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Palaeogeography, Palaeoclimatology, Palaeoecology 208 (2004) 23–30
PALAEO
www.elsevier.com/locate/palaeo

Drilling predation on *Gryphus vitreus* (Brachiopoda) off the French Mediterranean coasts

Jean Henri Delance[a], Christian C. Emig[b,*]

[a] *UMR CNRS 5561, Centre des Sciences de la Terre, Biogéosciences, Université de Bourgogne, 6, Boulevard Gabriel, 21000 Dijon, France*
[b] *CNRS UMR 6540, Centre d'Océanologie, Rue de la Batterie-des-Lions, 13007 Marseille, France*

Received 25 April 2003; received in revised form 27 January 2004; accepted 20 February 2004

Abstract

A total of 145 valves of *Gryphus vitreus* with naticid drillholes have been recorded from samples during 21 cruises in the Northwestern Mediterranean, out of about 30,000 empty valves. Drilling was lower than 1% in all stations, except in one station where it reached up to 25.5%. Selectivity of drillhole site by the naticid *Euspirella pulchella* seems to apply in *G. vitreus* as drillholes are mainly concentrated in the relatively meaty distal half of the shell, which is also the thickest part of the valve (about 0.6–2 mm). Attacks occur generally on the ventral valve (86.2%) according to the life position of *Gryphus*. The predation pressure on *G. vitreus* by drilling appears exceptional in that it has hardly any influence on the evolution of the species. This contradicts several previous statements on the fossil record.
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Keywords: Brachiopods; Gastropods; Mediterranean; Predation; *Gryphus*

1. Introduction

Drilling is one of the few modes of predation that can be recognized *post-mortem* in brachiopods, as well as scars and other structural damage caused by predators can be recognized in shells on occasions (Leighton, 2003). Population extinctions by predation pressure remain undemonstrated on extant brachiopod populations as well as on the biocenoses in which they are living (Babin et al., 1992). Evidence of predation by gastropods, as drillholes through the brachiopod shells, has been reported in the fossil record by many authors (see Kowalewski et al., 1998; Harper et al., 1999; Harper and Wharton, 2000; Leighton, 2003), but drilling in living brachiopods has been poorly investigated (Witman and Cooper, 1983; Noble and Logan, 1981; James et al., 1992).

Judging from population surveys on the upper continental slope in the western Mediterranean brachiopods are rare prey items, although *Gryphus vitreus* may reach up to 800 individuals/m^2 (Boullier et al., 1986; Emig, 1989, 1997). Little is known about predation on *G. vitreus*. Known predators in this area are decapods, especially the spiny lobster *Palinurus mauritanicus*, polychaetes, and naticid gastropods. Predator action is always restricted to a small percentage of a whole population of *Gryphus* (Emig, 1990; Babin et al., 1992). No individuals of other brachiopod species (i.e., *Terebratulina retusa*, *Mergerlia truncata*) living in the same area have been sampled with drill-

* Corresponding author. Tel.: +33-4-9104-1616; fax: +33-4-9104-1635.
E-mail address: emig@com.univ-mrs.fr (C.C. Emig).

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doi:10.1016/j.palaeo.2004.02.025

holes. In the same way, scars and other structural damage caused by predators have been recognized only in several shells on the nearly 6500 living specimens of various brachiopod species, recorded during the cruises. Thus, one can state that, along the continental slope of the French Mediterranean coast, drilling is the only mode of predation that can be recognized post-mortem on brachiopod shells.

The goal of the present study is to analyse the possible predator, predation frequency, size relationship, drillhole positions on the valves of *Gryphus vitreus*; a comparison with related drilling predation on fossil brachiopods is attempted.

2. Material and methods

Drilled valves of *Gryphus vitreus* have been sampled during 21 cruises along the continental slope of the French Mediterranean coasts with the French oceanographic vessels "N/O Catherine-Laurence", "N/O Korotneff" and "N/O Antedon" (CNRS–INSU) investigating the biocoenosis of the Bathyal Detritic Sands (Upper Bathyal zone), which is characterized by this brachiopod species. This biocoenosis extends between the shelfbreak at 100–110 and 160–300 m depth (Emig, 1989, 1997). Of about 20,000 disarticulated valves, 5000 empty articulated shells and 5500 living specimens sampled during those cruises, only 145 valves had been drilled by gastropods: 19 ventral valves recorded at the coast of Provence off La Ciotat and Porquerolles Island between 130 and 250 m depth; and 106 ventral and 20 dorsal valves along the northern coast of Corsica between 130 and 235 m depth. The sampling transects are shown in Fig. 1. Statistical analyses were conducted using StatView 5; a significance criterion of $\alpha = 0.05$ was used.

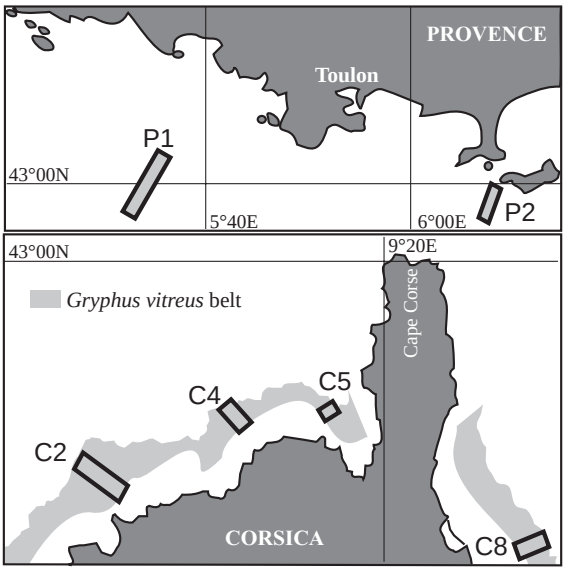

Fig. 1. Sampling areas off the French Mediterranean coasts; the drilled valves of *Gryphus vitreus* were collected along several transects.

3. Possible gastropod predators

In the investigated area several drilling gastropod species have been recorded or cited (Carpine, 1970; Falconetti, 1980; Houart, 2001), always occurring in a very low density.

The naticid *Euspirella pulchella* (Risso, 1826) (=*Natica nitida*) occurs along the coasts of Provence and Corsica: this species, living on the shelf, extends across the Upper Bathyal. Another naticid species *Cryptonatica operculata* (Jeffreys, 1885) is cited from the Provencal coast, but only exceptionally sampled.

The muricid *Pagodula echinata* (Kiener, 1840) and *Trophonopsis muricatus* (Montagu, 1803) occur off Provence and Corsica. Both species have a large geographic distribution: *P. echinata* has been recorded in the Atlantic Ocean from the Canary Islands to the Bay of Biscay and in the Western Mediterranean, from 80 to 150 m, exceptionally to 1100 m depth. *T. muricatus* extends from Turkey until the north of Great Britain, from 0.5 to 300 m depth, but this species has only been occasionally sampled along the coast of Provence. *Murex vaginatus* Cristofori and Jan, 1832 and *Murex carinatus* Bivona, 1832 refer to probably extinct taxa; both names have sometimes been used erroneously to identify the extant species *P. echinata* (see Houart, 2001). A third muricid species, *Muricopsis aradasii* (Monterosato, 1883), occurs in the western and central Mediterranean, along Turkey and the North African coast, and around the Canary and Madeira Islands (Houart, 2001). Along the coast of Provence, this species is known at few localities, from 0.5 to 105 m depth.

The conical shape of all drillholes and its outline (Fig. 2) are characteristic of a naticid gastropod

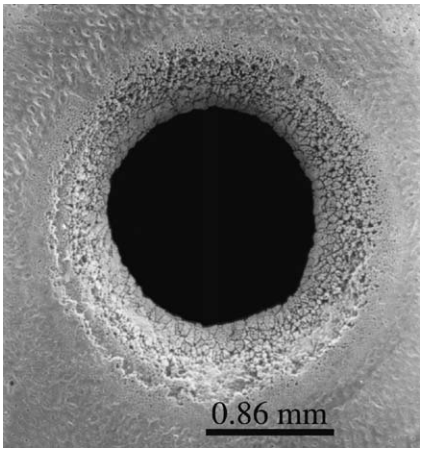

Fig. 2. SEM photography of a drillhole in a *Gryphus* valve (scale = 0.86 mm).

(Carriker and Yochelson, 1968; Martinell and de Porta, 1980), and cannot be confused with other drilling organisms, e.g. flatworms and octopuses. Incidentally, with the exception of gastropods, no other drilling predator has been reported in the investigated areas (Carpine, 1970; Falconetti, 1980). It is likely that *Euspirella pulchella* is responsible because it is the only naticid species recorded along the coast of Provence and of Corsica: this is the only manner to identify the naticid predator because the size and shape of the drillholes cannot identify unequivocally the naticid gastropod species or genus (see, among others, Carriker and Yochelson, 1968; Hoffman and Martinell, 1984). Naticids appear to be also epifaunal predators but probably concentrate on infaunal mollusc prey.

4. Predation frequency

In the biocenosis of the Bathyal Detritic Sands, the percentage of drilled valves of *Gryphus vitreus* has been estimated at less than 1% of the individuals in the semi-quantitative dredge samples. The *Gryphus* density is distributed in horizontal belts in relation to the characteristics of the continental slope and varies between some tens and about 800 individuals/m^2 (Emig, 1989, 1990). This brachiopod species is the dominant and characteristic species of the biocoenosis. In this biocoenosis, 13–42 molluscs species are known, representing about 15–32% of the total number of individuals. The dominant molluscs are the bivalves *Modiolus* (Mytilidae), *Venus* (Veneridae), and *Arca* (Arcidae). No data are available on drilling predation on those groups.

The density of the naticid and muricid gastropods is less that one individual/several m^2 to some 10 m^2, confirming the low predation pressure by gastropods on the *Gryphus* populations, in particular when taking into account the metabolic costs of boring gastropods (Harper and Peck, 2003). Low drilling frequencies, about 1%, have been reported also in Mesozoic brachiopods by Kowalewski et al. (1998). From Canadian subtidal habitats, Witman and Cooper (1983) reported only 3 *Terebratulina* drilled for 16 molluscs in 1978, and 2 for 19 in 1979; it seems that the brachiopod species of that genus are not affected by drilling predators. In our samples, no drilled *Terebratulina* shells have been recorded.

The proportion of drilled *Gryphus* shells may sometimes change between localities: in a dredge tract of the transect C2 (Fig. 1) of the 51 dead shells sampled 13 were drilled (25.5%). Such observations corroborate those of James et al. (1992), who reported that, in the sublittoral zone, approximately 30% of adult mortality of New Zealand brachiopods is due to muricid predation: the shells of *Liothyrella neozelandica* have drillholes produced probably by the gastropods *Xymene ambiguus* and *Argobuccinum tumidum*.

5. Size relationships

Drillholes penetrate the shell at right angles to the surface; the diameter is circular to subcircular, except at the two internal lateral folds of each valve (Fig. 6),

Table 1
Inner and outer diameters of the naticid drillholes in the brachiopod valves

	Ventral (n = 125)		Dorsal (n = 20)	
Diameter (mm)	Outer	Inner	Outer	Inner
Minimum	1.08	0.76	1.01	0.76
Mean	1.64	1.11	1.51	1.12
Maximum	2.22	1.49	1.90	1.33

No difference was found in relation to ventral or dorsal valves, $p < 0.001$, for both valves using a binomial test, $p = q = 0.5$ (see also Fig. 3).

where the drillholes may occasionally be slit-like. Although the shell is composed of two layers, and of three layers at the level of the body and muscle areas, holes are quite uniform and only the diameter of the holes varies (Table 1; Fig. 3A). Such variations agree with data from Verlaine (1936) on diameters of *Natica* holes, i.e. >0.5 to <1.5 mm. This author states that the hole diameter depends on the age of the predator, the larger the hole, the older the naticid. Drillhole size distributions (as an estimate of predator size) are similar on dorsal and ventral valve (Fig. 3A). The size–frequency histograms of the inner and outer diameter of the drillholes are represented in Fig. 4: inner mean diameter is 1.11 ± 0.14 mm and outer mean 1.62 ± 0.25 mm.

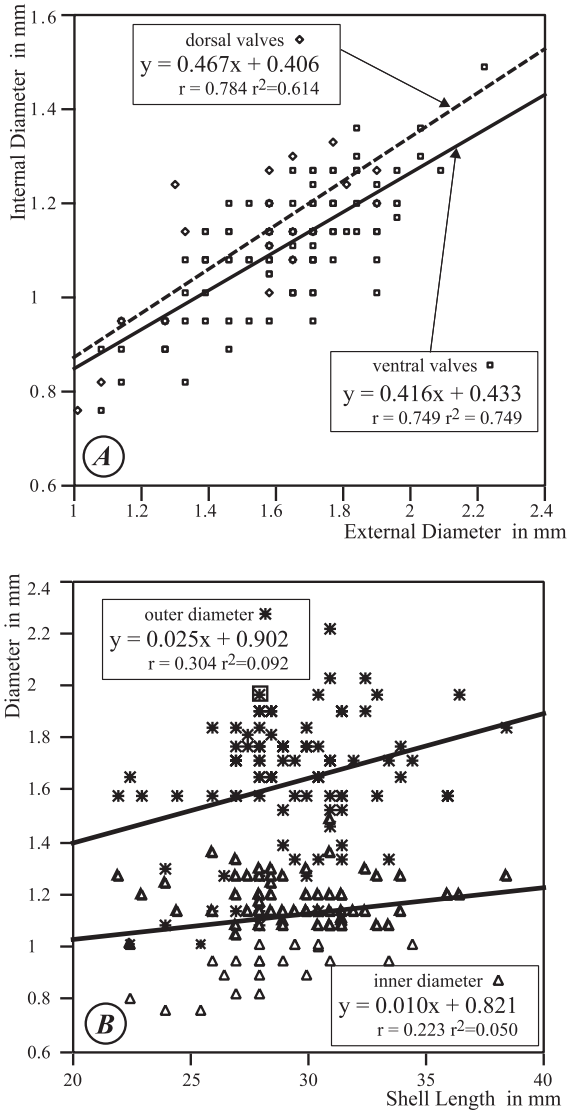

Fig. 3. Regression curves of the drillhole diameters, outer versus inner diameter (A), and outer/inner diameter versus length of the shell (B).

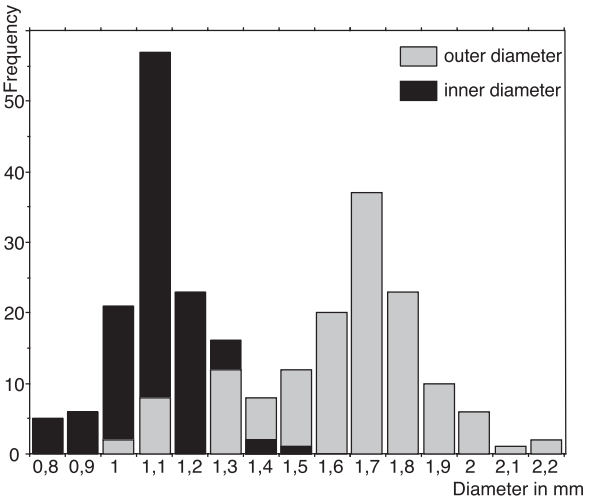

Fig. 4. Size–frequency histogram of the inner and outer diameters of the drillholes.

There is no statistically significant relationship between the size of the shell of *Gryphus*, i.e. length (Fig. 3B), width or *W*/*L* ratio, and the diameter of the drillholes (p is always >0.04; t varies from 0.819 to 0.849). One may argue that the naticid *Euspirella pulchella* does not select the brachiopod prey according to size. Similar results are given by Roopnarine and Beussink (1999) for bivalves drilled by naticids, but other naticids do clearly select (Verlaine, 1936; Martinell and de Porta, 1980; Alexander and Dietl, 2001).

According to the various authors dealing with drilling on molluscs (e.g., Carriker and Yochelson, 1968; Kitchell et al., 1986; Martinell and de Porta, 1980; Ziegelmeier, 1954; Alexander and Dietl, 2001), prey selection is or is not stereotyped by prey size; in fact, predator species and prey are often quite different (in size that may explain such variations). Nevertheless, for the western Mediterranean populations of *Gryphus vitreus*, the predation pressure by drilling gastropods is highest on medium to large shells, i.e. shells between 25 and 35 mm in length (Fig. 5). However, both length classes are also the most abun-

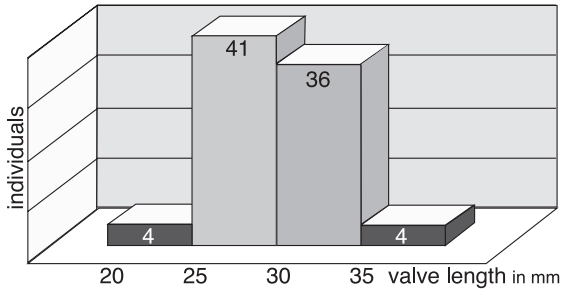

Fig. 5. Number of individuals drilled in relation to four size classes of the shell (20–24.9, 25–29.9, 30–34.9, and more than 35 mm).

dant ones in Mediterranean populations (see Boullier et al., 1986, for statistical analyses). Therefore, such results do not support the suggestion of Hoffman and Martinell (1984) that naticids choose their prey by size, at least in brachiopods.

6. Drillhole positions

In *Gryphus vitreus*, 13.8% of drillholes were in dorsal valves (20 valves sampled off Corsica, none recorded off Provence), while the other 86.2% were in ventral valves (125 valves): this difference is significant ($\varepsilon = 7.6$, binomial test, $p = q = 0.5$). This may be explained by the life position of the articulated brachiopod. The ventral valve is anchored via the pedicle to small hard substrates (pebbles, various fragments as shells, echinoderm tests, etc.) and oriented more or less vertical and perpendicular to the prevailing bottom current. The dorsal valve is generally close to or in contact with the sediment, at least the umbonal area (Fig. 6). This position prevents dorsal grasping and thus explains why the majority of drilled valves are ventral ones. In molluscs, the number of drilled left and right valves is often constant (Martinell and de Porta, 1980) because of their different life position. One may point out that no drillholes were found on *Gryphus* individuals having a minute foramen and/or a strongly incurved umbo, which are considered as indicators of a free-lying mode of life on the substrate.

Drillholes occur in various parts of the valves (Fig. 6), but are mainly concentrated in the relatively fleshy distal half of the shell, i.e. between the umbos, including the area near the hinge margin, and the posterior part of valves. In this zone, also the tertiary shell layer occurs, thus the shell is thicker in this part. A similar drilling area has been described by Martinell and de Porta (1980) and Alexander and Dietl (2001) in bivalves. Only two *Gryphus* individuals were bored at the edge. Multiple boring occurred only in three valves, which showed two or more drillholes (complete or incomplete). This suggests that almost every boring attempt was successful, because *Gryphus* has no possibility to escape predation actively, contrary to some molluscs (Kitchell et al., 1986).

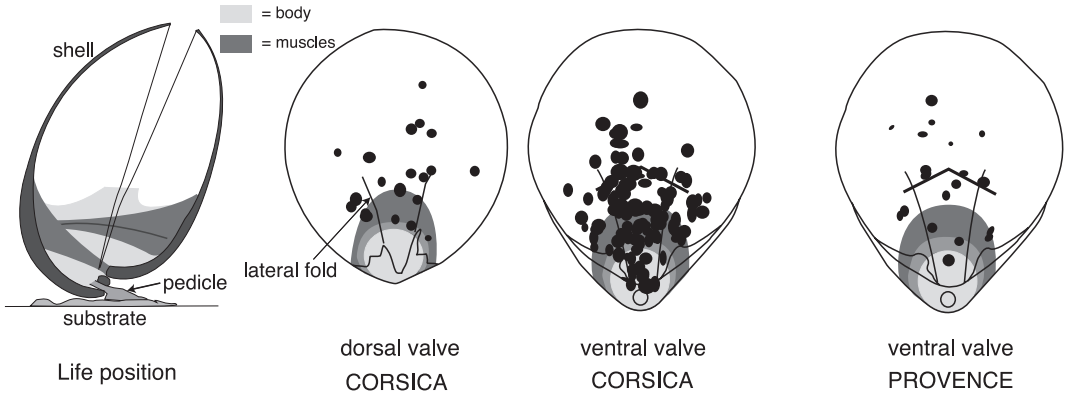

Fig. 6. Distribution of drillholes on normalized valves of *Gryphus vitreus* from the geographic areas, internal view. In the umbonal region, the grey area represents the surface occupied by the body and the dark grey area is the area occupied by the shell musculature (adductor and didductor muscles). The large remaining part (blank) corresponds to the lophophoral cavity, in which the plectolophous lophophore extends. A *Gryphus* in life position.

The brachiopods from Corsica show drillholes in a carefully selected zone (Figs. 6 and 7). Fifty-seven percent holes of the 106 records appear in the "fleshy" area (body and muscle parts). However, only 27% of the drillholes on the ventral valves off Provence and 35% on the dorsal valves off Corsica are located in this area. These differences are not significant (ε is 1.46, 1.86, and 1.60, respectively; binomial test, $p = q = 0.5$). The two latter results are less reliable given the low number of individuals sampled (19 and 20, respectively). Few drillholes in the fleshy area of the dorsal valves can be explained by the life position (see above).

Our observations fully agree with the data of Harper and Wharton (2000) on Cretaceous terebratulids and rhynchonellids. Latitudinal variations of drilling frequency and of shell sites in naticid predation have been demonstrated in bivalves by Alexander and Dietl (2001). Furthermore, the preferred drillhole site in brachiopods (Fig. 6) appears independent of the shell surface: Harper and Wharton (2000) suggested that crenulations may explain the absence of drillholes in the marginal area; however, the shell is totally smooth in *Gryphus*, but still no marginal boring occurs. No correlation between sculpture and drilling intensity in bivalves has been previously reported by Vermeij (1980).

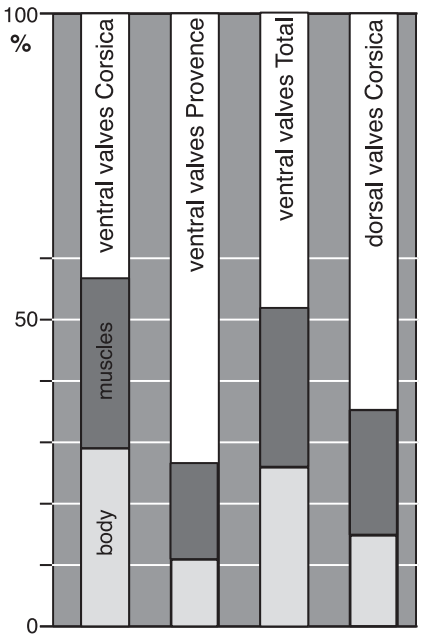

Fig. 7. Percentages of the drillholes in the three main parts of the internal volume of the shell of *Gryphus vitreus* (see Fig. 5).

The boring speed of muricids in molluscs is 0.2–0.5 mm/day and that of naticids is about 0.6 mm/day (Martinell and de Porta, 1980), in particular by *Euspirella pulchella* (Ziegelmeier, 1954). Recently, Harper and Peck (2003) indicated that the mean duration of attacks, drilling and feeding, by the muricid *Trophon longstaffi* on the Antarctic brachiopod *Liothyrella uva* was about 20 days.

The fleshy zone (body + muscles; Fig. 5) increases with age based on the length of the shell: in the ventral valve it varies from 28% to 37%, and in the dorsal valve from 32% to 37% of the whole valve length. The thickness of the valves in this part is variable in the same valve, and increases slightly with size; thickness is generally 0.6–2 mm in the ventral valves and 0.4–1.3 mm in the dorsal valves. Consequently, in the fleshy zone boring is expected to take between 1 and 2–3 days, and less than 1 day in the lophophoral cavity part.

7. Conclusions

Drilling gastropods appear to exert no more predation pressure on extant brachiopod populations than that estimated in Mesozoic and Cenozoic records. In general, the frequencies of drilled brachiopods reach as low as about 1% or less, but locally may reach values of 25–30%.

Although the brachiopods appear to be less resistant to drilling predators than bivalves, i.e. experimentally 3–10 times less according to James et al. (1992), they have significantly less tissue within the shell than molluscs, about by 7 to 14 times. In general, a predator has a relatively wide range of prey and there is no evidence that a boring gastropod would choose brachiopods on the basis of taste characters. Indeed, there is evidence that the opposite may be true (Witman and Cooper, 1983; Thayer, 1985; Peck, 1993). Yet, *Gryphus vitreus* does not exhibit any architecture, which can be considered as an antipredatory adaptation to being drilled by gastropods. Using the scores 0 to 3 assigned to antipredatory characters by Kelly and Hansen (1996) for the brachiopod *G. vitreus*, shell size is 2–2.5 (20–40 mm); thickness 1–1.5 (very thin to moderate thin); ornamentation 1 (smooth); margin 2 (no gape; margin smooth). These scores do not

agree with the hypothesis of an escalation between *G. vitreus* and naticid gastropods.

The occurrence of drilling naticid and muricid gastropods in the Proto-Mediterranean Atlantic region during the Early Miocene was rather sparse (Harzhauser et al., 2002) and remains low in the present-day Mediterranean deep-sea. There is not enough quantitative evidence since the Cenozoic to draw any conclusion in favour of an escalation-type relationship between terebratulid brachiopods and drilling naticids or muricids. In the perspective, it would be fruitful to record the proportion of drilled brachiopods that belong to terebratulid or/and terebratellid families since the end of the Miocene.

Predation rate by gastropods is probably overestimated in the fossil record or in collections (see Vermeij, 1980). The predation frequency is difficult to estimate because drilled valves or fragments are mixed with thousands of other empty or fragmented valves. In the same way, the moment of drilling cannot be estimated and it is impossible to date all drilled valves. Consequently, the presence of such valves or fragments in or on the substrate depends on the destruction rate of the shell of a given brachiopod species (see Emig, 1990).

The importance of predation pressure on the evolution of the Brachiopoda has been largely overemphasized from the fossil record. Boring predation is as low as 1% while pressure from other predators—i.e., polychaetes, other worms, crustaceans, echinoderms, and fishes—is difficult to estimate, but likely to be more important. For example, from experimental observations in aquaria (unpublished data), starving lobsters can eat dozens of *Gryphus* in a short time. The shell is brought to the mandibles by the pereiopods, cut and mashed along the commissure. Then, the first pereiopods, and sometimes the second ones, are inserted between the valves, which are pulled apart; this action causes fragmentation of valves. Only the distal part corresponding to the fleshy zone, which is also the thickest part of the valves, remains (Fig. 6), often still articulated. The interior of the shell is moved to the mouth.

Thus, crushing predation is largely underestimated (see also Harper and Wharton, 2000), at least in the Mediterranean Upper Bathyal Zone. The shell fragments remaining after crushing cannot be distinguished and will be rapidly incorporated into the sediment and mixed with the other detritic particles. The low rate of drilling on brachiopods may indicate a highly stereotypic behavioural response of naticid gastropods to select mollusc prey and not brachiopods. Only the selectivity of drillhole site by the naticid *Euspirella pulchella* seems to apply in *Gryphus vitreus* when, as an exception, an attack occurs.

Our results on boring predation are generally similar to those of Harper et al. (1998, 1999), Kowalewski et al. (1998) and Harper and Peck (2003), but the evolutionary history of the predators should be taken into account when boring frequency is compared through geological time. So the two main extant boring gastropods groups belong to the families Muricidae and Naticidae, which were absent prior to the Aptian–Albian (Lower Cretaceous) and to the Campanian (Upper Cretaceous), respectively, and diversified at a modern level in Eocene time (Tracey et al., 1993; Harzhauser et al., 2002; Kase and Ishikawa, 2003).

Finally, we may assume that boring predation in brachiopods is exceptional to occasional, and consequently such predation had and has a negligible influence on the evolution of this group, but may be locally important.

Acknowledgements

The program CNRS-RCP 728 has supported this research with the technical support of the CNRS–INSU (oceanographic vessels N/O Catherine-Laurence, N/O Korotneff and N/O Antedon) and the French Navy (vessel BISM Triton and submersible SMI Griffon).

We thank Roland Houart and Patrick Arnaud for their thoughtful comments on boring gastropods, Mireille Peyrot-Clausade for the statistical analyses, Liz Harper for helpful review on the manuscript and grammatical improvements, and the two P.P.P. referees, F.T. Fürsich and M. Kowalewski, for their constructive criticism on the early draft of this article.

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