



Drill hole predation on tubes of serpulid polychaetes from the Upper Cretaceous of Cuba



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ABSTRACT

The fossil record of drill holes in shelled invertebrates is focused primarily on bivalves and gastropods as prey. The still limited reports on drill holes in serpulid polychaetes are principally recorded from Cenozoic deposits and restricted to Europe and Antarctica. This study documents drill holes on the serpulid polychaete *Pyrgopolon onyx* from the Upper Cretaceous (Maastrichtian) of Pepito Tey (central Cuba). The oval-shaped drill holes, attributed to the ichnospecies *Oichnus ovalis*, were primarily caused by naticid gastropods, probably by individuals of *Gyrodes* sp. known from the same formation. Using five methods, the study on an assemblage of 53 non-moldic specimens shows that >17.0 and <22.2% of the specimens was drilled. This narrow range suggests that these methods can be used successfully for any time period for cylindrical shells including serpulids and scaphopods, if the specimens of the sample are reasonably well-preserved. Drill holes were randomly positioned with respect to the side of the tubes, but drill holes are preferentially located between the ribs and in the middle part to slightly towards the posterior end of the tube, suggesting that naticids selected the drill hole location efficiently on polychaetes with ornamentation already by the Cretaceous. The reasons for drilled tubes of *P. onyx* are probably related to the withdrawal of their soft body deep inside the tube and/or because of the presence of a calcareous operculum closing off the aperture. The record of drilling predation in *Pyrgopolon* is restricted to Cretaceous deposits, which may represent a bias in predation research focused only on Cretaceous specimens. More research on drilling predation of serpulids should be performed to better understand the function of ornamentation in deterring drilling, to determine how common drilling was on serpulids in deep time, and to evaluate the paleobiogeography of drilling predation.

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1. Introduction

The fossil record of predation in marine invertebrate shells has received a considerable interest because predator–prey interactions provide insight in paleoecological reconstructions, evolutionary trends, and behavior of predators (e.g., Kitchell et al., 1981; Kelley and Hansen, 1993; Kelley et al., 2001; Kowalewski et al., 1998; Harper et al., 2011; Huntley and Kowalewski, 2007; Martinell et al., 2010; Chattopadhyay et al., 2013; Mallick et al., 2014; Klompmaker and Kelley, 2015). The most studied evidence of predation in the fossil record is the presence of holes drilled in invertebrate shells (e.g., Kabat, 1990; Kowalewski et al., 1998; Klompmaker et al., 2013), mainly in bivalves and gastropods (e.g., Kabat, 1990; Kelley and Hansen, 2003; Klompmaker, 2009; Klompmaker and Kelley, 2015). However, drill holes occasionally have also been documented from other groups such

as scaphopods, ostracods, decapod crustaceans, barnacles, brachiopods, echinoderms, chitons, and serpulid polychaetes (Yochelson et al., 1983; Reyment et al., 1987; Leighton, 2003; Złotnik and Ceranka, 2005; Klompmaker, 2011; Martinell et al., 2012; Johnsen et al., 2013; Klompmaker et al., 2013, 2014, 2015; Rojas et al., 2014). Currently, only a few studies have reported on predation of serpulids, mostly on drill holes in Cenozoic serpulids: Eocene (Savazzi, 1995), Miocene (Sanfilippo, 1999), Pliocene (Sanfilippo, 1999; Klompmaker, 2012; Martinell et al., 2012), and Holocene (Morton and Harper, 2009; Morton and Salvador, 2009). Furthermore, only two detailed studies exist, both on Cenozoic serpulids (Klompmaker, 2012; Martinell et al., 2012). From Mesozoic deposits, we only know of a study by Müller (1969) documenting some drill holes in polychaetes from the Maastrichtian of Belgium, whereas other works only briefly mentioned holes in Cretaceous serpulids (Jäger, 1983; Macellari, 1984; Savazzi, 1995; Jäger and Kočí, 2007; Seilacher et al., 2008). Additionally, studies on drilling in serpulid polychaetes are restricted to European and Antarctic deposits thus far. Thus, Klompmaker (2012) emphasized the need for more studies and expressed that drill holes in fossil serpulids

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would be expected in assemblages from other regions to improve both the temporal and geographic coverage of this predator–prey interaction. Here we report on and assess new evidence of drill holes on tubes of *Pyrgopolon onyx* Morton, 1834, from the Pepito Tey locality, Cantabria Formation, Upper Cretaceous (Maastrichtian) of central Cuba. We also compare and contrast drilling predation to previous studies and a potential predator is inferred.

2. Geological and geographical setting

The specimens come from a small deposit of the Cantabria Formation at the Pepito Tey locality, Cienfuegos province, central Cuba (Fig. 1). The Cantabria Formation forms part of the infill of the Cienfuegos sedimentary Basin. The formation was first named and described by Kantchev et al. (1978) and its deposits are only exposed in the Cienfuegos province. The unit is assigned to the Cretaceous (upper Maastrichtian) based on its foraminifers and rudist associations (Seiglie and Ayala-Castanares, 1963; Kantchev et al., 1978; Rojas-Consuegra,

2004; Lex, 2013). The occurrence of the ammonite *Pachydiscus neubergicus* (von Hauer, 1858) indicates an age not younger than the early late Maastrichtian for a part of this unit (Kantchev et al., 1978; Pszczółkowski, 2002).

The deposits of the Cantabria Formation consist principally of biogenic, thick-bedded to massive limestones consisting of biocalcarenites and biocalcirudites. Sandy limestones, marls, and nodular limestones also occur (Kantchev et al., 1978; Pszczółkowski, 2002; Lex, 2013). The fauna of this unit is composed principally of large benthic foraminifers, gastropods, algae, bivalves, ammonites, corals, tube worms, and echinoids (Kantchev et al., 1978). Among the bivalves, the unit is known for its abundant rudist fauna (Kantchev et al., 1978; Rojas-Consuegra, 2004). The deposits of the Cantabria Formation have been interpreted as a neritic marine sequence (Rojas-Consuegra, 2004; Lex, 2013).

The tubes of the polychaete *P. onyx* reported here are found in a biodetritic, sometimes friable, calcareous clay marl. The fossils were found associated with orbitoid foraminifers and echinoids. In Cuba, *P. onyx* was previously recorded from Upper Cretaceous rocks of the San Pedro and Cantabria Formations by Kantchev et al. (1978).

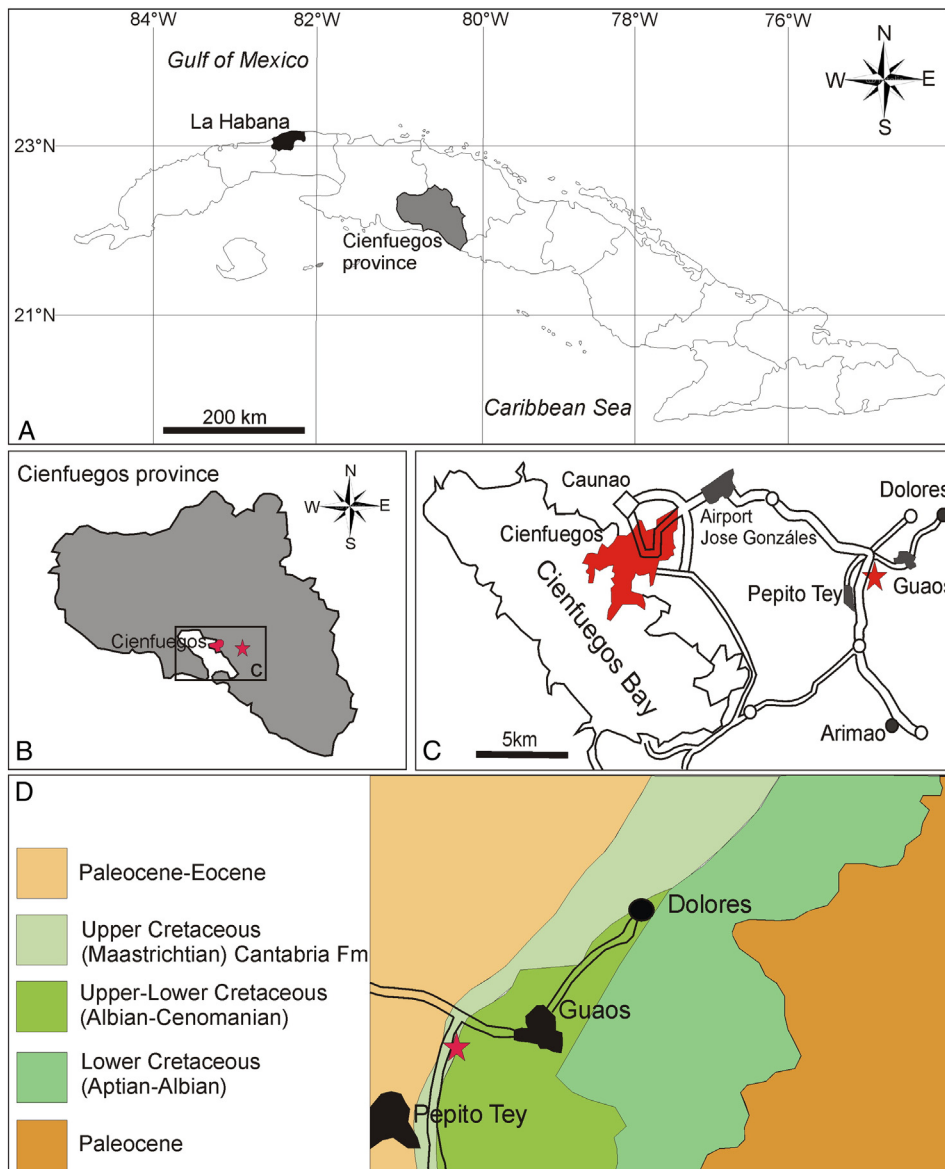


Fig. 1. Geographic location (A–D) of the study area (star) and the geological setting (D) of the Cienfuegos province, central Cuba.

Bermúdez (1950) mentioned its presence in rocks from the Paleocene, but those specimens were interpreted to be redeposited from the Upper Cretaceous Madruga Formation.

3. Material and methods

The studied material is housed in the paleontological collection of the Museo Nacional de Historia Natural de Cuba (MNHN Cu) under number MNHN Cu-9656. The studied specimens were discovered in the museum collection. All tubes were collected regardless of size and presence of drill holes in 1998 by Reinaldo Rojas-Consuegra. The material consists of 61 tubes with different degrees of preservation: fragmented (27), nearly complete and complete (26) tubes, and internal molds (8). Only the specimens with the shell preserved (53) were used for further analyses. For better observation of the polychaete tubes and the drill holes, the specimens were cleaned in an ultrasonic bath, the in many cases of the 20 specimens used it was not possible to remove the sediment remains and the infill of the tubes. Thus, the method of Martinell et al. (2012) to use the weight of tubes to estimate the total number of specimens and, subsequently, the predation intensity could not be used.

For each serpulid tube, the length was measured for three modes of preservation (Fig. 2): complete tubes (posterior and anterior end points are preserved), nearly complete tubes (posterior and anterior end points are partially preserved), and fragmented tubes (a substantial part of the tube is missing). Given the fragmentary nature of the tubes, we used the methods proposed by Klompmaker (2012) to estimate the true number of specimens. Furthermore, the tube diameter of the aperture was measured (note that this measurement estimates the true maximum width only in the case of complete specimens or fragments that preserve the anterior end point of the tube) and the number of ribs per tube was recorded. For each drilled specimen, the number of drill holes per tube was also noted.

For each drill hole, the following data were collected: (1) whether drill holes were incomplete or complete, (2) maximum outer diameters, and (3) maximum inner diameters (Fig. 2). The latter two were measured along of the longitudinal axis of the tube using a caliper. The profiles of the drill holes were determined using a microscope. For the ichnotaxonomy of the drill holes, we follow Wisshak et al. (2015).

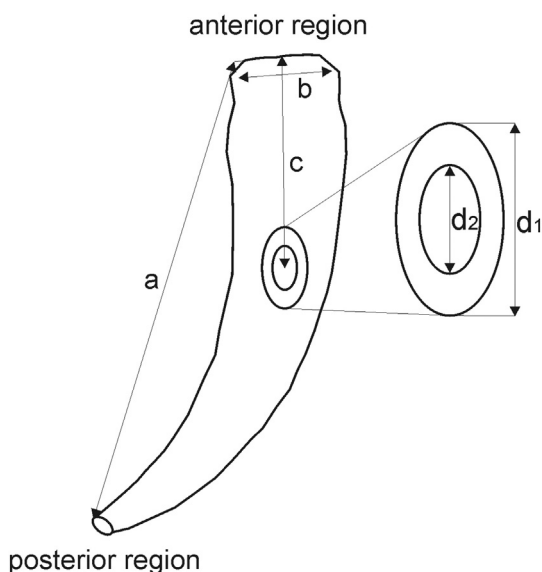


Fig. 2. Biometric measurements used in this study for the tubes of *Pyrgopolon onyx* and drill holes. (a) Tube length; (b) Maximum tube diameter; (c) Drill hole location relative to aperture; (d1) Maximum outer drill hole diameter; (d2) Maximum inner drill hole diameter.

The position of the drill hole was determined by measuring the distance from the anterior aperture tube to the drill hole to identify whether a part of the tube is preferentially drilled (Fig. 2) (only for complete and nearly complete specimens). The location of the drill holes with respect to the ribs and the side (lateral, concave, or convex) of the tube was also recorded.

The drill hole predation percentage was obtained using several methods (see also Klompmaker, 2012). The number of specimen was estimated as follows: (1) The total number of non-moldic specimens of the sample was counted regardless of their preservation. (2) The total length of all specimens combined was divided by the average length of complete and nearly complete specimens. (3) The number of specimens with apertures preserved was counted. (4) Only specimens with drill holes and apertures preserved were divided by the total number of specimens with apertures preserved. A fifth method uses only complete to nearly complete tubes. For all methods, the drilled specimens were divided by the estimated number of specimens and multiplied by one-hundred. The results were compared to obtain an accurate range of drilling percentages.

4. Results

4.1. Morphology and taxonomy of the serpulids

Specimens of *P. onyx* have never been described from the Cantabria Formation so we here provide a brief description. The white to gray tubes are conical, slightly curved, open on both ends, and hexagonal in external cross-section (Fig. 3). The inner surface of the tube exhibits fine lines laterally. The external surface is composed of six prominent subcircular ribs (Fig. 3Q) that extend longitudinally from the base to the apex of the tube. A narrow intercostal furrow is present between ribs (Fig. 3). Faint concentric growth lines are also visible laterally. These transverse or incremental fine lines are numerous in the majority of the individuals. The diameter of the tube increases towards the apex (anterior aperture). The complete to nearly complete tube length ranges from 7.5 to 16.3 mm (Appendix 1). The anterior aperture diameter of the tube ranges from 1.5 to 2.4 mm.

The morphology of the tubes, with the six longitudinal ridges, transverse ribs, and a semi-circular shape in cross-section allows us to assign the tubes to *P. onyx* (see Ten Hove and Kupriyanova, 2009, and Jäger, 2012, for diagnosis). Tubes of this morphology were previously attributed to *Hamulus onyx* described by Morton (1834) from the USA (Alabama and South Carolina), but the genus *Hamulus* was synonymized with *Pyrgopolon* De Montfort, 1808 (Jäger, 1993, 2004).

4.2. Morphology and location of the drill holes

The drill holes are found in fragments (4) and nearly complete (2) to complete (2) tubes of *P. onyx* and are preserved as complete drill holes. Each drilled specimen displays a single drill hole. The holes have an oval outline, with an outer diameter that is larger than the inner diameter (Fig. 4). One of the drill holes is located on the broken edge of a specimen and is preserved with an incomplete oval outline (Fig. 3N). The holes are parabolic in cross section (curved walls leading to a counter-sunk morphology). The outer edge is clearly defined (Fig. 4). The drill holes invariably exhibit an orientation with their long axis parallel to the posterior–anterior axis of the tube (Fig. 3H–N). The maximum outer diameter ranges from 1.03 to 1.43 mm (mean = 1.19 mm) (Appendix 2). The maximum inner diameter varies from 0.71 to 1.09 mm (mean = 0.87 mm). Three drill holes occur on the lateral sides of the tube, three on concave side, and two on the convex side. All drill holes are located between the ribs in the intercostal furrow (Fig. 3H–N). The drill holes are located preferentially towards the nearest half of the narrow end of the tube (Fig. 3). In nearly complete to completely drilled tubes (4), the drill holes are located 6.2 mm (tube length



Fig. 3. A sample of the studied specimens of *Pyrgopolon onyx* from the Upper Cretaceous (Maastrichtian) of the Pepito Tey locality, central Cuba. A–E. Nearly complete and complete specimens used to estimate the average length of specimens. F, G. Sample fragments of the specimens that preserve the anterior and posterior end, resp. H–N. Specimens with complete drill holes showing the location of the holes in the intercostal furrows in the middle to lower part of the preserved tube. The oval drill holes have a smaller inner than outer drill hole diameter (H–M). N. A drill hole on the edge of a broken specimen. O. Cross-sectional view of a specimen showing the six ribs. P. Internal mold of one of the tubes. Scale bars are 2 mm wide. Collective museum number: MNHNCu-9656.

10.2 mm), 7.0 mm (length 10.1 mm), 5.7 mm (length 9.2), and 6.3 mm (length 11.8 mm) from the anterior end of the tube.

4.3. Drill hole predation percentages

The number of drilled specimens (8) divided by the total number of non-moldic specimens (53) yielded an drilling percentage of 15.1% (Method 1). The total length of the 53 tubes taken together is 504.2 mm (mean length of 9.5 mm per specimen, length range of 4.5–16.0 mm). The mean length of the 26 nearly complete and complete specimens (Fig. 3) is 10.6 mm, with a range of 7.4–16.0 mm. This yields an estimated ~47 specimens for the sample, resulting in a drilling percentage of 17.0% (8/47) (Method 2). The total number of tubes with

the aperture preserved is 36 (total minimum number of specimens estimated), yielding an estimated maximum drilling percentage of 22.2% (8/36) (Method 3). Moreover, of the 36 specimens with the aperture preserved, five possess a drill hole (13.9%, Method 4). Using only complete to nearly complete tubes yields a drilling percentage of 15.4% (4/26) (Method 5). Thus, the range of drilling percentages based on the five methods is >17.0 to <22.2% (Table 1).

5. Discussion

5.1. Ichnotaxonomy of the oval drill holes

The morphology of the drill holes as rounded in outline and penetrating through the shell supports assignment to *Oichnus* (see Wisshak et al., 2015, for diagnosis). The parabolic profiles and the outer diameter that is larger than the inner one suggests that the drill holes can be ascribed to *Oichnus paraboloides* Bromley, 1981 (see Bromley, 1981, for diagnosis), but the holes studied herein are oval in outline as is the case for *Oichnus ovalis* Bromley, 1993 (see Bromley, 1993, for diagnosis), an ichnotaxon usually ascribed to drill holes produced by octopods (e.g., Bromley, 1993; Harper, 2002; Klompaker et al., 2014, 2015). The longer axis of the oval holes is always oriented parallel to the longitudinal axis of the tube in *P. onyx*. This characteristic of drill holes in serpulid tubes is a geometric effect: larger drill holes tend to become more oval in similar-sized cylindrical shells. The cylindrical morphology of the tube leads to the distortion of the typical circular morphology of the hole (Yochelson et al., 1983, for scaphopods; Morton and Harper, 2009; Klompaker, 2012; Martinell et al., 2012). Martinell et al. (2012) determined that this geometric artifact is better expressed in larger holes relative to the tube so that the effect of curvature of the tube is more pronounced. For that reason, they assigned their drill holes to *O. paraboloides*. However, this pattern was not identified in our specimens because drill holes are relatively small compared to the width of tube. Instead, the drilling organism selected the empty space between the ribs resulting in oval drill holes dictated by ornamentation. Therefore, it could be argued that these oval drill holes were caused by the behavior of the drilling organism in conjunction with the morphology of the ribs. In ichnotaxonomy however, the prime criterion for ascription to an ichnotaxon is the morphology of the structure and behavior of the producer is irrelevant (Bertling, 2007). For that reason, ascription to the ichnospecies *O. ovalis* seems more appropriate in this case.

5.2. The nature of the drill holes

The drill holes could be caused by predation or by a parasite, by association with an endolithic organism, or abiotically. The features of the holes in *P. onyx* from the Late Cretaceous (Maastrichtian) of Cuba suggest predation as the cause. They are the single perforations, the penetration axis is perpendicular to the surface of the tube, the hole was produced from the outside given the smaller inner diameter, the holes are positioned non-randomly on the tube (stereotypy), and the lack of a widely-ranging sizes of the holes all point to predation (Baumiller, 1990; Kowalewski, 2002; Harper, 2003; Kelley and Hansen, 2003; Daley, 2008).

5.3. The predator

Drill holes are caused by different groups including naticids, muricids, nudibranchs, pulmonates, platyceratids, cassids, eulimids, capulids, nassarids, marginellids, buccinids, nematodes, flatworms, and octopods (e.g., Bromley, 1993; Kowalewski, 2002; Kelley and Hansen, 2003). It is notoriously difficult to assign drill holes to a particular producer with any degree of certainty (Bromley, 1981). However, it is possible to make a number of deductions that, in this case, can indicate a most likely predator. The morphology of the drill holes in *P. onyx*, with a parabolic profile in cross-section, countersunk, and with outer

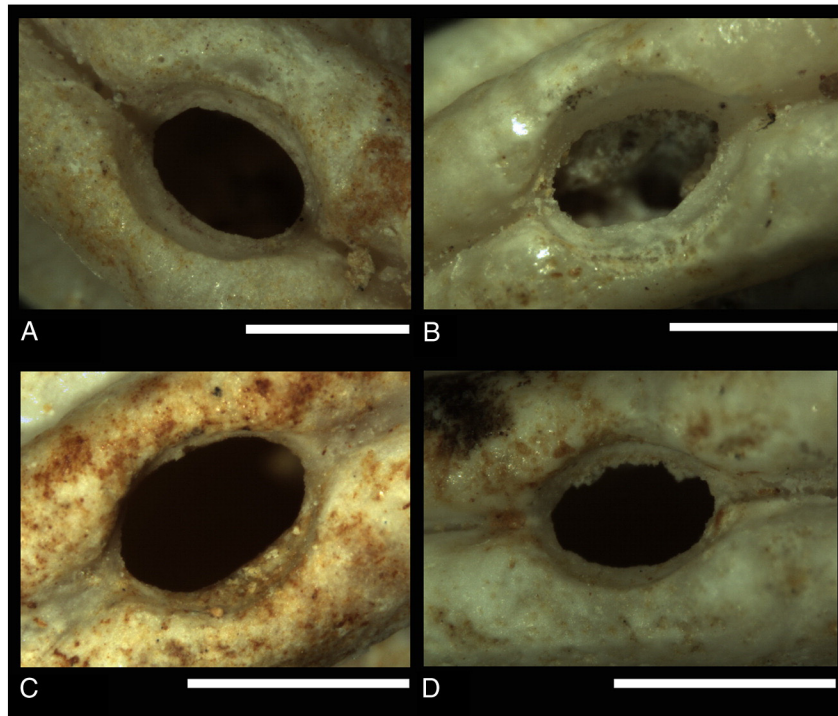


Fig. 4. Complete drill holes in *Pyrgopolon onyx* from the Upper Cretaceous (Maastrichtian) of the Pepito Tey locality, central Cuba. A–D. Close-ups of the holes from the specimens in Fig. 3H, 3J, 3K, and 3L. Scale bars are 1 mm wide.

drill hole diameters that are greater than the inner diameter are consistent with drill holes produced by a naticid predator (Bromley, 1981; Carriker, 1981, Kabat, 1990). The diameter of drill holes in *P. onyx* (1.0–1.2 mm) is also consistent with the size range of the drill holes produced by naticids (0.3–8.0 mm, Kowalewski, 1993). Drill holes with a similar morphology and size have also been recorded from serpulids and were attributed to naticid predation (Müller, 1969; Morton and Harper, 2009; Morton and Salvador, 2009; Klompmaker, 2012; Martinell et al., 2012). Klompmaker (2012) suggested that the drill holes in the serpulid *Ditrupa cf. arietina* (Müller, 1776) from the Pliocene of the Netherlands could be produced by small naticid specimens, probably juveniles, given the relatively small size of drill holes in serpulids compared to drill holes in bivalves. Naticids are also known to drill modern specimens of *Ditrupa*: Morton and Harper (2009) inferred that the naticid *Natica prietoi* Hidalgo, 1873, is the probable predator of specimens of *Ditrupa arietina* collected from the mid-Atlantic Azores, Portugal. Naticids are known from the Cantabria Formation. Kantchev et al. (1978) recorded specimens of *Gyrodont* sp. among its gastropod fauna. Thus, *Gyrodont* sp. is a plausible candidate as the tracemaker of the drill holes in *P. onyx* from the Maastrichtian of Cuba.

Table 1

A summary of the estimated drilling percentages for a sample of *Pyrgopolon onyx* from the Upper Cretaceous of Cuba based on five methods. The drilling percentages obtained by Klompmaker (2012) for much more fragmented specimens of *Ditrupa cf. arietina* from the Pliocene of the Netherlands are also shown for comparison.

	Total number of estimated specimens in the sample		Estimated drill hole predation percentage (%)	
	This work	Klompmaker (2012)	This work	Klompmaker (2012)
Method 1	53	915	15.1	9.5
Method 2	47	499	17.0	17.4
Method 3	36	140	22.2	62.1
Method 4	36	140	13.9	18.6
Method 5	47		15.4	

5.4. Comparisons of the drilling predation percentage

The first method resulted in a drilling percentage of 15.1%. The studied sample is not very large, but relatively well-preserved with abundant specimens that are complete to nearly complete (49%). However, some specimens of the sample are fragmented suggesting that the percentage may exceed 15.1%. The second method yields a higher percentage of 17.0%. The assumptions to be met for this method to work (Klompmaker, 2012) are: (1) all the drilled specimens exhibited only one complete drill hole per tube, (2) the specimens were randomly collected from the entire population, (3) the average length of complete serpulid tubes is comparable to the average length of specimens from the entire population, and (4) all the specimens can be ascribed to *P. onyx*. Only the third assumption is not met completely here because fragmented specimens with the anterior end preserved have a significantly larger reconstructed length on average than the complete to nearly complete specimens (Mann-Whitney $U = 43$; $p = 0.002$). The actual specimen length was reconstructed using the formula of the significant positive length/width relationship of complete specimens ($y = 9.016 \times -6.2642$, $R^2 = 0.78$, $p = 0.002$, Appendix 1). The average length is greater implying that the total number of specimens may be lower. Thus, the drilling percentage is probably $>17.0\%$.

In the third method, only specimens with the aperture preserved (36) were used to estimate the number of specimens yielding a drilling percentage of 22.2%. The assumptions for this method are (see Klompmaker, 2012): (1) only one drill hole per tube is present for complete specimen, (2) the samples were selected randomly, (3) the fragments or a part of the fragments are not broken so that they are become unrecognizable. The last assumption may not be met, implying that a part of the apertures have not been preserved in some specimens (18). The number of specimens estimated this way is, however, a minimum so that the actual number of specimens may be higher. Thus, the drilling percentage is likely $<22.2\%$. Taking into account only specimens with the aperture preserved (Method 4) yielded an estimated drill hole predation percentage of 14.3%. This may be an underestimation because drill holes may have been present in the absent parts of the posterior

end. Thus, the true drilling percentage could be >14.3%. The fifth method, by using only complete specimens, yielded a percentage of 15.4%. Once again this may be an underestimation because drill holes may weaken the serpulid shell (see Klompmaker, 2012, chapter 6.3.).

Based on the five methods used, the range for the estimated drilling percentage is >17.0 and <22.2%, which is higher than if only complete specimens were to be used (15.3%). Given the highly fragmentary nature (99%) of Pliocene *Ditrupa* cf. *arietina* from the Netherlands, Klompmaker (2012) obtained a much wider range based on four methods (>18.6 to <62.1%) (Table 1). The author mentioned that the methods are expected to result in a narrower range for samples that contain a higher percentage of complete serpulids. This is exemplified herein because the sample consists of a relatively high percentage of complete to nearly complete serpulid tubes (49%) resulting in a much narrower range.

5.5. Comparison to other studies of drilled serpulids

We note similarities and differences with previous studies on predation in recent and fossil serpulid polychaetes. The drill holes in *P. onyx* are preserved as complete holes and are always single, suggesting that successful drilling predation dominated this sample. Complete holes and the presence of only one drill hole per serpulid tube is also common in extant and fossil serpulids of *Ditrupa* Berkeley, 1835 (Morton and Harper, 2009; Klompmaker, 2012; Martinell et al., 2012). Incomplete drill holes and the presence of multiple complete drill holes in a same tube have been recorded in only a few specimens of this genus (Morton and Harper, 2009; Klompmaker, 2012; Martinell et al., 2012), suggesting that predators failed on occasion (Morton and Harper, 2009).

We estimate that the drill holes are located in the middle part to slightly towards the posterior end for four specimens of *P. onyx* (Fig. 3H–K). Naticid drilling in the central part of fossil and extant serpulid tubes is also reported in specimens of *Ditrupa mosae* (Bronn, 1837) (Müller, 1969) and *Ditrupa arietina* (Sanfilippo, 1999; Morton and Harper, 2009), respectively. Martinell et al. (2012) suggested anterior side-stereotypy for drill holes in *D. arietina*. Although sample size is limited for the polychaete tubes from the Maastrichtian of Cuba, no preference seems to exist for a particular side of the tube (lateral sides: 3; concave side: 3; convex side: 2), as was the case in for Pliocene *Ditrupa* from the Netherlands (Klompmaker, 2012). In contrast, the concave and convex sides were preferentially drilled in other fossil specimens of *Ditrupa* (Müller, 1969; Morton and Harper, 2009).

Only one specimen of *P. onyx* was found with a broken drill hole due to fragmentation of the tube through the drill hole. Frequent breakage across drill holes has been reported for specimens of *Ditrupa*, including a discussion of its potential biases (Klompmaker, 2012; Martinell et al., 2012). In *P. onyx*, the thick ribs on the external surface of the tube may have reinforced the tube wall, decreasing the possibility of breakage through the hole. Moreover, the holes are relatively small compared to the tube diameter. By contrast, the tubes of *Ditrupa* possess a thin wall and smooth external surface (Sanfilippo, 1999; Morton and Harper, 2009; Klompmaker, 2012). The outer diameter of the holes in the specimens from the Cuba (range: 1.03–1.43 mm) are overlapping with drill holes in specimens of *Ditrupa* cf. *arietina* from the Netherlands (range: 0.6–2.0 mm; Klompmaker, 2012), *D. arietina* from Spain (range: 0.58–1.69 mm, Martinell et al., 2012), and *D. mosae* from Belgium (range: 1.0–1.3 mm, Müller, 1969). This suggests that similar-sized predators caused these drill holes.

5.6. Drill holes and tube ornamentation in *Pyrgopolon*

The drill holes are found between the six longitudinal, thick ribs in *P. onyx* (Fig. 3). Drilling between ribs has not been clearly recorded on serpulids because most studies have focused on the smooth-walled *Ditrupa* (see Morton and Harper, 2009; Fig. 1; Klompmaker, 2012; Fig.

3; Martinell et al., 2012; Fig. 4). Jäger and Kočí (2007) briefly mentioned drill holes in the serpulid *Placostegus velimensis* Jäger and Kočí, 2007, from the Upper Cretaceous (Turonian) of the Czech Republic, but they did not report on the position of the drill holes relative to the longitudinally keel-shaped structures. Drilling between ribs by naticids is known from bivalve and ostracod prey (Arua and Hoque, 1989; Simões et al., 2007; Ottens et al., 2012; Klompmaker and Kelley, 2015). The latter authors conducted a study of drill holes in Cenozoic bivalves from the Netherlands and Florida. It was demonstrated that the presence of ribs influenced the drilling behavior of gastropod predators in that drill holes were predominantly sited between the ribs for bivalve with strong ribs, which saves energy and minimizes drilling time (see also Kitchell et al., 1986). These reasons probably explain the location of the drill holes in *P. onyx*, in which the shell thickness on the rib (0.64–0.98 mm) is greater than in the intercostal furrow (0.49–0.67 mm).

5.7. Drill holes and prey behavior

Predation of serpulids may occur through drilling the tubes or through feeding via the aperture, in which case the naticid inserts its proboscis into the opening of the tube to obtain food (Paine, 1963; Tan and Morton, 1998). Ten Hove (1994) explained that serpulids extend a number of radioles from the anterior end of the tube and normally occupy only the anterior part of tube, but they may withdraw deeply inside the tube when threatened. As a result of the latter, serpulid soft tissue may not be reached by inserting the proboscis in the anterior opening (see also Klompmaker, 2012, for Pliocene *Ditrupa*). This reason probably would explain the presence of drill holes in the tubes of *P. onyx* from the Maastrichtian of Cuba. Another reason for drilling this serpulid would be the presence of an operculum. Ten Hove (1994) expressed that the aperture can be closed with an operculum (a modified radiole) in some species of serpulids, protecting the animal against predators by blocking the tube entrance. Vinn and Ten Hove (2011) also suggested that the function of the operculum most probably is to protect the soft-bodied animal against predators. Specimens of modern *Pyrgopolon* are characterized by an entirely calcified opercular reinforcement (Ten Hove, 1973; Ten Hove and Kupriyanova, 2009). The calcareous operculum in *Pyrgopolon* has been recorded as early as the early Late Cretaceous (Lommerzheim, 1979; Cupedo, 1980; Jäger, 2004). Moreover, specimens of *Pyrgopolon*-like opercula have been recorded in deposits of different ages such as from the Eocene of Paris (Wrigley, 1951) and the early Oligocene of Italy (Rovereto, 1904). For *P. onyx*, a calcified, tack-shaped opercular structure is known with a three-pronged spike or tooth situated on the edge of the tack-head or basal circular plate, where the operculum is placed entirely behind the anterior margin of the aperture of the tube (Wade, 1926; Ten Hove, 1973). This structure was not found associated with specimens from the Maastrichtian of Cuba, probably due to the disassociation of the operculum from the tube shortly after death, but may have been present. The drill holes located approximately in the central region of the tubes could also be associated with the behavior the predator. The central part of serpulid tube is a favorite region to drill (Müller, 1969; Sanfilippo, 1999; Morton and Harper, 2009; see Section 5.5 above). Taking into account this data in polychaetes and the similar results obtained for fossil scaphopods, Klompmaker (2012) mentioned that naticids may have been able to locate the central position of the soft tissue in cylindrical tubes of *D. cf. arietina* after withdrawal of the animal inside its tube. This deduction may also apply to *Pyrgopolon* because this taxon also has a cylindrical morphology and drill holes in nearly complete and complete tubes are located approximately in the center of the tube.

5.8. Lack of study of drilling predation in *Pyrgopolon*

Drilling predation in specimens of *Pyrgopolon* has been recorded from Cretaceous deposits only. Specimens of the serpulid *D. mosae*

from the Maastrichtian of Belgium, including drilled specimens (Müller, 1969) attributed to naticids, were found in *Pyrgopolon clava* (Lamarck, 1818) (see Klompmaker, 2012: pers. Comm. M. Jäger to AAK, August 2010). Therefore, the drill holes reported from the Maastrichtian of Cuba represent the second record of predation of naticids in *Pyrgopolon*. Drilling predation on *P. onyx* after the Cretaceous is not expected because this species has been considered an index fossil for the Upper Cretaceous (Santonian to Maastrichtian) (Wade, 1921, 1926; Rutsch, 1939; Sohl and Koch, 1984; Housh, 2007). The record of drilling predation in other Cretaceous polychaete genera is, thus far, restricted to *Rotularia De France*, 1827, from the Campanian (Savazzi, 1995) and Maastrichtian (Jäger, 1983; Seilacher et al., 2008) of Seymour Island, Antarctica, in addition to drill holes in *Placostegus Philippi*, 1844, from the early Turonian of the Bohemian basin, Czech Republic (Jäger and Kočí, 2007). The restriction of predation to Cretaceous tubes of *Pyrgopolon* likely reflects a bias in research. Predatory drill holes in this genus should be expected from other periods and regions. Specimens attributed to *Pyrgopolon* are known from the Oxfordian (Jurassic) of the USA (Palmer et al., 2004), the Early Cretaceous and Eocene of France (Wrigley, 1951; Jäger, 2011), and the Late Cretaceous of Sweden (Sørensen and Surlyk, 2010), the Netherlands and Belgium (Jäger, 2012), the USA (Wade, 1921, 1926), Germany (Jäger, 1983), and the Czech Republic (Sklenář et al., 2013). However, most of these works are focused principally on taxonomic aspects. The absence of reports on predation in modern specimens of *Pyrgopolon* can be due to its biogeographic restriction and the few ecological studies available. The modern distribution of the genus is restricted to the tropical seas of the Americas: *Pyrgopolon ctenactis* (Mörch, 1863), from the US Virgin Islands (Saint Thomas), Caribbean, and tropical Pacific America; *Pyrgopolon differens* (Augener, 1922), from Barbados and Suriname; and *Pyrgopolon semiannulatum* (Ten Hove, 1973), from Barbados (Pillai, 2009; Ten Hove and Kupriyanova, 2009). Modern *Pyrgopolon* is understudied because the animals are difficult to find because their tubes are usually embedded into the substrate (Ten Hove and Kupriyanova, 2009). Thus, more research on extant and fossil *Pyrgopolon* is needed to assess whether drilling in tubes of *Pyrgopolon* is restricted to the Cretaceous.

6. Conclusions

The presence predatory drill holes (*O. ovalis*) in the serpulid *Pyrgopolon onyx* from the Cretaceous (Maastrichtian) of Cuba demonstrates that the restricted record of naticid predation on serpulids from Europe and Antarctica constitutes a geographical bias in research. Our research also increases the data on the diet of naticid gastropods in the Cretaceous because (1) the morphology of the drill holes resembles naticid drill holes and (2) naticids (*Gyrodès* sp.) are present in the same formation. The use of five different methods shows that drilling percentages for cylindrical shells such as serpulids and scaphopods can be determined successfully within a narrow range if specimens of the assemblage are reasonably well-preserved. Herein, the drilling percentage ranged from >17.0 to <22.2%, suggesting that *P. onyx* was a common prey for naticids.

The location of the drill holes between the ribs in tubes of *Pyrgopolon* probably demonstrates that this strategy of predation was utilized efficiently on polychaetes with ornamentation, as recorded in other groups with such ornamentation.

The reasons for drilling specimens of *P. onyx* may be the prey and predator's behavior and the morphology of the prey. In the case of danger, the prey's soft body may withdraw deep inside of the tube and an operculum may have closed off the aperture. The location of drill holes in the middle part of the tube to slightly towards the posterior end may indicate that naticids aimed for a spot where most soft tissue is located in these cylindrical tubes.

Drilling predation in *Pyrgopolon* is restricted to Cretaceous deposits, which likely represents a bias in predation research focused on Cretaceous specimens only. More research on drilling predation of serpulids

should be performed to understand the function of ornamentation in deterring drilling predation, to assess how common serpulids were as prey items for drillers, and to better document possible temporal changes in drilling predation.

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.palaeo.2016.05.009>.

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