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NATICID BOREHOLES ON A TERTIARY CYLICHNID GASTROPOD FROM SOUTHERN PATAGONIA

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INTRODUCTION

The fossil communities are in clear disadvantage when it comes to study the interactions among the species included in them. However, predation on shells gives us the possibility to examine at least some of these interactions. The diameter of the borehole, its placement, and the volume of the prey are parameters that can be easily recorded. Diverse combinations of these may allow inference about the size of the predator and the time spent on the perforation (Kitchell et al., 1981).

The morphology of two types of boreholes was described by Carriker & Yochelson (1968) that later Bromley (1981) described as ichnofossils. Taylor (1980) and later Bromley (1981) pointed out that externally wide and internally narrow predation marks with paraboloid walls are produced by naticid gastropods (*Oichnus paraboloides*), whereas those cylindrical with non-beveled edges are assigned to predators belonging to the Muricidae (Carriker, 1981).

Kelley (1988) developed a model in which predation of the Miocene naticids is stereotyped and predictable. The observed pattern of predation was revealed when analyzing the selection of perforation location and the size of the predators by means of the perforation diameter. Kitchell et al. (1981) showed that the main purpose of such patterns is an adaptive behavior to maximize energy efficiency and to select by prey size.

GEOLOGICAL SETTING

The material studied was collected in Neogene rocks exposed along the Atlantic coast of southern Patagonia. This is the first record of drilled gastropod shells from the Monte León Formation. Along the coast there are spectacular almost continuous outcrops of Tertiary rocks from the mouth of the Río Negro in northern Patagonia to the Straits of Magellan, and many authors have visited this area as they contain a very rich fauna of continental mammals and marine invertebrates. These beds have been subdivided based on their fossil content. These subdivisions – as well as the ages proposed for these rocks – have been a matter of great controversy, which has not yet been completely resolved.

The samples containing the studied material come from a locality along the southern margin of the Santa Cruz River first visited by Charles Darwin and by him called Mount Entrance (Fig. 1). They were collected in a very thin shelly bed of loose sediment lying within the Monte Entrada Member of the Monte León Formation (Fig. 2). The unit is richly fossiliferous, but the smaller specimens have generally escaped attention. The extraordinary abundance of *Kaitoa* in this particular bed has been overlooked, as most existing collections have only a few specimens. The Monte León Formation was formally introduced by Bertels (1970, 1978), and she subdivided it into a lower member (Monte Entrada) and an upper one (Monte Observación). The age of these rocks has been amply discussed and is presently believed to be late Oligocene to more probably earliest Miocene (Barreda & Palamarczuk, 2000).

Kaitoa patagonica (Ihering, 1897) (Fig. 3) is a small cylichnid first described from the Superpatagonian beds of Yegua Quemada, in the province of Santa Cruz and included in *Bulla*. However, the shell shape, ornamentation and columellar features suggest its affinities lie with *Kaitoa* Marwick, 1931 (type species *Kaitoa haroldi* Marwick, 1931), a genus described originally from Altonian (late early Miocene) rocks in New Zealand and which according to Beu & Maxwell (1990) occurs there from the Otaian (mid-early Miocene) to the Waipipian (early-late Pliocene). The occurrence of taxa peculiar to Australasia or Antarctica in South America has been variously recorded and this is just another example of such a connection (Beu et al., 1997).

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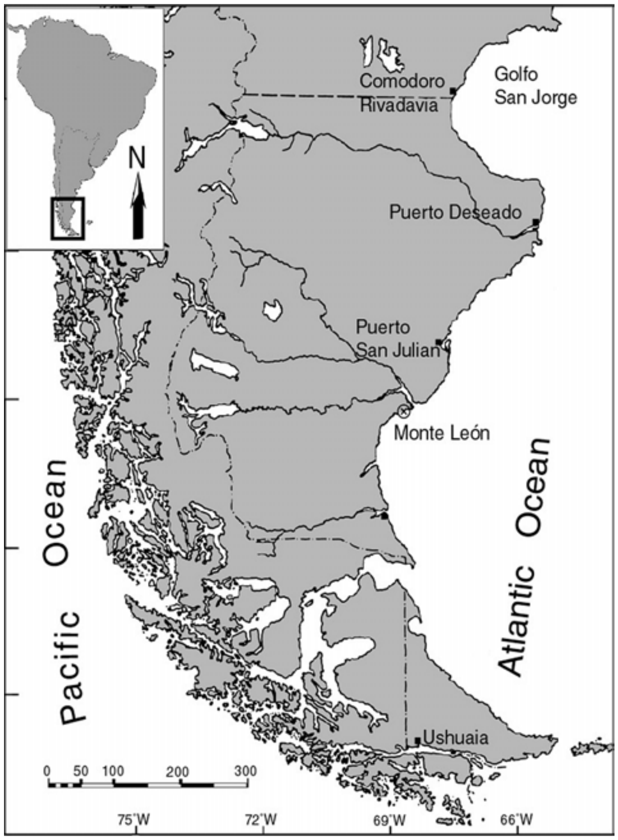


FIG. 1. Location map of the sampling area.

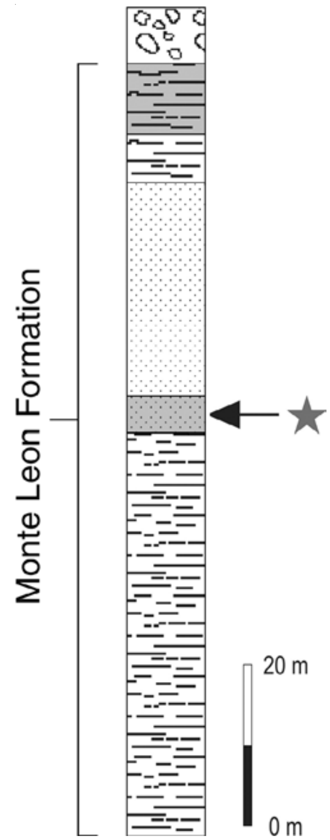


FIG. 2. Schematic Section of Monte León Formation.

MATERIALS AND METHODS

A total of 873 specimens of *Kaitoa patagonica* were considered in this study (Figs. 3–9). Internal and external diameters of 242 boreholes were measured using a stereoscopic microscope. The total length was measured in all 873 specimens, including those that were perforated. These three parameters were used to build a frequency table. SEMs pictures were done at MACN with a Philips XL30. All pictures were digitally processed.

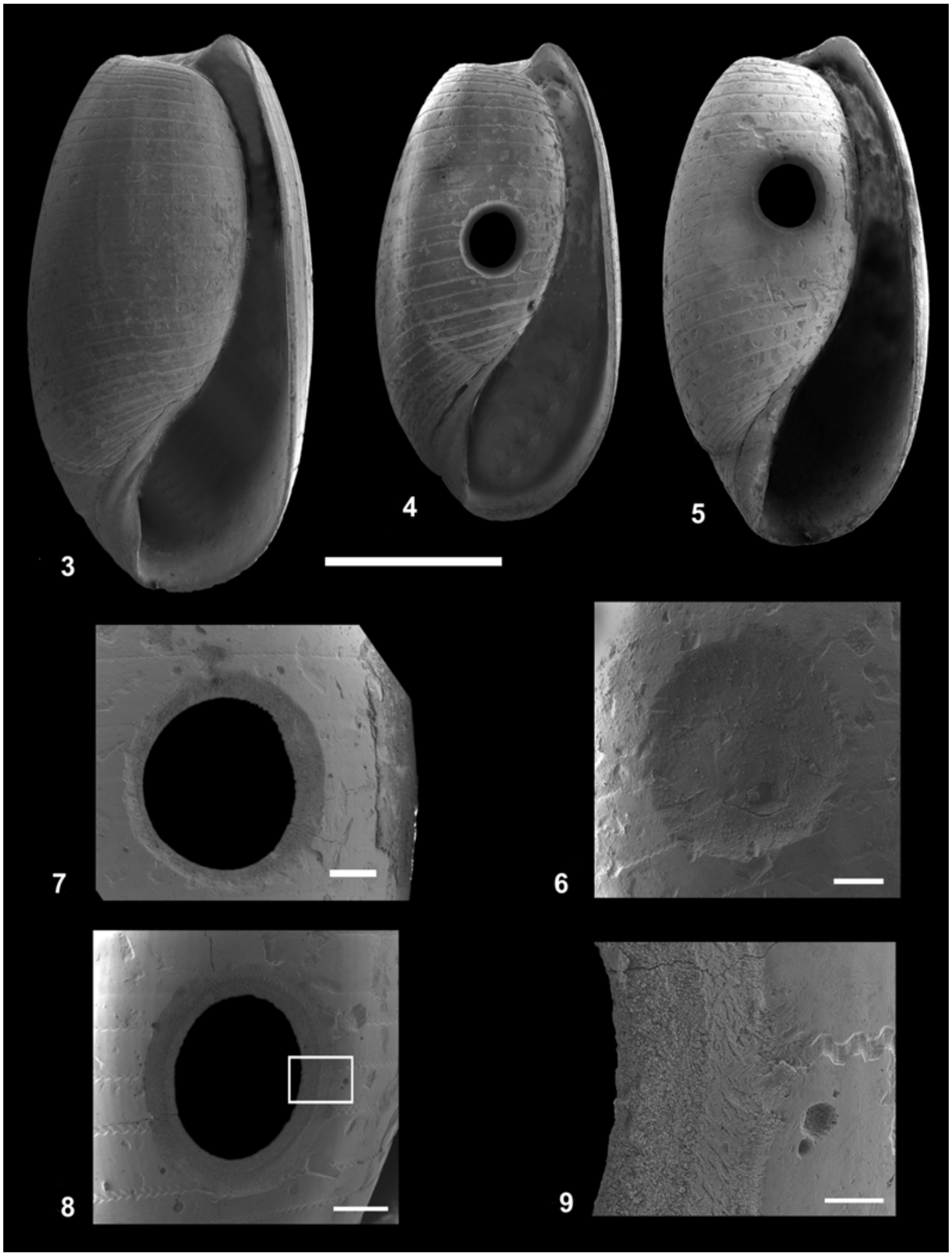
The studied material is housed in the Departamento de Ciencas Naturales, Facultad de Ciencias Exactas y Naturales, Universidad Nacional de La Pampa, under the numbers GHUNLPam26500, 26501, 26502 and 26503, for the illustrated specimens and GHUNL Pam26504 for the others.

RESULTS

All boreholes showed the same morphology. The perforations are conical, with the larger diameter on the external surface of the shell and the smaller diameter on the internal surface (Fig. 4).

Of all the boreholes measured in *Kaitoa patagonica*, 90% are placed on an area of the last whorl near the inner lip, that is, on the central part of the apertural side of the shell. The rest were found on the dorsal side of the shell (Fig. 5).

A very low percentage of incomplete boreholes were observed in the population. This does not allow us to draw any conclusion about predator behavior. However, the drilling mechanism was recognized due to the presence of a slightly prominent central boss (Fig. 6).



FIGS. 3–9. *Kaitoa patagonica* (Ihering, 1897). FIG. 3: UNLPam 26500; FIGS. 4–5: Two drilled specimens, UNLPam 26501, 26502. Scale bar = 2 mm (FIGS. 3–5); FIG. 6: Detail of an incomplete borehole, UNLPam 26503. Scale bar = 200 μm; FIGS. 7–8: Two complete boreholes. Scale bar = 200 μm; FIG. 9: Detail of the square from Fig. 8. Scale bar = 50 μm.

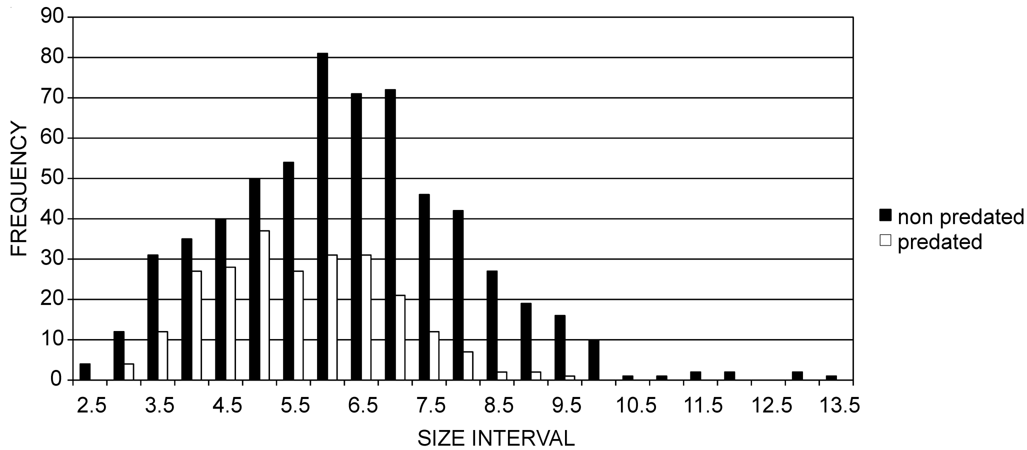


FIG. 10. Size intervals vs. number of specimens (predated and non-predated) of *Kaitoa patagonica*.

The size distribution curve of the population is normal in both predated and non-predated individuals. The most frequent size in the population is 6–6.5 mm of total length, whereas the most predated size is 5–5.5 mm of total length (Fig. 10). The distribution of borehole sizes is normal. The most frequent borehole size is 0.6–0.8 mm considering its internal diameter (Fig. 11). This borehole size curve is displaced to the left.

Correlation between internal diameter and the size-range of the population was analyzed with the software Statistica v. 4.0. The result was not significant ($R^2 = 0.1257$; $p < 0.000$), but there is a trend suggesting that the larger predators produced holes with a larger diameter (Fig. 12).

DISCUSSION

The conical shape of the perforations agrees with the morphology of boreholes referred to gastropods belonging to the Naticidae

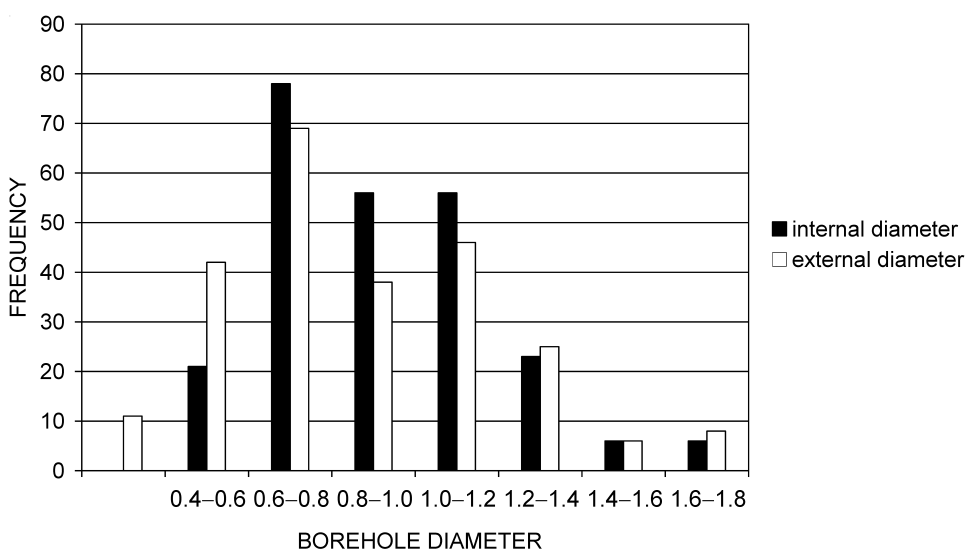


FIG. 11. Distribution of diameters of boreholes present in *Kaitoa patagonica*.

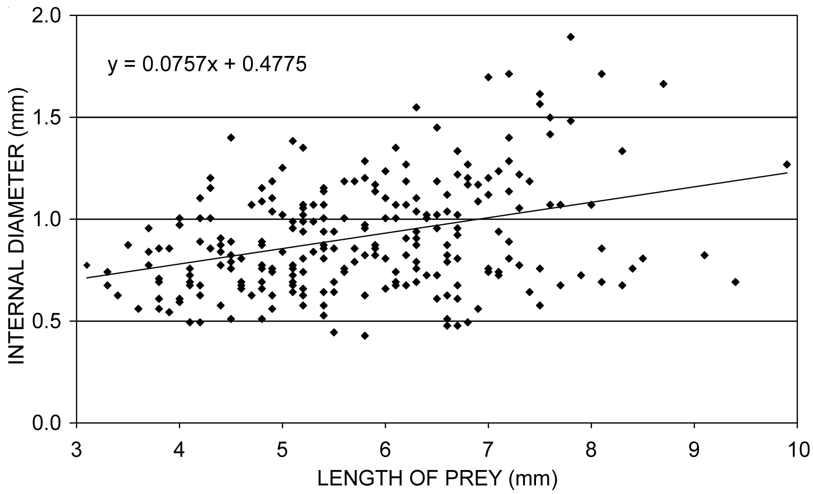


FIG. 12. Total shell length of prey vs. internal diameter of the borehole.

(Carriker & Yochelson, 1968; Taylor et al., 1980, among others). Among the species of this family described from coeval rocks in the same area are *Polinices santacruzensis* Ihering, 1897, and *Natica subtenuis* Ihering, 1897. These species were based on generally poorly preserved large adult shells, which seem unlikely to have been responsible for the borings on *Kaitoa*. There are numerous small juvenile naticid shells in this unit, but until further data become available on the different stages of the species described on the basis of large specimens, we cannot ascertain to which of them they may belong. Therefore, the identity of the *Kaitoa*-borer must remain as yet uncertain.

Borehole diameter provided an excellent tool to estimate the size of the predator. Such a size selection is a common behavior in naticids (Calvet i Catà, 1989). As reported here, the most abundant size in the population is not the most intensely attacked by the predator (Fig. 10). The reason for this discrepancy may lie in the fact that the predator could have been the very small, equally abundant naticid juvenile that appears in the same beds as *Kaitoa patagonica*. These presumably could prey on *Kaitoa patagonica* up to a certain size, but were somehow prevented of attacking the larger specimens, whether because of morphological constraints or because of a faster growth of the opisthobranch compared to naticids.

The non-predated population may constitute a size-refuge, such as those described for other groups of mollusks commonly attacked by naticids (Kabat, 1990; Pastorino & Ivanov, 1996).

A location selection for perforations (Hofmann & Martinell, 1986) is very well defined in most drilled shells of the Patagonian species. The area adjacent to the parietal callus carries the largest percentage of the perforations. This ellicits the question as to why it is so if the normal way of living is with the apertural side down. The possible answer to this may rest in the way in which the predator manipulated the prey. Additionally, this place is the easiest way to kill the prey because beneath the adapertural part of the shell, the most exposed, is where the foot is retracted, whereas a perforation on the ventral side assures the predator better chances of reaching vital organs and therefore enhancing its possibilities of killing the prey with minimum effort.

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