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## THE FIRST PREDATORY DRILLHOLE ON A FOSSIL CHITON PLATE: AN OCCASIONAL PREY ITEM OR AN ERRONEOUS ATTACK?

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**ABSTRACT:** Drillholes represent direct evidence of ecological interactions in the fossil record. Most of them have been interpreted as predatory in origin and enable the analysis of behavioral information of both predator and prey. Drillholes have been found in a variety of fossil organisms, but this is the first report of a bored fossil chiton plate. It was found in the La Coronilla deposit, a Late Pleistocene invertebrate assemblage from southeastern Uruguay. The drillhole belongs to the ichnospecies *Oichnus simplex* and is attributed to a muricid gastropod, which could likely have been the ocenebrid *Urosalpinx haneti*, recorded in the fossil assemblage. The drillhole features all traits for a predatory origin. However, the rareness of this particular interaction between chitons and gastropods in the fossil record and in the recent, could signify an event of arbitrary drilling. The reported occurrence here raises the question as to whether this behavior represents an understudied ecological interaction between polyplacophorans and gastropods.

### INTRODUCTION

Among signals of paleoecological interactions throughout the fossil record are small round holes on shells. These are one of the common trace fossils found in biological hard substrates with the oldest records reported in the late Precambrian (Bengtson and Zhao 1992; Hua et al. 2003). They can be found through the Paleozoic and Mesozoic, and have become more abundant in the fossil record since the Late Cretaceous (Vermeij 1987; Kowalewski et al. 1998; Harper 2003a; Kelley and Hansen 2003).

Drillholes have been thoroughly studied in terms of the evidence they provide for predator-prey interactions. They bring specific behavioral information such as prey preference, drill site selectivity, stereotypy, and rates of success or failure in the attacks (e.g., Taylor 1970; Hoffman and Martinell 1984; Kelley 1988; Arua 1989; Złotnik 2001; Signorelli et al. 2006). Together with other evidence of predation, the drilling record has allowed paleontologists to explore predation through time and to weigh its importance in evolutionary processes (Vermeij 1977; Kitchell 1986; Kowalewski et al. 1998; Harper 2003b; Kelley and Hansen 2003). Studies on drilling predation in the fossil record have also benefited from research concerning this interaction in the recent through field observation and laboratory experiments (e.g., Nebelsick and Kowalewski 1999; Simões et al. 2007; Visaggi et al. 2013). The mechanism of perforation, prey selection, prey-predator size relationships, and predator behavior have been extensively analyzed (Carriker et al. 1967; Carriker 1969a, 1981; Kitchell 1986; Hart and Palmer 1987; Palmer 1988; Urrutia and Navarro 2001; Harper and Peck 2003; Yanes and Tyler 2009). Moreover, many studies have incorporated morphometric analysis to aid in the identification of the tracemaker (e.g., Kowalewski 1993; Grey et al. 2005; Dietl and Kelley 2006). Besides overwhelming evidence for predation, some boreholes have been attributed or reinterpreted as other kinds of paleoecological interactions such as parasitism (Neumann and Wisshak 2009). Boreholes, especially older ones, have been reanalyzed as domiciles

(Wilson and Palmer 2001) or taphonomic artifacts (Lescinsky and Benninger 1994).

Drillholes are produced by several gastropod taxa, octopods, nematodes, and flatworms (see Bromley 1981; Kowalewski 2002), with very small holes not being attributed to any producer. In the literature, most attention has been on gastropods as borers (see Sohl 1969; Carriker 1981; Kabat 1990; Kowalewski 1993; Kelley and Hansen 2003). Drilled taxa include foraminiferans, brachiopods, echinoderms, bivalves, gastropods, scaphopods, crabs, barnacles, and ostracods (see Bromley 1981; Kowalewski 1993; Kelley et al. 2003). Polyplacophorans have only been reported to be drilled in the recent by octopods (Mather and Nixon 1990), which inject venom through the holes. The resulting drillholes reported by these authors are small and ovoid in shape. Taylor and Morton (1996) also mention that muricid gastropods drilled chitons as minor prey items, although we could not confirm that this was through the chiton shell (J.D. Taylor, personal communication, 2014). Chitons live on rocks or other hard substrates mostly in intertidal to shallow subtidal environments (e.g., Kaas and Van Belle 1985), a habitat shared with several drilling predators. No description or reports of drilled chitons has been found in the fossil literature. Thus, the aim of this paper is to report the first drillhole on a fossil chiton plate, to comment on the most plausible tracemaker and to interpret its possible origin and significance.

### STUDY AREA AND GEOLOGICAL SETTING

The drilled plate comes from the littoral fossil assemblage at La Coronilla locality, Rocha County in Uruguay (Fig. 1). The deposit outcrops in the abrasion platform of La Coronilla beach and may be assigned to the Villa Soriano or Chuy Formation (see Martínez and Ubilla 2004). It is composed of a greenish-grayish sandy claystone in which the fossils are well preserved. Taxa with delicate shells and

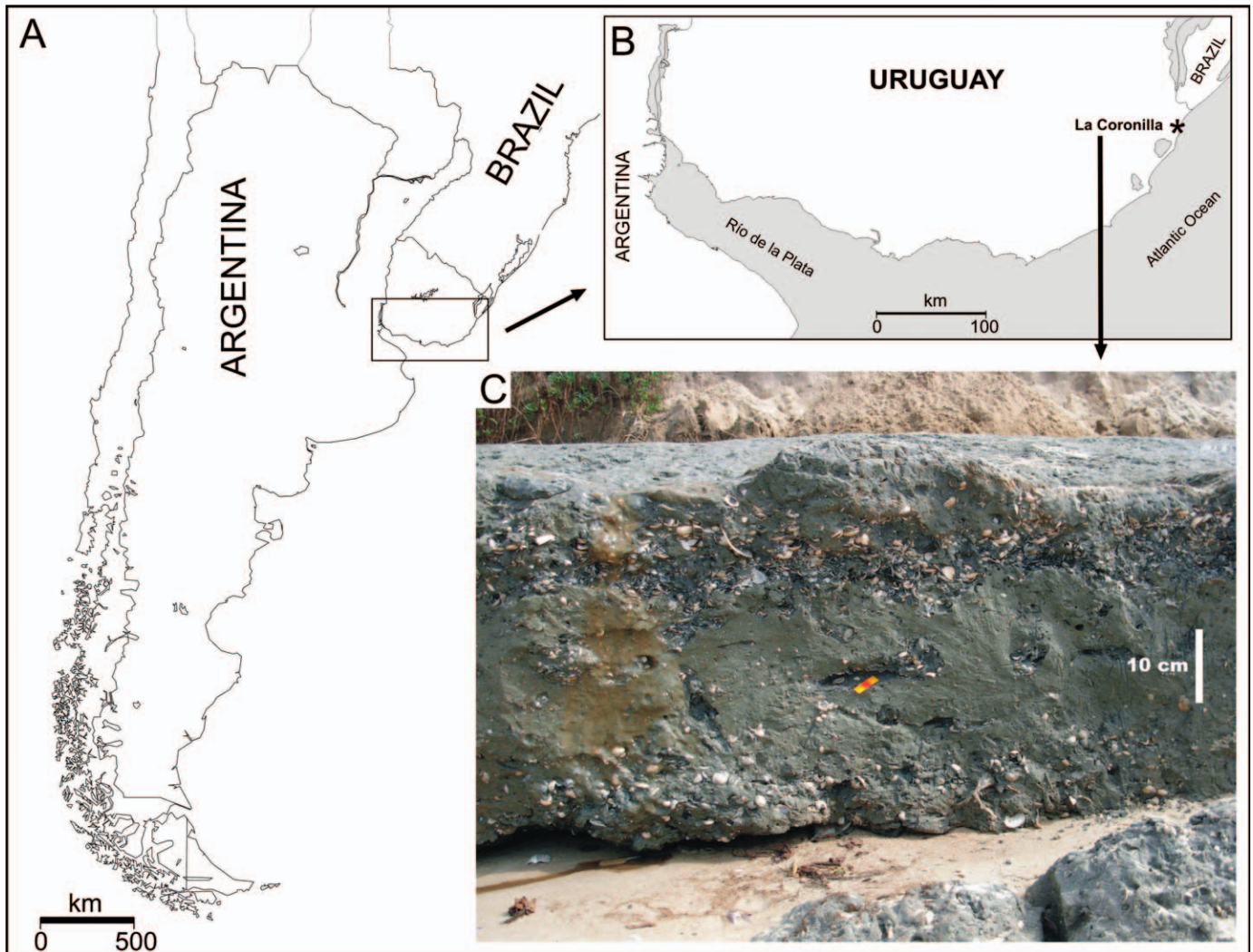


FIG. 1.—Geographic location of the La Coronilla fossil assemblage. **A)** Map of southern South America showing the location of Uruguay. **B)** Enlargement of the boxed area from view A showing the location in Uruguay of the study area. **C)** Image of the fossil bed from which the chiton valve was collected.

specimens in life position are commonly found. These features, along with the almost complete absence of fragmentation and abrasion of the shells and the lack of size sorting, suggest a predominantly autochthonous–parautochthonous assemblage without significant transport. The fossil assemblage is dominated by bivalves and gastropods and was first studied by Martínez et al. (2001) and more recently by Rojas (2007). It also contains remains of other taxa including crustaceans, corals, bryozoans, annelids, echinoids, chitons, and fish (Rojas 2007; Rojas and Urteaga 2011). A list of bivalve and gastropod taxa in this assemblage is provided in Martínez et al. (2001). Lorenzo and Verde (2004) reported drillholes only on oysters (mostly juveniles). These drillholes were attributed to muricids although no body fossils of these gastropods were found at that time in the fossil assemblage.

The La Coronilla assemblage has been dated, using radiocarbon dating as  $29,500 \pm 600$  years BP and  $35,500 \pm 1900$  years BP by Martínez et al. (2001), thus placing the study interval in the Late Pleistocene. The molluscan fauna includes warm water taxa not found today on the Uruguayan coast but living northward in Brazilian waters. Thus, the warm character of the fossil fauna indicates warmer conditions than present day. Based on this evidence Martínez et al. (2001) proposed a Late Interglacial (MIS 5e) age for the assemblage.

#### THE BOREHOLE

One of the samples analyzed from the La Coronilla fossil assemblage yielded a drilled intermediate valve of *Chaetopleura angulata* (Spengler, 1797) (Fig. 2). This species lives in shallow subtidal habitats up to 50 m depth on the Atlantic coast of South America from Rio de Janeiro to Cape Horn and the sub-Antarctic islands, and also on the Atlantic coast of Western Europe (Rochebrune and Mabile 1891; Kaas 1954; Leloup 1956; Castellanos 1988). The borehole is assigned to the ichnospecies *Oichnus simplex* Bromley 1981. The ichnogenus *Oichnus* has been recently considered a junior synonym of *Sedilichnus* Müller, 1977 (Zonneveld and Gingras 2014). However, we will refer to *Oichnus* in this paper due to the extensive usage of this name in the literature. The axis of the boring is almost perpendicular to the shell surface and penetration occurred from the shell exterior. Its overall shape is subcylindrical (with subparallel walls in longitudinal section), showing a decrease in diameter at the inner opening. The external diameter is 1.7 mm and the internal one is 1.2 mm. The boring openings are characterized by smooth edges. Shell thickness is 1.4 mm. Scanning electron microscope images do not show the presence of radula marks but only the ultrastructure of the shell (Fig. 3). The specimen is stored in the Paleontological Collection at Facultad de Ciencias, Universidad de la República, in Montevideo, Uruguay (FCDPI 4891).

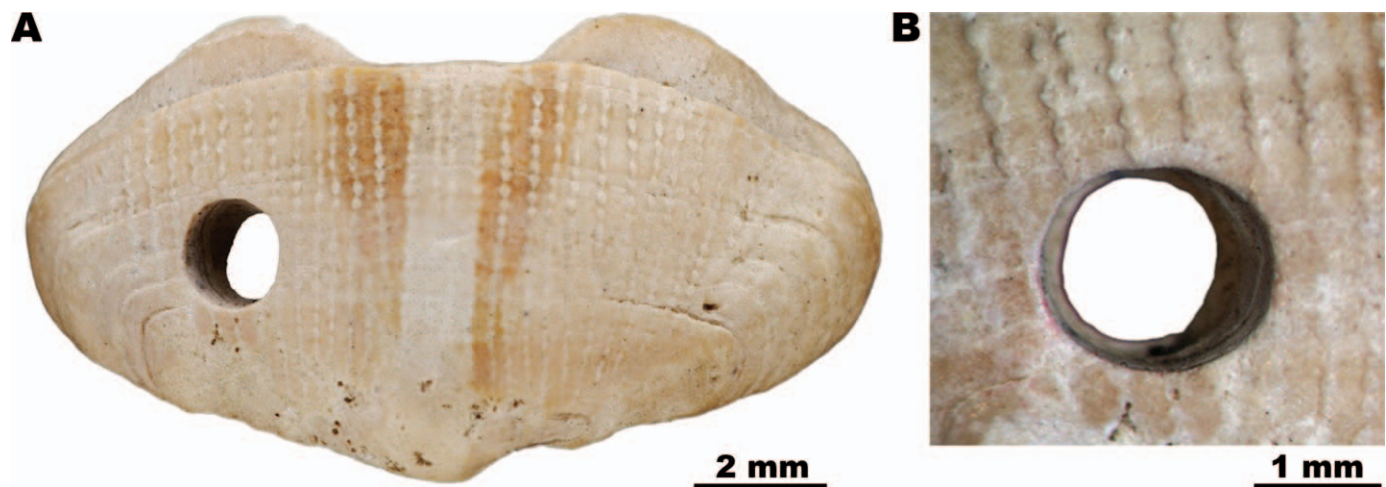


FIG. 2.—Drillhole on *Chaetopleura angulata* intermediate valve, FCDPI 4891. A) Image of the complete chiton valve. B) Close-up of the external surface of the valve showing the slightly larger external opening and slightly smaller internal opening of the drillhole.

#### DISCUSSION

##### *The Nature of the Drillhole and Tracemaker*

Regarding the nature of the borehole, abiotic factors such as abrasion as reported by Gorzelak et al. (2013) can be discounted for several reasons. First, the deposit in which the specimen was collected is fine grained and thus does not likely reflect significant transport or strong mechanical abrasion. The taphonomic characteristics of the fossil assemblage also preclude an abrasion-induced hole. Finally, the shape, as well as the ratio between its size and thickness, suggests that the valve would have been broken well before an abrasion-produced drillhole could have developed.

When considering potential biological factors, diverse ecological interactions between polyplacophorans and other organisms occur. Among these, the bivalve *Lithophaga aristata* has been reported to bore non-predatory holes in chiton plates (Bullock and Boss 1971). After the initial penetration of the shell, the bivalve bores horizontally, with the resulting holes dissimilar to the one described herein.

Predatory interactions must also be considered. Chitons are a source of food for several marine taxa, including other mollusks, crabs, sea stars, and some vertebrates (e.g., Talmadge 1974; DeBevoise 1975; Bernárdez et al. 2000; Tan 2003). The size and overall features of the boring discussed herein are coincident with those produced by carnivorous gastropods and octopods in a variety of shelled prey (e.g., Carriker and Yochelson 1968; Wodinsky 1969; Bromley 1981, 1993; Kowalewski 1993; Harper 2002; Todd and Harper 2011). The presence of microrasping traces would provide direct evidence of the boring activity of these organisms (see Schiffbauer et al. 2008). However, its absence in the drillhole reported here may be due to the etching action that takes place during the drilling process, which can erase previous radular marks from the walls of the hole (Carriker 1969b; Tyler and Schiffbauer 2012).

The chiton shell discussed herein is thick enough to avoid the common difficulties of identification between naticid and muricid drillholes (see Carriker and Yochelson 1968; Bromley 1981). Modern muricid gastropods typically produce cylindrical boreholes, whereas those drilled by naticids have a spherical, paraboloid nature (typically assigned to *O. paraboloides*), tapering from a larger external opening to a much smaller internal opening (Fretter and Graham 1961; Bromley 1981).

Chitons are epifaunal, hard substrate dwellers. Muricids commonly prey on epifauna, preferring those living on hard bottoms. On the contrary, most naticids are infaunal and prey on mollusks within the sediment (see Carriker and Yochelson 1968; Kelley and Hansen 2003)

although rare instances of naticid epifaunal predation also occur. Thus, the ecological setting and the morphology of the trace fossil renders a naticid gastropod an unlikely producer of the trace.

Considering other inhabitants of the epifaunal zone, many octopuses share habitats with chitons in shallow waters and chitons have indeed been reported to be part of the diet of some *Octopus* species (Pilson and Taylor 1961; Wodinsky 1969; Ambrose 1984; Mather and Nixon 1990). The record of this isolated drilled plate could be attributed to the attack of a generalist predator, such as one of many octopod species. However, the presence of soft-bodied octopods in fossil assemblages like that of La Coronilla can only be assured by the unequivocal identification of their traces on shelled prey. Octopods are the only known producers of macroscopic *O. ovalis*, a distinctive ovoid drillhole (Bromley 1993; Harper 2002) that differs from the circular borehole in the chiton plate described here. However, octopods can also produce borings that are circular in outline and cylindrical in morphology (see Wodinsky 1969; Bromley 1993; Harper, 2002). According to Bromley (1993), circular octopod drillholes normally exhibit a rounded external edge and a somewhat more irregular form than the predation holes produced by muricid gastropods. A short groove or gutter on the external periphery of the hole may also be present, a feature absent in muricid or naticid borings (Bromley 1993). *Oichnus simplex* on the bivalve *Venericor clarendonensis* from the early Eocene of England have been attributed to octopuses by Todd and Harper (2011). These drillholes have slightly irregular margins; particularly that of the inner perforation. Thus, we consider an octopod an unlikely producer of the trace as the borehole presented here lacks the characteristics described for circular octopod drillholes.

The sharp circular outline and smooth edges of the drillhole presented here are more likely to have been produced by a muricid gastropod than a naticid or an octopod. In fact, we recently found *Urosalpinx haneti* (Petit de la Saussaye, 1856) in the mollusk assemblage at La Coronilla, a muricid which belongs to the subfamily Ocenebrinae. Although we found no literature concerning the drillholes produced by this particular taxon, the borehole we report here is similar to material described by Carriker (1969a) based on modern observations of the North American species *Urosalpinx cinerea* on *Crassostrea virginica*. Thus, taking into consideration all of the information available, it is proposed herein that *U. haneti*, or a similar muricid, produced the drillhole observed. We were able to examine *Oichnus* specimens found on oysters in the La Coronilla assemblage reported by Lorenzo and Verde (2004). Although the authors classify all of them as *O. paraboloides*, those placed on thick shells are morphologically similar to that reported here, and should instead be

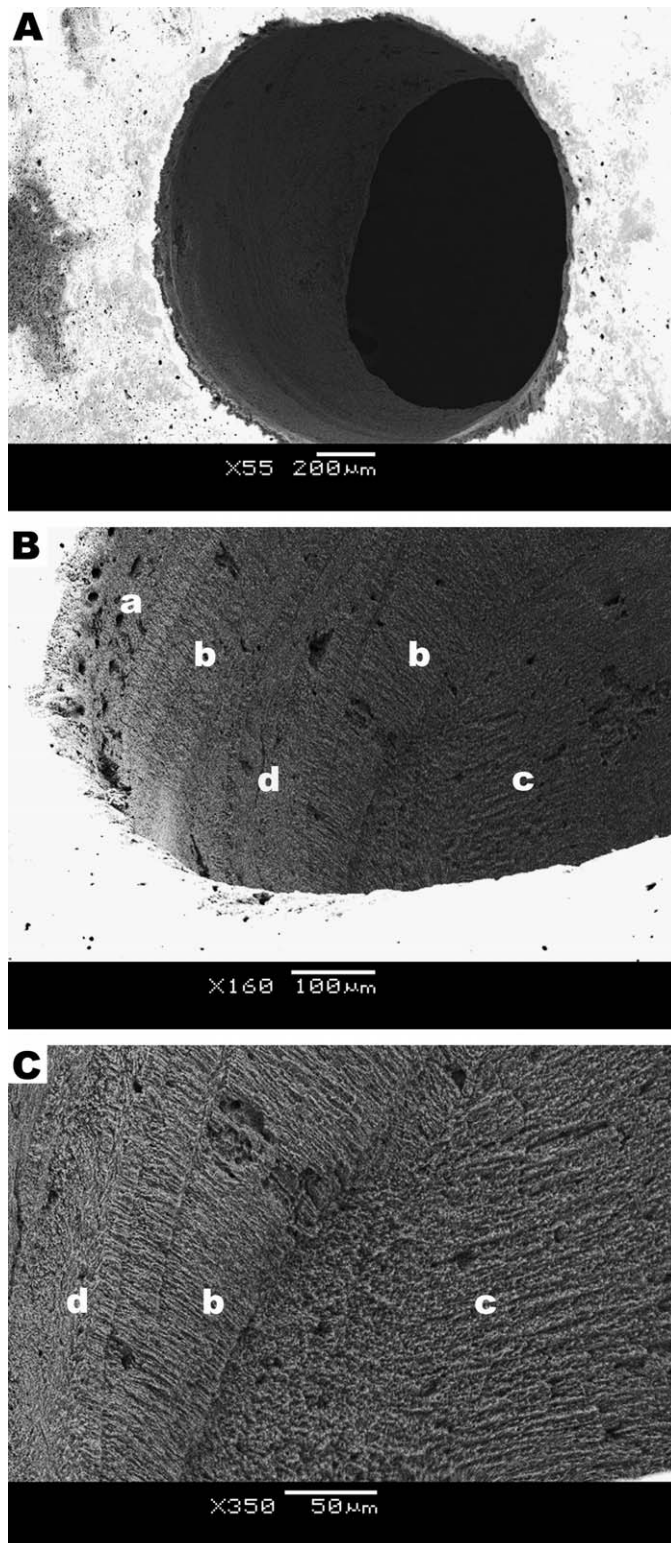


FIG. 3.—Uncoated scanning electron microscope images of the drillhole. **A**) Image of the drillhole. **B**) Close-up of the external surface of the valve and drillhole wall. **C**) Close-up of the drillhole wall showing the ultrastructure of the chiton shell (according to Laghi and Russo 1978) and the absence of radular marks. a = Tegmentum; b = Myostracum paleale; c = Hypostracum; d = Articulamentum.

included within *O. simplex*. These traces were also probably produced by *U. haneti* or a similar muricid. The geographic distribution of *U. haneti* ranges from Espírito Santo, Brazil to Puerto Belgrano, Argentina (Costa 1993). It occurs from the intertidal zone to a depth of 22 m, over and under rocks, lodged in crevices (Costa 1993). However, the current presence of this species on the coast of Argentina is doubtful (see Aguirre 1993). Ríos (1994) identified this species on rocky and calcareous aggregations feeding on mussels and oysters. In Uruguay, *U. haneti* lives today in consolidated substrates of the Atlantic coast, probably not beyond a depth of 20 m (see Scarabino et al. 2006). Demicheli and Scarabino (2006) reported the mytilid *Mytilus edulis* as the first prey recorded for this species in Uruguayan waters.

Although chitons have not been reported to be preyed upon by *U. haneti*, polyplacophorans have been found in the diet of muricids mostly by the analysis of gut content and/or field observation (e.g., Lewis 1960; Talmadge 1975; Hoffman and Weldon 1978; Taylor and Morton 1996; Tan 2003). Talmadge (1975) observed the attack of *Cryptochiton stelleri* by *Ocenebra lurida* (= *Ocenebrina lurida*) by rasping pits in the girdle of this chiton that bears internal valves. Similarly, Hoffman and Weldon (1978) noted that specimens of *Purpura patula* (= *Plicopurpura patula*) flipped over the chiton *Acanthochiton granulata* (= *Acanthopleura granulata*), reaching the viscera by making a hole through the foot. It is noteworthy that the authors use “drilling (eaten) a hole” (Hoffman and Weldon 1978, p. 364) to describe the behavior even though they refer to soft parts. Taylor and Morton (1996) mention that minor prey items such as the chiton *Acanthopleura japonica* (= *Liolophura japonica*) were drilled during feeding by the muricid *Thais clavigera* (= *Reishia clavigera*). Unfortunately, the specimens referenced in that paper are no longer available to compare the drillholes and to confirm that these were made through the shell of the chiton (J.D. Taylor, personal communication, 2013).

#### *The Cause of the Drilling: Predation or Anomalous Behavior?*

All morphological features are concordant with predation as the origin of the borehole (penetration from the shell exterior, perpendicular penetration of the shell surface, regular circular shape (e.g., Carriker and Yochelson 1968; Kowalewski 2002)). However, if we consider the novelty of this finding in the fossil record, the explanation for the cause of the drilling may not be that straightforward, particularly if we extrapolate from modern observations. Polyplacophorans and gastropods overlap in the littoral zone where predator-prey interactions are a fruitful subject of ecological research, but reports on their trophic relationship remain scarce and poorly described, with drillholes being rare as the result of this interaction. In addition, considering that muricids are versatile predators (see Harper and Peck 2003) that could more easily have access to the soft parts of a chiton than to other prey, why bore through a thick shell? The fossil assemblage at La Coronilla includes abundant oysters, many of which exhibit drillholes (Lorenzo and Verde 2004; A. Rojas, personal observation, 2013). Therefore, muricid gastropods probably had a high availability of other more abundant victims to prey upon. In this scenario, the putative attack to the chiton can be considered fortuitous or opportunistic with the lucky preservation of the bored chiton plate.

Still, there is another possibility to consider. The fossil record of drillholes and the study of recent predation show some anomalous behaviors. While describing the attack of *U. cinerea* on *C. virginica*, Carriker (1969a, p. 61) says that “in a dense mixed population of living and dead oysters, it will occasionally bore through a dead shell, and infrequently from the inside out, apparently unable to distinguish clearly the living from the non-living animals because of their close proximity”. Simões et al. (2007) considered erroneous attack on empty dead shells as one possible explanation for the rare occurrence of drillholes on brachiopod shells. Also, the same behavior has been documented for

other marine invertebrates like crabs (Walker and Yamada 1993). Thus, in the light of the novelty of this finding, the drilled chiton plate could have been the result of arbitrary drilling on a shell by a nonselective/opportunistic scavenger or predator rather than an instance of targeted predation.

Finally, predatory or not, the drillhole reported herein represents putative evidence of an ecological interaction between chitons and muricid gastropods that extends back to the Pleistocene. Focused studies in fossil assemblages as well as in recent littoral marine communities will resolve whether this record represents an exceptional or an understudied behavior between two relatively common marine molluscan taxa.

#### CONCLUSIONS

The analysis of the La Coronilla Late Pleistocene invertebrate assemblage in Uruguay yielded a drilled *C. angulata* intermediate plate. The borehole is identified as *O. simplex*. The morphology of the boring and the faunal and environmental context support the interpretation that this trace fossil was produced by a muricid gastropod. The tracemaker could have been the ocenebrinid *U. haneti* of which body fossils are found in the La Coronilla assemblage. Although the drillhole may have had a predatory origin, the rarity of this finding indicates that it may have originated from arbitrary drilling by a nonselective scavenger or predator. Further material and focused analyses of modern marine settings are necessary to assess whether this behavior represents evidence of understudied ecological interactions between chitons and gastropods.

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