simulations

Table 1. Data on drill hole distribution in *Megerlia truncata* from Sidi Youcef, Northern Algeria.

Species	Total specimens	Number undrilled	Number drilled	Drilled on ventral	Drilled on dorsal	Drilled on both valves
<i>Megerlia truncata</i>	261	171 (65.5%)	90 (34.5%)	60	29	1

Table 2. Data on drill hole shape in *Megerlia truncata* from Sidi Youcef, Northern Algeria.

Value	Shape of drill hole	
	Cylindrical	Conical
Ventral	43	18
Dorsal	19	11

revealed a non-random, clustered pattern of drill hole distributions on the dorsal ($p < 0.001$; Fig. 3A) and ventral ($p < 0.001$; Fig. 3B) valves for cylindrical holes and when cylindrical and conical drill holes were considered together, but a random distribution could not be rejected for conical holes on dorsal (Fig. 3C) or ventral valves (Fig. 3D; Table 3).

Discussion

The first question to ask about drill holes in the shells of invertebrates is whether they document biotic interactions or the interaction between a sediment borer and the shelly remains of dead organisms. There are numerous criteria for distinguishing between these two types of activities and the following drill hole features indicate that at Sidi Youcef they represent interactions between live organisms: (1) a circular outline, (2) orientation of the axis perpendicular to the shell surface, (3) penetration of only one valve in articulated specimens (with one exception), (4) the absence of multiple holes on individual valves, (5) a larger diameter always on the outer shell surface in conical holes, and (6) a degree of site selectivity (see Kelley & Hansen 2003 for a recent review).

Having established that the holes were drilled in live brachiopods, what type of a biotic interaction do they represent? Drill holes of the type found in brachiopods at Sidi Youcef have generally been ascribed to predatory gastropods, specifically muricids and naticids. Experimental work by Harper & Peck (2003) demonstrated that the muricid gastropod, *Trophon longstaffi*, could produce circular drill holes in either valve of the brachiopod, *Liothyrella uva*. However, capulids, a group

Table 3. Results of tests for site selectivity of drill holes on valves of *Megerlia truncata* using Monte Carlo simulations. Values correspond to the number of times the observed mean nearest neighbour (NN) distance was smaller than the mean NN distance of 1000 simulations. p -values in parentheses; NS: not significant.

Valve	Shape of drill hole		
	Cylindrical	Conical	Conical & Cylindrical
Ventral	1000 (0.001)	728 (NS)	1000 (0.001)
Dorsal	1000 (0.001)	849 (NS)	1000 (0.001)

of parasitic marine gastropods, are known to drill a circular hole in the shell of their host (Orr 1962; Sohl 1969; Matsukuma 1978). While their hosts are typically other molluscs, it has been recently shown that in the waters of Puget Sound (Iyengar 2004) the capulid *Trichotropis* kleptoparasitizes a brachiopod, *Terebratalia*. In that association, drilling has not been reported, but Taddei Ruggiero (1999) and Taddei Ruggiero & Annunziata (2002) have attributed holes in a few Pliocene and Pleistocene brachiopods to capulids. These supposedly parasitic drill holes were subcircular in outline and located on the commissure, features that do not characterize the drill holes found in *Megerlia truncata* from Sidi Youcef.

The fact that holes of two distinctly different shapes were found at Sidi Youcef, each shape associated with a different diameter (Fig. 5), could imply that they were produced by two drilling taxa. Given that muricid and naticid gastropods commonly drill their prey, that they have been common predatory drillers since the Cretaceous, and that both groups are known from the Lower Pliocene of Sidi Youcef (Dalloni, 1915 lists two species of *Murex* and three of *Natica*), it is possible that the holes were produced by these gastropods: the conical holes by naticids and cylindrical holes by muricids. However, the conical holes are not bevelled, making it unlikely that they were produced by naticids. Also, it has been shown by Harper & Peck (2003) that (1) a single species, the muricid *Trophon longstaffi*, can produce holes of different shapes and (2) the size of drill holes produced by even a single individual can vary by nearly a factor of 2, which could certainly accommodate the small, though statistically significant, difference in size between conical and cylindrical holes, especially given the amount of overlap in their sizes

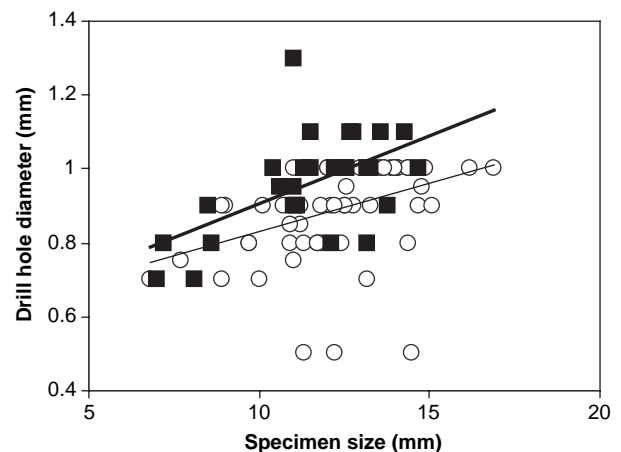


Fig. 5. The sizes of drill holes as a function of specimen size. Conical drill holes (solid squares; $n = 29$) and cylindrical holes (open circles; $n = 62$).

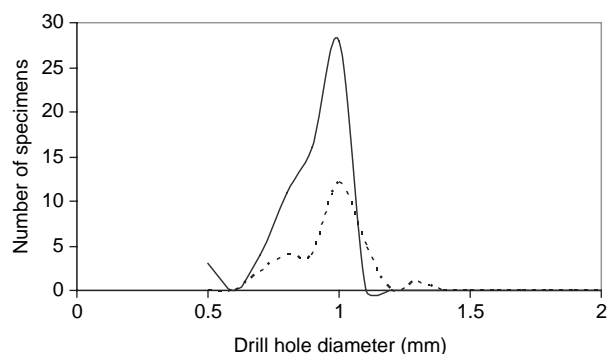


Fig. 6. Comparison of size distributions of different-shaped holes. Conical drill holes (dashed line; $n=29$) and cylindrical holes (solid line; $n=62$).

(Fig. 6). Therefore, one cannot dismiss the possibility that only a single predatory taxon was responsible for the drill holes at Sidi Youcef.

If the drill holes described herein represent the activities of a predatory organism, what does the 34.5% frequency of drilled individuals tell us about the intensity of biotic interactions in the live-live assemblage? Can one use that value as indicating that 34.5% of living brachiopods were affected by drilling enemies at Sidi Youcef, or are there reasons to suspect that this value is biased? For example, collector/collection bias could influence this value if drilled specimens were preferentially collected relative to undrilled ones, drilled (or undrilled) specimens were preferentially removed from the collection by curators or researchers, or drilled (or undrilled) specimens suffered preferential

destruction after they were collected. However, there is no reason to suspect that any of the above biases have influenced this collection.

Aside from collector/collection bias, the observed frequencies may still not be an accurate representation of the actual intensity of drilling predation if, for example, shell-crushing predators crushed, fragmented, or removed entirely undrilled specimens. If this were the case, the reported frequencies would be an overestimate of the actual intensity of interactions between drillers and brachiopods. In addition, differences in taphonomic characteristics of drilled and undrilled shells could introduce a bias, for example, if drilled specimens were taphonomically less resistant (Roy *et al.* 1994; Kaplan & Baumiller 2000; Zuschin & Stanton 2001). Likewise, hydrodynamic differences between drilled and undrilled specimens could generate a bias (Lever *et al.* 1961, Kaplan & Baumiller 2000). It is important to note, however, that studies of taphonomic and hydrodynamic properties of drilled and undrilled specimens have identified potential for bias for single valves rather than for articulated specimens and at Sidi Youcef brachiopods are represented by the latter.

Given the above caveats, if we consider the drilling frequencies as reasonably accurate, what information do such data provide and how do they compare to such data reported for brachiopods from other places and other times? It must be made clear that drilling frequency is not a measure of the frequency of attacks on brachiopods, as failed attempts are unaccounted for (except for one represented by a single incomplete hole

Table 4. Recently published studies documenting Cenozoic fossil brachiopods with drill holes.

Age	Locality or Formation	Country	Taxon	Number of specimens	Number of specimens drilled	Percent Drilled	Reference
Pliocene	Foggia	Italy	<i>Terebratula calabra</i>	600	15*	2.5	Taddei Ruggiero 1999
					2**	0.3	
					8***	1.3	
					25 (total)	4.2	
Pliocene	Coralline crag	UK	<i>Apletosia maxima</i>	248	17 (19)	6.9	Harper 2005
Miocene	Weglin	Poland	<i>Argyrotheca cuneata</i>	327	77	23.5	Baumiller & Bitner 2004
			<i>Megerlia truncata</i>	119	34	28.6	
			<i>Megathiris detruncata</i>	842	403	47.9	
	Weglinek		<i>A. cuneata</i>	257	8	3.1	
			<i>Argyrotheca cordata</i>	454	19	4.2	
			<i>M. detruncata</i>	113	6	5.3	
	Szczaworyz		<i>A. cuneata</i>	514	4	0.8	
			<i>A. cordata</i>	1016	9	0.9	
			<i>M. detruncata</i>	1117	45	4.0	
Eocene	Central Pyrenees	Spain	<i>Terebratulina tenuistriata</i>				Bitner 2000
			<i>Argyrotheca vidali</i>	1606	5	0.3	
			" <i>Terebratula</i> " n. sp.				

Taddei Ruggiero (1999) distinguished holes made by predatory gastropods (*), capulid gastropods (**), and octopods (***). Harper (2005) reports reported number of drilled specimens and, listed in parentheses, number of drillholes.

(Fig. 2G, I). It is also not a measure of frequency of brachiopod mortality because: (1) other predators may have hunted brachiopods, and (2) even drilling predators may subdue their prey without drilling. It is thus best to consider the reported metric as a measure of drilling predation intensity, or, more precisely as a measure of frequency of mortality from drilling predation (see Leighton 2002). How does the 34.5% value at Sidi Youcef compare to other reported brachiopod drilling frequencies? As mentioned in the Introduction, the phenomenon of drilled Tertiary brachiopods went largely unrecognized by palaeontologists until recently. The few studies that have reported drilling in Tertiary brachiopods since 1999 indicate that in Tertiary deposits drilled brachiopods are relatively rare, in most instances accounting for fewer than 5% of the sample (Table 4), suggesting that the high frequencies at Sidi Youcef may be unique. However, an even higher frequency was reported from Roztocze, a Miocene locality in south-eastern Poland, where over 500 specimens representing 40% of the total sample were drilled (Baumiller & Bitner 2004). Also, recently published reports indicate that while the 'common observation that there is little predation pressure on living brachiopod populations' (Peck 1993, p. 18) may hold true, there are at least instances where drilling predation may be high, such as in the northwestern Mediterranean, where Delance & Emig (2004) found at one collecting site in Corsica 25.5% of *Gryphus vitreus* to have naticid drill holes, or in the waters of the Pacific where 29.1% of specimens of *Basiliola becheri* had been drilled (Baumiller *et al.* 2003). Thus, far from being unique, the Sidi Youcef data represent one of several examples of high drilling frequencies and illustrate the existence of a great deal of heterogeneity in rates of drilling of Cenozoic brachiopods.

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