# *Oichnus* Bromley as evidence of predator presence in the Canadian High Arctic

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Molluscan predators are rarely preserved in Late Pleistocene and Holocene marine sediments from the Canadian High Arctic. Predator-prey interactions in molluscan assemblages recorded as round holes in shells, recognized as the trace fossil *Oichnus*, are even less well known for Quaternary molluscan assemblages from the High Arctic. Because these biological interactions recorded in molluscan shells are an essential source of information for palaeoecological and environmental reconstructions, this study aims to identify *Oichnus* ichnospecies in bivalve shells to unveil the possible gastropod predators that were not recorded in Quaternary sediments from the Canadian High Arctic, particularly on Axel Heiberg Island (AHI). The whole assemblage consisted of a total of 3586 shells, where drilling frequency was 0.013 and prey effectiveness was 0.58. Boreholes were observed mainly in *Astarte borealis*, *Hiatella arctica* and *Mya truncata* (96% of the total assemblage) with a low drilling frequency. Those borings showed two different designs identified as *Oichnus simplex* and *O. paraboloides,* which could be produced by predatory gastropods belonging to the Naticidae and Muricidae families. The higher number of *O. paraboloides* observed in different prey species indicates that naticid gastropods produced a greater number of boreholes than muricid gastropods. These boreholes are preferentially located on the central area of *A. borealis* valves in the Late Quaternary bivalve shell assemblages from AHI. These findings provide evidence of predator-prey interactions, and therefore palaeoecological evidence that help us to understand the trophic structure of Late Quaternary benthic communities of the Canadian High Arctic. □ *Bivalves, drill holes, muricid, naticid, Quaternary, Axel Heiberg Island.*

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The Late Pleistocene-Holocene glacial and sea-level history of the eastern Canadian Arctic Archipelago (CAA) has been examined by several authors (Hodgson 1985; Bednarski 1986; Lemmen 1989; England 1990; Hein & Mudie 1991; Stewart 1991; Lemmen *et al.* 1994; Bell 1996; O'Cofaigh *et al.* 2000). However, there are few studies focused on the palaeoecology of marine invertebrates recovered from Late Quaternary raised marine sediments in this region (Dyke *et al.* 1996a; Aitken & Bell 1998; Gordillo & Aitken 2000, 2001). These studies analysed the presence and mode of preservation of the most common mollusc macrofossils in relation to sedimentary environments, comparing subfossil mollusc assemblages with the ecology of modern mollusc faunas observed in fjord and inner continental shelf environments in the CAA (Andrews 1972; Dale

*et al.* 1989; Syvitski *et al.* 1989; Aitken 1990; Aitken & Fournier 1993; Gilbert *et al.* 1993; Aitken & Gilbert 1996; Dyke *et al.* 1996a).

These studies found that benthic community composition from the CAA is influenced by local controls such as the rate of sedimentation, water depth, substrate type, and seasonal changes in water temperature and salinity, factors that may modulate the distribution of molluscs (Syvitski *et al.* 1989; Dyke *et al.* 1996a; Aitken & Gilbert 1996). However, these molluscan assemblages may also reflect regional immigration patterns in response to Late Pleistocene–Early Holocene deglaciation and oceanographic changes (Dyke *et al.* 1996a). In addition, morphological (i.e. shell structure, Dyke *et al.* 1996), ecological, and geological factors such as the presence of permafrost, sediment permeability and acidity, and rates of

sedimentation in proximal glacimarine environments may affect the presence or absence of certain species and therefore, the presence or absence of body and trace fossils (Syvitski *et al.* 1989; Dyke *et al.* 1996a; Aitken & Bell 1998).

According to Aitken (1990), the macrofauna inhabiting fjords and nearshore waters from the CAA exhibited the greatest preservation potential and consisted mainly of shelled bivalves and gastropods, especially infaunal suspension feeders and epifaunal browsing organisms, which is also reflected in the Late Quaternary fossil assemblages. However, the presence of organisms whose bodies have low preservation potential may be deduced by searching for their traces (Aitken 1990). These Late Quaternary fossil assemblages differ from living Arctic marine benthos as a result of the loss of soft-bodied carnivorous and deposit feeding organisms due to their poor preservation potential in shallow marine environments rather than changes in nearshore oceanography during the Late Pleistocene and Holocene (Aitken 1990).

Little is known, however, about predator-prey interactions recorded in these subfossil mollusc assemblages, since molluscan predators are rarely preserved in raised marine sediments from the Canadian High Arctic. Predator-prey interactions in molluscan assemblages are recorded as small round holes in shells. Aitken & Risk (1988) examined biotic interactions by studying the body and trace fossils in shell samples ranging in age from 500 ka B.P. to the present from the eastern Canadian Arctic. They analysed gastropod boreholes and epizoan borings observed in bivalve mollusc shells to partially reconstruct the trophic structure of these subfossil faunas. Gordillo & Aitken (2000) employed the presence of gastropods in subfossil mollusc assemblages recovered from Late Quaternary glacimarine sediments in the central CAA to similarly reconstruct biotic interactions in these faunas.

Biological interactions involving molluscs are also recorded as epizoan borings. The presence of these biogenic structure is even less well known from Pleistocene-Holocene mollusc assemblages from the High Arctic (Blake & Dean 1973; Bromley & Hanken 1981; Petersen 1982; Aitken & Risk 1988; Hanken *et al.* 2012). Round holes in shells may be a clue for predator-prey interactions in molluscan assemblages. The round holes or borings observed in this study were assigned to the ichnogenus *Oichnus* Bromley 1981. The main producers of different *Oichnus* ichnospecies observed on bivalve shells are gastropods (e.g. Bromley 1981; Carriker 1981; Kabat 1990; Kowalewski 1993; Zonneveld & Gingras 2014). In the case of muricid and naticid gastropods, they drill a hole in a valve allowing the proboscis to be inserted through the shell and facilitate consumption of the soft tissues within (Carriker 1981).

This study aims to identify *Oichnus* ichnospecies in bivalve shells to unveil the possible gastropod predators in subfossil mollusc assemblages from the Canadian High Arctic, particularly on Axel Heiberg Island (AHI), Nunavut. We propose the following hypothesis, that there is evidence of muricid and naticid gastropods producing different ichnospecies of *Oichnus* in Late Pleistocene-Holocene bivalve shell assemblages from AHI.

## The study area

Axel Heiberg Island is the second most northerly island in the CAA (Fig. 1). Glaciers currently cover 30–35% of AHI (Pollard 2005) and together with sea ice, have significantly influenced the fjords and nearshore environments present in the study area throughout the Late Quaternary. Most of this island and adjacent Ellesmere Island share the highest peaks of eastern North America, and one of the great fjord systems of the Canadian Arctic, the Greely Fjord system (Dawes & Christie 1991). Topographic relief declines southeastward from the highlands towards
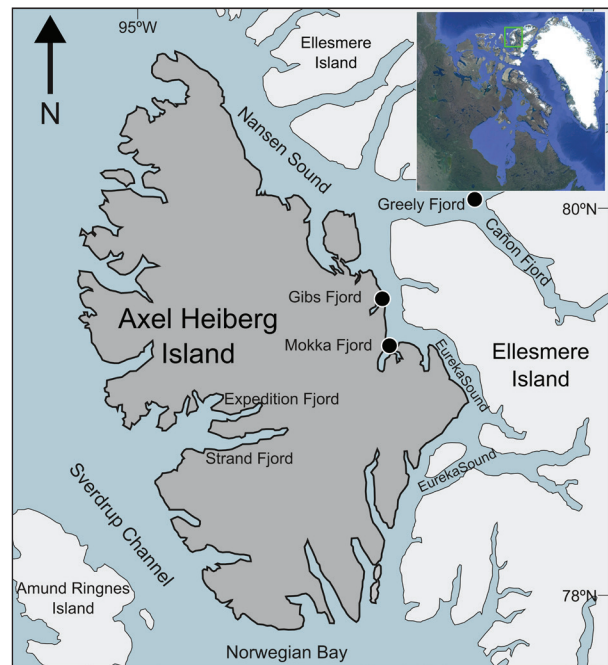


*Fig. 1.* Location map showing study sites (dots) at Axel Heiberg Island (79°26′N 90°46′W), Canadian High Arctic. Cañon Fjord (80°N, 82°W), Gibs Fjord and Mokka Fjord (79°N, 87°W) Expedition Fjord, and Strand Fjord (79°N, 90°W).

a narrow coastal plain bordering Nansen Sound and Eureka Sound (Fig. 1), dissected by glacially modified valleys and fjords. Eureka Sound is the inter-island channel that separates Ellesmere and Axel Heiberg islands. Modern glaciers are limited to small, upland ice caps, but the region is bordered immediately to the east and west by extensive ice fields on central Axel Heiberg and Ellesmere islands.

### Geological background

Raised marine sediments, deltas and strandlines are common along the AHI coasts, reflecting extensive and repeated sea level adjustments following Late Pleistocene-Holocene deglaciation (Lemmen *et al.* 1994; Bednarski 1998). Also, other environmental changes such as variations of the sea ice cover, positions of glacier margins, and temperature within AHI have been interpreted from proxy data such as changes in driftwood and whale bone abundance in strand lines, and the melt water production record of the Agassiz Ice Cap during the Late Pleistocene and Holocene (Bradley 1990; Hein *et al.* 1990; Koerner & Fisher 1990; Fisher *et al.* 1995; Dyke *et al.* 1996*b*).

Sedimentary processes that contributed significantly to the deposition of glacimarine sediments on and adjacent to AHI during the Late Quaternary include: (1) settling of fine-grained sediments from suspension in overflowing melt-water plumes; (2) deposition of sediments from turbidity currents; and (3) deposition of coarse-grained sediments from gravity flows or by rafting from sea ice and icebergs (Hein & Mudie 1991; Stewart 1991; Gilbert *et al.* 1993; Bell 1996; Aitken & Bell 1998; Bednarski 1998; Pollard 2005).

## Material and methods

### Sampling

The shell collections were recovered from sediments representing a variety of glacial and post-glacial sedimentary environments over the course of field campaigns conducted in 1994, 1998 and 2000 by Alec Aitken, Trevor Bell (Memorial University of Newfoundland) and Donald Lemmen (Geological Survey of Canada, Calgary) (Supplementary Table 1). Bulk samples were collected from natural exposures in raised marine sediments using a Mason's trowel. Each sample contains 30+ molluscan shells and the enclosing sediment. Whenever possible, samples were recovered from discrete beds; however, in massive sediments shells were recovered from a

minimum volume of 1000 cm³. Shell collections were also obtained from surface exposures of glacial tills (>30ka BP). Two or three members of the research team walked adjacent linear transects across the till surface, collecting shells and shell fragments visible to the naked eye. Every reasonable effort was made to avoid sampling bias (e.g. selecting shells of only one taxa). Collecting continued for 20–30 minutes and the shells collected by each researcher were pooled to create a single bulk sample.

### Taphonomic considerations

The mollusc shells recovered from AHI glacimarine deposits presented the typical mode of preservation affected by the presence of sediment acidity, where mollusc shells with significant levels of postmortem solution were recovered (Lemmen *et al.* 1994; Bednarski 1998; Gordillo & Aitken 2000). Most of the material was found neither in life position nor articulated, and showed signs of transport; however, many shells exhibited periostracum and the absence of encrusting organisms, which suggests a rapid burial (Lemmen *et al.* 1994; Dyke *et al.* 1996*a*; Gordillo & Aitken 2000).

The studied material can be categorized into two different preservation patterns: 1) samples with poor preservation in terms of fragmentation but with little or no indication of bioerosion and encrustation; and 2) samples with a fair or low degree of fragmentation with no evidence of bioerosion or encrustation, contributing to good shell preservation (Cai 2006).

### Radiocarbon dates

A complete list of radiocarbon-dated shell samples acquired in the study area is presented in Supplementary Table 1. The samples were recovered by Alec Aitken, Trevor Bell (Memorial University of Newfoundland, Canada), and Donald Lemmen (Geological Survey of Canada, Ottawa), assisted by undergraduate research assistants. Holocene marine limit varies throughout the study area; 78–102 m above sea level (a.s.l.) in Expedition Fjord (Lemmen *et al.* 1994), 95–120 m a.s.l. in Strand Fjord (Lemmen *et al.* 1994), and ca. 116 m a.s.l. in Mokka Fjord (Aitken, unpublished). Shell samples acquired at elevations below Holocene marine limit yield radiocarbon ages younger than 8400 a BP throughout the study area (Supplementary Table 1). Shell samples acquired from the surface of glacial tills above Holocene marine limit in eastern AHI are believed to be older than 30 ka BP based on 2 dates from Mokka Fjord: 31,310 ± 1110 a BP (Beta-117279) and 33,400 ± 790 a BP (GSC-5666) (Supplementary Table 1).

The ages of shell samples recovered from eastern AHI (Gibs Fjord, Mokka Fjord, coast of Eureka Sound) that have not been submitted for radiocarbon dating were estimated using an emergence curve for northern Fosheim Peninsula (Eureka Sound-Ellesmere Island) presented by Bell (1996). Similarly, the ages of shell samples recovered from western AHI (Expedition Fjord, Strand Fjord) were estimated using an emergence curve for the head of Expedition Fiord, Axel Heiberg presented by Lemmen *et al.* (1994) (Supplementary Table 1).

## Mollusc species composition and Oichnus *ichnospecies*

In the laboratory, specimens were identified to the level of species if possible, and, in the case of bivalves, only those shells with umbos were considered as one specimen. Shells with drill holes were photographed with a scale (10 mm). Bivalve shells were examined carefully to find trace fossils on each valve surface. Each boring was identified at the level of ichnospecies following the classification of the ichnogenus *Oichnus* revised by Wisshak *et al.* (2015). Boring positions on the shells were recorded with respect to a nine-sector grid following Kelley (1988). Bivalves could grow after a failed attack, therefore incomplete drill holes may change their location on the grid concerning the original position. We considered the final place of the incomplete drill holes. To determine whether site selectivity occurred, we tested each distribution against the null hypothesis that drilling frequencies for each sector are equal. Frequency of complete drill holes versus frequency of incomplete drill holes site selectivity were sufficiently large to use a chi-squared test. A two-sample Kolmogorov-Smirnov test (Siegel 1956) was used to assess site selectivity between bivalve species with small sample sizes of drill holes.

Two metrics were calculated to characterize predator-prey interactions across AHI: (1) drilling frequency, which consists of the degree of mortality caused by drilling predation (DF = number of complete drill holes divided by half the number of whole valves); and (2) prey effectiveness, which consists of the incidence of failed drilling predation attempts relative to all attacks (PE = number of incomplete drill holes divided by the total number of complete and incomplete drill holes; Vermeij 1987; Kelley & Hansen 2003; Neely *et al.* 2021). These metrics (DF and PE) were also calculated from other Canadian Arctic sites (Baffin Island, BI) using the dataset from Aitken and Risk (1988). Then, Pearson's chi-squared tests ($X^2$) were conducted to test the statistical significance of differences in DF and PE between AHI and BI. Statistical analyses were conducted in R Software (R Core Team 2015).

# Results

## *Molluscan species composition*

A total of 3586 specimens were examined in this study. The faunal assemblages consisted of 24 mollusc species, including bivalves and gastropods. *Mya truncata* (n = 1436; 40.04%), *Hiatella arctica* (n = 1117; 31.15%) and *Astarte borealis* (n = 853; 23.78%) were the dominant species contributing more than 95% of the preserved hard parts. Other bivalve species were found in lower proportions such as *Portlandia arctica* and *Serripes groenlandicus* (1.33% and 1.28% respectively) among others (Supplementary Table 2). Gastropod specimens represented 1.31% of the total fossil assemblages.

## *Traces on bivalve shells in this study*

We could identify different ichnospecies only in bivalves. Predators or trace fossil producers can be identified according to the morphology of drill holes, (Carriker & Yochelson 1968; Bromley 1981a; Carriker 1981; Kabat 1990; Kowalewski 1993, 2004; Kelley & Hansen 2003; Dietl & Kelley 2006 and many others), although different predators can make similar drill holes (Carriker & Yochelson 1968; Klompmaker *et al.* 2016). Among those borings, we observed small drill holes (millimetric) with a round or circular shape which consisted of a wider outer borehole than the inner borehole, with smooth walls and oriented perpendicular to the shell surface (Carriker & Yochelson 1968; Bromley 1981; Carriker 1981). This type of drill hole is reported as being produced by modern predatory gastropods belonging to the Naticidae and Muricidae families. Some traces that we observed are cylindrical holes with a circular outline typical of muricean boreholes, called *O. simplex* (Carriker & Yochelson 1968; Bromley 1981; Carriker 1981; Kowalewski 2004), while others are parabolic holes with a circular outline but have a bevelled edge distinctive of naticid boreholes, called *O. paraboloides* (Carriker & Yochelson 1968; Carriker 1981; Kelley & Hansen 2006*a*). These borings were observed in the bivalves *M. truncata, H. arctica, A. borealis, Portlandia arctica, Serripes groenlandicus, Nuculana pernula, Thracia* sp. and *Macoma* sp. (Fig. 2; Supplementary Table 3).

From a total of 3586 shells, only 24 of them exhibited complete drill holes (0.66%) and 27 incomplete drill holes (0.75%), where drilling frequency was
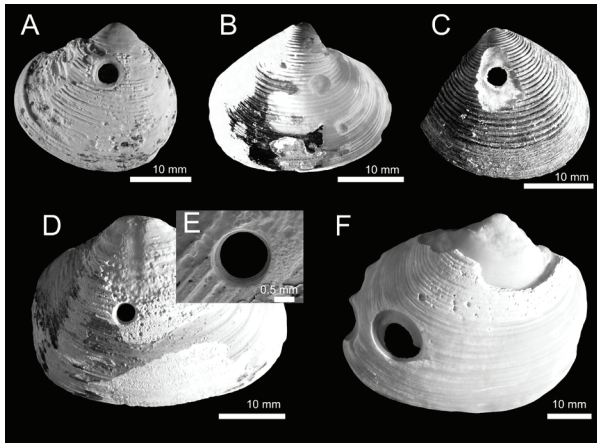
*Fig. 2.* Shells of bivalve species from AHI showing *Oichnus* isp. A, F, *Oichnus paraboloides* on *A. borealis*. B, incomplete drill hole on *A. borealis*. C, *Oichnus simplex* on *A. borealis*. D, E, *O. simplex* on *Thracia* sp. with special focus on drill hole shape.

0.013 and prey effectiveness was 0.58 for the complete data set. Considering each bivalve species, drilling frequency was very low for *A. borealis* (DF = 0.0027), *H. arctica* (DF = 0.0044) and *M. truncata* (DF = 0.0016). On the other hand, *A. borealis* showed a PE of 0.81 which was the highest prey effectiveness amongst all bivalve species, while *M. truncata* (PE = 0.25) and *H. arctica* (PE = 0.15) showed lower prey effectiveness (Supplementary Table 2). Considering other Canadian Arctic sites on Baffin Island (BI; Aitken & Risk, 1988), the DF for *A. borealis* is significantly different from the DF for this species from AHI ($DF_{Baffin\ Island}$ = 0.017; $X^2$ = 17.344; p<0.0001). Similarly, the DF for *H. arctica* is significantly different from the DF for this species from AHI ($DF_{Baffin\ Island}$ = 0.067; $X^2$ = 96.749; p< 0.0001). On the other hand, there was no significant difference for DF in *M. truncata* ($DF_{Baffin\ Island}$ = 0.001; $X^2$ = 2.7824e-30; p = 1) in shell assemblages from Baffin Island in comparison to AHI assemblages. With respect to prey effectiveness, there was a significant difference for *A. borealis* from Baffin Island ($PE_{Baffin\ Island}$ = 0.3783; $X^2$ = 10.373; p = 0.0012), while for *M. truncata* ($PE_{Baffin\ Island}$ = 1; $X^2$ = 0.75; p = 0.3865) and for *H. arctica* ($PE_{Baffin\ Island}$ = 0.3181; $X^2$ = 0.8345; p = 0.361 ) there were no significant differences between PE from Baffin Island and AHI assemblages.

The borings corresponding to *Oichnus simplex* Bromley 1981 exhibited a simple cylindrical shape penetrating perpendicular to the shell surface and those of the partially penetrating holes were flat, while those *O. paraboloides* Bromley 1981 showed a spherical parabolic form, and when it is not penetrative, it can be identified by a raised central boss.

*Astarte borealis* and *H. arctica* were the species that exhibited the greatest occurrence of drilling predation. The null hypothesis of equal drilling frequency for each shell sector was not rejected for *A. borealis* ($X^2$ = 17.532; df = 26; p = 0.8921) nor for *H. arctica* ($X^2$ = 9.5; df = 9; p = 0.3925). On the other hand, there were no significant differences in the preferred sector for drill holes between *A. borealis* and *H. arctica* (Kolmogorov-Smirnov D = 0.22963; p = 0.8363), nor for complete vs incomplete drill holes in *H. arctica* (D = 0.3125; p = 0.6749). However, there was a significant difference in the preferred sector for complete vs incomplete drill holes in *A. borealis* (D = 0.777; p = 0.0494). (Fig. 3; Supplementary Table 3).

## Discussion

The samples examined in this study were characterized by the three most abundant bivalve mollusc species, *M. truncata*, *H. arctica* and *A. borealis,* which represented more than 95% of the total assemblage. These three species presently exhibit an Arctic-Boreal distribution with a preference for heterogeneous substrates of mud, sand, and gravel, a water temperature range from –2°C to 15°C, at depths ranging from 5 to 60 metres (Dale *et al.* 1989; Aitken & Fournier 1993; Aitken & Gilbert 1996; Rosenberg 2009). Both *O. paraboloides* and *O. simplex* were recorded from *M. truncata* and *H. arctica*, while. only *O. paraboloides* was recorded from *A. borealis*. Knowing the bivalve prey's living requirements will allow us to discover which other species shared this habitat, and which possible predators could be the *Oichnus* producer on these bivalve species.

Besides bivalves, seven species of gastropods were recorded in the subfossil assemblage (representing 1.31% of the total assemblage). All these species exhibit Arctic-Boreal distributions and different substrate and food preferences. *Trichotropis borealis* is an epifaunal suspension feeding gastropod and *Margarites olivaceus* is a grazing gastropod, therefore they are not considered to be the *Oichnus* producers. Although the remaining gastropods, *Buccinum totteni*, *B. finmarkianum*, *Colus togatus*, *Cylichna* sp. and *Oenopota cinerea*, are carnivorous, none of them are known to produce a drill hole in their prey during their attacks (Nielsen 1974; Himmelman & Hamel 1993). We did not observe any gastropods that can produce drill holes in their prey such as those observed in our assemblages from the Late Quaternary glacimarine sediments on AHI. Therefore, the only evidence of drilling gastropods in the shell assemblages are the presence of *Oichnus* on bivalve shells.
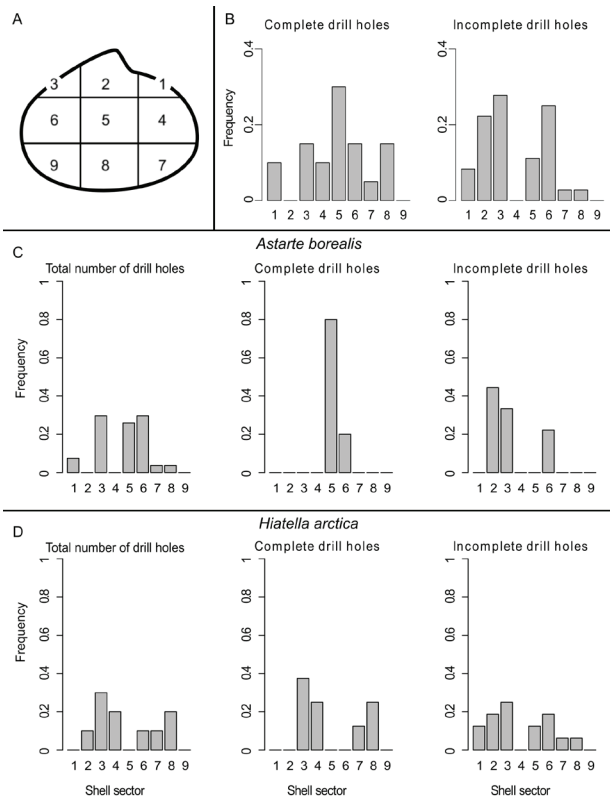
*Fig. 3.* Location and bar-plots frequency of complete and incomplete drill holes in a shell sector. A, nine-sector grid on a hypothetical valve for records of boring positions on the shells (Kelley 1988). B, frequency of complete and incomplete drill holes in a shell sector from the total assemblages of AHI. C, frequency of the total number, complete and incomplete drill holes in a shell sector on *A. borealis.* D, frequency of the total number, complete and incomplete drill holes in a shell sector on *H. arctica*

## Which gastropod species could produce these drill holes?

According to some experiments, muricids hunt and drill prey epifaunally (Carriker & Yochelson 1968; Carriker 1981; Kowalewski 2004). Epifaunal organisms, with the exception of *Hiatella arctica*, constitute less than the 2% of the preserved hard parts of the Late Quaternary Canadian Arctic shell collections examined by Aitken and Risk (1988) and Gordillo and Aitken (2001). However, muricid boreholes were also found in infaunal bivalves in the same shell collections (Aitken & Risk 1988; Gordillo and Aitken, 2001). Among these faunas, *A. borealis, A. montagui, Macoma calcarea, Mya truncata* and *Serripes groenlandicus* are infaunal bivalves that represent more than 80% of the fossil assemblages (Aitken & Risk 1988; Gordillo & Aitken 2000, 2001). Gordillo and Aitken (2001) recorded six specimens of *O. simplex,* attributed to muricid drill holes, in *Astarte borealis,* one of the most abundant species in some of these

assemblages. The same muricid traces were also recorded on *M. truncata, Thracia* sp. and *Portlandia arctica* (Gordillo and Aitken 2001). We also recorded *O. simplex* on *M. truncata, H. arctica* and *Macoma* sp. valves from AHI assemblages.

On the other hand, naticids hunt on the seafloor as well as prey on infaunal molluscs, in particular venerids, tellinids and lucinids, and usually drill and feed within coarse-grained sediments (Bromley 1981b; Yochelson *et al.* 1983; Kabat 1990; Kowalewski 1993, 2004). Aitken and Risk (1988) found that only *Macoma calcarea*, an infaunal bivalve, exhibited naticid borings in the fossil assemblages dated older than 8180 years B.P. from the Canadian Arctic. However, we found *O. paraboloides* on other bivalve species such as *M. truncata, A. borealis, H. arctica, N. pernula, Macoma* sp.*, T. myopsis* and *P. arctica,* probably produced by naticid predators. The latter ichnospecies also was reported in East Greenland Pleistocene faunas where *A. borealis* is the most abundant species and is preyed upon in preference to other bivalve prey (Petersen 1982).

## Frequency and location of drill holes

Drilling frequency on the bivalve species *A. borealis* and *H. arctica* from AHI were lower than Baffin Island. The latter fossil assemblage showed a higher proportion of drill holes and the presence of predator shells, such as *Amauropsis* sp.*, Boreotrophon clathratus* and *Natica* sp. (Aitken & Risk 1988). Also, prey effectiveness in *A. borealis* was significantly higher in AHI assemblages due to more incomplete drill holes recorded than in BI assemblages.

On the other hand, the distribution of boreholes on prey valves showed no preferred shell site on *A. borealis* nor on *H. arctica* shells. Furthermore, there was no significant difference for sector preference between complete and incomplete drill holes on *H. arctica*. However, there are differences in the locations of complete and incomplete drill holes on *A. borealis*, where complete drill holes had a higher frequency in sector 5 while incomplete drill holes had a higher frequency in sector 3. This bivalve species, *A. borealis*, recorded just one *Oichnus* isp. which was *O. paraboloides*. This agrees with naticid predation behaviour that is highly selective of drilling site (Kelley 1988; Neely *et al.* 2021). Naticid predators were reported to be highly selective of drilling site on A. borealis, which typically occur on the central area of the shell, in Miocene and Pliocene shell assemblages from North America and Iceland, respectively, (Kelley 1988; Neely *et al.* 2021). Similarly, naticid boreholes are also concentrated in the central area

of *A. borealis* shells from AHI assemblages (Fig. 3; Supplementary Table 3), which may facilitate complete consumption of prey tissues (Kabat 1990).

In the case of *O. simplex*, drill holes were positioned more frequently in sector 8, close to sector 5. However, we note that there were only six records of this trace to document the tendency of site selection. (Fig. 3, Supplementary Table 3). Therefore, the absence of drilling predators' shells and the low values of drilling frequency on AHI bivalves may reflect a low abundance of muricid and naticid gastropods living in the Late Quaternary benthos of the Canadian High Arctic.

## Absent but suspected Oichnus producers

In the absence of drilling predator specimens, we will try to elucidate the possible muricid and naticid species that could produce the named traces by comparison with other authors' findings in neighboring study areas (Fig. 4). Roy *et al.* (2014) recorded the presence of the following muricid and naticid gastropods among the megabenthic communities inhabiting the Canadian Arctic: *Boreotrophon clathratus* (Linnaeus, 1767), *Boreotrophon pacificus* (Dall, 1902), *Boreotrophon truncatus* (Strøm, 1768), *Cryptonatica affinis* (Gmelin, 1791), *Euspira pallida* (Broderip and Sowerby, 1829),



*Fig. 4.* Naticid and muricid species records during the Late Quaternary. These gastropods are the probable producers of the *Oichnus* traces from AHI. Map taken from Google Earth.

and *Scabrotrophon fabricii* (Møller, 1842). In a comprehensive study of the living marine gastropods from the Canadian Arctic, Macpherson (1971) listed the same species but also *Bulbus smithii* (Brown, 1839) and *Amauropsis islandica* (Gmelin, 1791).

Three of the species, *Amauropsis* sp., *B. clathratus* and *B. truncatus*, as well as gastropod borings in bivalve shells, were observed in Holocene and Pleistocene marine assemblages from the eastern Canadian Arctic by Aitken and Risk (1988) and Aitken (1990). Some of those species, *Natica* sp., *B. truncatus, E. pallida, S. fabricii* and *Lunatia* sp., as well as *Oichnus* isp., were recorded in Late Quaternary assemblages from Greenland by Bennike *et al.* (1994) and Simonarson *et al.* (1998). Furthermore, Neely *et al.* (2021) recorded naticid gastropod drilling predation during the Pliocene of Iceland and found an increase in abundance of naticids relative to bivalves across the trans-Arctic invasion (TAI *ca.* 3.5 Ma). Several specimens of naticid gastropods recorded in Tjörnes Peninsula deposits correspond to the species of *Natica* cf. *exvarians, Euspira helicina, Euspira catenoides, C. affinis, B. smithii, Amauropsis islandica, Natica* sp. (Neely *et al.* 2021). Moreover *C. affinis* and *Natica* sp. were also observed in Pleistocene deposits from Iceland together with *B. clathratus, E. pallida,* and *Trophon (Sipho)* (Norton 1975; Eiriksson *et al.* 2004). *Cryptonatica affinis* and *B. truncatus* were also reported in Pleistocene records from Alaska (Barth 1956; MacNeil 1957; Allison 1973). On the other hand, *A. islandica, B. clathratus, B. truncatus, C. affinis, Pseudopolinices nanus* (Møller, 1842), *E. pallida* and *Euspira tenuistriata* (Dautzenberg & Fisher, 1911) were found living in the Novaya Zemlya Arctic archipelago (Nekhaev & Krol 2017). In addition, predatory borings attributed to naticid and muricid gastropods were reported in Holocene bivalves from the eastern Canadian Arctic (Eyvindson, 1986) as well as in Pleistocene bivalves from East Greenland (Petersen 1982), Iceland (Eiríksson *et al.* 1992) and Vestnesa Ridge (Thomsen *et al.* 2019). Some of these species occurred repeatedly in the neighboring area of the Canadian High Arctic during the Late Quaternary, especially *C. affinis* and *E. pallida* among naticids; and *B. clathratus* and *B. truncatus* among muricids. These species could be considered as the probable producers of *Oichnus* from our study area (Supplementary Table 4).

Although we did not observe any naticid or muricid specimens in the fossil assemblages, we could elucidate their presence in the fossil record by studying their predatory behaviour traces. The study of these predatory traces allowed us to add information related to the biodiversity of the Late Quaternary benthos
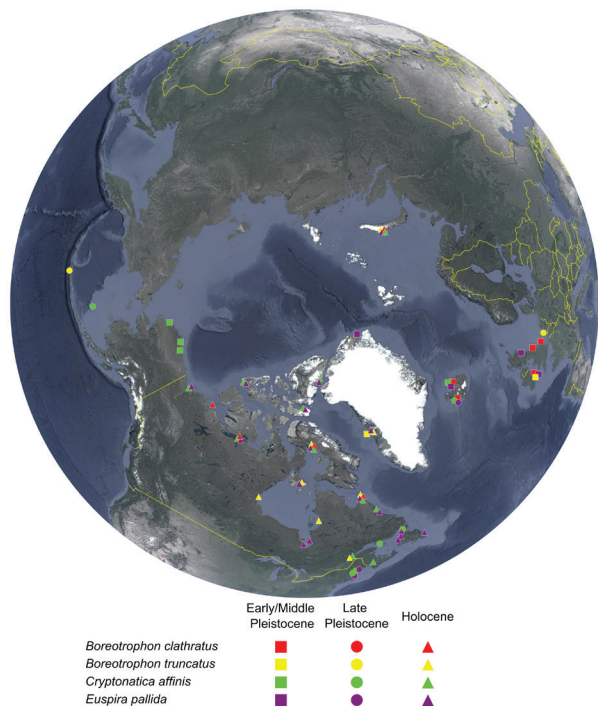
from the Canadian High Arctic despite the absence of both families of gastropod shells. The presence of *O. simplex* and *O. paraboloides* on bivalves shells from AHI allows us interpret the presence naticid and muricid gastropods living and predating in the Late Quaternary benthos of AHI.

## Conclusions

Drill holes occurred only in bivalve shells corresponding mainly to *Astarte borealis*, *Mya truncata* and *Hiatella arctica* (96% of the total assemblage). A low drilling frequency was reported in AHI as in other sites from the Canadian Arctic. Those borings were identified as *Oichnus simplex* and *O. paraboloides,* that could be produced by predatory gastropods belonging to Naticidae and Muricidae families. *Oichnus paraboloides* was observed in greater numbers and on different bivalve species than *O. simplex.*

According to previous studies in modern and Quaternary molluscan assemblages from the Canadian High Arctic, some naticid and muricid gastropods species could be consider as the producers of *Oichnus* isp.: *C. affinis* and *E. pallida*, *B. clathratus* and *B. truncatus.*

The greater number of *O. paraboloides* relative to *O. simplex* recorded in AHI fossil assemblages and the variety of mollusc prey exhibiting *O. paraboloides*, implies a greater number of naticid gastropods than muricid gastropods in the Late Quaternary benthos from AHI.

Despite the absence of drilling predators' shells in the studied assemblages, the presence of *Oichnus* issp. with a very low drilling frequency, allowed us to conclude that drilling gastropods were relatively rare in the Late Quaternary benthos of AHI.

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