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Non-predatory borings in *Phanerotrema* (Gastropoda), Early Silurian, Anticosti Island, Québec, Canada

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Abstract

Borings found in Early Silurian *Phanerotrema* sp. gastropod shells from the Goéland Member, Jupiter Formation (Anticosti Island) were analyzed to determine if the borings are evidence of predation. The analysis included a comparison of the borings to published criteria for predatory borings, scrutiny of the functional morphology and biostratinomy of the gastropod shell, and contextual information about borings produced as dwelling structures in skeletal substrates from the Anticosti sequence. Four of nineteen *Phanerotrema* contain borings having a roughly circular cross-section and a length that is slightly conical. Although the borings meet several predatory criteria including taxon-specificity and site-specificity of the borings, the occurrence of multiple borings within the same shell and the variable angle of penetration are atypical of most predatory borings. The functional morphology and stratinomy of the shell further supports a non-predatory origin. When the shell is oriented in life position, several borings penetrate anterior to where the snail would be if retracted into the shell as an anti-predatory action and two of the borings are shown to cut into the sediment infilling the shell. The borings therefore are interpreted as *Trypanites* dwelling cavities. The distribution of *Trypanites* in coralline substrates from Anticosti provides an explanation for the apparent taxon- and site-specificity of the borings observed in *Phanerotrema*. Absolute height of a substrate is demonstrated to positively correlate with *Trypanites* boring frequency, since high relief substrates are more likely to remain above the sediment–water interface than low relief substrates. *Trypanites* boring frequencies show that substrates from the Goéland Member are 1.6 times more likely to be bored by *Trypanites* as compared to background levels observed for all Anticosti members. This factor would facilitate the probability of borings in the large shells of *Phanerotrema*, which likely had longer exposure times to the water column and settling larvae of bioeroders. The peripheral band was the preferred target as it was the highest point on the recumbent conch, and the rugosity of the site also may have favoured settling and initiation of boring larvae. Borings in shells are evident throughout the fossil record, and are commonly used as evidence of predation. Viewed individually, some of the borings in this case study could convincingly be

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interpreted as resulting from predation. This study demonstrates the importance of using multiple criteria to interpret trace fossil evidence.

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1. Introduction

From the advent of protective biomineralized shells in the latest Neoproterozoic and early Cambrian, breakage and trace fossils record predator–prey interactions (e.g., Bengtson and Conway Morris, 1992; Bengtson, 1994, 2002; Hua et al., 2003). Many aspects of the evolution of predator–prey interactions have been studied and intensely debated, and the expanding literature and numerous topical symposia reflect the interest and potential applications of these studies (e.g., Kowalewski and Kelley, 2002; Kelley et al., 2003). In particular, inferred predator–prey interactions through time have been used to test theoretical evolutionary concepts such as coevolution and escalation (Vermeij, 1983, 1987, 2002; Dietl and Kelley, 2002).

The history of predation by drilling appears to have been continuous throughout the Phanerozoic (Kowalewski et al., 1998), though questions related to the tempo and modus of the drilling activity are still being resolved (Harper et al.,

1999; Kowalewski et al., 1999, 2000; Leighton, 2002). Few unambiguous examples of predatory borings exist from the Lower Palaeozoic (for list of references see Rohr, 1976, 1991; Conway Morris and Bengtson, 1994; Ebbestad and Peel, 1997; Streng, 1999; Brett and Walker, 2002; Kowalewski, 2002; Kelley and Hansen, 2003). Fundamental to the debate is the identification of borings as either predatory, parasitic, or dwelling excavations (Kaplan and Baumiller, 2001; Wilson and Palmer, 2001; Kowalewski, 2002), and to this end, a number of criteria have been proposed (Table 1). In addition, the true origin of holes in shells is not always easy to decipher. Many interpretations are plagued by a small sample size of bored shells, especially for the Lower Palaeozoic (but see Harries and Schopf, 2002 for the Mesozoic) or by a significant overprinting by domichnial borings (e.g., *Trypanites*: Richards and Shabica, 1969; Wilson and Palmer, 2001). Although little can be done to ameliorate the small sample size, previous studies have attempted

Table 1

Criteria in the literature and used to infer predatory origin of boreholes, applied to the Anticosti samples

Predatory boring criteria	Occurrence in <i>Phanerotrema</i>	Requires large <i>n</i> ?	Reference
1. Boreholes perpendicular to shell surface	No	No	2, 4
2. Boreholes oval to circular in cross-section tapering baseward and smooth-sided	Yes	No	4
3. Boreholes penetrate from outside of shell	Yes	No	1, 2, 3
4. Only one complete borehole per shell	No	No	4
5. Boreholes preferentially occur at particular sites on the shell (site-selective)	Maybe	Yes	3
6. Boreholes preferentially occur in particular shell taxa (taxon-selective)	Yes	Yes	5
7. Boreholes preferentially occur in shell of a particular size class (size-selective)	Yes	Yes	6
8. Borehole size correlated to shell size	Maybe	Yes	4
9. Boreholes common in assemblage	Maybe	Yes	1

Maybe=evidence suggests 'yes', but data is not statistically adequate.

Key to references: 1) Fenton and Fenton, 1931; 2) Bucher, 1938; 3) Cameron, 1967; 4) Carriker and Yochelson, 1968; 5) Kowalewski, 2002; 6) Hoffmeister et al., 2003.

to account for domichnial borings by using taphonomic analysis and probabilistic modelling (Kaplan and Baumiller, 2000).

The case study presented here discusses drilled holes found in a species of *Phanerotrema* (Mollusca, Gastropoda) from the Early Silurian Jupiter Formation on Anticosti Island, Québec, Canada. As in most other case studies of possible early Palaeozoic predatory borings, the sample size of bored *Phanerotrema* is small. Furthermore, domichnial bioerosion is common in the Anticosti sequence, and particularly so in corals and stromatoporoid skeletons from the Jupiter Formation (Tapanila and Copper, 2002; Tapanila et al., 2004). With these two factors in mind, a three-pronged approach will be used in our analysis. We seek not only to describe the formation and character of these borings to evaluate whether they have a predatory or non-predatory origin, but also to elucidate why they predominantly occur in this particular gastropod shell. Cited criteria for distinguishing predatory borings will be applied in concert with functional morphology analysis of the *Phanerotrema* shells. These observations are placed in the context of bioerosion and the potential role of domichnial borings in shelly and coralline fossils of the Jupiter Formation, using primary data from a comprehensive study by Tapanila (2001).

2. Geologic setting

Limestone and calcareous shale outcrops on Anticosti Island represent both Upper Ordovician and Lower Silurian strata of the Anticosti Basin (Fig. 1). Extensive geological, stratigraphical and palaeontological work has produced a broad and detailed knowledge of this region (see Long and Copper, 1994; Jin and Copper, 2000), which is being refined by ongoing systematic studies of various fossil groups. The sediment succession on the island is subdivided into seven formations, including the Jupiter Formation, which is the main focus of this study.

The basal Goéland Member of the Jupiter Formation is roughly 55 m thick, and divided into nine units (Copper and Long, 1990). It consists of calcareous grey shale and lesser interbedded light-grey micrites. Increasing calcarenites typify the middle and upper parts of the member. Here, large in situ shells of *Pentamerus palaformis* typically occur, and become gigantic (up to 10 cm length) in units 8 and 9 (Jin and Copper, 2000). Associated with *P. palaformis* are large specimens (>5 cm in largest dimension) of the isostrophic planispiral gastropod *Salpingostoma* and the low spired pleurotomarioidean *Liospira*. The beds are of late Aeronian age, within the *P. palaformis*–*Stricklandia gwelani* concurrent

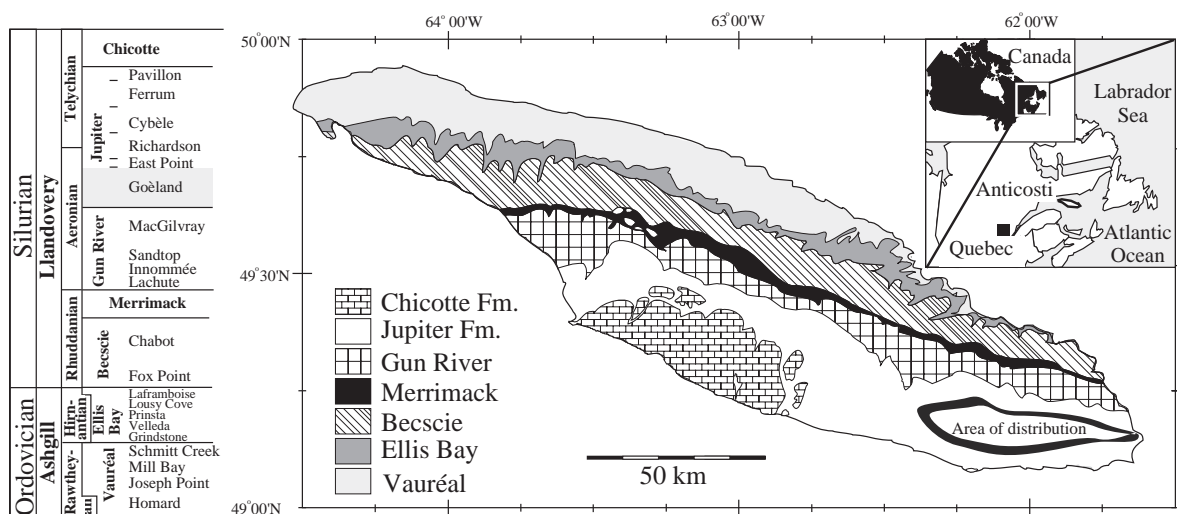


Fig. 1. Geologic map of Anticosti and stratigraphic column (adapted from Jin and Copper, 2000). The area of distribution of known specimens of *Phanerotrema* is indicated by the irregular loop in the eastern tip of the island.

Zone (Jin and Copper, 2000). Specimens of *Phanerotrema* occur in units 5–9 on the eastern part of the island (Fig. 1, Appendix 1).

The Jupiter Formation represents a shallowing-upward cycle, which is also evident in the Goéland Member. The presence of large and laterally consistent in situ pentamerid shell beds in units 2–8 suggest a position below normal storm wave base. The pentamerid community disappears towards the top of the member, where shallower water environments occur in the reefal and crinoidal East Point Member (Jin and Copper, 2000).

3. Material and methods

Nineteen specimens of *Phanerotrema* sp. are available from the collections investigated (P. Copper research collection, Laurentian University, Sudbury (LU); Royal Ontario Museum, Toronto; Geological Survey Canada (GSC), Ottawa; Yale Peabody Museum, New Haven). This survey includes material collected over the past 100 years, and new specimens

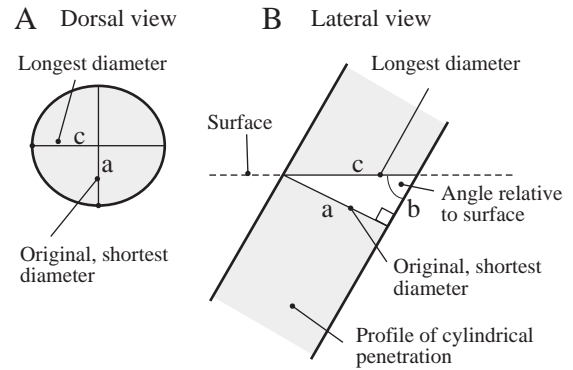


Fig. 2. Generalized figure showing the application of the Pythagorean Theorem, $a^2 + b^2 = c^2$, to estimate angle of penetration for individual holes. (A) Dorsal view of oval hole, where the longest (oblique) vector is c , and the true diameter (orthogonal to depth) is a . (B) Lateral view of the hole shown in (A), with the corresponding measurements superimposed. It is assumed that the drilling organism made holes with a circular cross-section.

are therefore likely to surface only through future fieldwork. The specimens are deposited in the type collection at the Geological Survey of Canada (GSC), Ottawa. The extensive reference material of tabulate

Table 2
Drilling statistics

Total number of specimens, holes, and position on shell relative to the peripheral band							
Species	<i>n</i> specimens	<i>n</i> drilled	Drilled (%)	<i>n</i> holes	<i>n</i> at band	At band (%)	
<i>Phanerotrema</i> sp.	19	4	21	13	8	67	
Properties of individual specimens and individual holes on these (hole id)							
Specimen no. (GSC)	Specimen height (mm)	Borehole elevation (mm)	Hole id	Hole ϕ (mm)	Angle of penetration	Width of band (mm)	Hole ϕ /Width of band
GSC 10924	49	30	a	0.3	30°	–	–
			b	0.8	75°	–	–
			c	2.9	65°*	2.7	1.07
			d	2.6	85°	?	–
			e	1.1	50°	1.3	0.85
			f	1.0	30°	–	–
			g	1.5	60°*	–	–
			h	0.8	45°	–	–
GSC 10925	31	20	a	1.4	60°	1.2	1.16
			b	1.4	55°	1.2	1.16
GSC 10926	36	20	a	0.9	50°	1.7	0.52
GSC 10927	40	30	a	1.2	60°	2.0	0.60
			b	1.5	55°	2.0	0.75

Specimen height is maximum preserved height along axis of coiling. Borehole elevation refers to the height of the borehole above the substrate, when the shell is positioned with the borehole upward and the drilled surface horizontal. Hole diameter (ϕ) is based on the shortest vector of the holes. Angle to surface was estimated using the Pythagorean theorem (Fig. 2).

* Holes incomplete or precise measurements otherwise made difficult.

corals and stromatoporoids for the analysis of bioerosion comprises part of a research collection compiled by P. Copper and it is currently stored at LU.

The small sample size of bored gastropod shells does not permit rigorous statistical analysis, but we apply criteria for identifying the nature of drilled holes discussed in Carriker and Yochelson (1968) and elaborated upon by subsequent authors (see Introduction and Table 1).

Where numerous holes are found on one specimen, they are in the descriptive part referred to by small letters in subsequent order, starting with the hole nearest to the gastropod aperture. Borehole elevation

(Table 2) refers to the height of the borehole above the sea bottom (assuming no burial) when the shell is positioned with the borehole upward and the drilled surface horizontal. This was estimated by orienting the shell loosely on a bed of sand with the drilled holes positioned as described. Problems using this estimate are discussed below.

The angle of penetration of the holes relative to the shell surface was estimated using the Pythagorean theorem, $a^2 + b^2 = c^2$. At the plane where penetration occurs (i.e., the shell surface) the smallest, original diameter of the hole is taken as a . The longest vector of the hole represents c . In profile, the angle between

Table 3

Summary of data correlating the frequency of domichnial macroborings (e.g. *Trypanites*) with respect to the maximum height (0.5 cm interval) of massive tabulate corals and stromatoporoids

	Maximum height intervals, H (cm)	Calculated height intervals (cm)	# Bored samples	Total # samples	Frequency bored (%)
All Anticosti mbrs ($n=1986$)	0.5 to 1.0*	0.93	26	95	27.37
	1.5	1.50	28	112	25.00
	2.0	2.00	67	230	29.13
	2.5	2.50	67	183	36.61
	3.0	3.00	86	304	28.29
	3.5	3.50	56	137	40.88
	4.0	4.00	74	185	40.00
	4.5	4.50	41	91	45.05
	5.0	5.00	67	128	52.34
	5.5	5.50	30	66	45.45
	6.0	6.00	37	87	42.53
	6.5	6.50	21	37	56.76
	7.0	7.00	31	64	48.44
	7.5	7.50	16	24	66.67
	8.0 to 8.5*	8.16	22	55	40.00
	9.0 to 9.5*	9.10	22	44	50.00
	10.0 to 10.5*	10.16	25	37	67.57
11.0 to 11.5*	11.14	20	25	80.00	
12.0 to 13.5*	12.63	26	35	74.29	
14.0 to 16.5*	14.94	15	24	62.50	
17.0 to 32.0*	22.28	17	23	73.91	
Goéland Mbr. only ($n=227$)	0.5 to 1.0*	0.89	6	19	31.58
	1.5	1.50	4	17	23.53
	2.0	2.00	11	27	40.74
	2.5	2.50	9	16	56.25
	3.0	3.00	11	19	57.89
	3.5	3.50	24	32	75.00
	4.0 to 4.5*	4.10	19	26	73.08
	5.0 to 5.5*	5.15	18	24	75.00
	6.0 to 7.5*	6.64	20	21	95.24
8.0 to 21.0*	11.88	25	26	96.15	

Data subdivided to include all members of the Anticosti sequence and only the Goéland Member of the Jupiter Formation. See Fig. 4 and text for further details.

* Inclusive.

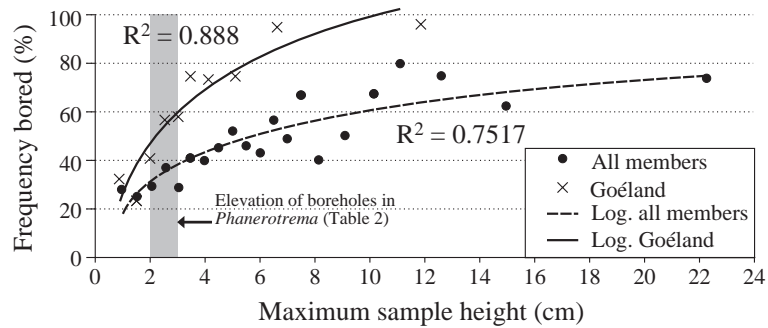


Fig. 3. Frequency of domichnial macroborings (e.g., *Trypanites*) in tabulate corals and stromatoporoids is positively correlated with the maximum height of the specimen. Samples from the Goéland Member ($n=227$) are particularly more likely to be penetrated by domichnial borings when compared to all Anticosti samples ($n=1986$). Data summarized in Table 3.

b and c in the resulting triangle thus represents the angle of penetration (Fig. 2, Table 2). The underlying assumption is that the drilling organism would have produced cylindrical holes with a circular cross-section if the penetration was perpendicular to the surface. Although some modern predatory drillers, e.g., *Octopus*, regularly produce non-circular holes (Cortez et al., 1998), all well-preserved borings in *Phanerotrema* appear to be circular in cross-section. Studies on the geometry of Silurian and Devonian *Trypanites* show that this boring typically is circular in cross-section and roughly isodiametric in length (Pemberton et al., 1980, 1988), adding further justification to our assumed geometry of the borings in *Phanerotrema*. Measurements were taken from enlarged digital photographs of the holes, with the shell surface on which they occur oriented horizontally. The resulting angle was rounded up to the nearest 5° .

Data used to characterize domichnial bioerosion for the Anticosti sequence are derived from a larger study that analyzed macroborings (diameter >0.5 mm) in more than 2500 massive tabulate corals and stromatoporoids (Tapanila, 2001). Samples came from all exposed formations of the Anticosti sequence (Fig. 1), starting at the basal Vauréal Formation (Ashgill, Late Ordovician) through to the upper Chicotte Formation (Telychian, Silurian), and include several reefal and biostromal shallow marine facies.

A subset of nearly 2000 specimens was used for this study to analyze the relationship between vertical height of a substrate above the seafloor and the frequency of domichnial macroborings (i.e., *Trypanites*) (Table 3). The vertical height metric in this study

is a proxy for the actual height of the substrate above the seafloor. Since some proportion of the substrate was covered by seafloor sediments prior to its ultimate burial, the actual height of the substrate above the seafloor is overestimated by the vertical height metric used in this study. As a result, exposure time of the substrate to the water column, and would-be borers, is greater for the tallest parts of the substrate.

Anticosti tabulate corals and stromatoporoids grew to attain a wide range of vertical heights above the seafloor, from 0.5 up to 21 cm in the Goéland Member and 32 cm for all Anticosti members. For each specimen, the maximum vertical height of the tabulate coral or stromatoporoid colony was measured to the nearest 0.5 cm, and the presence/absence and type of macroborings were noted. Encrusting specimens were eliminated from the subset if the height of the encrusted substrate was unknown or suspect. Samples bored only on the undersurface were eliminated from the subset, since biostratinomic reorientation might compromise the fidelity of the measured maximum vertical height of the specimen.

Percent boring frequency (no. macrobored specimens \div total no. of specimens $\times 100\%$) was calculated for each height class at 0.5 cm intervals for all Anticosti specimens and exclusively for the Goéland Member (Fig. 3, see Discussion). Where sample size (n) was less than 15 for a height class, pooled intervals were used. For pooled intervals, a weighted mean height class was generated using the following equation;

$$\sum_{i=1} (H_i \times n_i) \div \sum_{i=1} (n_i),$$

where, H is the height class in cm, and n is the number of specimens in the height class.

4. Results

The following is a descriptive analysis of the bored gastropod shells and the macroborings encountered. Observations focus on the presence and position of the holes with reference to the shell geometry and inferred life orientation of the snail shell, i.e., aspects of functional morphology. The quantitative assessment of the bioerosion record on the marine deposits of Anticosti Island is included in the final discussion to provide real-data context for understanding the occurrence of the borings in the case study.

4.1. The shell of *Phanerotrema*

Silurian species of *Phanerotrema* were earlier assigned to *Pseudoscalites* (*sensu* Boucot and Johnson in Boucot et al., 1967; but see Peel, 1983), which was a preoccupied name (Wagner, 2002). Recent phylogenetic analyses remove the genus from association with raphistomid gastropods, suggesting that similarities in shell morphology arose from convergence (Wagner, 2002); the genus is placed in the Phanerotrematidae Knight (1956), with *Brachytomaria* Koken in Koken and Perner (1925), and *Ulrichospira* Donald (1905).

Mature shells of *Phanerotrema* are among the largest gastropod conchs in the Goéland Member, with the height of the shells reaching 4 cm (measured along the axis of coiling). All the bored specimens are larger than 3 cm in height (Table 2). The shell of this taxon has four whorls, characterized by a low spire and a large final whorl, owing to low translation along the axis of coiling combined with rapid whorl expansion. The upper whorl surface appears nearly flat, but has a low-angle slope (convex or concave) towards the peripheral band. This creates a step-like profile in lateral view, with the peripheral band positioned high up on the whorl profile. The surface of the band is not parallel to the axis of coiling, but rather positioned in a 45° angle relative to the axis (lateral view, for instance Fig. 4: 12). The band is ornamented by prominent lamellose lunulae, representing a distinctive character for the genus. The

ornamentation on the shell consists of distinct lamellose growth lines (with lesser amplitude than the lunulae), intersected by prominent spiral lirae to create a corrugated surface.

The Anticosti species occurs exclusively in the eastern end of the island (Fig. 1). It is hitherto undescribed, but may be compared closely to *Phanerotrema lindstroemi* (Boucot and Johnson in Boucot et al., 1967) from Wenlock beds on Gotland, Sweden. The major differences are paucity of spiral cords on the upper whorl surface and a deeper slit. Other comparable species are *P. jugosum* (Pitcher, 1939) from the Llandovery of Shropshire and *P. aff. jugosum* from the earliest Llandovery of Arisaig (Peel, 1977). These species carry 2 and 5 spiral cords, respectively, on the upper surface. The Anticosti species carries between 3–5 cords on the upper surface, which suggests that this character is susceptible to intraspecific variation. However, further discussion on affinities awaits closer taxonomic studies.

Peel (1977, 1983) noted that the raised, flange-like peripheral band becomes more prominent in large specimens of *Phanerotrema*, which makes sense when the shell is oriented in life position. The tangential apertural plane and its elongated shape suggest that the shell was oriented with the aperture plane parallel to the substrate with the spire turned backward through detorsion (*sensu* Linsley, 1977). The slit and emargination would thus be directed to the right of the snail (dorsal perspective), and the raised and drawn-up flange would ensure an efficient transport of the waste-water away from the mantle cavity. This is assuming a normal pleurotomarioid arrangement of the mantle cavity, i.e., two gills—the sinus and slit would thus represent the position of the exhalant currents after ventilating the gills (Knight, 1952; Knight et al., 1960). In this position, the peripheral band on the last whorl becomes the highest point of the shell above the substrate, and it is also sub-parallel to the substrate.

The band and flange have the thickest shell deposition of the conch. Shell surfaces above and below the band are proportionally thin, while the inner margin of the aperture again is thicker. Specimens of the Anticosti species are generally well preserved with little alteration of the shell. However, several specimens have a crushed spire, likely owing to the thin

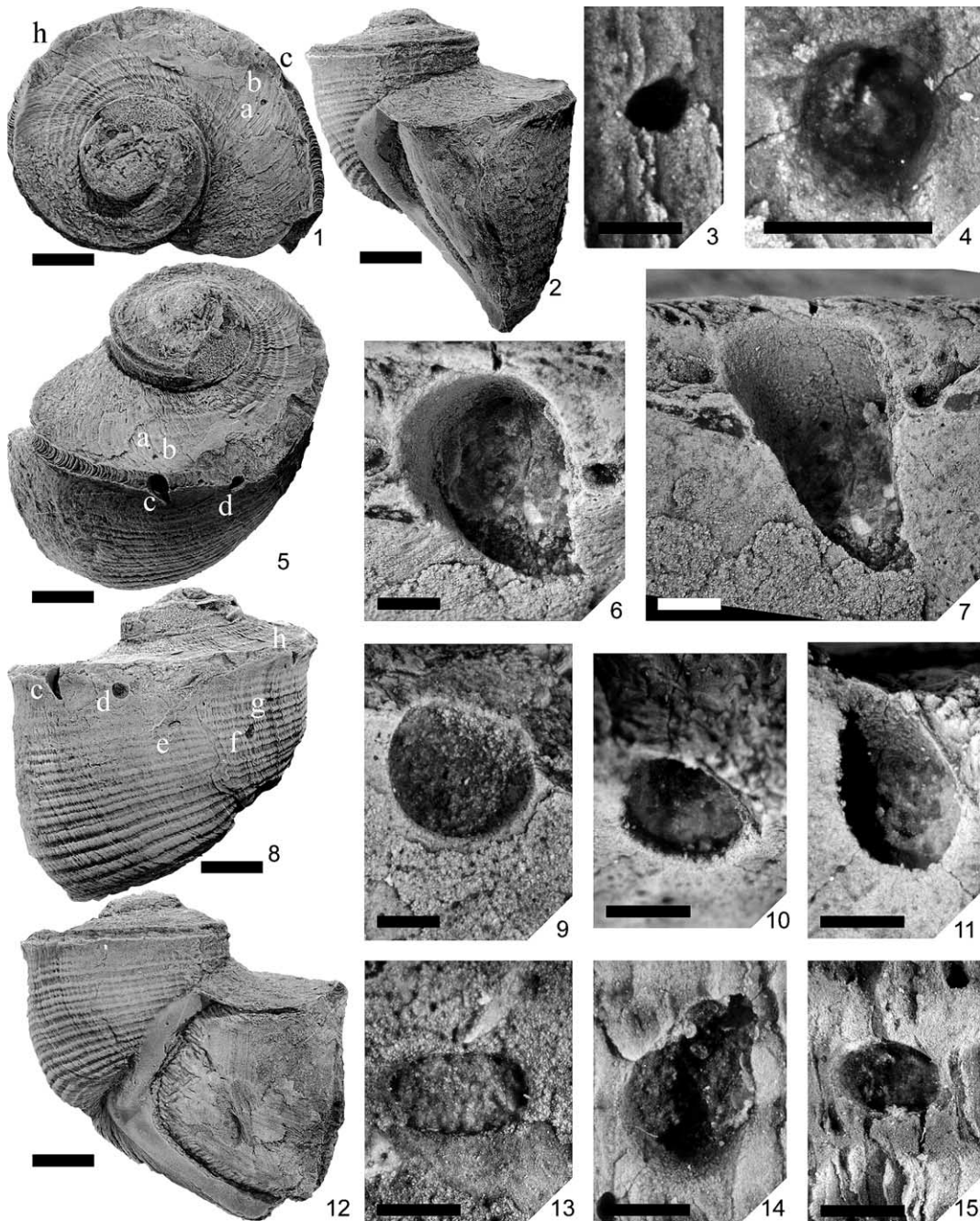


Fig. 4. Bored *Phanerotrema* from Goéland Member, Jupiter Formation, Anticosti Island. All images of specimen GSC 10924, locality A513. Images 1, 2, 5, 8, 12; General shell morphology, scale bar=10 mm. (1) Dorsal view. (2) Lateral view. (5) Dorsal oblique view. (8) Lateral view. (12) Apertural view. Images 3, 4, 6, 7, 9–11, 13–15; Borings in shell, scale bar=1 mm, except image 3; scale bar=0.5 mm. (3) Boring a, plane view. (4) Boring b, plane view. (6) Boring c, plane view. (7) Boring c, lateral view. (9) Boring d, plane view. (10) Boring h, plane view. (11) Boring h, lateral view. (13) Boring e, plane view. (14) Boring f, plane view. (15) Boring g, plane view.

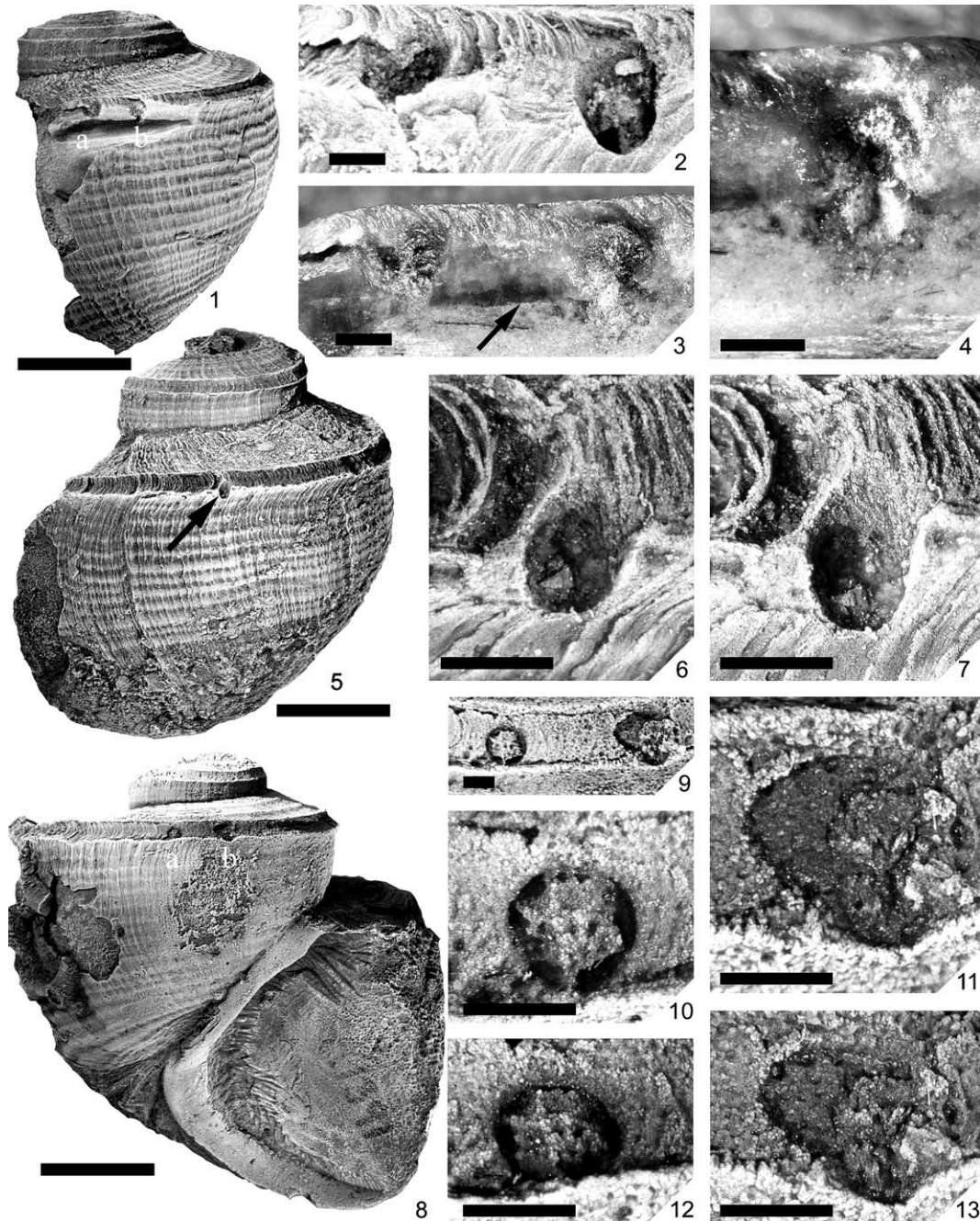


Fig. 5. Bored *Phanerotrema* from Goéland Member, Jupiter Formation, Anticosti Island. Images 1, 5, 8; General shell morphology, scale bar=10 mm. Images 2–4, 6, 7, 9–13; borings in shells, scale bar=1 mm. (1–4) Specimen GSC 10925, locality A846; (1) Lateral view of shell. (2) Lateral view of boring a. (3) Lateral view of boring a and b sectioned. Arrow points to shell boundary. (4) Sectioned detail of boring b. (5–7) Specimen GSC 10926, locality A1110; (5) Lateral view of shell. Arrow points to hole. (6) Plane view of boring. (7) Lateral view of boring. (8–13) Specimen GSC 10927, locality A1391. (9) Boring a and b. (10) Plane view of boring a. (11) Plane view of boring b. (12) Lateral view of boring a. (13) Lateral view of boring b.

shell and/or the shell not having been filled with sediment. The breakage is probably syndepositional in origin because the broken elements of the shell are in place but distorted and pressed down into the matrix. Weathering and general abrasion of more recent origin tend to degrade the appearance of otherwise good specimens.

4.2. Hole geometry and the drilled specimens

Drilled holes occur in four out of the 19 specimens (21%), but with a total of 12 completed holes (i.e. penetrating the shell) and one partial or unfinished hole (Figs. 4 and 5; see Table 1 for summary of statistics). They are circular to oval in outline, wide and cylindrical to conical with depth. The inner walls of the holes appear smooth, and the penetration at the surface is simple and lacks bevelled or countersunk margins. The holes range in diameter between 0.3 and 3 mm. All boreholes clearly penetrate the shell from the outside.

The largest specimen (GSC 10924; Fig. 4) has 8 of the total holes (67%), with 3 on the peripheral band, 2 on the upper whorl surface, and 3 on the lower whorl surface. In all the other specimens, the holes occur directly on the peripheral band or just at the margin of the peripheral band, so that 8 of the 12 holes are positioned here (67%). On specimen GSC 10924, a few other small (<0.5 mm) pits or holes occur, but it is uncertain whether these are structures similar to the well-defined holes described above (e.g., the pit to the right of hole GSC 10924c, Fig. 4: 6, 7).

The peripheral band is completely obscured in 7 of the 19 specimens (37%), due to weathering or poor preservation (GSC 10928, 10935, 10936, 10939, 10940, 10941) or epibiotic overgrowth (GSC 10942). Holes are not seen on any exposed whorl surfaces in these specimens. The last whorl of *Phanerotrema* expands and embraces the lower whorl surface of the spire, so that any holes here would be obscured. Furthermore, most available specimens have the upper part of the spire eroded or crushed, as explained above, thus obliterating any structures.

It is evident that several of the holes did not penetrate perpendicular to the shell surface (Fig. 4:6, 13, 14). Estimates of the angle of penetration were made (Table 2), under the assumption that the holes when made had a circular outline. The angle of

penetration varies considerably, even where multiple holes exist on one specimen. Most holes are, however, directed towards the base of the shell when it is oriented in the conventional position (i.e., the axis of coiling horizontal and the aperture facing the viewer). Three holes in GSC 10924 are exceptions to this, in that the angle seems to be directed towards the spire of the shell when this is oriented in a conventional position (GSC 10924g, h). This is particularly evident in GSC 10924g (Fig. 4:14).

5. Discussion

5.1. Predation vs. dwelling

Interpretation of the drilled holes on shells of *Phanerotrema* discussed herein as non-predatory may seem straight-forward. But is this really so? The literature on drilled holes in the fossil record is increasing, especially concerning predatory induced injuries. A number of criteria have been proposed to help identify predatory borings (Table 1), but still the available sample size ultimately limits the statistical certainty of an interpretation (see for instance Harries and Schopf, 2002).

The complications of using published predatory boring criteria are evident when applied to the small sample size of *Phanerotrema* from Anticosti. Of nine criteria commonly used in the literature for diagnosing predatory borings, the *Phanerotrema* examples meet seven (Table 1). (1) Their circular to oval outline, conical shape, and size range (0.3–3 mm) are consistent with the predatory boring *Oichnus* (Bromley, 1981). They also conform to types A and B predatory boreholes of Ausich and Gurrola (1979) with the exception of the countersunk margins in the latter. (2) The boreholes all clearly penetrate the shell from the outside. Most likely they penetrate to the interior (for instance specimen GSC 10925) as distinct from penetrating into the shell (i.e. for instance representing failed predation). (3) The boreholes may be 'site-specific' with relation to the peripheral band of the shell, though the statistics are too limited to substantiate this. Measurements show that there is no correlation between the diameters of the holes relative to the width of the peripheral band where they occur (Table 2), but this may not necessarily refute

site-specificity. This property and criterion 5 (below; prey size) is particular to selectivity (or stereotypy) of prey in modern shell-drilling gastropods and indeed in the fossil record (Kelley, 1988; Kelley and Hansen, 2003). (4) Because these borings only are found in one species of gastropod in the Goéland Member, the borings may be considered taxon-specific. This is supported by the study of more than 50 specimens each of *Salpingostoma* and *Liospira?* co-occurring with *Phanerotrema*. Though of comparable size, not a single specimen have holes drilled into them. (5) Observations also suggest that borings preferentially occur in a particular size of shell, i.e., the bored shells ranging in maximum height of 3–5 cm (Table 2). With the limited material available, it is unclear how size classes are reflected in the dataset. If not size classes, alternatively any preferential size distribution of bored shells may relate to the height of the boring above the substrate (2–3 cm). Height above substrate may in fact be the controlling factor for the origin of the holes in the interpretation preferred here, though certain assumptions need to be invoked (see discussion in Section 5.3). (6) Finally, because of the small sample size of *Phanerotrema* shells, we cannot refute the possibility that the size of the boreholes may be correlated to the size of the *Phanerotrema* shells or (7) that these types of borings are common in the assemblage.

In spite of these predatory-boring indicators, two criteria in Table 1 are not met. Though the applications of these criteria are not clear-cut, failure to meet them fully significantly reduces the possibility that the *Phanerotrema* borings are of predatory origin. (1) Multiple successful borings (i.e., fully penetrating the shell) in a single shell is less common for predatory borings (Carriker and Yochelson, 1968), although exceptions exist (Leighton, 2001). A particularly intriguing example was presented by Streng (1999). In six phosphatic brachiopod species from the Cambrian of Morocco, he reported the unusual occurrence of both several successful borings and aborted drillings of predatory origin in single shells. This was explained by the presence of unspecialized and less efficient types of predators. In *Phanerotrema* all drilled specimens, except GSC 10926, have two or more holes, mostly located at the peripheral band. Although this part of the whorl is greatly thickened, most of the holes

appear to have fully penetrated the shell. (2) The boreholes are not oriented perpendicular to the shell surface, but rather they are oriented at a variety of angles (Table 2). Where the holes are associated with the peripheral band, they all penetrate with angles between 50–85° relative to the surface (the surface of the band being positioned horizontally). This is evident from the way the holes cut outside the shell margin or the way many of them are elongated (see for instance Fig. 4: 6, 7, 10, 11, 14, 15; Fig. 5: 2, 6, 11). It was argued by Carriker and Yochelson (1968) that oblique holes resulted from biochemical etching of a tilted substrate, and as a general rule penetration of predatory origin usually is perpendicular to the surface and gives rise to circular holes. The drilled surface may be inclined, but the penetration is still oriented perpendicular to the inclined surface. The underlying criterion is that a smooth surface is being drilled, whereas an irregular surface or ornamentation may severely distort the shape of the drilled hole (Carriker and Yochelson, 1968, p. 7). Some of the holes drilled in the shell of the highly ornamented peripheral band and shell of *Phanerotrema* therefore may have been originally directed perpendicular to the surface, possibly fulfilling the criterion of predatory origin.

Functional considerations of the shell morphology further support a non-predatory origin. In the presumed life position of the shell, only two drilled holes would penetrate perpendicular to the shell (GSC 10924d; GSC 10926). In the life position of GSC 10927, the two holes would face down toward the substrate. Rohr (1976, and references therein) reported predatory holes in brachiopods made by an infaunal predator, which could be argued for the holes in GSC 10927 as well. However, a different boring organism would be required, and no morphological evidence of the borings supports the hypothesis of a second boring organism.

An additional observation to bolster the non-predatory origin is the simple fact that most holes penetrate the shell near the apertural edge, a position anterior to where the snail would be if retracted into the shell as an anti-predatory action. This includes the four holes placed near the aperture in the shell of GSC 10924, as well as both holes in GSC 10925 and GSC 10926. Furthermore, most holes penetrate the thickest part of the shell, which is not economical in terms of

energy spent during drilling for food. On the contrary, predators already in the Cambrian selected for the thinnest, non-marginal parts of the shell in brachiopods (Miller and Sundberg, 1984). A primary observation to strengthen the non-predatory origin is that the holes in shells of GSC 10925 clearly penetrate the shell and distort the matrix infilling of shell (Fig. 5: 3, 4). This is decisive evidence demonstrating that these two borings were produced *post-mortem*, and suggests the likelihood that many of the other borings discussed herein were made into an empty or sediment-filled shell.

5.2. Background domichnial bioerosion

If the holes in *Phanerotrema* are not predatory in origin, what may have caused them, and why do they occur here? Macroborings are common in the Ordovician–Silurian limestones of Anticosti Island (Tapanila and Copper, 2002; Tapanila et al., 2004). These are dominated (>99%) by *Trypanites* domichnial borings that most commonly penetrate tabulate corals, stromatoporoid sponges, bryozoans and hard-ground surfaces. These borings were most commonly excavated in dead substrates (i.e., *post-mortem*) and they are concentrated on the uppermost surface of the substrate.

Tapanila et al. (2004) found that *Trypanites* was more common in substrates having higher vertical relief, greater skeletal density, and which grew in off-reef, deeper water settings. Thus, the chief control on the occurrence of *Trypanites* in a substrate was concluded to be related to the maximum time that the substrate was exposed to the water column, i.e. not buried by sediment. Indeed, there also seems to be a strong correlation between height above the sediment surface and the likelihood of being bored by *Trypanites* (Fig. 3). Analysis of the large reference collection with both sample groupings, the 2500 and the subset of 2000, show that the frequency of domichnial borings increases with increased vertical height of the coral or stromatoporoid substrate (Fig. 3). The positive correlation between boring frequency and substrate height appears to fit a logarithmic function for both groupings (All Anticosti members: $r^2=0.75$, $d.f.=20$; Goéland Member only: $r^2=0.89$, $d.f.=9$). Analyzed separately, samples from the Goéland Member are roughly 1.6 times more likely to

have domichnial borings than the background levels observed for all Anticosti members. For example, a coral or stromatoporoid that grew to a height of 3.5 cm above the seafloor during the deposition of the Goéland Member had a 75% likelihood of being penetrated by domichnial borings. This is significantly higher than the 40% Anticosti average for 3.5 cm tall substrates.

5.3. Controlling factors

The greater frequency of *Trypanites* in samples from the Goéland as compared with all Anticosti members can be related to the low rate of net sedimentation in this member (Copper and Long, 1998). As a result, substrates from the Goéland were exposed to the water column for greater lengths of time. In addition, Goéland substrates having a small vertical relief are more likely to contain *Trypanites* than in other Anticosti members. For example, a substrate such as *Phanerotrema* that has a stabilized *post-mortem* height of 3 cm would have a 50% likelihood of containing *Trypanites*, based on results for stromatoporoid and tabulate coral substrates. The inferred size range, or rather elevation height, is between 2–3 cm for boreholes in a recumbent shell in our interpretation (Fig. 3). This prediction is higher than the observed frequency, and therefore other controlling factors on the distribution of borings (e.g., shell thickness, density, taphonomy) may have contributed to this result.

Other controlling factors are evident when considering other large benthic shells in the Goéland Member. Various forms of large brachiopods and gastropods occur abundantly, but conspicuously they lack *Trypanites* borings or potential predatory borings. Shells of the large gastropods *?Liospira* and *Salpingostoma* would similarly be raised several centimetres above the substrate, yet not a single boring has been encountered (more than 50 specimens of each species investigated). We speculate that the reason may be found in the shell ornamentation, which in *?Liospira* and *Salpingostoma* is smooth compared with that of *Phanerotrema*. The possible site-specific occurrence of borings at the highly rugose peripheral band of *Phanerotrema* may suggest a settling preference by the larvae of the *Trypanites* tracemaker.

Similarly, shells of the comparably large and numerous brachiopod *P. palaformis* are devoid of macroborings. This may be due to the fact that these only sit 1.5–2 cm above the seafloor as *Pentamerus* occurs in nests, with the thickest, posterior hinge part of its shell buried in the sediment, and the almost paper-thin anterior commissure uppermost (Copper, 1997). Lack of marks that could be of predatory origin in brachiopod shells may be explained by three reasons: 1) brachiopods offer very little potential food for predators; 2) the soft tissues were probably foul-tasting as are those of the surviving brachiopods such as rhynchonelloids, terebratuloids, and thecideids (Thayer, 1985; Thayer and Allmon, 1991), and 3) that modulation of the substrate by these colonies deters macro-bioturbators (Copper, 1997, pp. 140, 145).

6. Conclusion

In this study *Trypanites* borings are described specifically from the Goéland Member and compared with the entire Anticosti sequence. In addition, the qualitative observation that vertical relief influences boring frequency (Nield, 1984; Segars and Liddell, 1988; Lebold, 2000; Tapanila et al., 2004) is quantified for the first time in Palaeozoic substrates, suggesting that height above the sea floor increases exposure time and acts as a significant controlling factor for preferential boring density. These results can help determine the likelihood of domichnial boring occurrence and may account for the apparent taxon-specificity of the *Phanerotrema* borings.

The possible site-specificity on the peripheral band of most holes in *Phanerotrema* may be explained by the rugosity of the site, which may have favoured settling and initiation of boring larval organisms. This may indicate a stable position of the recumbent shell partly or wholly embedded in the sediment, where the drilled site of the peripheral band would be the highest point above the substrate. Occurrences of multiple holes with varying angles of penetration, as in GSC 10924, would assume that the shell was shifted about and changed position in the sediment. It may therefore be speculated that the occurrence of borings in *Phanerotrema* is more fortuitous than directed and intentional, suggesting

that within the range of optimal vertical relief the *Trypanites* tracemaker was opportunistic with respect to an appropriate settling substrate. However, this cannot be tested without the possibility of a statistical evaluation.

The *Phanerotrema* case study illustrates the potential difficulties in diagnosing predatory boreholes, especially from a limited data set. Such small, locality-specific sample sizes are most commonly available in the fossil record (e.g., Carriker and Yochelson, 1968; Rohr, 1991), but they will continue to be important for discerning and describing the early Palaeozoic record of trophic relationships.

In this case, our examples of Silurian *Phanerotrema* from Anticosti were not preyed upon, but rather were passive substrates that served as the site for domichnial borers. Previous authors have rightly cautioned against using the traditional criteria for predatory borings as definite indicators (e.g. Kowalowski, 2002, and references therein). These criteria, used individually, are inaccurate tests for predation, and indeed the size class criterion discussed above illustrates how the interpretations can only be conjectural when the true origin of the drilled holes is obscure. Used together they are potentially very useful, but often require a larger sample size than is typically available for early Palaeozoic examples. This study shows the importance of using multiple criteria to interpret trace fossil evidence, including a broader understanding of the actual regional record of bioerosion, and the biostratinomy and functional morphology of the target shell.

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Appendix A. Locality data

A418 Jumpers section [=A105]. Outcrop at contact Pavillon and Chicotte, <500 m west of junction N SW Point road. Section 12.47 m thick. (5) 530 cm blue-grey thin, irregular bed lenticular coquinoids, calcarenites and 40% soft fossils, blue-grey shale with diverse brachiopods. Uppermost 30 cm with *Costistricklandia*. Pavillon Mbr., 12E/5 ca 60950:69900. Specimen number GSC 10934.

A513 [=A733, A770] Main road, intersect with access creek flowing under culvert 50 m north to Schmitt Creek; 11.2 km east of A512. Large spill heaps on both sides of road for about 50 m, exposing ca 2–3 m soft weathering blue-grey shales, orange coloured, with rich giant *Pentamerus* and *Joviatrypa brabyla*. Goéland Mbr., units 7–9. 12E/1-556600:5453870 (59400:55280). Specimen number GSC 10924.

A846 Chaloupe Road, 2.4–2.5 km south of main Chaloupe River tourist camp, 3.3 km north of easterly turnoff to Chaloupe River access; trenches on west side of road with 3–5 m soft, blue-grey top yield weathering shales and micrites, contains rich giant *Pentamerus* fauna, with *Joviatrypa brabyla*, large domed stromatoporoids. Goéland Mbr, units 7–8 high. 12E/1-538400:5454900. Specimens number GSC 10925, 10928, 10937.

A854 [=A710] Sandtop Road end at turn-around point, 300 m south-east of A853; 3.0 km south of South Sandtop Creek, ca 2 m exposed with *Pentamerus* coquinite at base, capped by 1 m of micrites, then upper 30–70 cm of very rich *Coolinia* and *Stricklandia* beds. Goéland Mbr, unit 5, stratigraphically above A853. 12F/4-592520:5449200. Specimen number GSC 109 Specimen number GSC 10940.

A886b Dauphine Road, outcrop along riverside, at bridge-intersection of east branch Dauphine River, 1.8 km south of main road. Jupiter Fm., Goéland Mbr., unit 2 directly above *Pentamerus* unit capping Gun River contact on south side of bridge. Has *Joviatrypa* and *Hyattidina*. 12E/8-545900:546900. Specimen number GSC 10933.

A889 Dauphine Road, 2.6 km S of bridge, 500 m south of A888; ca 150–200 m northwest of sharp bend-winter road transect, on north side of culvert crossing. Soft-weathering, blue, yellow-grey micrites, shales with *Joviatrypa brabyla*, rare *Triplexia*, *Lep-*

taena. Goéland Mbr., high (unit 9?). 12E/1-544700:5454820. Specimen number GSC 10938, 10939.

A1109 [=A888] Dauphine road, north side of creek intersect ca 200 m north of winter-road intersect. South of A1106. Approx. 7–10 m of section exposed here on small creek flowing west into Dauphine River. A1109a, lowest level with small *Eoplectodonta* just above creek level; A1109b, 2 m higher than A1109a, with first levels of *Joviatrypa* sp. A1109c, ca 3 m higher than A1109b, unit with medium-large *Pentamerus*, *Joviatrypa cuspis* (larger than A1109b below), *Ptychopleurella* [this level is still slightly below unit with even larger *Pentamerus* shells]. All units here in Goéland Mbr., levels 4–5? 12E/1-545280:5455100. Specimen number GSC 10932.

A1110 Dauphine road, on south-side of same creek as in A1109. Roadcuts and ditches for about 30 m south, with larger excavation on east side of road above the creek, repeating same levels but with the larger *Pentamerus* from the units above A1109c, *Joviatrypa* here occurs abundantly in two beds, at about level of A1109b, but 60 cm apart, with large *Pentamerus* about 5–7 m higher. Goéland Mbr. 12E/1-5445270:5454970. Specimen number GSC 10926.

A1188 Dauphine River, east bank, ca 400 m south of short (<100 m) easterly access road from main road, 150 m long outcrop exposing 1–2 m soft weathering clayey shale, micrite, blue-grey with abundant giant *Pentamerus*, strophomenids, no atrypids. Goéland Mbr., higher 6–7? 12E/1-5442950:5451950. Specimen number GSC 10942.

A1189 Dauphine River, east bank, 700 m downstream from access road. Continuous low outcrop in light grey shales, micrites with repetitive local beds at several levels of *Pentamerus* in massive *in situ* nests, few *Leptaena*, common nautiloids, stromatoporoids (bored, domed, large), Goéland Mbr. 12E/1-5442770:5451750. Specimen number GSC 10930.

A1202 [=A935, A1149] Main road, road-fill quarry on south side of road at east branch of Box River (which runs south of and around this quarry). Exposing ca 2 m of strata including hard grainstones in the road-bed and upper 50 cm of quarry (east point basal beds with *Palaeoporella*), and underlying blue-green shales of Goéland Mbr with abundant shells *Stegerhynchus*, rare athyrids, *Pentamerus*. Collections from uppermost 1–1.5 m of Goéland Mbr. with

rhynchonellids. 12E/8-5452560:5455900. Specimen number GSC 10931.

A1391 [=A888, A1109, A1287] Dauphine road at south bank, second small creek, 2.4 km south of bridge. Intersect with ca 10 m soft blue-grey shales. Loose collections on roadside going uphill above creek on south side of creek. Soft weathering micrites and shales yield giant *Pentamerus* at top [A1391b], overlying *Joviatrypa* unit 2 m below [=A1391a] and shales at creek level. Goéland Mbr., unit 7–8. 12E/1-5445300:5455080. Specimens number GSC 10927, 10929.

A1493 Sandtop road, 1.2 km east of East Point Mbr contact. Adjacent, south to Schmitt River, roadside of *in situ* bulldozed nest of *Pentamerus paliformis* in blue-grey shales/micrites, weathering orange. Goéland Mbr. units 7–8. 0558607E:5454608N; 12E/1-5958607:5454408. Specimen number GSC 10935, 10936, 10941.

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