

The distribution of worm borings in brachiopod shells from the Caradoc Oil Shale of Estonia.

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Abstract: Abundant worm borings were found in some brachiopod shells (*Clitambonites*, *Estlandia*, *Nicolella*) from the Ordovician (Caradoc) oil shale in North Estonia. 9 of 21 brachiopod genera (43 %) have been bored. Excluding the size and thickness of valves, no common morphological feature discriminates the brachiopods with borings from those without them. The *Trypanites* are host-specific, and the frequency of bored valves varies from 6.5 % in *Bekkerina* to 51 % in *Estlandia*. The worm larvae preferred hosts with thick lamellose shells, such as those of the clitambonitids, especially *Clitambonites schmidtii*. The boring organisms were size-selective; they preferred large adult specimens. The majority of the borings are oriented, and living hosts were preferred to dead shells. Some clitambonitid brachiopods, like *C. schmidtii* tolerated a large number of the borer's shafts in their valves. Few bored valves have the blister-like shell-repair structures in their interior.

Key Words: Ordovician; Estonia; oil shale; Brachiopoda; *Trypanites*; palaeoecology

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Résumé : *Distribution des perforations de vers dans les coquilles de brachiopodes des schistes bitumineux du Caradoc d'Estonie.*- Des perforations dues à des vers sont observées en abondance sur les coquilles de quelques brachiopodes (*Clitambonites*, *Estlandia*, *Nicolella*) des schistes bitumineux caradociens du Nord de l'Estonie. Ainsi, 9 des 21 genres de brachiopodes (43 %) étudiés ont des valves perforées. La présence ou l'absence des perforations est liée à taille et l'épaisseur des valves. Les autres traits morphologiques semblent n'avoir aucune importance. Dans l'ensemble, en effet, les larves des vers marquent une préférence pour des coquilles épaisses et lamelleuses, comme celles des clitambonitidés, particulièrement *Clitambonites schmidtii*. On note, cependant que les représentants de l'ichnogène *Trypanites* marquent quelques préférences spécifiques, ainsi leur fréquence varie de 6.5 % chez *Bekkerina* à 51 % chez *Estlandia*. La majorité des perforations sont orientées et les coquilles d'individus vivants étaient préférées aux coquilles vides. Certains brachiopodes clitambonitidés, comme *Clitambonites schmidtii*, ont toléré un grand nombre de perforations dans leurs valves. Seul un petit nombre de valves trouées ont révélées des calcs de réparation de la coquille sur leur face interne.

Mots-Clefs : Ordovicien ; Estonie ; schistes bitumineux ; Brachiopoda; *Trypanites* ; paléoécologie

Introduction

It appears that the oldest macroborings in the world are specimens of *Trypanites*: small, simple holes reported in localized Early Cambrian archeocyathid reefs in Labrador (JAMES *et alii*, 1977; KOBLUK *et alii*, 1978). Essentially no macroborings of any kind are known during the remainder of the Cambrian Period. The next oldest macroborings, found in carbonate hardgrounds, are of Early Ordovician age (PALMER & PLEWES, 1993; EKDALE & BROMLEY, 2001; DRONOV *et alii*, 2002; TAYLOR & WILSON, 2003). Macroborings in brachiopod shells are known from the Ordovician (CAMERON, 1969; PICKERILL, 1976; OPALINSKI & HARLAND, 1980; VINN, 2004).

In Baltoscandia borings in brachiopods of medial Late Ordovician age have been recorded from the Mjøsa Limestone (Rakvere to Nabala stages) of Southern Norway, but the borings of

Vermiforichnus occur very rarely there. The Mjøsa Limestone was deposited during the middle Upper Ordovician (Upper Caradoc) at the western margin of the extensive Lower Palaeozoic epicontinental sea of Baltoscandia (Fig. 1). It consists predominantly of carbonate sediments deposited in shallow to very shallow marine environments (OPALINSKI and HARLAND, 1980).

In the Oil Shale basin worm borings are known in the bryozoan colonies of the Leningrad area (Russia). These borings were originally identified as *Hicetes* (HECKER, 1928), but they may be *Trypanites* (personal observations; see KOBLUK & NEMCSOK, 1982).

In the oil shales of Estonia abundant borings in brachiopods are slightly older (lowermost Caradoc, see Fig. 2) than the *Trypanites* described from Wales and Norway, but closely resemble them. During Kukruse (Early Caradoc) time in the Baltoscandia Basin (Fig. 1), light-

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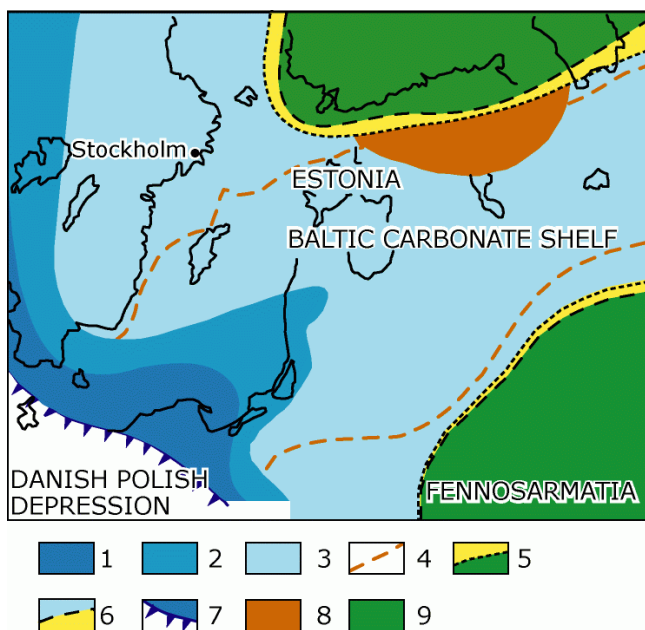


Figure 1: Setting of the oil shale-bearing deposits in the Upper Ordovician (Caradoc) of Baltoscandia (modified after PUURA *et alii*, 1988). 1 - black shales; 2 - argillaceous detrital limestones; 3 - detrital limy marls; 4 - supposed boundary of oil shale occurrences; 5 - erosion boundary; 6 - boundary of the oil shale accumulation area; 7 - TORNQVIST lineament; 8 - rich oil shale occurrences (with bored brachiopods); 9 - exposed land during Late Ordovician.

brown organic-rich muds formed oil shale interbeds in calcareous sediments (NESTOR & EINASTO, 1997). The oil shale is composed of almost equal portions of carbonates, clayey siliciclastics and organic matter. The existence in the Estonian oil shales of a rich and diverse marine bottom fauna (RÖÖMUSOKS, 1970, p. 172) together with a very low pyrite content suggest that conditions in the bottom waters were fully oxic (BAUERT & PUURA, 1990). Most of the organic matter is conjectured to have been derived from algal mats (KÖRTS & VESKI, 1994), that covered extensive tidal flat areas. Their organic matter was transported to shallow subtidal environments (PUURA *et alii*, 1988) during the Late Llanvirn-Early Caradoc regression (PUURA *et alii*, 1988).

The Estonian oil shale taphocoenosis includes a mixture of invertebrate remains from several different but adjacent parts of the basin. However, the extraordinarily well-preserved colonies of large, fragile bryozoa (e.g., *Chasmatoporella*) along with unweathered brachiopod shells, and rare, almost pristine trilobites, were neither transported nor affected by post mortem hydrodynamic movements. Nevertheless, many brachiopods (e.g., *Clitambonites*, *Estlandia*, *Nicolella*, *Cyrtototella*, *Kullervo*, *Glossorthis*) are preserved as discrete valves and presumably were not buried *in situ*. Strophomenids and *Porambonites* are usually preserved as complete shells presumably

because of the structures of their articulations. The taphocoenosis here is comprised mainly of the remains of brachiopods from nearby areas, and a small amount of weathered, obviously allochthonous shell material.

Methods and materials

Methods

As The borings were cleaned using ultrasound and brushes. Casts of some of them were made using the universal instant adhesive "Super Attak", Loctite Ltd. All borings were counted in relation to their occurrence on a single valve. They were measured and digitally photographed using a binocular light microscope. To determine the importance of the characteristics of the valve in relation to its role as a substrate for boring organisms the following measurements were made on each specimen: size (length and width), thickness, structure (lamellose or homogeneous), and surface relief. Specimens of *Estlandia marginata*, *Clitambonites schmidtii* and *C. squamatus* were studied to determine the average frequency of borings per discrete valve (pedicle and brachial valves counted separately) and their orientation noted. Conclusions are based on measurements of least six valves (both ventral and dorsal) of a particular taxon.

GLOBAL SERIES		BALTIC SERIES, STAGES	
UPPER	ASHGILL	HARJU	PORKUNI
			PIRGU
			VORMSI
	CARADOC	VIRU	NABALA
			RAKVERE
			OANDU ●
KEILA			
MIDDLE	LLANVIRN	HALJALA	
		KUKRUSE ●	
	ARENIG	OELAND	UHAKU ●
			LASNAMÄGI
LOWER	TREMADOC	ASERI	
		KUNDA	
		VOLKHOV ●	
		BILLINGEN	
			HUNNEBERG
			VARANGU
			PAKERORT

● A ■ B

Figure 2: Stratigraphical subdivisions of Baltoscandian Ordovician. A: Worm borings in brachiopod shells; B: Main oil shale deposits.

Material: Brachiopods in oil shale

A total of 29 articulate brachiopod genera

(about 90 species) are recorded in the oil shales of the Kukruse Stage in northeastern Estonia (HINTS & RÕDMUSOKS, 1997); 21 genera (about 30 species) were examined for this study of the distribution of borings (Table 1). The following taxa had one or more borings in at least a single valve: *Estlandia marginata*, *Clitambonites schmidtii*, *Clitambonites squamatus*, *Kullervo* ssp., *Glossorthis* ssp., *Nicolella* ssp., *Bekkerina*

ssp., *Bilobia* ssp., *Cyrtonotella* ssp., and *Septomena* ssp. Borings were not seen in *Oxoplecia* ssp., *Platystrophia* ssp., *Paucicrura* ssp., *Porambonites* ssp., *Leptestia* ssp., *Leptelloidea* ssp., *Estonomena* ssp., *Sowerbyella* ssp., *Actinomena* ssp., *Bicuspina* ssp. and *Kierulfina* ssp. A craniate brachiopod *Orthisocrania* was studied too, but no borings were discovered (Table 1).

Species/genus	Number of studied valves	Number of bored valves	Boring frequency
<i>Estlandia marginata</i>	267	131	51 %
<i>Clitambonites squamatus</i>	271	130	48 %
<i>Clitambonites schmidtii</i>	397	180	45.3 %
<i>Nicolella</i> ssp.	29	5	20.8 %
<i>Glossorthis</i> ssp.	6	1	16.7 %
<i>Bilobia</i> ssp.	7	1	14.3 %
<i>Kullervo</i> ssp.	9	1	11.1 %
<i>Cyrtonotella</i> ssp.	11	1	9.1 %
<i>Septomena</i> ssp.	29	2	6.9 %
<i>Bekkerina</i> ssp.	46	3	6.5 %

Table 1: List of studied brachiopods from oil shale (Kukruse Stage) and their boring frequency with *Trypanites* aff. *fimbriatus*.

Borings occur in specimens of nine of the 21 brachiopod genera examined. Their frequencies range from 6.5 % in *Bekkerina* ssp. to 51 % in *Estlandia marginata*. The two genera that occur in large numbers in oil shale, *Estlandia* and *Clitambonites*, have the highest frequency of borings. The two were selected for detailed studies of site specificity and the morphology of borings, and were chosen as a control group for the comparison of the boring frequency in the brachiopod fauna of the oil shale with that of stratigraphically older and younger brachiopods from the same area in the Baltoscandian Ordovician Basin (i.e., the North Estonian confacies belt of JAANUSSON, 1973).

Material preservation

Valves are considered to be strongly weathered if their shape is obviously rounded by wear and they lack the original sculpture and articulation. Rounded cardinal extremities or flattened ribs are considered to be the result of weathering. About 8 per cent of valves with borings are strongly weathered (most of these are the resistant ventral valves of *Clitambonites squamatus*). Borings in weathered valves are sparse; the majority were probably made on undamaged fresh valves. However, strongly weathered valves of *Clitambonites* and *Estlandia* have never been found without borings, but about one-third of these strongly weathered valve were not rebored after having been weathered. Large thin-shelled strophomenids (*Leptestia* and *Estonomena*),

Leptelloidea and *Sowerbyella* do not contain borings. They too were unweathered.

Borings in other fossil groups

The shells of molluscs may have been substrates for boring organisms, but in the strata studied their fossils are mainly internal moulds. Several well preserved echinoderm specimens (*Echinosphaerites*) were examined for borings, but none were found. Bryozoans too lack borings like those in brachiopods, but some bryozoans are covered with scratch marks that obviously were created differently from the borings in brachiopods. Borings similar to *Trypanites* are recorded in the *Monticulipora* bryozoans of the Haljala and Kukruse stages of the Leningrad area of the Oil Shale Basin of northeastern Russia (HECKER, 1928).

Borings in other Ordovician brachiopods from the East Baltic

The percentage of borings in brachiopod populations both preceding and succeeding the oil shale fauna seem to be remarkably lower. The collection of *Estlandia* (13 specimens) from the Uhaku Stage (in the shallow water [near-shore] area of the Baltic Basin), stratigraphically older than the Oil Shales, found no specimens with borings (Figs. 1-2). The collection of *Clitambonites schmidtii* from North Estonia yielded only one specimen with borings. Collections of *Estlandia* (ten specimens), *Clitambonites* (seven specimens) and *Bekkerina* (six specimens) from the stratigraphically younger Haljala Stage did not

yield even one specimen with borings (Fig. 2). So the frequencies of boring are certainly lower in sites other than the oil shale milieu.

The oldest specimens of articulate brachiopods (*Antigonambonites* and *Iru*) with sporadic borings are from the Volkhov Stage (Arenig) of the Baltic Ordovician (Fig. 2). Three borings in *Antigonambonites*, one large (0.7 mm wide) and two small ones (0.1 mm wide), resemble those of *Trypanites* in the oil shale brachiopods (see Plate 1.a) (VINN, 2004). The others are morphologically different from those seen in the brachiopods of the Kukruse Stage for they penetrate the shell at right angles to the outer surface (see RICHARDS & SHABICA, 1969; CARRIKER & YOCHELSON, 1968). *Trypanites* borings occur sporadically in stratigraphical younger brachiopods, as in *Ilmarinia dimorpha* from the Oandu Stage (Late Caradoc), of the Ordovician of the Baltic.

Systematic ichnology

Ichnogenus: *Trypanites* MÄGDEFRAU, 1932

Type ichnospecies: *T. wesei* MÄGDEFRAU, 1932

Remarks: The genus as redefined by BROMLEY (1972) and later by BROMLEY & D'ALESSANDRO (1987), includes simple, unbranched cylindrical or sub-cylindrical borings in a hard substrate (rock, shell, wood) with a single opening to the surface.

Trypanites aff. *fimbriatus*

Figs. 3-5; Pls. 1-2

Description: Single, elongate and cylindrical borings. Shafts smooth, commonly straight to slightly curved, more rarely sinusoidal, with few irregularities; cross-section generally circular, but may be oval or flattened. Majority of borings never intersect, and are almost always inclined at a low angle to or are parallel to their substrate. Diameter ranges from 0.2 mm to 1.6 mm, commonly 0.2-1.0 mm, and may be as long as 8 mm (Fig. 3). A few borings are joined, situated side by side (Plate 1.c). In some of the intersecting borings the younger ones cross older borings, which may have been abandoned then (Plate 1.f). Terminations of borings are rounded (Figs. 4-5; Plate 1.e). About half of the borings are oriented with their apertures towards the brachiopod commissure.

Discussion: *T. aff. fimbriatus* resembles *T. fimbriatus* STEPHENSON 1952 (p. 51, pl. 8, figs. 4-6, BROMLEY & D'ALESSANDRO, 1987, pl. 42, fig. 5) in diameter and shape. In contrast to *T. fimbriatus* the specimens of *T. aff. fimbriatus* sometimes cross and interpenetrate each other. Neither the shape nor the size of the shafts differ in the non-oriented borings so they cannot be assigned a discrete ichnospecies from those directed toward the brachiopod

commissure. However, it is possible that discrete species of borers created the oriented and randomly situated shafts.

Remarks: Structures associated with the apertures of a few borings in a single *Glossorthis* sp. valve could be either the calcareous linings produced by boring worms or were secreted by the brachiopod in reaction to the boring worm (Plate 1.c).

Occurrence: Abundant borings in hundreds of brachiopods from the oil shale strata of the Kukruse and Kohtla localities NE Estonia, Kukruse Stage, Caradoc, Upper Ordovician.

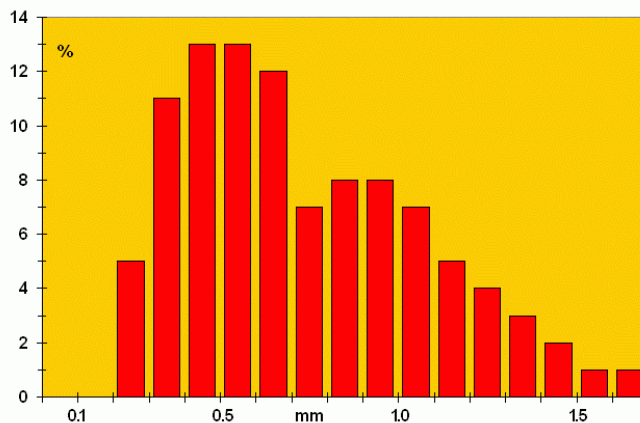


Figure 3: Frequency histograms of maximum diameter of *Trypanites* aff. *fimbriatus* borings in 20 valves (100 borings examined) of the brachiopods *Estlandia marginata*, *Clitambonites squamatus*, *C. schmidti* and *Septomena* sp.

Host specificity of borings

Brachiopod characteristics that may have influenced the intensity of boring include both shell morphology and the ecological aspects of the relationship (e.g., orientation, valve preference: see Tables 2-4). Morphological characteristics of the host that may have affected the borer larva's choice of substrate include the thickness of the shell, the shell macrostructure as it relates to ease of penetration, and the relief of the shell surface.

Size of the host

The organisms were able to bore into valves that were at a minimum 0.5 mm thick (*Septomena* sp.). However, the least possible thickness of a valve to be attacked was determined by the diameter of the smallest borer (0.15 mm recorded in *Septomena*). In the brachiopod genera most subject to boring (*Estlandia* and *Clitambonites*), the majority of the shafts range in diameter between 0.9 mm to 3.6 mm (recorded maximum width in *C. squamatus*). The wall thickness of most thin-shelled brachiopods without borings (e.g., *Estonomena*) ranges from 0.4-1.1 mm, so shell thickness may have been a limiting factor for the borers.

Species	Number of ventral valves	Boring frequency of ventral valves %	Number of dorsal valves	Boring frequency of dorsal valves %	Boring frequency of shell interiors %
<i>Estlandia marginata</i>	105	47.6 %	162	53.1 %	6.7 %
<i>Clitambonites squamatus</i>	176	40.3 %	95	62.1 %	1.8 %
<i>Clitambonites schmidti</i>	193	43.5 %	204	47.1 %	1.5 %

Table 2: *Trypanites* aff. *fimbriatus* boring frequency of the ventral and dorsal valves, and shell interiors.

Species	Number of dorsal valves studied (no. of studied dorsal borings)	Borings on average per a dorsal valve	Number of ventral valves studied (no. of studied ventral borings)	Borings on average per a ventral valve
<i>Estlandia marginata</i>	44 (250)	5.7	21 (67)	3.2
<i>Clitambonites squamatus</i>	19 (207)	10.9	14 (83)	5.9
<i>Clitambonites schmidti</i>	33 (368)	11.2	28 (173)	6.2

Table 3: Average number of *Trypanites* aff. *fimbriatus* borings in dorsal and ventral valves of *Estlandia marginata*, *Clitambonites squamatus* and *C. schmidti*.

Species	Number of dorsal valves	Average area of dorsal valve	Borings per 10 mm ²
<i>Estlandia marginata</i>	44	26.8 mm ²	2.1
<i>Clitambonites squamatus</i>	19	43.5 mm ²	2.5
<i>Clitambonites schmidti</i>	33	20.5 mm ²	5.5

Table 4: Boring density on the dorsal valves in *Estlandia marginata*, *Clitambonites squamatus* and *C. schmidti*.

Brachiopod specimens in the examined collection range in size from a 4.5 mm long juvenile *Estlandia marginata* to a 47 mm *Estonomena* sp. The smallest brachiopod with a boring (0.3 mm in diameter) is a juvenile *Nicolella* (6.0 mm long, 7.2 mm wide), and the largest is *Cyrtonotella* sp. (35 mm long, 47 mm wide). Immature brachiopods have thinner shells. The possible size specificity of *Trypanites* borings was examined on 14 small specimens (<10 mm long, <15 mm wide, and <1.0 mm thick) of *Estlandia marginata*. Although for the whole population of specimens of *Estlandia marginata* in the collection the boring is 51 %, only 28 % of these 14 small specimens are bored, and commonly just once. Thus, the borers appear to have been size-selective; they preferred the larger and thicker shells among the population of the same species. Large hosts have borings of a greater diameter; the valves of smaller hosts are commonly too thin to accommodate large shafts.

The size specificity of substrates for Ordovician *Vermiforichnus* (= *Trypanites*, personal communication with Mark WILSON) was

recorded by PICKERILL (1976) in assemblages of *Macrocoelia* and *Heterorthis*; the borings are invariably associated with the larger individuals. Here again it is probable that the small shells are too thin to accommodate boring and large shells offer an increased surface area for a larva to settle (see THAYER, 1974). However for *Trypanites* this areal advantage is valid only within the same host taxon. Dorsal valves of *C. schmidti* with the highest recorded density of borings have less than half the area of *C. squamatus* (Table 4) but in area have a boring density more than twice as great.

Shell structure

In *Clitambonites schmidti* an especially large number of borings occur in the fibrous secondary shell layer (Plate 2.a) of the lamellose anterior region of the shell: the thickest portion of the both valves. In *Estlandia* (Plate 2.b) and *C. squamatus*, which are thin anteriorly and have a less lamellose structure, boring frequency is highest slightly farther back from the anterior margin and the shafts are distributed more equally over the anterior two

thirds of the shell. However, boring density per square mm is about half that of *C. schmidtii* (Table 4). In the two most bored genera, *Estlandia* and *Clitambonites*, the structure of the shell is respectively fibrous pseudopunctate and fibrous unpunctate.



Figure 4: *Trypanites* aff. *fimbriatus*, Caradoc, Kukruse Stage, Kohtla, Estonia. Artificial cast of the boring preserved in *Estlandia marginata* shell, TUG 1121/20, scale bar 1 mm.

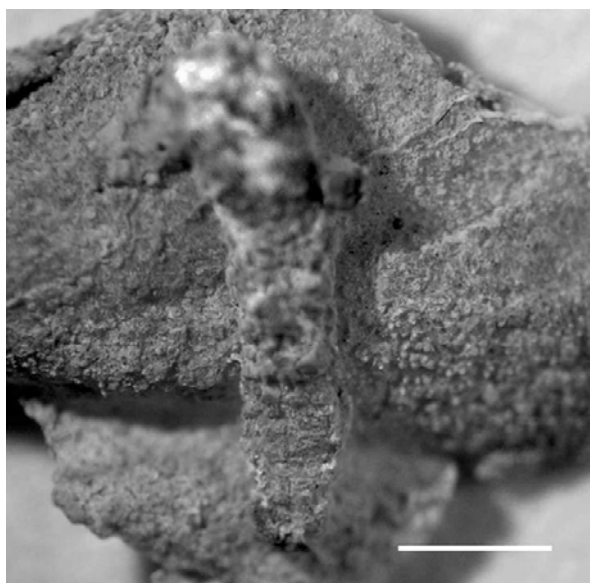


Figure 5: *Trypanites* aff. *fimbriatus*, Caradoc, Kukruse Stage, Kohtla, Estonia. Artificial cast of the boring preserved in *Estlandia marginata* shell, TUG 1121/21, scale bar 1 mm.

Shell surface

All types of shell surfaces have been bored, from the entirely smooth *Bilobia* (Plate 2.d) to the strongly ribbed *Glossorthis* (Plate 1.c), and in a unique case even within a rib. This suggests that the borers' larvae were able to attach to and bore all of the types of surfaces represented by brachiopod valves.

PICKERILL (1976) suggests that the host specificity of Ordovician *Vermiforichnus* borings (= *Trypanites*) is related to the delicate and parvicostellate nature of its hosts. Several authors have suggested (RICHARDS, 1972; HURST, 1974) that ectozoa avoided coarse-ribbed and angular-ribbed brachiopods. The brachiopod genera examined in this study do not support this idea. The high frequency of borings (20.8 %) in the strongly costate, angular-ribbed *Nicolella* demonstrates (Table 1; Plate 2.c) that high costa were not a limiting constraint for that borer. Moreover, borings are relatively infrequent on flat surfaces, with the exception of *Septomena* and a single boring in *Bilobia* (Plate 2.d). Borings usually occur between the ribs or in any type of depression, including the shell interior or the hinge line cavity. This suggests that cavities were preferred to flat surfaces., for after attachment these niches may have provided the borer larva with a safer place to start operations. The moderately costate brachiopods *Clitambonites* and *Estlandia* have the highest boring frequencies (Table 1), but this may be ascribed to various ecological factors or to their relatively thick and lamellose shell.

Results and discussion

Distribution and orientation of Trypanites

Most borings are on the outer surfaces of the valves. Only in intensely bored shells of *Estlandia* (Plate 2.b) and *Clitambonites* (Plate 2.a) are borings found in the interior (Plate 2.e), and they occur in only 3.3 % of all bored shells (see also Table 2). The valves with interior borings are always strongly weathered.

A selective orientation of borings with respect to the host has been documented for *Vermiforichnus* (= *Trypanites*) by PICKERILL (1976, see p. 161-162), and was confirmed for *Trypanites* in this study. A majority of borings were located at the anterior margin and oriented perpendicularly to the commissure (Plate 2.a). Presumably these borings were made in the shells of living brachiopods (PICKERILL, 1976).

Similar observations were made by HEMPEL (1957), who found a concentration of recent spionid polychaetes (*Polydora ciliata*) at the valve margins of *Mytilus*. *Polydora hoplura* has been described as oriented perpendicularly to the edge of oyster shells, and GALTISOFF (1964) discovered that larvae of *Polydora websteri*

settled in a similar orientation. These Recent polychaetes appear to have no detrimental effect on the host, and in the same way the boring worms of the Ordovician may have benefited from the feeding currents produced by the host (PICKERILL, 1976).

An increased density of *Trypanites* borings has been ascribed to its association with the shells of living hosts. In addition to the advantages of feeding mentioned, living hosts would provide better protection from sedimentation, overturning, breakage or abrasion than empty shells could offer (PICKERILL, 1976). When worms in empty shells were buried by sediment, they probably succumbed.

In *Clitambonites* and *Estlandia*, the great majority (about 90 %) of multiple borings in brachial valves and in the anterior two-thirds of pedicle valves are oriented perpendicularly to the commissure or inclined towards it (when not situated at the anterior margin itself). This pattern is best exhibited in *Clitambonites schmidti* (Plate 2.a; see also Table 2) and is apparent in other taxa when the density of borings on the host is high (*Nicolella*, *Glossorthis*, and *Septomena*). The particularly high concentration of oriented borings near the commissure of both valves in *C. schmidti* (up to a maximum of 24 on a brachial valve) presumably owes its existence to two favoring factors in that location: the specific lamellose structure of the shell and the extraordinary thickness of the anterior margin, both of which facilitated the successful attachment of borer's larva. The density of borings in *C. schmidti* is twice as high as in the other two species *C. squamatus* and *E. marginata* (Table 4), and this may be due to the attachment advantages offered by the thick lamellose anterior part of the shell, made even more attractive by the improved feeding associated with a location close to the commissure.

The number of borings on the brachial valves is about twice that on the pedicle valves in all three of the species studied (*C. schmidti*, *C. squamatus* and *E. marginata*). So the brachial valve was a preferred substrate for larvae when they attached to a living brachiopod (Table 3) with its brachial valve up. The living adult brachiopods *C. schmidti* and *C. squamatus* presumably lay on the pedicle valve, with the posterior third of that valve either on or slightly below the sediment line. There are only a few unorientated borings of a clearly post-mortem origin. It is possible that young specimens of *Estlandia*, that may have retained a functional pedicle longer, were oriented on the substrate with their anterior ends upwards. That would explain the presence of a few oriented borings in the center of some pedicle valves (see Plate 2.b). The pedicle valve of *Clitambonites* is never so attacked.

The concavo-convex strophomenids rested on the pedicle valve while boring took place, but presumably all borings were made after death, for the boring on *Bilobia* penetrates the brachial valve of the tiny shell (Plate 2.d), and all the borings in *Bekkerina* are on the hinge line, a phenomenon functionally impossible in a living brachiopod.

Influence of borings on the living host

The relatively short length of *Trypanites* borings and their large apertures suggest suspension feeding using to advantage the feeding currents produced by the living brachiopod.

There are few shells with repaired borings showing that the borings had disturbed the living host (Plate 2.f). The few blisters (see also BRICE & HOU, 1992, p. 253-260) found in the interiors of bored brachiopods (see Plate 2.g) obviously formed when the boring organism approached soft tissues. These features are rare but they indicate clearly that the relationship of the borer and its host was not always neutral. To some extent boring animals may have benefited as parasites by taking nutrients from the shell material of a living brachiopod. However, if that were the case they were presumably immobile. It is certain that in dead shells, the borer's larva attached and made borings only as habitations.

Conclusions

Brachiopods with borings are divided into two groups: those with many borings, the clitambonitids *Estlandia marginata*, *Clitambonites squamatus*, and *Clitambonites schmidti*; and the moderately bored *Nicolella*, *Glossorthis*, *Kullervo*, *Cyrtonotella* and *Bekkerina*. Similar host-selective-distribution patterns has been recorded for *Vermiforichnus* (= *Trypanites*) borings in Middle Ordovician brachiopods from Wales (PICKERILL, 1976). The moderately costate and relatively thick-shelled clitambonitids may have been preferred by the borers because of their thick shell, lamellose structure, and large size. Depressions such as the areas between costa and between the shell lamellae could have protected newly attached larvae from possible predators, such as grazing snails.

The absence of borings in several brachiopod taxa (*Porambonites*, *Oxoplecia*, *Leptestia*, *Leptelloidea*, *Estonomena*, *Sowerbyella*, *Actinomena*, *Orthisocrania*) has two possible explanations: either the brachiopods with borings lived in environments other than those occupied by brachiopods without borings, or the boring animals avoided certain taxa completely. With the exception of size and valve thickness no common morphological feature distinguishes

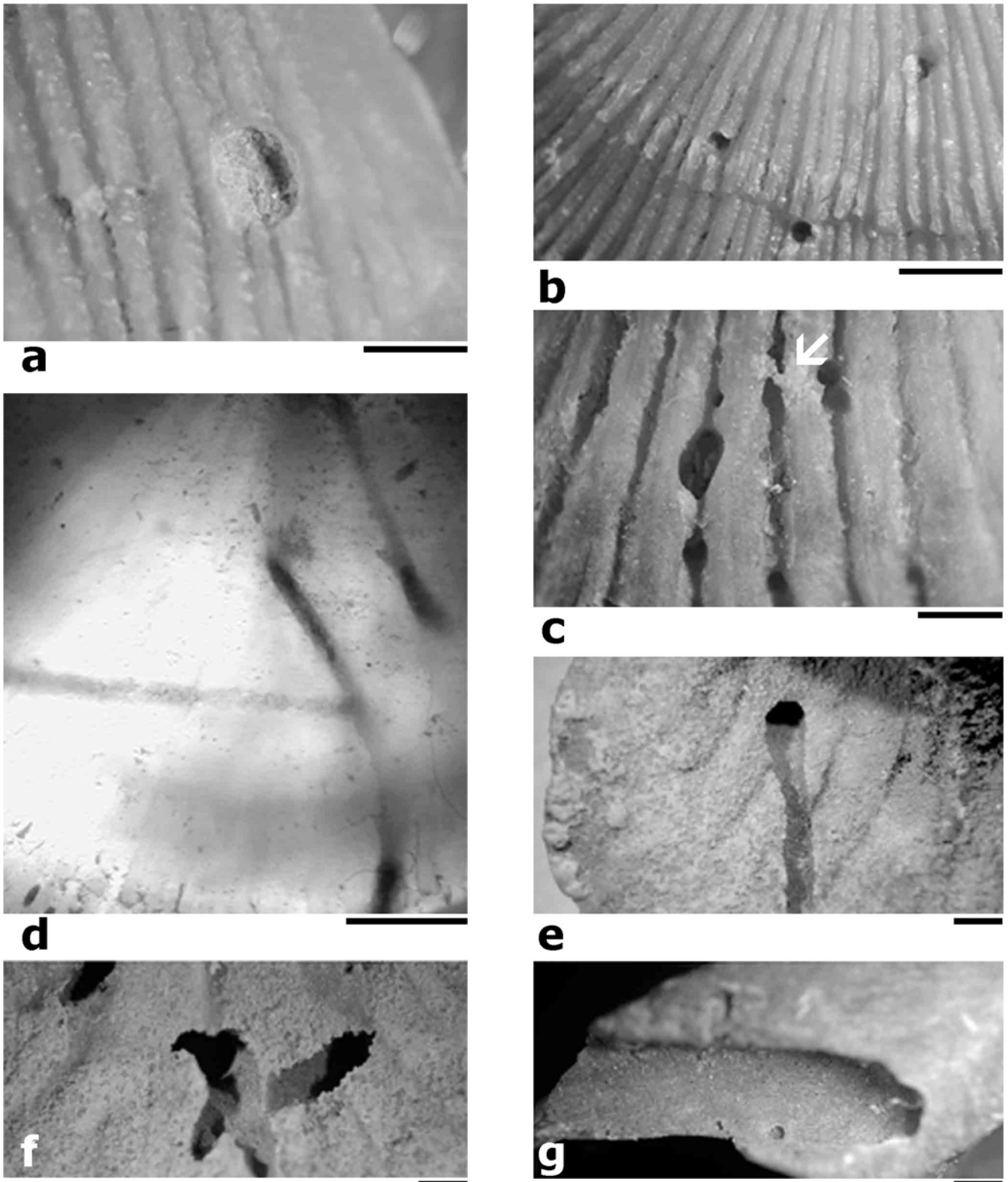


Plate 1: *Trypanites* ssp. borings (scale bars 1 mm):

- (a) in exterior of ventral valve of Arenig *Antigonambonites planus*, Volkhov Stage, Lava River, NW Russia, TUG 1121/1;
- (b) in dorsal exterior of *Antigonambonites planus*, Volkhov Stage (Arenig), Volkhov, NW Russia, TUG 1121/2;
- (c) in ventral exterior of *Glossorthis* sp., note the two joined borings, and the possible mud constructions associated with the aperture of a boring in the central upper part of figure, TUG 1121/3;
- (d) TUG 1121/2 translucent view;
- (e) longitudinal section of a broken out boring in ventral interior of *Estlandia marginata*, TUG 1121/4;
- (f) broken out crossing borings in dorsal interior of *E. marginata*, TUG 1121/5;
- (g) longitudinal section in a ventral valve of *Clitambonites squamatus*, TUG 1121/6.

brachiopods with borings from those without them. Even if the articulates in the oil shale taphocoenosis had a discrete autoecology that does not explain the lack of borings in the dead shells. Even if one were to assume that the life style of certain brachiopods kept the borers away, some of their dead shells would have been accessible to them. In the concavo-convex *Bekkerina* a lack of oriented borings may have been caused by the unfavourable autoecology of the living brachiopod. It is possible that some brachiopods repelled the larvae of borers by some chemical means or protected their shells against larval settlements by poisonous secretions on their surface.

As a rule, brachiopods without borings are thin-shelled, but *Porambonites* is an exception. The thickest parts of the shell of large thin-shelled strophomenids and that of all large individuals of other genera provide adequate space for the small borings discovered in young *Estlandia* and *Nicolella* and in adult specimens of thin-shelled *Septomena*. Borers avoided flat surfaces, but could bore in them. Flat surfaces are bored in weathered shells of *Clitambonites* and *Estlandia* (about 2 % of the total number of borings). Some borings have been found in the interior of shells, and an exceptional boring exists in the middle of a flat brachial valve of *Bilobia* (Plate 2.d). The strophomenid *Septomena* has several oriented borings, although its sculpture is very fine.

Presumably the relief of the substrate was not a controlling factoring in the placement of borings. Recent boring polychaetes, such as *Polydora*, bore into diverse substrates including limestone pebbles (see BOEKSCHOTEN, 1966, p. 352-354). Available data on the specificity of the relationships between boring polychaetes and their hosts seems to display a generic monoxenous pattern. About 37 % of polychaetes infest a single host species, 63 % infest three or fewer host species (MARTIN & BRITAYEV, 1998). The host specificity of *Trypanites* borings in the oil shale brachiopods may reflect a similar pattern. The biological affinities of the organisms that bored the oil shale brachiopods are unknown. These *Trypanites* borings could have been produced by polychaetes, but they may well have been made by some kind of boring lophophorate, for example, the phoronids. Borings by representatives of this soft-bodied worm-like phylum are known from the Palaeozoic (EMIG, 1982). However, other soft-bodied, suspension-feeding invertebrates can not be ruled out as possible borers.

Taphonomic analyses of an assemblage of the bored Ordovician brachiopod *Onniella meeki* performed by KAPLAN and BAUMILLER (2000) suggested that 10-15 % of the borings in the assemblage were predatory. Thus, some borings discussed here may represent predation: those that penetrate the valves.

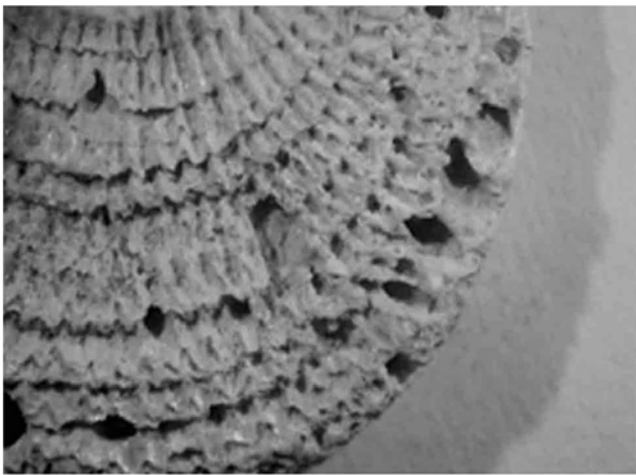
However, it is more likely that all borings in Ordovician brachiopods are simply habitations (WILSON & PALMER, 2001).

Acknowledgements

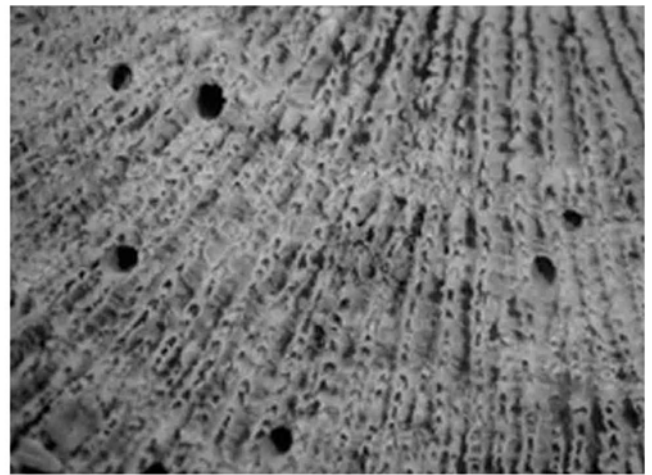
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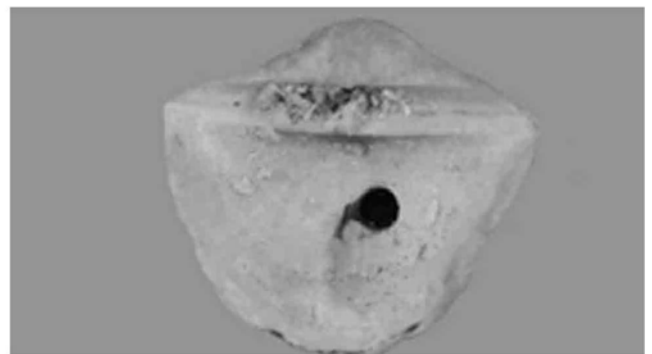
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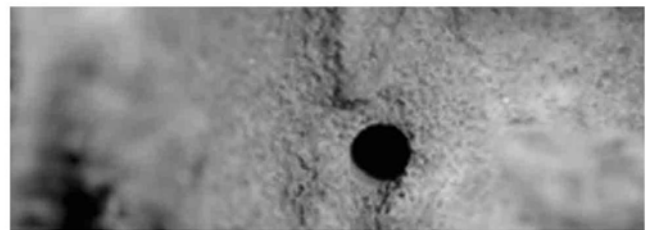
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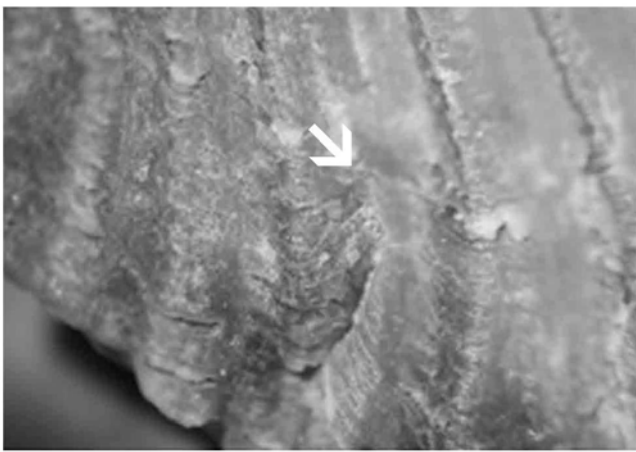
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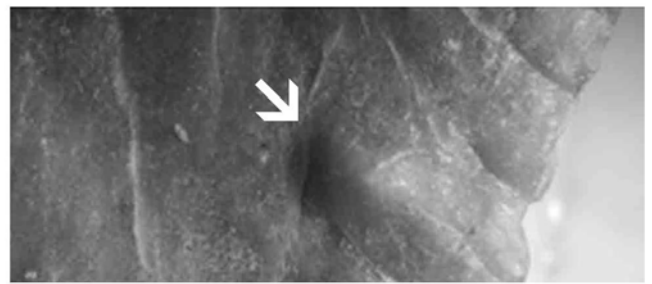
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Plate 2: *Trypanites* aff. *fimbriatus* borings, Caradoc, Kukruse Stage, Kohtla, Estonia (scale bars 1 mm):
 (a) oriented borings in anterior commissure of dorsal valve of *Clitambonites schmidtii*, TUG 1121/7;
 (b) oriented external borings in anterior half of ventral valve of *Estlandia marginata*, TUG 1121/8;
 (c) oriented borings in dorsal exterior of *Nicolella* sp., TUG 1121/9;
 (d) in dorsal valve exterior of *Bilobia* sp., TUG 1121/10;
 (e) in ventral interior of *Estlandia marginata*, TUG 1121/11;
 (f) repaired boring in ventral exterior of *Glossorthis* sp., TUG 1121/3;
 (g) 'blister'-like structure in ventral interior of *Glossorthis* sp., below the repaired boring, TUG 1121/3.

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