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Patterns of drilling predation in relation to stratigraphy, locality and sieve size: Insights from the Eocene molluscan fauna of the Paris Basin

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ABSTRACT

Predatory drilling traces are routinely used to evaluate temporal patterns in animal behaviour. However, for testing such trends it is important to consider natural and methodological variability that may play a role in shaping drilling patterns. The present study attempts to test this notion by evaluating the drilling patterns of the molluscan fauna in relation to stratigraphy, locality, sieve size (4 mm, 2 mm, 1 mm) and taxonomic affinity at class level. We studied drilling predation using molluscan specimens from three localities (Grignon, La Ferme de l'Orme, Fleury-la-Rivière), representing a variety of elementary depositional sequences (EDS) from the Middle Lutetian strata of the Paris Basin.

The overall drilling frequency (DF) averaged over the three localities is 17%; bivalves show a significantly higher overall DF (18%) compared to gastropods (14%) and scaphopods (<0.01%). For all higher taxa and at all localities DF is highest in the medium size class (2–4 mm), which we relate to the dominance of preferred prey species in this category. Despite having similar diversity profiles of molluscan fauna, the three localities show distinct drilling patterns with highest frequencies in Grignon (overall 25%, bivalves 29%, gastropods 20%), followed by Fleury-la-Rivière (overall 18%, bivalves 17%, gastropods 18%) and almost a complete lack of drill holes in La Ferme de l'Orme. This pattern is true for each sieve size of molluscs, bivalves and gastropods. The results are similar for common species found in all three localities. EDS2-3 representing a mesotrophic environment during a regressive phase shows a slightly higher DF compared to oligotrophic EDS4, from the following transgression. Locality emerges as the strongest predictor of DF when evaluated for the relative role of stratigraphy, locality, sieve size and higher taxa. The occurrence of incomplete drill holes is relatively rare and increases with sieve size, implying a possible existence of handling limit of the predatory gastropods. There are very few occurrences of edge drilling. The combined variation documented in this study is comparable in magnitude with many temporal shifts documented previously. Therefore, in order to establish any temporal pattern in drilling behaviour it is vital to evaluate and control for the potential gradient of other natural variabilities in predatory behaviour.

Species composition and diversity has been used previously to resolve the debate on climate conditions of the Eocene Paris basin through a comparison to modern analogues. We have used a similar approach by comparing predation patterns with Recent localities of subtropical and temperate regions. The available data from the Eocene Paris basin, from the warm-temperate northern Adriatic Sea and from the sub-tropical Red Sea show very heterogeneous patterns, depending on the drilling metric considered. Considering the strong patchiness of drilling predation within each of these basins and reported from many other studies, we conclude that a climatic affiliation of the Eocene Paris basin based on drilling metrics is not yet possible.

1. Introduction

Drilling by predatory gastropods, such as naticids and muricids, has captured the interest of paleontologists because it preserves biotic interactions of the past that can be studied quantitatively. Such data are

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critical in testing evolutionary hypotheses such as coevolution and escalation (Kelley and Hansen, 2003). However, for testing such hypotheses it is important to consider various sources of natural and methodological variability that may play a role in shaping drilling patterns.

Temporal variability in drilling predation is intensely studied (Kelley and Hansen, 2003 for review). Predation is often considered the most important agent of natural selection and response to predation pressure is often claimed to bring long-term evolutionary change in populations (Vermeij, 1987). Therefore, we may expect to see temporal change in predation intensity. This idea leads to the development of evolutionary ecological hypotheses like coevolution and escalation and the subsequent effort to document them using drilling frequency data (Kitchell, 1986, 1990; DeAngelis et al., 1984, 1985; Dudley and Vermeij, 1978; Kelley and Hansen, 1993, 1996; Kowalewski et al., 1998).

In order to recognize such temporal change, the variation in drilling pattern within a time interval should be much smaller in magnitude in comparison to the changes between subsequent time intervals. Biotic interaction depends on the composition and density of predator-prey communities (DeAngelis et al., 1985). As many of the communities are quite patchy in their distribution, we may expect to see spatial variation in drilling intensity at different scales.

Studies focusing specifically on spatial variation in drilling behaviour are relatively rare as compared to reports on local drilling predation. In studying spatial variation in drilling patterns, scale becomes an important issue. Researchers have recognized variation from a few meters to multiple latitudinal bins. Variation along a several km long transect was recognized in the modern northern Adriatic Sea (Sawyer and Zuschin, 2010) and within and between localities in the Lower and Middle Miocene of the Vienna basin, Austria (Sawyer and Zuschin, 2011). Using Recent molluscs of the Red Sea, Chattopadhyay et al. (2014a, 2015) reported a change in overall and edge drilling frequencies in various depositional environments in one bay of about 75 km^2. Using Eocene molluscs of North America from multiple depositional environments, Hansen and Kelley (1995) demonstrated the variation in naticid drilling predation. Hoffmeister and Kowalewski (2001) documented such variation in drilling pattern for Miocene molluscs between multiple depositional basins of central Europe. Chattopadhyay and Baumiller (2010) reported a case of spatial variation in drilling predation in Pleistocene deposits from various basins of the United States. Some researchers expanded such analyses to a global scale. Vermeij (1980) documented variation in DF for terebrid gastropods by analyzing specimens of Cenozoic occurrences from all over the globe. Often such large-scale spatial variation in DF has been causally linked to latitudinal variation. Some of the studies demonstrated an increase in drilling intensity towards the equator (Visaggi and Kelley, 2015) while others found an opposite trend (Hansen and Kelley, 1995) or none at all (Marincovich, 1977; Taylor and Taylor, 1977; Dudley and Vermeij, 1978; Vermeij et al., 1989; Allmon et al., 1990). A useful approach to evaluate the extent of spatial variation is to study samples from different localities within one depositional basin with distinct environmental characteristics, because ecological processes operate at local scales and local communities receive species from a biogeographically delimited metacommunity (Hubell 2001). In the fossil record, paleoecological studies in basins with tectonically and sedimentologically meaningful frameworks can be performed at low taxonomic levels and with highly resolved stratigraphic control (e.g., Zuschin et al., 2011).

Another important source of variability that could affect the final drilling pattern is the taxonomic composition of the prey. As each prey presents a different location on the cost-benefit landscape for a given predator (Kitchell et al., 1981; DeAngelis et al., 1985; Chattopadhyay and Baumiller, 2009), we may find different drilling patterns among different taxa. Such preference for taxa has been documented in Recent as well as fossil ecosystems (Hoffman and Martinell, 1984; Kohn and Arua, 1999; Sawyer and Zuschin, 2010, 2011; Chattopadhyay and Dutta, 2013).

Body size is another source of natural variability. Drilling pattern is often size dependent primarily because of two factors: 1. Ontogenetic variation in drilling behaviour of the predator, 2. Cost-benefit relationship. Consequently, each size class of the prey may represent a unique drilling pattern (e.g., Ansell, 1960; Allmon et al., 1990; Kitchell, 1986; Kelley 1988, 1991; Anderson, 1992; Harper et al., 1998). Therefore, using a specific size class of prey for the study of drilling predation could present an incomplete result. Moreover, the sampling method (see Kowalewski, 2002) could act as a source of variability that affects specimen size; several studies have evaluated this potential source of bias (Ottens et al., 2012, Hattori et al., 2014, Visaggi and Kelley, 2015).

The natural and methodological variabilities discussed above play important roles in fossil and Recent assemblages. However, apart from a few studies (Hoffmeister and Kowalewski, 2001; Ottens et al., 2012; Hattori et al., 2014), rarely has an effort been made to disentangle their relative effects. In this study, we evaluated the individual and relative effects of stratigraphy, locality, sieve size and higher taxa on drilling patterns of molluscan fauna. We evaluated these effects on drilling predation using molluscan specimens from three localities, representing a variety of elementary depositional sequences (EDS) from the Middle Lutetian strata of the Paris basin (Fig. 1).

2. Materials and methods

2.1. Geologic setting

The lists of the macro- and microfossils of the middle Lutetian of the Paris Basin have been worked out to a large extent (see references in Merle, 2008, Lozouet, 2014). Notwithstanding the basin was located around 30–35°N, sample-level species richness of the molluscan fauna matched values of modern tropical hotspots (Dominici and Zuschin, 2016). The thickest part of this interval is composed of unlithified fine-grained hybrid arenites (in the sense of Zuffa, 1980), with a very large carbonate fraction of biogenic origin (mainly mollusc shells or foraminifer tests), a quartz component and occasional glauconite. Bedding is usually massive, and field correlations among distant outcrops are mainly based on the molluscs (Gely, 1996).

2.2. Stratigraphy

We have sampled the middle Lutetian at three localities: La Ferme de l'Orme, Grignon (both near Paris) and Fleury-la-Rivière (near Reims). Strata are roughly horizontal and individual unconformity-bound units have been correlated between outcrops as far as 160 km (Fig. 1, modified from Dominici and Zuschin (2016), and references therein), following the detailed sedimentologic description of the “Falunière de Grignon” by Jean-Pierre Gély and Didier Merle (in Guernet et al., 2012), interpreted based on available multiproxy data (Huyghe et al., 2012, Guernet et al., 2012, Dominici and Zuschin, 2016). We distinguished several elementary depositional sequences (EDS) from bottom to top:

EDS1-EDS2 contain bioturbated calcareous sandstone (3–4 m), with abundant glauconite and quartz, and sparse shell material. The association is characterized by *Cardium (Orthocardium) subporulosum*. A tabular shell bed in the upper part contains sparse gravels and *Turritella* shell debris. Transgressive gravels are present at Fleury, in association with bones of marine vertebrates. EDS 2 sediments at Fleury are interpreted as lower shoreface deposits. Two samples were analyzed in EDS2, at one locality (Fleury).

EDS 3 contains cross-bedded, locally bioturbated calcareous sandstones (2 m), rich in quartz and glauconite, interpreted as an upper shoreface deposit, and a highly-bioturbated massive calcareous sandstone (1.5 m), with abundant quartz and glauconite. Loosely-packed shell beds are characterized by *Campanile giganteum*. The