Borings in trepostome bryozoans from the Ordovician of Estonia: two ichnogenera produced by a single maker, a case of host morphology control

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The evolution of borings has shown that the morphology of borings is a function of both the borer and its substrate. This study investigated the effect of bryozoan internal skeletal morphology on the dimensions and distribution of borings. One hundred and forty-three trepostome colonies from the Middle and Upper Ordovician strata of northern Estonia were examined. Of these, 80% were matrix entombed, longitudinally sectioned ramose and hemispherical colonies, and 20% were matrix-free hemispherical colonies that allowed examination of the colony surfaces. Seventy-one percent of the ramose colonies were bored, whereas 88% of the hemispherical colonies were bored. On average, only 8% of colony surface areas were bored out. Borings were more randomly oriented in the hemispherical colonies. In contrast in the ramose colonies, the borings tended to more restricted to the thin-walled endozone and thus parallel to the branch axis. This is interpreted to be a function of the thick-walled exozones controlling to some extent where the borer could bore. Based on morphology, the borings in the hemispherical colonies are referred to *Trypanites* and those in the ramose colonies to *Sanctum*. *Sanctum* is revised to include two possible openings and to recognize that boring shapes were inherently constrained by the thick-walled exozones of the host bryozoan colonies. Both trace fossils were probably produced by a boring polychaete that used the tubes as domiciles. ☐ *Estonia, Ichnotaxa, Ordovician, Sanctum, trace fossils,* Trypanites.

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Trace fossil classification is complicated by the competing components of trace morphology, that is, the morphology of the trace maker and the substrate on or in which the trace is made. Bertling *et al.* (2006) argued that ichnotaxa should be based primarily on the morphology of the trace resulting from the behaviour of the trace maker without regard to size, producer, age, facies, and preservation. For bioerosion traces such as borings, substrate is crucial as well (Bertling *et al.* 2006). This is illustrated in the ichnogenus *Sanctum* as it is partly defined by its substrate, that is bryozoans with distinct exozones and endozones (Erickson & Bouchard 2003).

What are the implications for ichnotaxonomy if the morphology of the substrate creates two morphotype traces for the same trace maker (Bromley 1996)? More specifically, should *Sanctum* be synonymized with *Trypanites* simply because the only difference between the two is that the morphology of a ramose trepostome bryozoan substrate results in a different shaped trace than in a hemispherical bryozoan substrate? Ichnotaxa are determined by morphology, not producer (Ekdale *et al.* 1984). Ramose trepostome bryozoans have a peripheral thick-walled exozone and an axial thin-walled endozone. The exozone is more difficult to bore through due to its thicker walls, and therefore the borer was postulated to be forced into the endozone (Erickson & Bouchard 2003). Hemispherical trepostome bryozoans possess a thin endozonal portion close to the basal budding plate. The endozonal chambers are recumbent on the basal plate but after a very short distance bend into the exozone to become vertical to subvertical (Boardman & Utgaard 1966) and grow away from the basal zone in all directions. In this upright exozonal region chamber walls are no thicker than the endozonal walls seen in many ramose bryozoans. These thin exozone walls in the hemispherical colonies should create less constraints than ramose colonies on the borer resulting in more randomly oriented borings. Thus, the same borer may make two distinctly shaped borings simply due to the morphology of its host substrate.

Bryozoans often provided a substrate for macroboring organisms, which became prevalent during the Middle and Upper Ordovician. The Ordovician

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radiation in bryozoan biodiversity (Taylor & Ernst 2004) may have contributed to the rapid diversification of macroboring ichnotaxa at this time, which is now referred to as the Ordovician Bioerosion Revolution (Wilson & Palmer 2006). It may be a result of the Ordovician radiation of marine invertebrates and the concurrent differentiation of hard substrate niches (Wilson & Palmer 2006). *Trypanites* predated this revolution as it started in the Early Cambrian (James *et al.* 1977; Kobluk *et al.* 1978; Palmer 1982; Wilson & Palmer 2006). *Sanctum* certainly is part of the revolution as it is first reported in the Upper Ordovician (Erickson & Bouchard 2003).

Geological setting and stratigraphy

This study is based on bryozoan colonies collected from the Middle and Upper Ordovician of northern Estonia. The Ordovician strata lie almost horizontally with a regional southward dip of 2.5°–3.5° (Männil 1990). During the Ordovician, the Baltic basin experienced a period of regional intracratonic platform subsidence (Nikishin *et al.* 1996). As sea level rose, there was progressive overstepping of the basin's margins, and shallow marine carbonates and shales were deposited on the platform (Hints *et al.* 1989). From the Middle to Late Ordovician, Estonia (part of the Baltica Plate) drifted from 45 to 30°S latitude (Torsvik *et al.* 1992; Raukas & Teedumäe 1997; Cocks & Torsvik 2004, 2005). Carbonate deposition in the Baltic basin extended over Scandinavia and East Baltic (Nestor & Einasto 1997; Ainsaar *et al.* 1999; Dronov & Homer 1999; Sivhed *et al.* 2004). Deposition in the basin is characterized by concentric confacies belts (Jaanusson 1976, 1995). The Northern Estonia Confacies belt is characterized by laminar, nodular, argillaceous, bioclastic limestones and pure biomicritic limestones (Ainsaar *et al.* 1999). Bryozoans are major contributors to the biogenic carbonate of these limestones (Bassler 1911; Männil 1961a; Polma 1972).

During the Lower to early Middle Ordovician, the Baltic basin was dominated by cool-water, condensed carbonates/marls, which by the late Middle to Upper Ordovician were replaced by warm water carbonate and build-up accumulation (Sivhed *et al.* 2004). The change in depositional style was related to the progressing collision of Baltica with Avalonia (Nestor & Einasto 1997; Meidla & Ainsaar 2004).

Eight stratigraphic stages from the Middle and Upper Ordovician of northern Estonia were sampled (Table 1). To avoid any biases from fragmentary colonies, only the most complete bryozoans were selected. The bryozoans came from 16 different localities (Fig. 1) including quarries (Aluvere, Harku, Kohtla, Kunda-Aru, Pääskula, Peetri (near Harku), Saka, Väo (in Tallinn), Vasalemma), coastal exposures (Pakri, Põõsaspea, Ristna), road cuts (Laagna Tee (in Tallinn), Madise), and subsurface cores (Kuusiku, Rooküla) (for stratigraphy and locality details of many of these localities see Hints & Ainsaar 2004).

Table 1. Stratigraphic distribution of bryozoan colonies and borings through the Baltic Middle and Upper Ordovician (Global Series and Baltic Series and Stages follow stratigraphic scheme for Estonia and Baltoscandia outlined in Nõlvak (1997, Table 7, p. 54); Webby (1998, fig. 4); and Meidla & Ainsaar (2004, fig. 3).

Global series	Baltic series	Baltic stages	Number of bryozoan colonies examined	Percentage of bryozoan colonies bored
Upper Ordovician	Viru	Oandu	7	57
		Keila	62	90
		Haljala	16	81
		Kukruse	33	64
Middle Ordovician		Uhaku	8	88
		Lasnamägi	10	100
		Aseri	0	
	Oeland	Kunda	6	50
		Volkov	1	0

Materials and methodology

One hundred and forty-three trepostome bryozoan colonies were utilized in this study, of which 68 (48%) were ramose erect branching colonies all preserved in matrix, and 75 (52%) were hemispherical dome-shaped massive colonies, some of which were free of matrix and some were preserved in the matrix. All but 34 were sectioned longitudinally. Three were sectioned obliquely, two transversely, and 29 matrix-free hemispherical colonies were not sectioned so their colony surfaces could be examined. In the former, these surfaces were polished which allowed for the borings to be more easily examined. A number of hemispherical colonies were then slabbed to reveal internal structures. All the ramose colonies were sectioned for interior examination, and a few were sufficiently free of matrix as to allow examination of surface borings. All the material is housed in the Geological Museum, Trinity College, Dublin (specimen prefix TCD).

On each colony various characters were measured or scored (Fig. 2). The following five characters were measured: (1) Cross-sectional area of the colony was the area of the colony in cross-section view; except in matrix-free hemispherical colonies, it was simply the area of the top of the colony in plan view. (2) The number of borings was simply a count of the number of individual borings visible. This underestimates

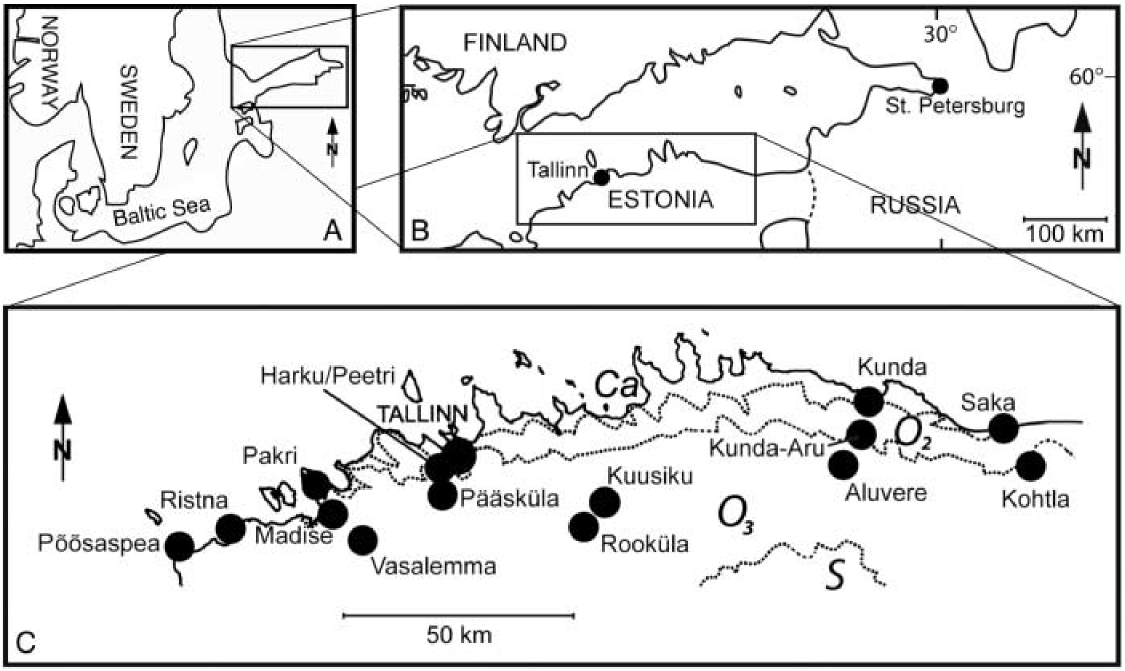

Fig. 1. Schematic geological map of northern Estonia showing collecting localities. Ca = Cambrian, O_2 = Middle Ordovician, O_3 = Upper Ordovician, S = Silurian. □A. Southern Scandinavia and the Baltic Sea. □B. Location of Estonia. Modified from Vinn (2004, fig. 1). □C. Collecting localities and geology. Modified from Meidla & Ainsaar (2004, fig. 1).

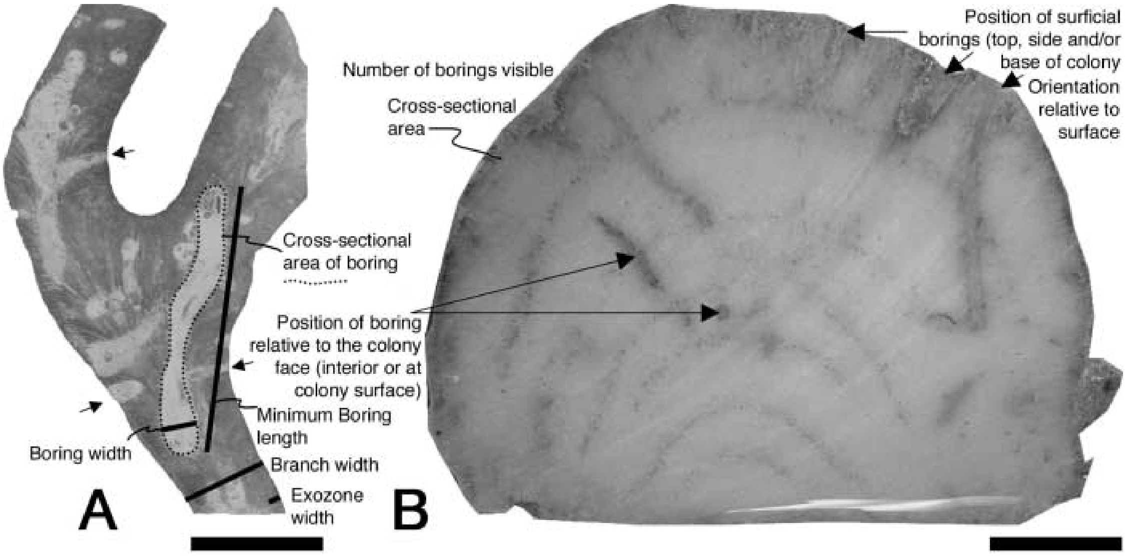

Fig. 2. Parameters measured on borings in trepostome bryozoan colonies in this study. Scale bars 10 mm. □A. Ramose colony. TCD.58168, Vasalemma Quarry, Saue Member, Kahula Formation, Keila Stage, Upper Ordovician. Short arrows point to boring openings to colony surface. Boring cross-sectional area depicted with dotted line. □B. Hemispherical colony. TCD.58620, Kohtla Quarry, Kiviõli Member, Viivikonna Formation, Kukruse Stage, Upper Ordovician.

the number of borings as cross-cutting borings were counted as one boring since we could not differentiate the two. (3) Cross-sectional area of boring. This underestimates the true area as rarely did the section intersect the borings along their long axis. (4) The minimum length of each boring is also correlated with the orientation of the cross-section to the boring. Boring lengths are complicated measurements as they combine biological information about the borer, ecological information about the host colony's ability to be bored, and the orientation of the boring to the thin section. As a result, boring length undoubtedly underestimates the true length of the borings. (5) The maximum width measured perpendicular to the length of each boring is independent of the orientation of the cross-section to the boring; as a result it contains more biological information about the boring and/or borer. In addition for the ramose colonies, we measured (6) branch width and (7) exozone width. All measurements were made to the nearest 0.01 mm on a digital image analysis system with a measurement error of 3.7%.

For each colony we calculated the mean boring area, mean minimum boring length, mean boring width, total area of borings, and the percentage of the colony cross-sectional area that was bored.

For each colony we scored the following five characters: (1) Position of the boring relative to the colony surface (i.e., completely in the interior or at the colony surface). (2) Position of the surficial borings within the colony (i.e., at top, side, and/or base of the colony). (3) Orientation of the surficial borings relative to the colony surface (i.e., perpendicular, oblique, or parallel). (4) Infilling material (i.e., sparry cement, matrix, or both). (5) Relationship between zooecial walls of the colony and the boring (i.e., trunctated or deflected). In addition for the ramose colonies, we scored the following two characters: (6) Orientation of the boring relative to the branch axis (i.e., parallel, oblique, or perpendicular). (7) Position of the boring relative to the endozone and exozone. The exozone is defined as the thick-walled surficial part of ramose colonies, whereas the endozone is the thin-walled axial part of ramose colonies (Boardman & Cheetham 1983) (Fig. 3B, C).

We also measured, calculated, and scored the same characters for ghosts in the sectioned ramose and hemispherical colonies. Ghosts are defined as smaller sparry cement-filled voids within larger matrix-filled borings. We interpret ghosts as the sparry cement-filled cast of the boring organism that was killed by infilling of matrix into the larger boring it had excavated. Matrix infilling would have occurred during a storm event that involved burial of the host colony. As the boring organism decayed, a void was left in the matrix-filled boring that was later filled by diagenetic sparry cement. Even though the soft-bodied animal would likely be compressed by post-mortem decay and shrinkage as well as by sediment compaction, the minimum length dimension of the ghosts represent the minimum length dimension of the boring organism better than the minimum length of the matrix-filled borings. The borer's width was probably the same as the boring width as most extant borers are the same width as their borings (Tapanila 2001), but that post-mortem shrinkage or other factors outlined above have reduced the width seen here in the ghosts.

Observations and results

In total 623 borings were measured on 143 colonies (Table 2). Colonies ranged in size from small delicate ramose forms (colony cross-sectional area = 18 mm^2) (Fig. 3A–C) to giant hemispherical forms (24,293 mm^2) (Fig. 4). The ramose colonies on average were significantly smaller (mean cross-sectional area = 167 mm^2) than the hemispherical colonies (mean = 1,066 mm^2) (*t*-test, $P = 0.008$).

To determine if there was any bias in the counting and measuring of borings for the two types of hemispherical colonies (matrix-free or matrix-entombed), we compared the results of hemispherical colonies whose borings were measured from thin sections (46 colonies) *versus* those measured from exterior surfaces (29 colonies). The percentage of colonies bored was similar (89% for matrix-entombed thin sectioned colony interiors, 86% for matrix-free exterior surfaces), and the mean boring widths were not significantly different (*t*-test, $P > 0.05$). Thus it was concluded that the boring data taken from the colony interiors from thin sections were comparable with those taken from exterior surfaces.

Boring intensities

Overall, 80% of the colonies were bored (Table 2). More of the hemispherical colonies (88%) were bored than the ramose colonies (71%). The number of borings per colony ranged from zero for nine of the hemispherical colonies and 20 of the ramose colonies to 79 in the largest hemispherical colony (Fig. 4G). The hemispherical colonies also had significantly more borings per colony (mean = 4.3) than the ramose colonies (mean = 1.7) (*t*-test, $P < 0.001$). This was partly due to the greater size of the hemispherical colonies which should have had more borings simply because they were bigger. By way of comparison, we note that Vinn (2005) reported on bored brachiopods from the same stratigraphical and geographical area as our study. Only 43% of the brachiopods he examined were bored as opposed to 80% of the bryozoans studied here. (Vinn (2005) noted that *Trypanites* was host-specific: over 40% of the valves of *Estlandia* and *Clitambonites* were bored, while less than 10% of valves of *Cyrtonotella*, *Septomena* and *Bekkerina* were bored. The boring organism was also size selective preferring large adult shells.)

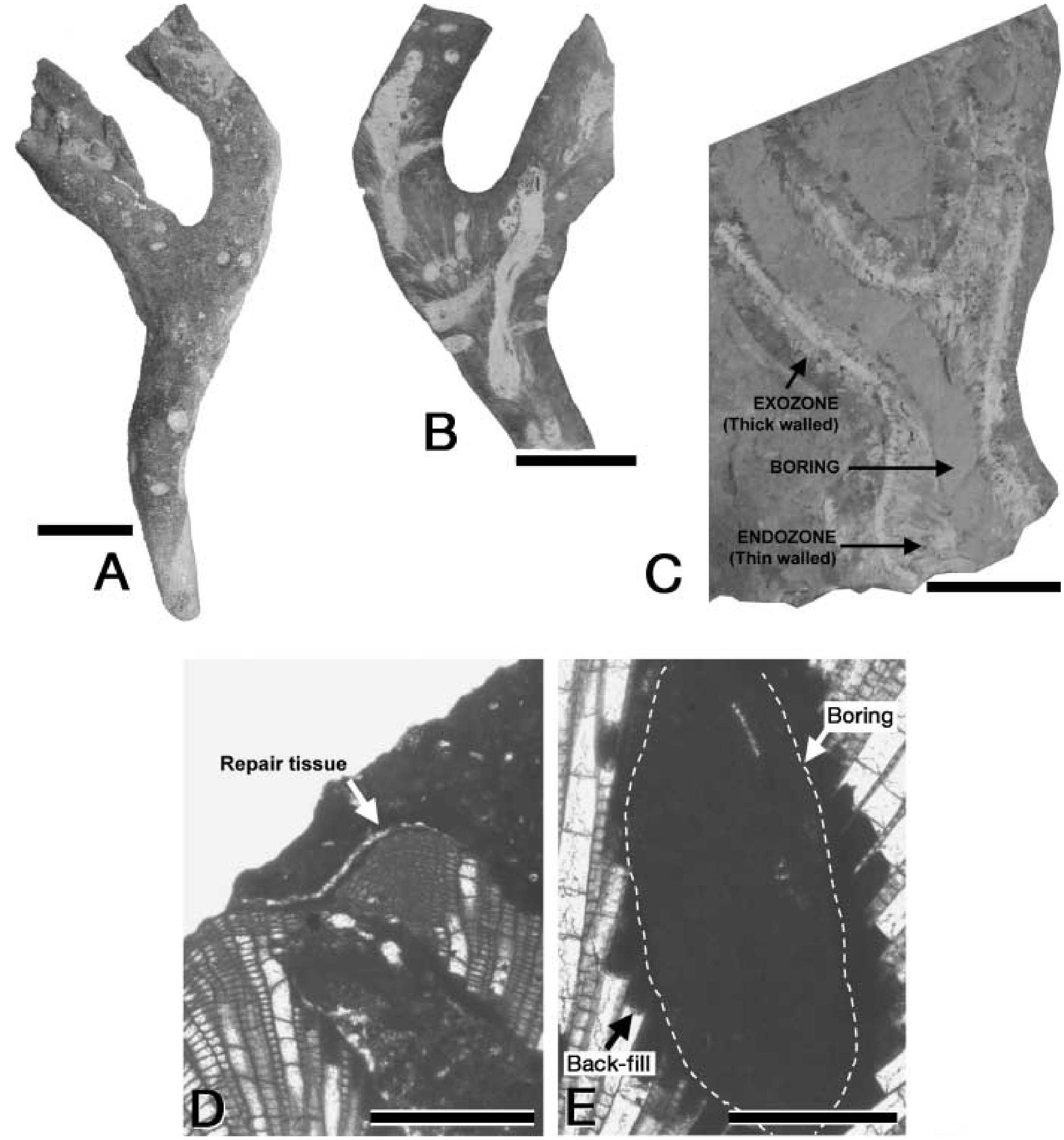

Fig. 3. Ramose trepostome bryozoans with *Sanctum* borings. □A, B. TCD.58168, Vasalemma Quarry, Saue Member, Kahula Formation, Keila Stage, Upper Ordovician. Scale bars 10 mm. □A. Exterior view of ramose colony with nine circular boring openings to surface. □B. Longitudinal section through A showing some perpendicular borings through outer thick-walled exozone (arrowed), and general pattern of longitudinal borings through the interior thin-walled endozone, roughly parallel to branch axis. □C. Longitudinal section through branched colony showing exozone and long longitudinally orientated boring that has removed most of the endozone through the colony on one side. TCD.58353, Ristna Cliff, Kahula Formation, Keila Stage, Upper Ordovician. Scale bar 10 mm. □D. Oblique longitudinal section showing skeletal repair tissue (arrowed) adjacent to a boring, TCD.58214, Pakri Peninsula, Väo Formation, Uhaku Stage, Middle Ordovician. Scale bar 2 mm. □E. Oblique transverse section through a boring (dotted line (arrowed)) with jagged broken exozonal walls and back-filled sediment (arrowed) lateral to the boring. TCD.58300, Madise Village, Madise Member, Kahula Formation, Haljala Stage, Upper Ordovician. Scale bar 2 mm.

As expected the number of borings in our study was significantly positively correlated with colony size (linear regression, $R^2 = 0.62$, $P < 0.001$). The percentage area of the colony bored was not significantly correlated with colony size (linear regression, $R^2 = 0.00$, $P > 0.05$), which suggests that the borers settled more on the larger colonies simply because they were larger, and not because they actively selected larger colonies. To correct for this we calculated the percentage of each colony's cross-sectional area that was bored out. We only used the 46 thin-sectioned hemispherical colonies as they have the same

Table 2. Summary statistics for colony and boring quantitative characters for ramose and hemispherical colonies.

	Ramose colonies	Hemispherical colonies (longitudinally sectioned)	Hemispherical colonies (both surfaces)	Total	Ghosts in borings
No. of colonies sampled	68	46	29	143	18
No. of colonies bored	48	41	25	114	na
% colonies bored	71	89	86	80	na
Mean no. of borings per colony	1.7	2.8	6.8	4.4	na
Mean no. of borings per bored colony	2.3	3.2	8.6	5.3	2
Mean colony cross-sectional area (mm^2)	167	356	2034	639	na
Mean total boring cross-sectional area (mm^2) [includes non-bored colonies]	20	29	186	50	na
Mean % colony cross-sectional area bored [includes non-bored colonies]	10	8	4	8	na
Mean boring cross-sectional area (mm^2)	19	12	17	16	5
Mean minimum boring length (mm)	7.1	5.5	4.9	6.0	3.9
Mean boring width (mm)	2.1	2.1	2.6	2.2	1.2
Minimum boring length/width ratio	3.4	2.6	1.9	2.7	3.3

na, not applicable.

geometric relationship between the borings and the longitudinal cross-sections as the ramose colonies. The ramose colonies had a higher percentage of area bored (10%) than the hemispherical colonies (8%), but the difference was not significant (*t*-test, $P > 0.05$).

Boring dimensions

Minimum boring length ranges from a mean of 4.9 mm in the matrix-free hemispherical colonies to 7.1 mm in the ramose colonies (Table 2). Boring width is a more useful character as maximum boring width should approximate true boring diameter regardless of the orientation of the boring to the thin section. Boring widths were less variable and did not significantly differ among the different colony morphologies (Fig. 6). Mean boring widths ranged from a mean of 2.1 mm in matrix-entombed hemispherical colonies and ramose colonies to a mean of 2.6 mm in matrix-free hemispherical colonies (Table 2). Vinn's (2005) borings in brachiopods were on average smaller (mode = 0.5 mm) than those in the bryozoans (mode = 1.54 mm).

Ghosts

Ghosts were found in 18 of the 114 (16%) sectioned colonies, eight in ramose colonies and ten in hemispherical colonies (Fig. 5). These differ from the 'ghost rims' observed by Kobluk & Nemcsok (1982, Fig. 1b) which are diagenetic recrystallization of micritic linings of borings, and from the geopetal fills at the bottom and lateral margins of *Trypanites* noted by Tapanila *et al.* (2004, p. 297). The degree of post-mortem shrinkage of the soft-bodied borer can be seen in the significantly smaller ghost widths (mean = 1.2 mm) compared to the boring widths (mean = 2.3 mm) (*t*-test, $P < 0.001$) (see Fig. 5). If our interpretation of ghosts as remnant body cavities is correct, then ghosts should have shorter minimum lengths than borings. This proved to be the case in the thin-sectioned colonies with the mean boring minimum length (6.4 mm) being significantly longer than that for the ghosts (3.9 mm) (*t*-test, $P = 0.014$).

Effect of borings on colonies

Did the borings have a negative impact on the bryozoans? Before this question can be answered, we must address the question of whether the colonies were alive at the time of boring. As the colonies were also bored on their bottom surfaces, the colonies must have rolled along the substrate during storms (Cuffey 1997; Sanders *et al.* 2002). When this happened for an extended period of time, the zooids on the colony surface in the sediment presumably died. Therefore, parts of the colony surface were undoubtedly bored where there were no living zooids. As clonal animals, it is typical for bryozoan colonies to have living and necrotic parts, therefore it is likely parts of the colony surface were alive when bored. The truncated nature of the zooecial walls at the edges of borings does not help resolve this. The truncated walls simply indicate that the zooecia were dead before or were killed during the boring.

In the matrix-free hemispherical colonies, on average only 4.2% of the colony surface was bored. This suggests that borings did not have a great impact on the number of feeding zooids. However, it is possible that if the boring organism was a filter feeder, then its filtration fan when active would have had a deleterious effect on the ability of bryozoan zooids

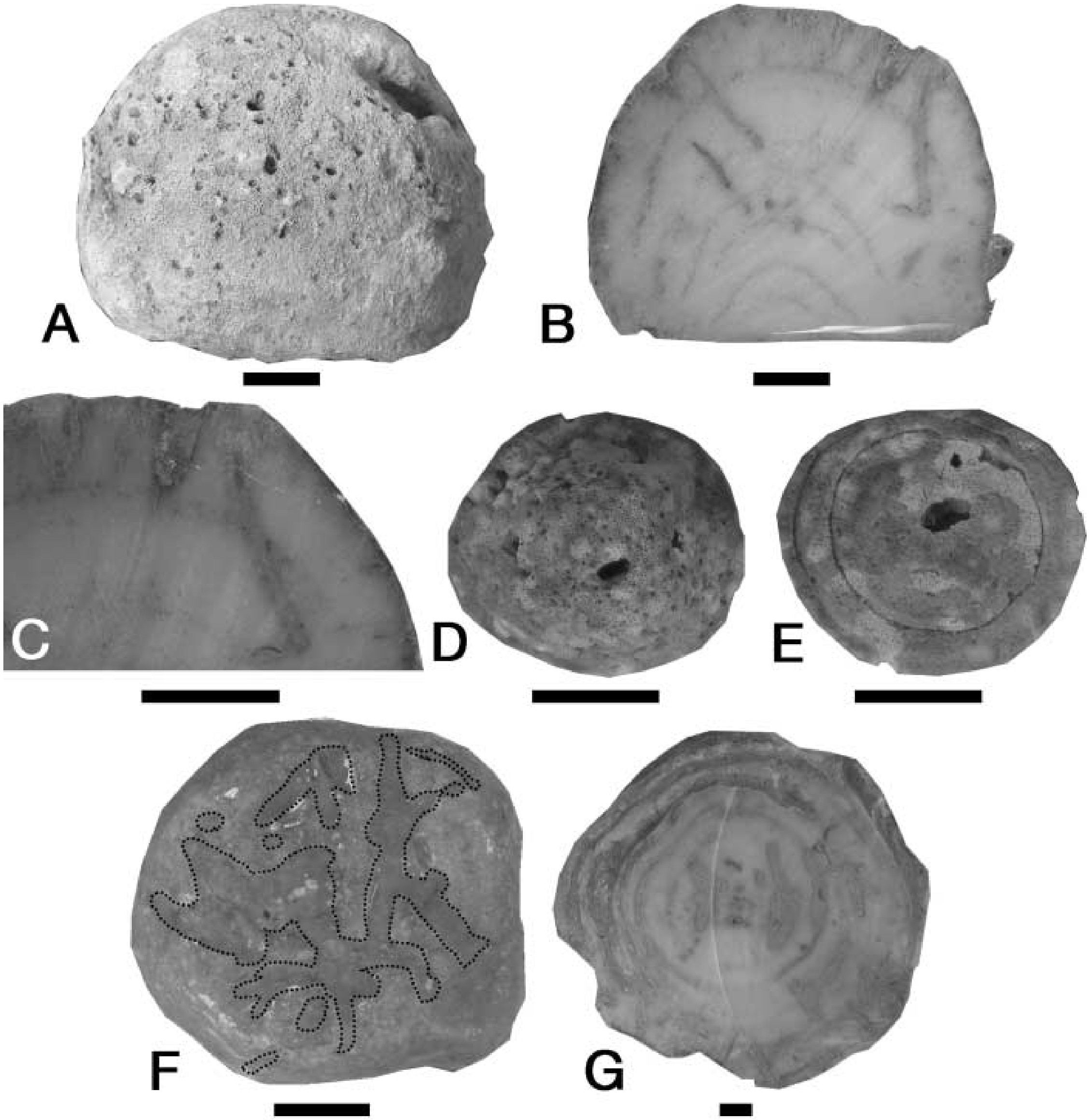

Fig. 4. Hemispherical trepostome bryozoans with *Trypanites* borings. All scale bars 10 mm. □A, B, C. TCD.58620, Kohtla Quarry, Kiviõli Member, Viivikonna Formation, Kukruse Stage, Upper Ordovician. □A. Exterior surface with circular boring openings with a range of diameters. □B. Longitudinal section through A showing thin-walled exozonal skeleton transversed by several tubular borings; most enter perpendicular to the surface and then become more randomly orientated. The concentric darker zones represent earlier growth stages of the colony. □C. Detail of B. □D, E. TCD.58388, Ristna Cliff, Kahula Formation, Keila Stage, Upper Ordovician. □D. Upper surface of colony in plan view showing autozooecial apertures, and scattered boring openings. The majority of openings are small representing borings by juveniles whereas the four larger ones are interpreted to have been made by adults. □E. Basal surface in plan view showing radiating growth pattern of colony and two large boring openings. □F. TCD.58371, Ristna Cliff, Kahula Formation, Keila Stage, Upper Ordovician. Upper surface plan view of truncated colony which has been extensively bored with tubular borings in various orientations. Borings outlined by dotted lines. □G. TCD.58620, Kohtla Quarry, Kiviõli Member, Viivikonna Formation, Kukruse Stage, Upper Ordovician. Plan view of basal surface with tubular borings in centre. The outer dark concentric zones are undulations in the basal surface of the colony.

situated immediately underneath the fan to feed. Another potential threat to the colonies, at least the ramose ones, was the effect of borings on the structural integrity of the colony. Erickson & Bouchard (2003) argued that bored out endozones in ramose colonies could compromise the strength of ramose branches leading to breakage. This is certainly possible, but any potential effect is lessened by the fact that the strength of ramose branches comes from their exozone width and branch width, not the endozone skeletal material (Key 1991). This is analogous to the strength of an I-beam as opposed to a solid cylinder.

Kobluk & Nemcsok (1982, p. 680) argue *Prasopora* was only bored when dead, as does Tapanila *et al.* (2004) for stromatoporoids. However, in this study we show that boring into living bryozoan colonies

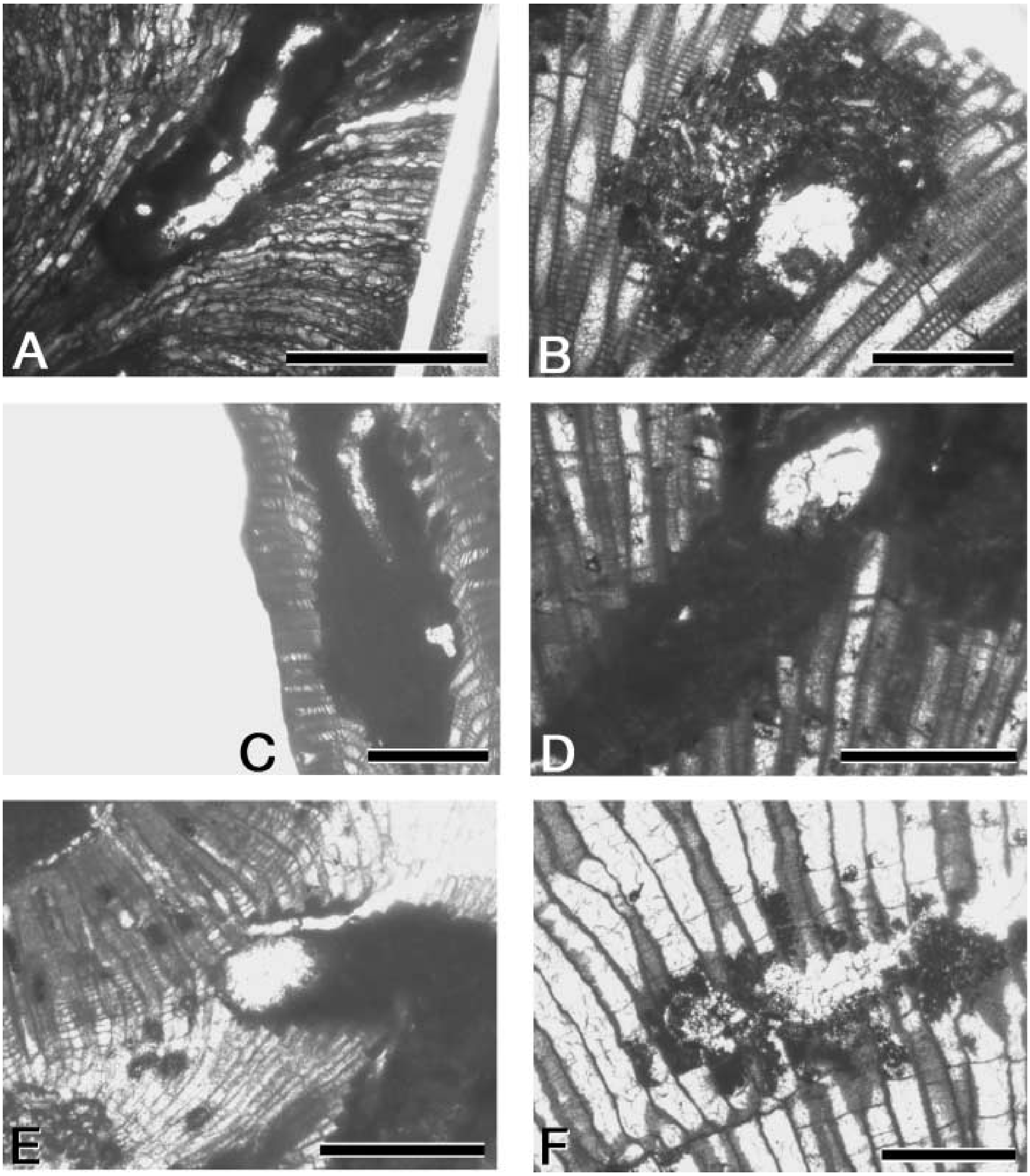

Fig. 5. □A–F. Ghosts and faecal pellets in *Sanctum* and *Trypanites* borings. These are infilled by sparry calcite and contrast sharply with the matrix filled borings. All scale bars 2 mm. □A–C ramose bryozoan colonies, and □D–F hemispherical bryozoan colonies. □A. Oblique longitudinal section; calcitic ghost in centre of *Sanctum* boring. TCD.58168, Vasalemma Quarry, Saue Member, Kahula Formation, Keila Stage, Upper Ordovician. □B. Oblique tangential section; circular ghost profile on lateral margin of *Sanctum* boring. TCD.58152, Vasalemma Quarry, Pääsküla Member, Kahula Formation, Keila Stage, Upper Ordovician. □C. Longitudinal section with most of endozone removed. Thin curved ghost representing long profile of boring animal in *Sanctum* boring. TCD.58156, Vasalemma Quarry, Saue Member, Kahula Formation, Keila Stage, Upper Ordovician. □D. Oblique section through *Trypanites* tube with ghost profile. TCD.58007, Väo Quarry, Väo Formation, Uhaku Stage, Middle Ordovician. □E. As □D. TCD.58002, Väo Quarry, Väo Formation, Uhaku Stage, Middle Ordovician. □F. *Trypanites* boring containing small dark faecal pellets in right-hand side. TCD.58215, Pakri Peninsula, Väo Formation, Uhaku Stage, Middle Ordovician.

certainly does occur, as evidenced by the presence of repair tissue adjacent to some borings (Fig. 3C) but it is impossible to determine if *in vivo* boring occurred extensively (see Lamond & Tapanila 2003).

Typically only the outer surface (periphery in a hemispherical colony and exozone in a ramose colony) of a bryozoan colony contains living zooids. The rest of the interior of the colony generally does

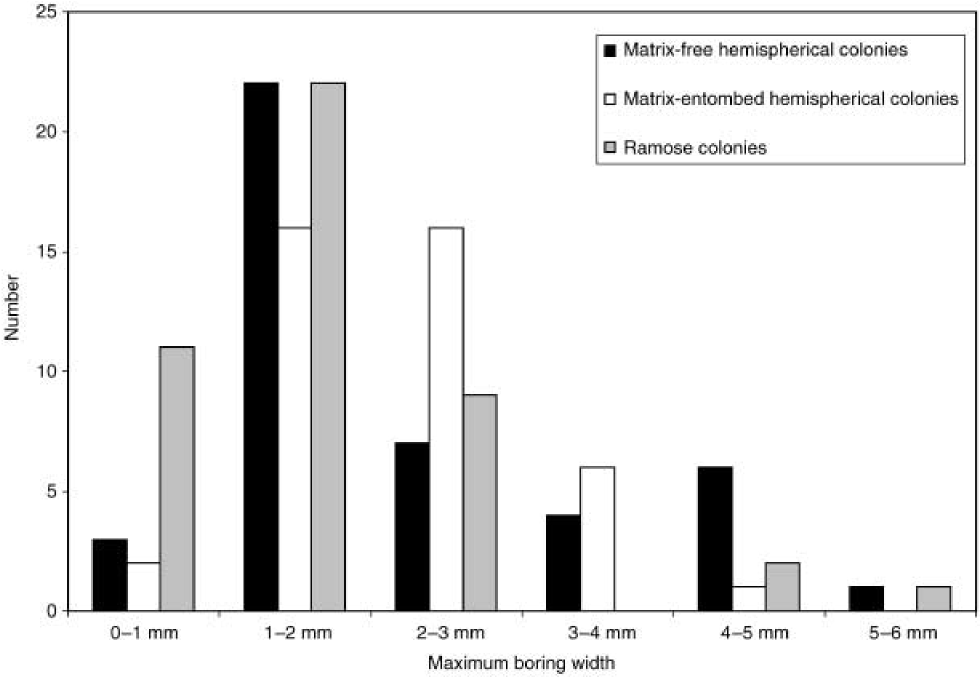

Fig. 6. Frequency histogram of maximum boring widths for exterior surfaces of hemispherical colonies, interiors of hemispherical colonies, and interiors of ramose colonies.

not. As a result, only the initial surface boring would potentially kill zooids. In the matrix-free hemispherical colonies, on average only 4.2% of the colony surface was bored. This low number suggests that there was not a large negative impact on the number of feeding zooids by the borings. It is likely that *Trypanites* developed in both living and dead bryozoan hosts. This also suggests the reasons for and function of the boring – as we demonstrate these borings are found mainly in the endozone which lacks zooids and other living tissue, and they were used as a domicile and not produced by a boring animal seeking nutrients.

Could the internal borings have compromised the structural integrity of the colonies? The percentage of the internal cross-sectional area of the colonies that was bored out averaged 8% and ranged from 0% for the unbored colonies to 78% for one ramose colony (Table 1). These internal borings were almost entirely restricted to the thin endozonal zooecial walls. As this percentage is so low, there probably was not much of an impact on the strength of the colonies. The loss of the endozone should not significantly decrease the strength of the ramose colonies (Key 1991).

The boring organisms are endoskeletozoans (an animal that inhabits any organic hard substrate that is either dead or alive, see Taylor & Wilson 2002). Even though we only have one example of synvivo boring (Fig. 3D), we assume that most of the colonies were alive (around their peripheral margins, as outlined above) at the time of boring due to a lack of fouling organisms on the colony surfaces. In this case the boring organism lived within live host bryozoan colonies of both morphologies and we suggest that this has no serious impact on living polypide numbers. As such they may be regarded as being in endosymbiosis with the host bryozoan. Unlike many endosymbiotic relationships with a host, we do not have a case for suggesting that the boring organism here forms a bioclaustration. Bioclaustrations are formed when an endosymbiont becomes embedded within the growing skeleton of the host, which results in the formation of a cavity in which the endosymbiont lives (Tapanila 2005). In this study we have evidence of rare regeneration and repair of outermost exozonal skeletal tissue subsequent to it having been bored (Fig. 3C). It is clear that the cavities formed within the bryozoan colonies were not developed around an endosymbiont during growth of those colonies, but that they were bored subsequent to colony growth, and therefore they are not bioclaustrations.

Spatial distribution of borings within colonies

The number of borings and the percentage of surface area bored on hemispherical colonies did not differ significantly between the top of the colony and the bottom (*t*-tests, $P > 0.05$). This suggests that the borers did not have a preference for either surface and/or that the bryozoan colonies were bored when upright as well as overturned by storms. These types of massive colonies that are repeatedly overturned during their life have been termed ectoproctoliths (Thiel *et al.* 1996).

Borings on colonial organisms that were not flipped during life by storms such as stromatoporoids, corals, and some bryozoans exhibit a preference for the topographically high points of the hosts (Kershaw 1980; Kobluk & Nemcsok 1982; Nield 1984; Habrant & Lathuiliere 2000; Wilson & Lazzuri 2000; Tapanila *et al.* 2004). The contrast between these stable host colonies and our hemispherical bryozoans may be due to repeated flipping of the bryozoans during their life. Dome or bell-shaped massive bryozoan colonies are hydrodynamically more stable in an upside-down position (Wyse Jackson *et al.* 2002). Experimental modelling has shown that the right-side up orientation is effective at maintaining upright orientation in low to medium energy wave regimes, but once the colonies are entrained, they tend to settle upside down (Wyse Jackson *et al.* 2002). Additional support that our hemispherical colonies may have been overturned comes from Kershaw (1980, p. 331) who demonstrated that *Trypanites* did not occur in the cryptic niches found under some Silurian stromatoporoids, and that it was restricted to the upper surfaces of colonies. He reasoned that where the underside of colonies was bored, the colonies had been overturned.

If the borers were actively selecting their host colonies, then we would predict that the ramose colonies with thinner exozones would be more bored than those with thicker exozones. This is in marked contrast to the findings of Tapanila *et al.* 2004, who found that borers favoured those corals and sponges with a higher substrate density. Highsmith (1981) found that modern borers tend to selectively target denser coral substrates, and that *Trypanites* is abundant in really dense coccoserids, proporids and clathrodictyids (Tapanila, personal communication, 2006). Exozones in ramose trepostomes are composed of thicker walls (often by two orders of magnitude) than in the endozone (Fig. 3C) and could create a deterrence to borers. The number of borings was not significantly correlated with exozone width (linear regression, $R^2 = 0.03$, $P > 0.05$), which suggests that the borers were not actively selecting for ramose colonies with thinner exozones and/or against those with thicker exozones. The borers probably lacked a way to determine exozone width from the colony surface.

Were the orientations of the borings constrained by the presence or absence of a thick-walled exozone? To test this, we calculated the boring length:width ratio. A ratio of 1:1 indicates that the borings were as long as wide. This would occur if the boring was oriented perpendicular to the longitudinal section of the thin section. A larger ratio indicates that the borings were oriented more parallel to the thin section. Our results (Table 2) show that the ramose colonies (mean = 3.654) had a significantly larger ratio than the hemispherical colonies (mean = 2.76) (*t*-test, $P < 0.0047$). This suggests that the borings in the ramose colonies were oriented more parallel to the branch axes (i.e., were constrained by the exozone), and that the borings in the hemispherical colonies were oriented more randomly. This analysis requires the assumption that the borings were the same length in both colony shapes. As discussed above, the hemispherical colonies are significantly larger than the ramose colonies and thus should have had longer borings. Thus our data should have been biased against finding the length:width ratio to be higher in the ramose colonies.

Borings entered or exited the colony roughly perpendicular to the colony surface 68% of the time in ramose colonies and 55% of the time in hemispherical colonies (mean = 60%). Kobluk *et al.* (1978) and Kobluk & Nemcsok (1982) reported that borings intersected the colony surface from 60 to 90°, with most at 90° (Nield 1984). Our findings are consistent with these observations. A minority of the borings intersected the colony surface obliquely or parallel. Borings oriented roughly perpendicular to the colony surface would have minimized intersection with skeletal walls of the bryozoan zooecia which would have provided more resistance than the empty zooecial chambers. This is especially true with the ramose colonies with their thicker zooecial walls in the exozone. In these colonies the borings seemed to parallel the zooecial chamber axes (Fig. 3B). This same pattern is seen in *Favosites* corals where the borings are oriented down the center of the corallites to avoid the corallite walls (Tapanila *et al.* 2004). This is supported by the higher percentage of borings intersecting the colony surface roughly perpendicular in the ramose as opposed to the hemispherical colonies. In the ramose colonies, 57% of the borings were roughly parallel to the branch axis and 79% were in the endozone. This suggests that the borers were actively avoiding the exozone with its thicker skeletal walls. Rarely did borings go straight through a colony, suggesting that these may have been bored after burial by a different organism boring through the sediment and any clasts (e.g., bryozoan colonies) it encountered.

Identification of the Estonian borings

Borings are frequent bioerosional features (Palmer & Plewes 1993) within Lower Palaeozoic faunas (Kobluk *et al.* 1978; Wilson 2000; Wilson & Palmer 2006) where they have been identified variously as predatory borings or domiciles (see references in Wilson & Palmer 2001). Such borings are known to affect many taxa including brachiopods (Clarke 1921; Kaplan & Baumiller 2000; Vinn 2004, 2005), bryozoans (Cameron 1969a, b; Cuffey 1977; Kobluk & Nemcsok 1982; Spjeldnaes 1981; Pickerill *et al.* 1984; Buttler & Wyse Jackson 1997; Wilson & Lazzuri 2000), corals (Elias 1986; Tapanila & Holmer 2006), and stromatoporoids (Clarke 1921; Nield 1984; Pemberton *et al.* 1988; Wilson & Palmer 1988; Tapanila *et al.* 2004; Tapanila & Holmer 2006).

Borings in Lower Palaeozoic bryozoans

Borings made in Lower Palaeozoic bryozoans, particularly in the trepostome genera *Diplotrypa* Nicholson, 1879 and *Prasopora* Nicholson & Etheridge, 1877, have been assigned to various ichnogenera including *Trypanites* Mägdefrau, 1932; *Palaeosabella* Clarke, 1921; *Vermiforichnus* Cameron, 1969a; *Petroxestes* Wilson & Palmer, 1988; and most recently *Sanctum* Erickson & Bouchard, 2003. From the Cincinnatian of Ohio, Palmer & Wilson (1988) described the unusual trace fossil *Catellocaula* which they found on the trepostome *Amplexopora*, but this they showed to be a pseudoboring, recently recognized as a bioclaustration (Tapanila 2005).

Trypanites has been the most widely reported of these ichnotaxa, and is characterized by being a simple, unbranched, long cylindrical boring with length-to-width ratio of > 20:1, that may be up to 4.9 mm in diameter (Palmer *et al.* 1997; Cole & Palmer 1999). Wilson & Palmer (2006) note a word of caution that many borings attributed to *Trypanites* twist and are not necessarily elongate and may represent ichnogenera that are not simply filter feeders. They suggest that better ichnosystematics of *Trypanites* may yield a greater diversity of boring ichnotaxa in the Ordovician than hitherto recognized. Of the borings observed here, the length-to-width ratio is < 20:1 for two reasons; first, our sections are orientated randomly to the long axis of the borings, and therefore we never know the true length of the borings. Second, the dimensions of the host colonies may restrict the length of the borings to less than one-twentieth of their diameter.

Vermiforichnus, a boring described in the hemispherical trepostome *Prasopora orientalis* from the Ordovician of New York (Cameron 1969b), is a synonym of *Trypanites* (Pemberton *et al.* 1988).

Palaeosabella is a clavate boring with length-to-width ratio of < 10:1, and although morphologically different from *Trypanites*, the two ichnogenera have often been confused.

Petroxestes is a surficial elongate boring produced by bivalves and is known from hardgrounds and bryozoan colonies from the Ordovician of North America (Wilson & Palmer 1988, 2006) and from the Lower Silurian of Anticosti Island, Canada (Tapanila & Copper 2002).

Sanctum was described as being a domichnia with a single, circular opening 1.1 to 3.2 mm in diameter that formed a variety of chamber shapes (clavate, flabellate, or irregular) in the endozonal skeleton of both ramose and frondose Lower Palaeozoic trepostome bryozoans.

The Estonian borings

It is clear that in the material examined two ichnogenera are present.

1. In the large hemispherical bryozoan colonies, the borings are curved elongated tubes with a mean minimum length of 5.5 mm and a mean width of 2.1 mm (Fig. 4B, C). They are randomly orientated as indicated by a low minimum boring length/width mean value of 2.76. This is due to the fact that there are no space or morphological skeletal restrictions imposed by the host colony on their propagation and development. In transverse section, borings can be seen to have a cross-cutting relationship, and the intensity of boring was so great in some of the colonies that their apexes were lost due to mechanical breakdown caused by the borings (Fig. 4F).

   The orientation and pattern of boring are not restricted by the orientation and thickness of the zooecial walls in the hemispherical bryozoans (Fig. 4B–C, F–G). Zoarial skeleton of most trepostome bryozoans is divided into a thin-walled endozone and a thicker outer walled exozone (Fig. 3C), but these fully mature, hemispherical bryozoan colonies that had a full complement of feeding polypides at the growing surface are unusual in that the endozone was restricted to a narrow zone close to the basal budding plate (Boardman & Utgaard 1966), and that the outer exozone was composed of thin zooecial walls (see Mänill 1961b for a discussion of colony morphology in hemispherical trepostomes, and Madsen 1987 for a discussion of skeletal growth in trepostomes). Although noting Wilson & Palmer's

(2006, p. 111) caution regarding the possible complexity of the ichnosystematics of *Trypanites* Mägdefrau, 1932 we have referred the borings in these hemispherical colonies to this ichnogenus.

2. In the ramose erect bryozoans, borings had a mean length of 7.1 mm, some 1.6 mm on average greater than in the hemispherical colonies, but had an identical mean width of 2.1 mm. However, the boring length/width mean value was higher in the ramose forms (3.74) which indicates that the borings were influenced by the tubular morphology of the erect bryozoans (see Fig. 3B). The borers were preferentially avoiding the exozone with the thicker skeletal walls and favoured excavating the thin-walled endozone. Consequently, the borings in the ramose bryozoan colonies were in a more axial orientation (Fig. 3B) than the borings in the hemispherical colonies which have a more random orientation. The traces in the erect ramose bryozoans are referable to *Sanctum* Erickson & Bouchard, 2003, although unlike *Sanctum* previously diagnosed, may have had more than one opening to chambers (Fig. 3A).

In both cases it is clear that the morphology of these traces is directly controlled by the morphology of the colonies, the disposition and development of the thickened exozonal skeleton in the ramose forms or the thin-walled nature of the exozone in the hemispherical colonies. These parameters had a direct bearing on the ability with which the boring organism could excavate borings. The morphology of borings seems to have been affected by the ramose form, while the hemispherical form allowed *Trypanites* to form the way the animal 'normally' would make it.

What produced the borings in the Estonian trepostome bryozoans?

Various organisms have developed lithophagy and produce borings or dissolve shelly material and produce circular openings. In modern oceans, a vast array of organisms have the ability to bioerode (Neumann 1966; Bromley 1970, 1992; Warme 1977; Wilson 2000), either by boring or by grazing (Taylor & Wilson 2003). A high percentage of bioerosion is carried out by boring bivalves (such as *Lithodomus*) and by boring clionaid sponges, and to a lesser extent by crustaceans such as barnacles and amphipods, and by echinoids and polychaete worms. Wilson (2000) has argued that through the Phanerozoic there was a change in the style of bioerosion and that in the Palaeozoic and early Mesozoic bioerosion rates were low and generally confined to the production of small holes in hard substrates, but that by the later Mesozoic bioerosion rates increased as bivalves and sponges became more prominent and various organisms sought out endolithic niches to exploit.

In the Palaeozoic, *Trypanites* was perhaps the most prevalent bioeroded ichnofossil and the animals that were responsible for producing these trace fossils have undoubtedly changed over the course of the Phanerozoic (Kobluk *et al.* 1978; Kobluk & Nemcsok 1982). This is not surprising as the ichnogenus ranges from the Cambrian (James *et al.* 1977) to the Recent (Kobluk *et al.* 1978). *Trypanites* probably represents sessile annelid polychaete worm dwelling structures (Elias 1986) or protection structures (Cole & Palmer 1999), although other organisms postulated as being the *Trypanites* 'animal' include bivalves, sipunculid peanut worms, polychaetes, acrothoracican barnacles (see Kobluk *et al.* 1978, Table 1), or phoronids (Pemberton *et al.* 1988). That some *Trypanites* was produced by polychaetes is supported by the fact that Kobluk & Nemcsok (1982) found annelid polychaete microfossils in bored bryozoan colonies; these may be a derived from a detrital polychaete jaw, and that Cameron (1969a, b) reported the presence of the spionid polychaete *Vermiforafacta rollinsi* preserved within a *Vermiforichnus* [= *Trypanites*] boring. *Trypanites* can occur by itself, indicating monospecific recruitment of trace makers (Kobluk & Nemcsok 1982; Bertling 1999) or with other trace makers (Ebbestad & Tapanila 2005).

In this study we provide evidence that suggests that the borings found in both the erect ramose bryozoans and the hemispherical bryozoan colonies were produced by *an identical organism*, but of significance is the fact that the form of the trace made in each colony type may be *different* simply because of the different internal morphologies of the colonies. As outlined above, the ghosts of the boring organism naturally had a smaller width than the borings in which they were found, and significantly there was no difference in the ghost width between ramose colonies and hemispherical colonies (Fig. 5A–E), thus pointing to their common body profile and biological type. Associated with the ghosts in a number of borings are faecal pellets which add further weight to their biological nature, although Tapanila *et al.* (2004, p. 297) suggest that such material may be introduced subsequently due to a secondary bioturbating organism. There is a slight possibility that the ghosts represent the remains of a nestler, an animal that inhabited the borings subsequent to their formation by another animal. However, this is unlikely in this case, because for this to be a possibility, one would expect to see bioturbated sediment in the borings and such reworked material was not developed in the borings described here.

It is possible that the boring organism was a sipunculan worm, some of which can bore into hard substrates. Equally it may have been a polychaete similar to modern spionid or vermiform worms, with a mean body diameter (excluding any appendages) of 1.2 mm, but if one considers any appendages that it would have possessed then these would account for the larger width borings observed. These appendages were not preserved as ghosts with only the trunk of the animal sufficiently robust for such preservation to take place. The polychaete produced tubes nearly twice its body diameter by mining through endozonal skeleton, and this action accounts for the broken margins of borings (Figs 3E, 5). The maximum length of tubes is unknown. We found 11 borings with two openings – these could simply be overprinted borings that cannot be distinguished one from another. Within the larger hemispherical colonies, movement would have been unrestricted and so elongated tubes characteristic of *Trypanites* are frequently observed (Fig. 4B–C), whereas in the restricted space offered within the endozonal portion of the ramose colonies any movement by the polychaete would have mined away much of the endozonal skeleton (Fig. 3B–C), producing a chamber characteristic of the ichnogenus *Sanctum*.

As was noted earlier, the *Sanctum*/*Trypanites* organism that produced the borings in the bryozoans under study selectively bored through low density bryozoan substrates. This is in contract with findings for some modern corals (Highsmith 181) and fossil corals and sponges (Tapanila *et al.* 2004). This suggests that there may be some fundamental behavioural difference between the *Sanctum*/*Trypanites* organism reported here, and other *Trypanites* occurrences; this may allow for the recognition of different types of *Trypanites*.

Reinterpretation of *Sanctum* (Erickson & Bouchard, 2003)

The shape of the chambers described by Erickson & Bouchard (2003) is a direct consequence of containment of the boring organism by the exozone skeleton, and we contend that in other similar trepostomes the shape of such chambers would reflect the characteristics of the outer thickened exozonal skeleton. Erickson & Bouchard (2003, p. 1002) gave the diagnosis of *Sanctum* as follows: 'Domichnia originated by boring a single, circular opening through exozonal skeleton, followed by removal of endozonal skeleton to produce dwelling cavities. Chambers of varying shapes, linear, clavate, flabellate or irregular, rather roughly, mechanically excavated out of endozonal skeleton in both ramose twig or frondose-blade growth forms of Paleozoic Bryozoa. Characteristics of openings and chambers as presently known are those of the type species.' To this should be added the important observation that *chamber morphology is defined and controlled by the exozone.* Equally chambers may be reached by *more than one opening.*

Erickson & Bouchard (2003, p. 1008) suggested that the chambers in *Sanctum* may have been produced as a domicile for an amphipod-like or isopod-like crustacean, and that they were occupied by a small colony of these creatures that fed outside their domicile. They compared the galleries with those of modern haustoriid amphipod galleries and rejected the possibility that the chambers and borings were made by polychaete or boring bivalves. However, in the light of earlier observations and discussion regarding the evidence for the producing organism, we suggest that *Sanctum* was produced by a polychaete worm with a diameter of approximately 2 mm, and that this organism was using the bryozoan host as a domicile rather than a source of nutrients.

Conclusions

Borings are frequently found in both ramose and hemispherical trepostome bryozoans from the Ordovician of Estonia. These bryozoan colony forms are distinctive and have a different skeletal arrangement, with the ramose bryozoan skeleton differentiated into a thicker-walled peripheral exozone and a thinner-walled axial endozone. The hemispherical colonies do not develop a thick-walled exozone, rather the exozonal walls are thin. These skeletal differences influence the morphology of borings made within them. Borings in the hemispherical colonies are generally unbranched and tubular, and typical of the common ichnogenus *Trypanites*. Borings in erect ramose colonies remove much or all of the endozone producing irregular shaped borings that are generally aligned parallel to the exozone and growth direction of the bryozoan colony. These borings are characteristic of the rare ichnogenus *Sanctum* hitherto only described from the Cincinnatian of North America. Significantly, both ichnogenera were probably produced by an identical boring organism, which we suggest was a spionid or vermiform polychaete, but whose borings reflect the different morphologies of the host bryozoans into which and through which it bored. In other words, the same borer makes two distinctly shaped borings simply due to the morphology of its host substrate. According to Bertling *et al.* (2006) this is legitimate so *Sanctum* and *Trypanites* should not be synonymized. The morphology of *Sanctum* traces is revised as controlled by the morphology of the exozonal skeleton of the bryozoan in which it is found.

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