Shell repair in *Anticalyptraea* (Tentaculita) in the late Silurian (Pridoli) of Baltica

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Abstract: Shell repair is common in the late Silurian (Pridoli) encrusting tentaculitoid tubeworm *Anticalyptraea calyptrata* from Saaremaa, Estonia (Baltica), and is interpreted here as a result of failed predation. *A. calyptrata* has a shell repair frequency of 29 % (individuals with scars) with 17 specimens. There is probably an antipredatory adaptation, *i.e.* extremely thick vesicular walls, in the morphology of Silurian *Anticalyptraea*. The morphological and ecological evolution of *Anticalyptraea* could thus have been partially driven by predation.

Key Words: Predation; shell repair; Tentaculita; *Anticalyptraea*; Pridoli; Silurian; Estonia.

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Résumé : *Réparation de la coquille chez Anticalyptraea (Tentaculita) dans le Silurien supérieur (Pridoli) du bouclier balte (Baltica)*.- La réparation de coquilles est habituelle chez *Anticalyptraea calyptrata*, un vers tentaculitoïde encroûtant du Silurien supérieur (Pridoli) à Saaremaa, Estonie (bouclier balte), et est interprétée ici comme la conséquence d'une prédation qui aurait échoué. *A. calyptrata* a une fréquence de réparation de la coquille de 29% (individus présentant des cicatrices) pour 17 spécimens. Ceci est probablement une adaptation contre la prédation, c'est-à-dire la présence de parois vésiculaires et très épaisses, présentes dans la morphologie de l'*Anticalyptraea* du Silurien. L'évolution morphologique et écologique d'*Anticalyptraea* pourrait donc pour partie avoir été provoquée par la prédation.

Mots-Clefs : Prédation ; réparation de la coquille ; Tentaculites ; *Anticalyptraea*; Pridoli ; Silurien ; Estonie.

1. Introduction

There is a single previous record of possible predation on *Anticalyptraea* from the Pridoli of Saaremaa (Estonia), but the predation frequency or details of the shell repair was unknown (VINN & ISAKAR, 2007): Fig. 1. The material for this study was collected from two outcrops – Kaugatuma cliff and Ohesaare cliff - (Fig. 1) during five field expeditions in 2006-2010. In addition collections of the Natural History Museum, University of Tartu, were studied. *Anticalyptraea* is a rare fossil in the Pridoli of Saaremaa. It belongs to encrusting tentaculitoid tubeworms and is closely related to cornulitids, microconchids and tentaculitids (VINN & ISAKAR, 2007; VINN, 2010). *Anticalyptraea* occurs as an encruster on various shelly fossils, such as brachiopods, stromatoporids, corals, but also on hardgrounds (VINN & WILSON, 2010b).

Figure 1: Location of Kaugatuma (lower Pridoli) and Ohesaare (upper Pridoli) cliffs. Locality of *Anticalyptraea calyptrata* with shell repair marked with red.

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The aims of this paper are: 1) to describe in detail the shell repairs in the encrusting tentaculitoid tubeworm *Anticalyptraea* for the first time; 2) to assess how often *Anticalyptraea* was attacked by predators in the late Silurian; 3) to describe shell repair mechanisms in *Anticalyptraea*; 4) to find correlations between shell repair rate and size of *Anticalyptraea* specimens; and 5) to discuss possible antipredatory adaptations in *Anticalyptraea* morphology and behavior.

2. Material, methods and geologic setting

17 specimens from Kaugatuma cliff and five specimens from Ohesaare cliff were examined for shell repair and predatory drillings under an Olympus B061 binocular light microscope. The photography was done with a digital camera mounted on the binocular microscope. In addition, shell repair was studied with a Hitachi S-4300 FE-SEM at the Swedish Museum of Natural History. The diameters of *Anticalyptraea* shells at the lowest edge of each shell repair was measured and catalogued to record the location of the shell repairs.

There are two common methods of determining shell repair frequencies: 1) the "individuals with scars" method which involves dividing the number of individuals with at least one scar by the total number of individuals in the sample (KOWALEWSKI, 2002; ALEXANDER & DIETL, 2003: p. 163, and references therein); and 2) the "scar per shell" method which involves dividing the total number of repairs by the total number of individuals in the sample (ALEXANDER & DIETL, 2003: p. 163, and references therein). KOWALEWSKI (2002: p. 17) and ALEXANDER & DIETL (2003: p. 163) have advocated standardization of data tables so that data from both methods are available, which is followed in this paper (Table 1, Fig. 4). All figured specimens are deposited in the Museum of Natural History, University of Tartu (TUG), Estonia.

The Pridoli (uppermost Silurian) rocks (Fig. 2) are distributed in the southwestern part of Saaremaa island (Fig. 1). The major outcrops are coastal cliffs at the western coast of Sõrve peninsula.

Specimen n°	Shell max. width (mm)	Number of repairs	Shell width at the repair (mm)
TUG 1607-1	7.0	3	6.8 - 6.7 - 3.7
TUG 1607-2	5.6	1	5.0
TUG 1607-3	5.5	1	3.5
TUG 1607-4	5.1	1	4.8
TUG 1116-1	4.8	1	4.2

Method	Number
individuals with scars	5 of 17 (29%)
Scars per shell	0.41

Table 1: Shell repairs in *Anticalyptraea calyptrata* EICHWALD, 1860, from the Kaugatuma cliff, lower Pridoli (upper Silurian) of Saaremaa, Estonia.

3. Kaugatuma Cliff

The Kaugatuma cliff (2.5 m high) is situated on the western coast of the Sõrve Peninsula, some kilometers south from its neck and about 100 meters from the sea (58°7'22"N, 22°11'36"E): Fig. 3. The rocks belong to the middle part of the Äigu Beds of the Kaugatuma Stage (Fig. 2):

- 0.5+ m — greenish-grey nodular argillaceous wackestone of open shelf origin. Skeletal debris consists mostly of echinoderm and brachiopod fragments. Complete large crinoid holdfasts and fragments of columnals occur in great numbers. Ostracods, trilobites, gastropods, bryozoans and fish fragments occur. Detached specimens of *Anticalyptraea calyptrata* have been found in the argillaceous interlayers
- 1.5+ m — yellow-grey coarse-grained wavy-bedded crinoidal limestone of forereef origin. Grain size and sorting degree of skeletal debris is variable. Some bedding plains show erosion marks. Large colonies of *Syringopora blanda* (30 cm in diameter).

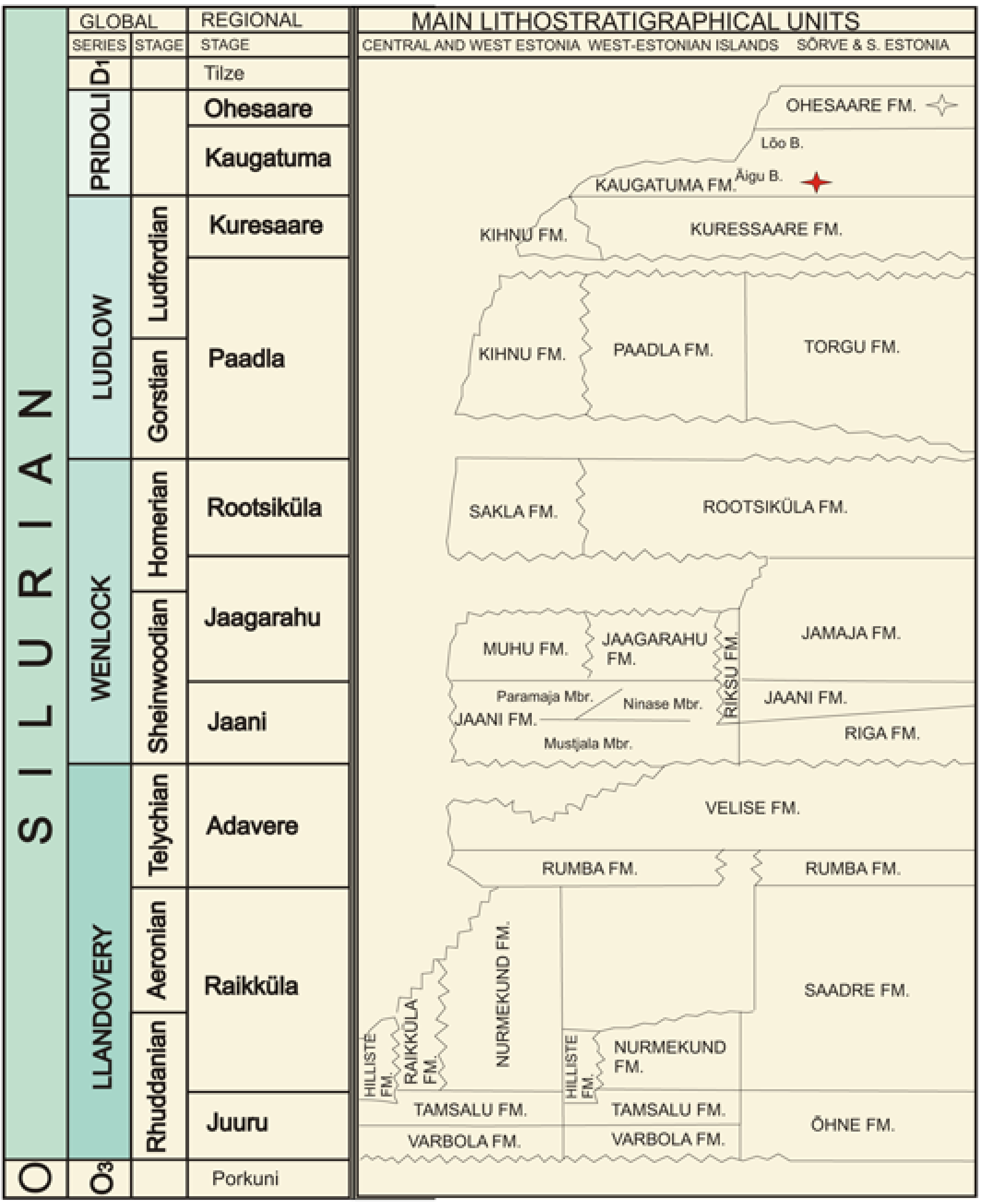

Figure 2: Stratigraphy of the Silurian of Estonia (after HINTS *et al.*, 2008). *Anticalyptraea* with shell repair marked with red star.

A great number of fossils have been recorded from the Kaugatuma locality, including large crinoid holdfasts and columnals, trilobites, tabulate corals and stromatoporoids. Major predators include acanthodian fish and cephalopods. The following vertebrate remains have been found from the lower beds of the cliff: *Nostolepis striata*, *Gomphonchus sandelensis*, *Poracanthodes porosus* (HINTS *et al.*, 2008).

4. Results

Shell repairs were found in five of 17 specimens from the Kaugatuma cliff (Table 1, Fig. 4). Most of the shell repairs are very large as compared to the size of *Anticalyptraea calyptrata* specimens, extending up to 50% of the shell diameter (from 1.5 to 3.5 mm wide): Figs. 5 - 6 - 7 - 8. Studied shell repairs of *A. calyptrata* display a meandering or zigzag fracture which outlines a jagged piece of the shell surface that was removed and resecreted (Figs. 5 - 6 - 7 - 8). The regenerated growth lines are oblique to the antecedent growth lines lateral to the fracture in the studied shell repairs. Five specimens (29 %) of *A. calyptrata* (n=17) from the Kaugatuma cliff (lower Pridoli) of Saaremaa have scars (n=7) of shell repair (Table 1, Fig. 4). One of the five specimens of *A. calyptrata* has a multiple shell repairs (three repair marks). No shells smaller than 3.5 mm in diameter have repair marks. There are 0.41 scars per shell (Table 1).

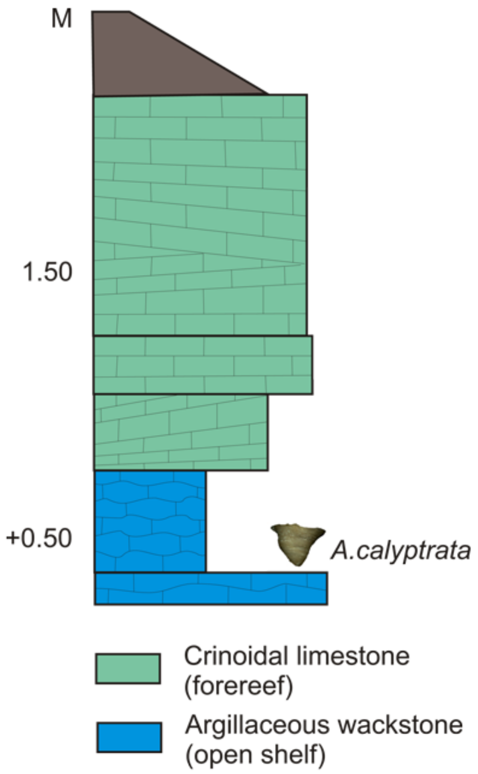

Figure 3: Kaugatuma cliff after EINASTO (1990). *Anticalyptraea calyptrata* with shell repair occurs in the lower part of section.

All shell repairs in *A. calyptrata* are carried out by resumption of shell growth from underneath the broken edge so that the newly secreted repaired shell lies mostly below the surface of the damaged shell. In one specimen the newly secreted shell is flush with the surface of the damaged shell.

No shell repair was found in five specimens from Ohesaare cliff (upper Pridoli). No predatory drillings were discovered in any *Anticalyptraea* specimens studied.

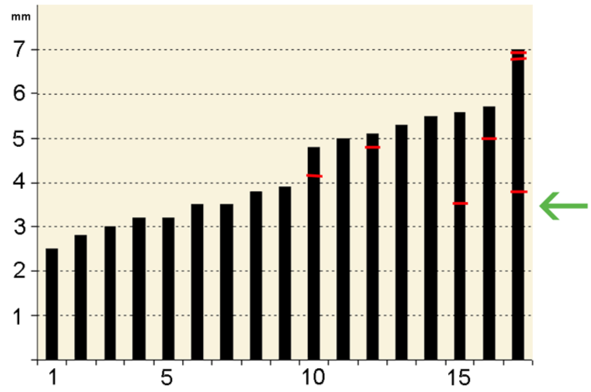

Figure 4: Graphic showing size distribution (max. diameter) of studied *Anticalyptraea calyptrata* specimens (n=17) from Kaugatuma cliff (lower Pridoli) of Saaremaa and location of the shell repairs (red lines). Green arrow points to the minimum diameter of the shells with repair marks.

5. Discussion

The morphologies of shell repair in *A. calyptrata* and sizes of the scars resemble those known in Ordovician cornulitids (VINN, 2009: p. 88, fig. 1A), and Silurian to Devonian tentaculitids (LARSSON, 1979; BERKYOVÁ *et al.*, 2007). The minute size of *A. calyptrata* shells makes direct comparison difficult with the larger molluscs and brachiopods. However, even smaller sized shell repairs are known in recent tiny pelagic gastropods (BERKYOVÁ *et al.*, 2007: p. 411, fig. 4). The shell repair in various organisms has often been interpreted as results of failed predatory attacks (*e.g.*, ALEXANDER, 1986; EBBESTAD & PEEL, 1997; ALEXANDER & DIETL, 2003; WILSON & TAYLOR, 2006). The proposed predatory cause of shell repair in *A. calyptrata* herefollows from morphological similarities to the predator-caused shell repair in the Paleozoic mollusks and brachiopods, but especially in similar size shells of tentaculitids (BERKYOVÁ *et al.*, 2007: p. 409, fig. 2, and p. 410, fig. 3) and cornulitids (VINN, 2009: p. 88, fig. 1A). Alternatively, shell repair could have resulted from the natural breakage of shell in intense water movement during the storms. This kind of damage and repair has also been observed in molluscs (HOLLMANN, 1968).

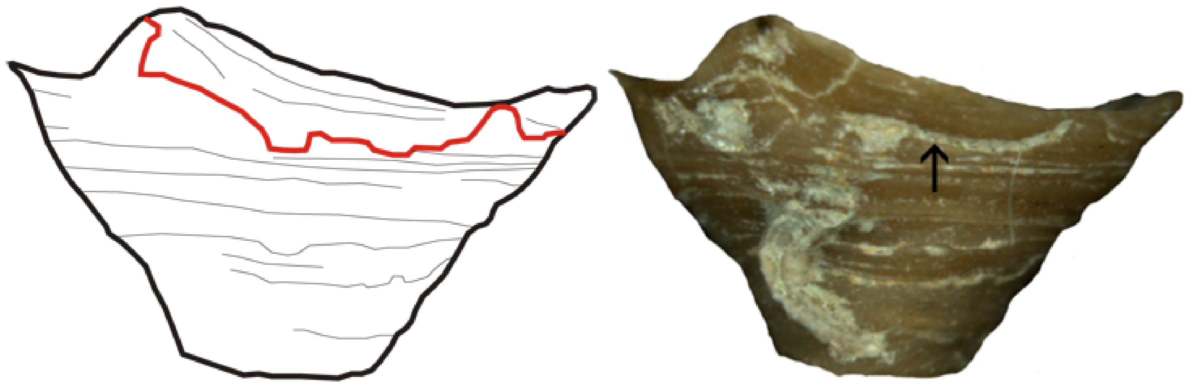

Figure 5: *A. calyptrata* EICHWALD, 1860, from Kaugatuma cliff (lower Pridoli), lateral view. Arrow points to shell repair. Max. diameter of the shell 7.0 mm.

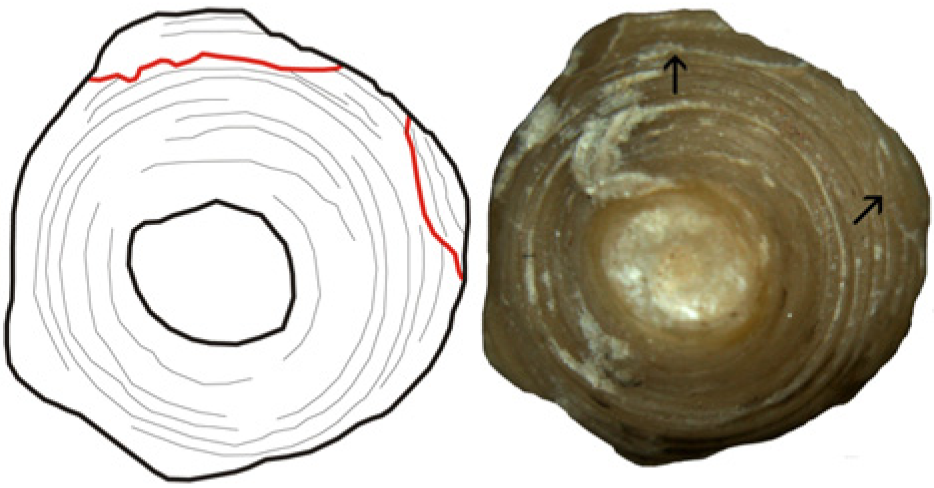

Figure 6: *A. calyptrata* EICHWALD, 1860, from Kaugatuma cliff (lower Pridoli), apical view. Arrow points to shell repair. Same as Figs. 5. Max. diameter of the shell 7.0 mm.

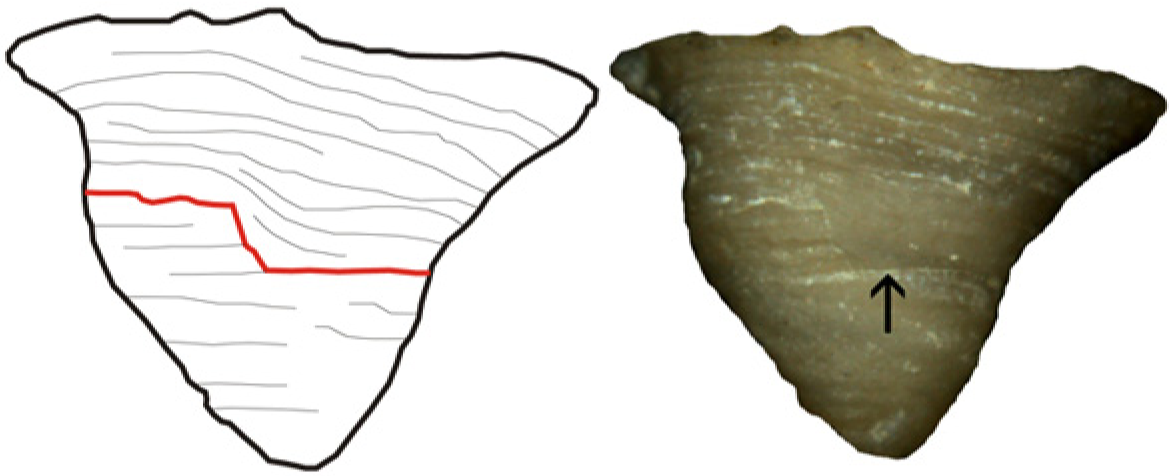

Figure 7: *A. calyptrata* EICHWALD, 1860, from Kaugatuma cliff (lower Pridoli), lateral view. Arrow points to shell repair. Max. diameter of the shell 5.5 mm.

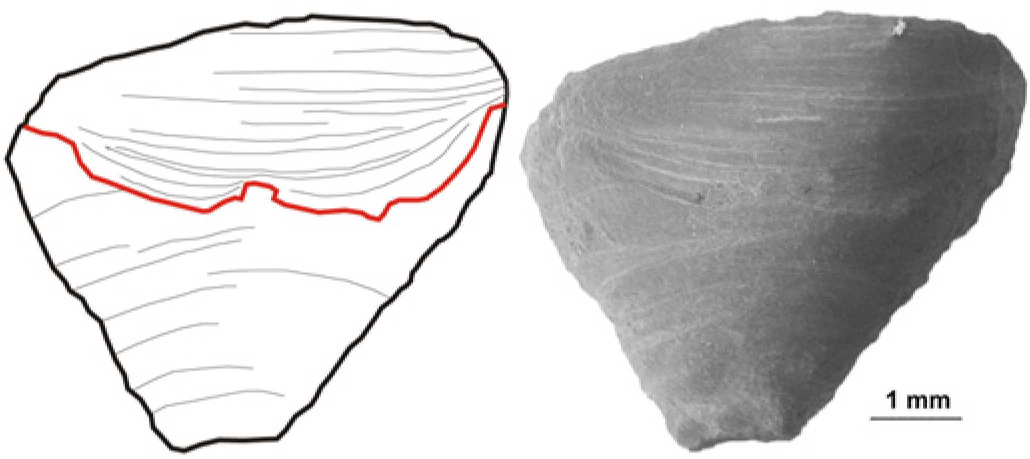

Figure 8: *A. calyptrata* EICHWALD, 1860, from Kaugatuma cliff (lower Pridoli), lateral view. Arrow points to shell repair.

The shell repair carried out by resumption of shell growth from underneath the broken edge in *Anticalyptraea* (Figs. 5 - 6 - 7 - 8) is characteristic of the encrusting tentaculitoid tubeworms (VINN, 2009) and their probable close relatives the hederelloids (WILSON & TAYLOR, 2006). A similar method of shell repair has also been reported from free-living tentaculitids (LARSSON, 1979; BERKYOVÁ *et al*., 2007).

Recent large gastropod shells usually show higher proportions of shell repair because they have been exposed for longer times to predators as compared to their smaller relatives (VERMEIJ *et al.*, 1980, 1982). Similar patterns would also be expected for *A*. *calyptrata* because their shell growth was similar to that of the molluscs. All shell repairs in *A*. *calyptrata* occur only in relatively large specimens (≥3.5 mm in diameter): Table 1, Fig. 4. This could indicate that after a certain size is reached, *Anticalyptraea* became less vulnerable to lethal attacks and shell repairs accumulated as a result of predation being more likely to fail (LEIGHTON, 2002; ALEXANDER & DIETL, 2003, and references therein). Alternatively, the predators may have been size selective, and only large adult *Anticalyptraea* specimens contained enough food to attract an attack.

The shell repair frequency of 29% (individuals with scars) in *A*. *calyptrata* is comparable to the shell repair frequencies in Late Ordovician and Silurian gastropods (ranging from 2.4 to 35.7%; LINDSTRÖM & PEEL, 1997, 2005; EBBESTAD & PEEL, 1997; EBBESTAD & STOTT, 2008): Table 1, Fig. 4. Molluscs were likely among the primary targets of Paleozoic predators. Brachiopods were probably secondary casualties of mistaken or opportunistic attacks (KOWALEWSKI *et al.*, 2005). However, the highest recorded shell repair frequencies (26%, individuals with scars) in Late Ordovician brachiopods (ALEXANDER, 1986) are slightly less but still comparable to that observed in *A*. *calyptrata*. The relatively high shell repair frequency in *A*. *calyptrata* alone does not prove whether the *Anticalyptraea* was among primary prey for Early Paleozoic predators, but it indicates their interest. The shell repair frequency is an ambiguous indicator that may either indicate a high rate of attacks or a high rate of failed attacks or both.

Predation presumably has influenced evolution of cornulitids (VINN, 2009; VINN & MUTVEI, 2009) and encrusting tentaculitoid tubeworms in general (VINN, 2010). In *Anticalyptraea*, the external wall that were in contact with seawater are thick and vesicular, while internal walls are thinner and do not contain vesicles. In cornulitids, the vesicular wall structure may have evolved as an antipredatory adaptation (VINN, 2009, 2010). Thus, the vesicular shell structure of *Anticalyptraea* could be a protective morphology. In addition to thick vesicular walls, *Anticalyptraea* has reported to have some preference for the cryptic surfaces when associated with the hardgrounds in Pridoli of Saaremaa that can indicate predation pressure (VINN & WILSON, 2010b). The latest known *Anticalyptraea*-like fossils belong to *Streptindytes* (Middle Devonian to Carboniferous), which lived embedded in the host coral skeleton. If the coral endobiont *Streptindytes* is a derived *Anticalyptraea*, it is possible that predation pressure may have led their evolution from encrusting life style to more protected endobiotic one. Similarly, in cornulitids predation pressure may have led to evolution of defensive morphologies and an endobiotic life style (VINN & MÕTUS, 2008; VINN, 2009, 2010; VINN & WILSON, 2010a).

There are just few palaeoecological studies on the skeletal benthos from the Pridoli of Saaremaa. At the present there is no data on the shell repair in other groups of skeletal benthos. The future studies should demonstrate how common the shell repair in the Pridoli of Saaremaa was in general.

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