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Size matters – Analysis of shell repair scars in endocerid cephalopods

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Abstract

Nearly one third of all conchs of *Anthoceras buchi* (Lesnikowa, 1949) from Baltoscandia display healed apertural breakages. Often multiple of these repair scars can be found in single conchs. Most of the scars are less than 2 mm deep, but deeper slit-like repaired breakages occasionally occur. Small injuries are usually around the entire apertural circumference, but the larger scars are concentrated at the ventral side of the conch, which is interpreted as result of a protection from a hood. The adult diameter of *Anthoceras buchi* is > 40 mm. Conch regions that exceed 30 mm in diameter rarely contain evidence of multiple repair scars. The relative frequency of deep healed breakages is highest at regions with diameters of 25–30 mm. This pattern is interpreted as evidence for a size limitation of the predator: large specimens with conch diameters above 30 mm had a considerably lower risk to get injured and the preserved injuries were less severe. This potentially explains the strong evolutionary trend of size increase in endocerids during the Lower to Middle Ordovician as escalation between them and shell breaking predators. Additionally, a specimen of *Anthoceras buchi* is described and figured, which displays colour marks with a mottled pattern.

Introduction

Endocerids are the dominant cephalopod group in the lower–middle Darriwilian limestones in Baltoscandia which historically were named "*Vaginatum* Limestone" ("Vaginatenkalk", Schmidt 1858). These limestones range from south-eastern Sweden to the St. Petersburg region, Russia, and are today subsumed under the Kunda Regional Stage limestones in Estonia, the Lynna, Obukhovo, and Simonkovo formations in the St. Petersburg region (Ivantsov 2003), and the Formation D in Öland, Sweden (Stouge 2004). Boulders of these formations are common in Northern Germany and northern Poland in the Pleistocene erratics, here the older stratigraphic terms "Lower Grey Orthoceratite Limestone" and "Lower Red Orthoceratite Limestone" are still in use by private fossil collectors.

The predominant endocerids in these limestones are the name giving straight, irregularly annulated longicones, that were subsumed under *Anthoceras vaginatum* (Schlotheim, 1820) by earlier authors. The conch of these endocerids is characteristically ornamented with prominent transverse striae. Five or more striae occur between two ribs. The largest specimens known measure nearly 50 mm in diameter. Adult size was usually reached at diameters exceeding 40 mm (indicated by septal crowding). A considerable variation in conch ornamentation occurs between different specimens. In some specimens the transverse striae appear more irregularly spaced, while in others, they are very regularly spaced. The amplitude of the annulation varies between different specimens and in some specimens irregularly spaced constrictions occur on the steinkerns (Fig. 1). These cephalopods exceptionally often preserve traces of shell breakage and repair. Nearly a third of all conchs (29 %) in the collection of the Naturhistoriska Riksmuseet, Stockholm, Sweden, have traces of healed breakages.

Traces of failed predation are reported from other Ordovician mollusks (gastropods, monoplacophorans and tergomyans: Ebbestad & Peel 1997; Ebbestad 1998; Isakar & Ebbestad 2000; Alexander & Dietl 2003; Lindström & Peel 2005; Frisk & Ebbestad 2007; Ebbestad & Stott 2008). The shell repair frequencies documented in these reports range from 5–36 %. Ebbestad & Stott (2008) demonstrated that differences in shell repair frequency can vary strongly between gastropod species in coeval rock samples. The authors inter-

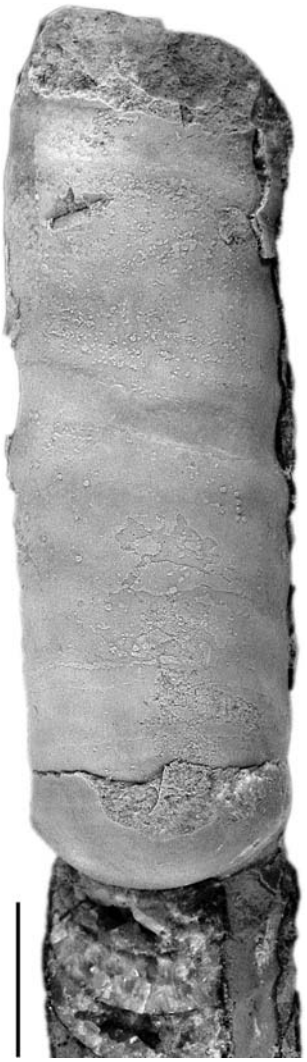

Figure 1. Complete body chamber steinkern and part of the phragmocone of *Anthoceras buchi* (Lesnikowa, 1949), TUG TUG 1309-1, from Kadaka railroad trench, Tallinn, Estonia (59.23.888N, 024.38.657E), Kunda Limestone, Middle Ordovician. The slightly oblique constriction of the body chamber is a result of an internal shell thickening. These shell thickenings occur at irregular distances in *Anthoceras buchi*. They are parallel to the peristome and are interpreted here as antipredatory traits. Scale bar 10 mm.

preted the different injury frequency as a result of interspecific differences in predation intensity and emphasize the need for more detailed analyses in the background of the emerging complex (Ordovician) shell repair frequency pattern.

Leighton (2002) demonstrated that shell repair frequencies themselves are a poor predictor to predation intensity. Quantification of repair frequencies in individual size classes of injured conchs and of frequencies of multiple injuries in individual conchs is necessary to infer predation intensity (see also Ebbestad & Stott 2008).

Here, I counted the repair scars in the Middle Ordovician endocerids of *Anthoceras buchi* (Lesnikova, 1949), = *A. vaginatum*, measured their size and position, and photographed the most spectacular injuries among them. The position, size, and shape of the repair scars potentially provide information of predator-prey interactions, on the shape of the endocerid soft body anatomy, the lifestyle, and the causes of some evolutionary trends of these common cephalopods.

The description and analysis of *Anthoceras buchi* required a short review of this common annulated endocerid, which is better known by its older, but invalid, name "*Endoceras vaginatum*".

Finally, I included in this analysis the description and illustration of an exceptionally preserved specimen of *Anthoceras buchi* which revealed the original colour pattern of this species.

Material

The Naturhistoriska Riksmuseet Stockholm (NRM) has a collection of about 236 specimens of these endocerids from Öland, Västergotland, Dalarna, and Östergotland. The specimens are conch fragments of different diameter, usually with a length of 50–150 mm. Only in a few cases the conch fragments are more complete. The analysis of the material at the NRM was completed with single specimens from Harku near Tallinn, Estonia, which are in the collection of the Tartu Ülikool Geoloogia Muuseum (TUG), and from boulders of Pleistocene erratics of northern Germany which are in the collection of the Naturkunde Museum Berlin (MB).

Taxonomic remarks

The list of endocerids assigned to *Orthoceratites vaginatum* Schlotheim, 1820 is very long. Originally the name was given as a *nomen nudum* to specimens of probably Jurassic age from the Swabian Alb in Germany by Schlotheim (1813). Schlotheim (1820, p. 53–54) described annulated and transversely striated longicones from Reval (Tallinn), Estonia as *O. vaginatus*, and refers to the figures in Knorr & Walch (1768–1774, Volume III, tab. IVb) and Breynius (1732, tab. V, fig. 2b). But the table V, figure 2 in Breynius (1732) illustrates a smooth longiconic endocerid, and figure IVb in Knorr & Walch (1768–1774, Volume III) an indeterminable fragment of a siphuncle. Because a type specimen was previously designated neither originally nor subsequently, the name "*O. vaginatus* Schlotheim, 1820" cannot be used.

The first illustration of a species named "*O. vaginatus* Schlotheim" appears to be published in Buch (1841, p. 592, pl. 33, fig. 11), which was later synonymised with *Cyclendoceras buchi* Lesnikowa, 1949. According to the opinion of Balashov (1968) *Cyclendoceras buchi* belongs to *Lobocyclendoceras* and "*Endoceras vaginatum* Schloth" in Eichwald (1860, pp. 1243–1245, pl. 48, figs 1a–e) is identical with *Paleocyclendoceras eichwaldi* Balashov, 1968. Dzik (1984) finally subsumed these species under "*Anthoceras vaginatum* (Schlotheim, 1820)". Additional annulated endocerids of the Kunda stage limestones that were synonymised with "*A. vaginatum*" by Dzik (1984) are *Paracyclendo-*

ceras cancellatum (Eichwald, 1860), *Paracyclendoceras compressum* Balashov, 1968, *Protocycloceras balticum* Balashov, 1968, *Protocycloceras iruense* Balashov, 1968, and *Lobocyclendoceras kundense* Balashov, 1968. The different taxa are mainly distinguished by their shape of the endosiphuncular deposits.

The revision of this common and relatively variable annulated endocerids, which would include a detailed analysis of the shape of the endosiphuncular structures is not within the scope of this paper. Herein, I refer to it provisionally as *Anthoceras buchi*, because "*O. vaginatum* Schlotheim, 1820" is indeterminate and *Cyclendoceras buchi* Lesnikowa, 1949 is the first available name representing this group of annulated and striated endocerids of the Kunda Regional Stage limestones and its equivalents in Baltoscandia. The specimens are classified within *Anthoceras*, because it is an annulated endocerid with subholochoanitic septal necks (see e.g. Balashov 1968, pl. 20, fig. 2g, pl. 23, fig. 3b).

Methods

I investigated all specimens of *Anthoceras buchi* in the collections of the NRM, counted, classified and measured the conch breakages. The specimens observed in the MB and TUG were not included in the statistical analyses. The depth of the breakages were measured with calipers. The depth was measured as the distance of the deepest point of the scar posteriorly from the anterior margin of the scar. The frequency of different repair scar depth classes was calculated. The individual conch diameter at each repair scar position was measured and the frequency distribution of repair scars in classes of conch diameter was calculated. The measurements were directly taken from the specimens with a precision of $+/-$ 1 mm.

The frequency of repaired injuries was calculated in different ways (Table 1), following Kowalewski (2002), Alexander & Dietl (2003), and Ebbestad & Stott (2008). Three types of abundance ratio are the result of the calculations: 1) the ratio of specimens with at least one, or multiple injuries against the total number of specimens, 2) the ratio of total number of scars against the total number of specimens (scars per shell method, Ebbestad & Stott 2008), and 3) the ratio of specimens with multiple repair scar against total number of specimens (see Ebbestad & Stott (2008) for further references of this method).

The position of the repair scars around the circumference was determined by measuring the angle departing from the venter, where ventral is 0°, dorsal 180°, the right flank viewed in direction of growth (adapical view) is 90°, the left flank 270°. The conch was separated into 18 zones with 20° degree widths (0–20°, 20–40°, 40–60°, etc). The frequency of injuries at each zone was calculated. The preservational potential of the individual zones was estimated as a function of missing conch parts in the available specimens against the total number of measured specimens. This was realized by measuring the range of angles departing from the venter of the preserved conch parts in each specimen. The percentage of the ranges with conch parts preserved against the total number of specimens is the preservational potential. A zone of the conch was considered as "not preserved" when the shell in more than half of the length of the specimen was abraded in this zone.

The frequency distribution of injuries at individual ranges of positions then was corrected by the probabililty of the parts of the conch of not being preserved.

Results

Size and shape of repair scars

All the documented injuries in *Anthoceras buchi* in the collections of the NRM and MB are original breakages from the aperture at different growth stages. Because nautiloids have accretionary shell growth, the non-lethal breakages were healed and are preserved as irregularities or scars in subsequent shell growth.

The regeneration of the fractured shell of *Nautilus* was described in detail by Keupp (1998). In *Nautilus* the repairing shell is substructed forming a wedge under the margin of the broken shell. The repair technique, which involves an intermittent withdrawal of the peristomal mantle margin, is probably common in most molluscs with accretionary growth. The resulting repair pattern, with sometimes slightly outward bulged conch portions and irregular sculpture pattern was named "*forma substructa*" in a terminology of ammonoid pathological conch forms by Hölder (1973) (see also Hengsbach (1996) for a review of the "forma types"). Without exception, the documented injuries in

Table 1. Abundances and frequency of injuries in *Anthoceras buchi* (Lesnikowa, 1949), Kunda Regional Stage, middle Darriwilian, Sweden. All specimens are in the collection of the NRM. ° calculated as ratio of the total number of repair scars against the total number of specimens, * calculated as ratio of specimens with multiple repair scars against the total number of specimens with breakages, ^ calculated as mean depth of breakage against the mean diameter of conch at the position of injury (at the interimistic conch margin).

	Specimens total	with scars (percentage of specimen with at least one injury)	with multiple scars (percentage of specimen with multiple scars)	scars per shell°	multiple versus injured*	mean relative depth of breakages^
Dalarna	52	20 (38 %)	10 (19 %)	0.75 (39 scars)	0.5	0.15
Västergötland	19	3 (16 %)	2 (11 %)	0.47 (9 scars)	0.67	0.27
Östergötland	120	26 (22 %)	7 (6 %)	0.3 (36 scars)	0.27	0.1
Öland	45	19 (42 %)	6 (13 %)	0.71 (32 scars)	0.32	0.12
Total	**236**	**68 (29 %)**	**25 (11 %)**	**0.49 (129 scars)**	**0.36**	**0.14**

Anthoceras buchi represent shell malformations of the type "*forma substructa*".

Most of the breakages are pit-like (= *typus parvus*, Kröger 2000) with depths less than 2 mm from the interimistic apertural conch margin (n = 61 of $n_{ss\text{-}total}$ = 121, 50 %; with $n_{ss\text{-}total}$ = subsample of classified scars within total sample number of 129 scars). Small u-shape breakages (= *typus stupidus*, Kröger 2000) with depths of 2–5 mm are also common (n = 14, = 12 %) (Fig. 2). The small pit-like and u-shaped scars can be classified as "divots" *sensu* Alexander & Dietl (2003). Often (n = 25, = 19 %) multiple small breakages (= "scallops" *sensu* Alexander & Dietl 2003) occur along an interimistic apertural conch margin (Fig. 3B). The largest breakages are often slit-like (Fig. 2), with depths significantly larger than widths (= "embayments" *sensu* Alexander & Dietl 2003). Remarkably the slit-like breakages in some cases show distal widenings (Fig. 2A). Rarely, deep breakages occur that comprise large parts of the apertural margin (Fig. 4). Only in one case (Fig. 2C), the breakage is deep and v-shaped (= *typus acutus*, Kröger 2000; = "divot" *sensu* Alexander & Dietl 2003). The greatest measured depth of a breakage in the material of *Anthoceras buchi* in all collections investigated is 27 mm (specimen NRM Mo 167603 from Ljung, Östergotland, Sweden). It occurs at a conch diameter of 29 mm.

The average depth of breakages in specimens of different size classes reveals a specific pattern: In specimens with injuries at conch diameters of 25–30 mm the breakages are significantly more severe. The deepest breakages occur in conchs of these size classes and the breakages are also in the average deeper at conch regions with diameters of 25–35 mm (Fig. 5).

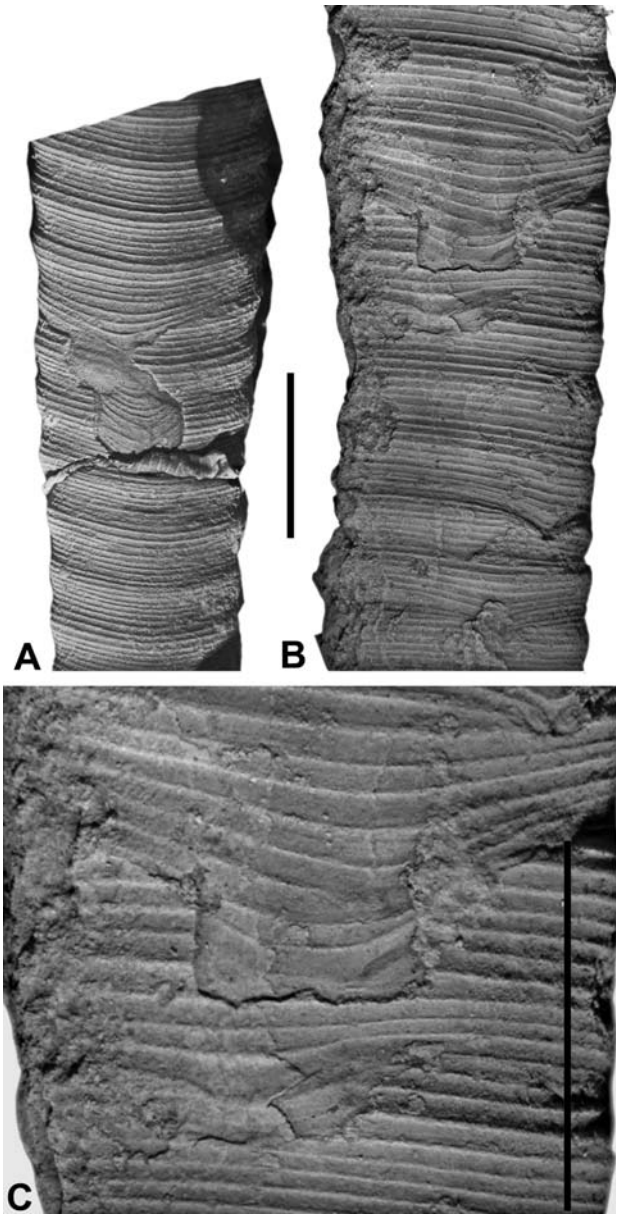

Figure 2. *Anthoceras buchi* (Lesnikowa, 1949), Kunda Regional Stage, with u-shaped or slit-like repaired shell breakages. **A.** NRM Mo 167604 a–b, from Mölltorp, Billingen, Sweden with narrow slit-like repaired breakage with distal widening; **B–C.** NRM Mo 8948, from Digerberget, Dalarna, Sweden. Scale bar 10 mm.

Position and abundance of injuries

Nearly one third (29 %, Table 1) of all specimens of *Anthoceras buchi* in the collection of the NRM have shell injuries. The relative abundance of healed shell fractures is very similar in the specimens from Dalarna, Östergotland, and Öland. In these specimens, multiple injuries are also very common. Repair scars are less common in specimens from Västergötland. Multiple repair scars are more common in conch portions with smaller diameter. The relative number of multiple scars at different size classes is highest in conch fragments with diameter 15–20 mm. Multiple scars do not occur in fragments with diameter > 30 mm (Fig. 6).

The relative abundance of repair scars at individual positions around the circumference of the conch before and after correction against preservation probability of the related conch parts is uneven. Generally repair scars are slightly more common on the left side of the conch. The ratio of scars at the left against scars at the right is 1.26 (n = 120), 56 % of the scars occur at the left side. Because the left side has a significantly higher potential not to be preserved and eroded or dissolved (Fig. 7A) the left/right discrepancy of the breakage frequency nearly disappears after correction against the preservation potential (51 % of the breakages occur at the left side after correction). The causes of this preferential right side preservation of the shell are unknown.

Small breakages which penetrated less than 3 mm posteriorly beneath the anterior margin of the scar show conspicuous peaks at positions 20–40°, 100–120°, and 220–240° after correction against preservation potential (Fig. 7B). The larger breakages with depths of more than 5 mm are concentrated at the ventral half of the conch with frequency maxima at 20–40°, 60–80°, and 300–320° (Fig. 8).

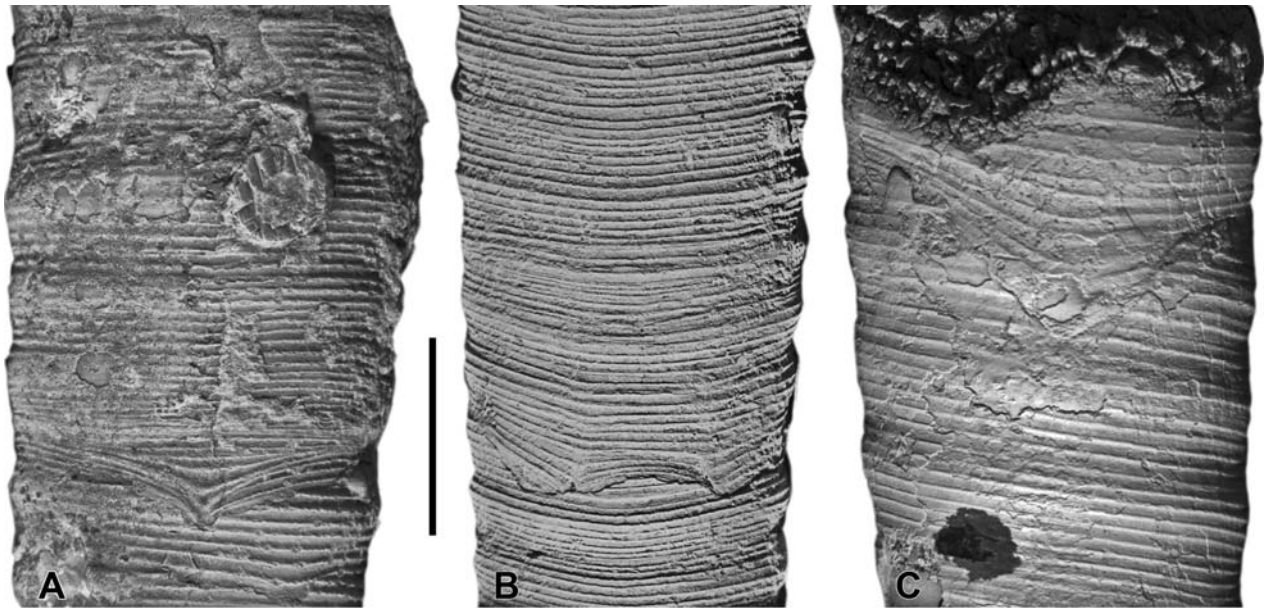

Figure 3. Small or v-shaped repaired shell breakages in *Anthoceras buchi* (Lesnikowa, 1949), Kunda Regional Stage. **A.** NRM Mo 14636, Norre Udde, Öland, Sweden with pit-like repaired breakage; **B.** NRM Mo 167604 a–b, from Mölltorp, Billingen, Sweden, same specimen as in Figure 2A, with wide irregular shallow repair scar; **C.** NRM Mo Mo 167602 a–c, from Sjurberg, Dalarna, Sweden with relatively deep v-shaped breakage. Scale bar 10 mm.

Interpretation

Conch size matters

Because it was affected by the several taphonomical and ecological variables the interpretation of shell repair frequency is not trivial. The probability of the individual of getting attacked during its life time, the severity of attacks, the type of attacks (the rate of unsuccessful attacks), and the resilience of the prey are important factors to be considered. The shell size, and the probability of different shell portions to be preserved affect the abundance of repairs.

In the fossil material, the severity of attacks can be evaluated based solely on the preserved repairs after unsuccessful attacks. The mean depths posteriorly from the anterior margin of the scars and the rate of multiple traces can be considered as good proxies of the severity of the average attack (and as a side note: potentially as evidence for a size limitation of the predators "tool"). A relatively high number of deep and large scars can be interpreted as concentration of severe attacks. Con-

Figure 4. *Anthoceras buchi* (Lesnikowa, 1949), NRM Mo 10005, labelled "Red *Orthoceras* Limestone", Kunda Regional Stage, from Kinnekulle, Västergotland, Sweden, with multiple large and deep repaired shell breakages comprising the entire circumference. From left to right: lateral view from the left side, dorsal view, lateral view from the right side. Scale bar 10 mm.

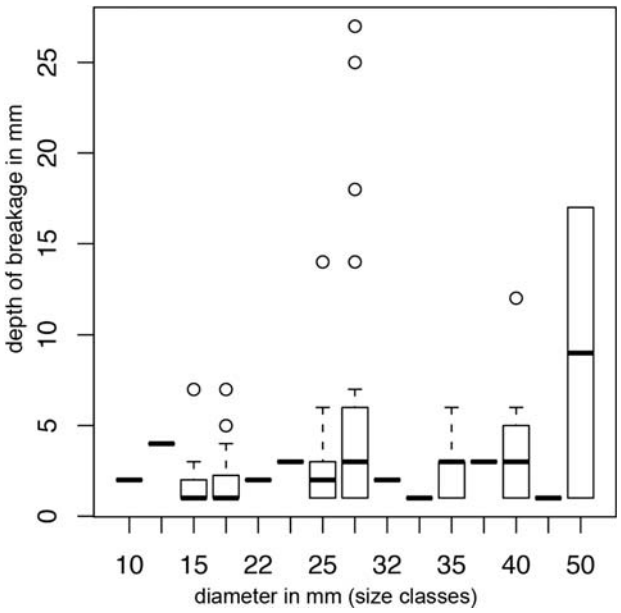

Figure 5. Box plot of depth of repair scars in different size classes of *Anthoceras buchi* (Lesnikowa, 1949), $n = 129$, circles = maximum values, bold bars mean values, empty box 95 % confidence interval, dotted lines 65 % confidence interval. Note the maximum values at conch diameters of 25–30 mm. The large depths in the size class > 45 mm is based on two values only.

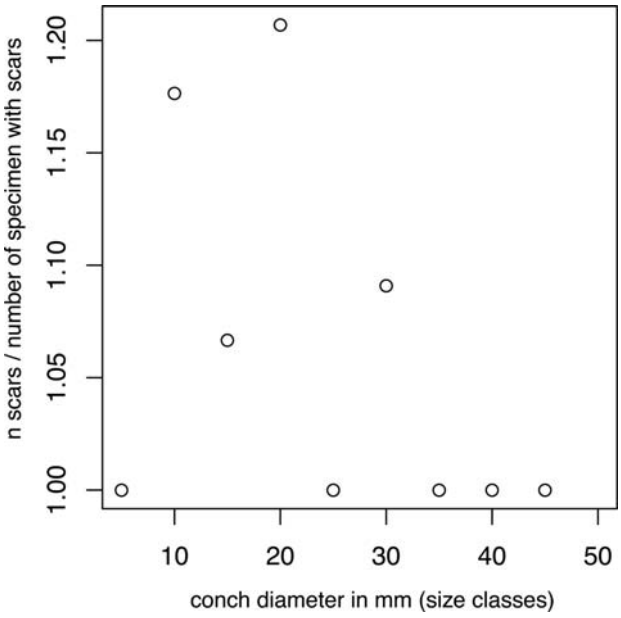

Figure 6. Plot of relative number of multiple injuries in conchs of different size classes. Note the decreasing trend of multiple injuries with increasing diameter of the conch.

trarily, a high rate of multiple traces in individual shells indicates abundant interaction of low severity.

Small specimens of *Anthoceras buchi* often contain small breakages and multiple breakages, while specimens with diameter of 25–30 mm contain the deepest breakages and also often contain multiple breakages. Larger specimens rarely contain breakages at all. The probability of getting injured is highest at diameters of 15–20 mm. This pattern can be interpreted as evidence for a size limitation of the predator: large specimen with conch diameters exceeding 30 mm had a considerably lower risk to get injured, and the preserved injuries were less severe. This implies that the large endocerid

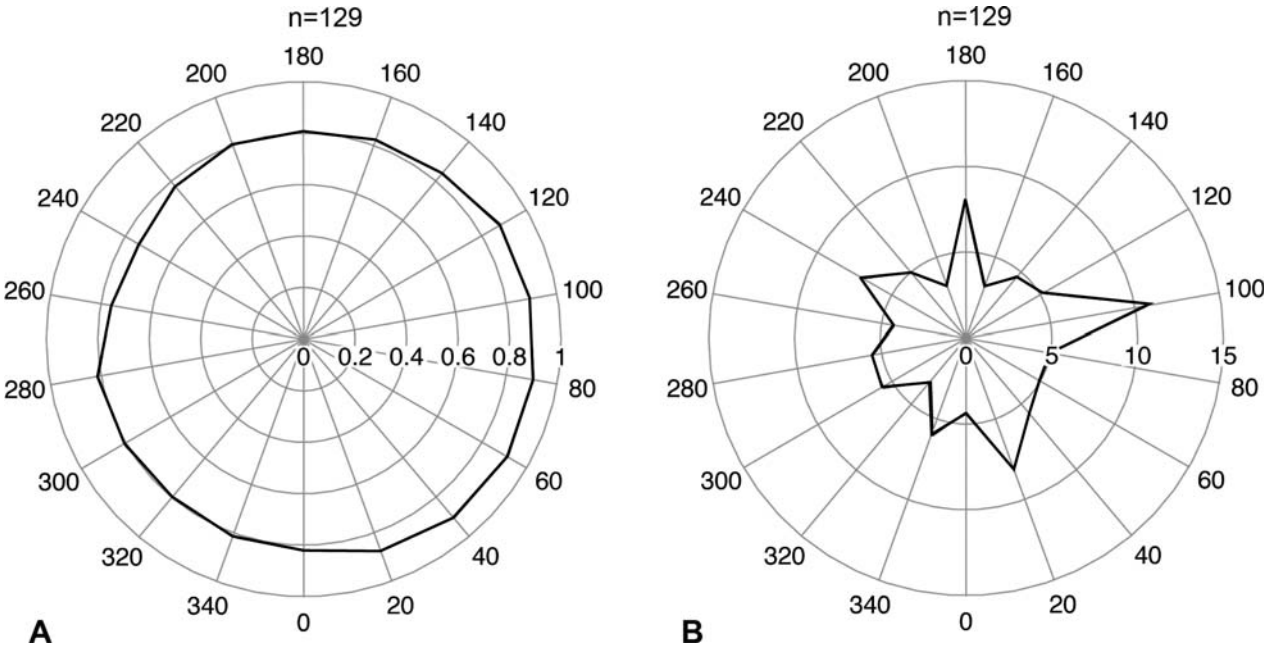

Figure 7. Frequency distribution of healed injuries around circumference of aperture in degrees, 0° = ventral, 180° = dorsal, in adapical view. **A.** Preservational potential of the conch in different sections. Conch sections with lowest probability are the least common preserved with shell in the documented specimen. Note the left/right discrepancy. **B.** Frequency distribution of all documented injuries around circumference, in percentage.

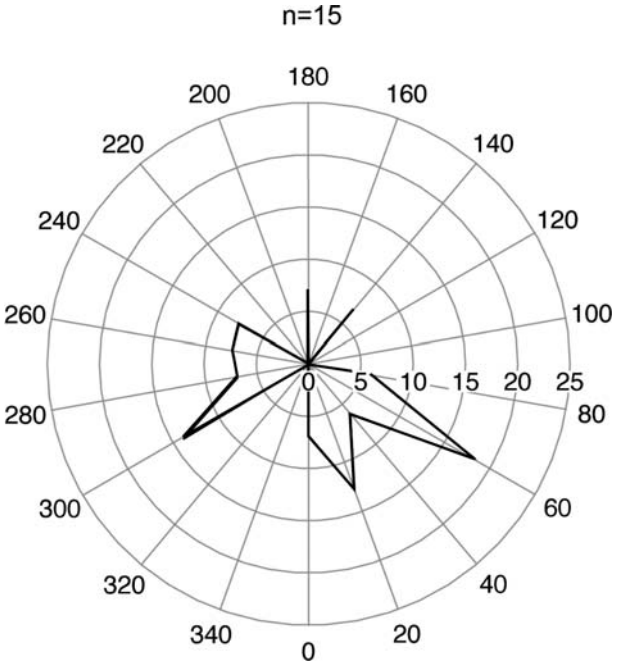

Figure 8. Frequency distribution of large healed injuries (breakages penetrated more than 5 mm posteriorly from anterior margin of scar) around circumference of aperture in degrees, 0° = ventral, 180° = dorsal, in adapical view. Note the concentration at the ventral parts of the aperture.

conchs reached a functional size refuge where they became big enough so that very few injuries occurred (see e.g. Leighton (2002) and Harper et al. (2009) for the discussion of this specific aspect of predator/prey relationship).

Conch position matters

Repair scars nearly have the same frequency on both sides of the conch when corrected for the preservation potential of the respective conch parts (left/right: 51/49 %). Nonetheless, the frequency distribution of injuries around the circumference of the interimistic aperture is not even (Figs 6–7). It is difficult to compare these frequency pattern with patterns known from *Nautilus* or ammonoids, because the coiling of the shell in these cephalopods by itself prevents dorsal breakages. But in ammonoids a clear concentration of repair scars at ventral shell parts is apparent (Kröger 2002; Klompmaker et al. 2009). This is not the case for small repair scars in endocerid shells. Thus, endocerids were attacked not only from the bottom-directed side but also from the water column, from swimming predators.

Figure 9. *Anthoceras buchi* (Lesnikowa, 1949), MB.C. 21996, from erratic boulder, Grey Orthoceratite Limestone, Kunda Regional Stage, Nienhagen, Mecklenburg, Germany, with irregularly mottled colour marks. Colour marks highlighted in the right figure. Scale bar 10 mm.

The colour pattern of *Anthoceras buchi* is known from a specimen from the erratics of northern Germany (Fig. 9). The preserved conch part displays an irregular network of dark broad bands forming irregular light deltoids or a mottled pattern. This pattern resembles irregular shadows of elongate objects like e.g. *Posidonia*-like water plants at the ground and probably indicates an habitat in seaweed fields or a bottom with small irregular ripples. The specimen gives no evidence of a dorsal/ventral differentiation in colour pattern. No correlation of a shell side with the colour pattern and injury frequency can be detected.

The aperture of *Anthoceras buchi* is nearly directly transverse (Fig. 1). A shallow broad ventral sinus is developed and at the lateral sides the aperture runs slightly oblique in apical direction toward the venter. The ventral emargination may be interpreted as a hyponomic sinus. The concentration of large repair scars at the ventral side is thus probably a result of the relatively low protection potential of this part of the aperture when assuming a dorsal hood. However, no direct correlation between apertural shape and injury frequency can be detected.

Because the repair scar frequency appears unrelated to apertural shape and colour pattern, the concentration of repaired scars at specific ranges along the circumference may reflect specifically unprotected areas, which were more susceptible for bites. A dorsal hood may have played an important role for protection.

Noteworthy, only a single injury of the apertural mantle epithelium is known from *Anthoceras buchi* (TUG 860–1640, from Kunda regional stage, Nehatu, northern Estonia). This type of injury forms narrow lateral furrows or scars in the shell and can reach considerable depths. Hölder (1956) termed this type of injuries *forma verticata* (Hengsbach 1996; = "tracked clefts" sensu Alexander & Dietl 2003). In Jurassic ammonoids healed injuries of the type *forma verticata* occur sometimes in up to 40 % of the conchs (Kröger 2002) and are generally more common. In ammonoids a correlation of the relative frequency of injuries of the peristomal mantle epithelia and the frequency of multiple injuries is obvious. Additionally, injuries of the peristomal mantle epithelia and multiple injuries are often more common in ammonoids with long body chambers and a high ability of withdrawing the body into the shell. In *Anthoceras buchi* the body chamber is very short, suggesting only little potential for withdrawing of the soft body into the shell. The scarcity of injuries of the peristomal mantle epithelia supports the interpretation of a high vulnerability of the soft body against predatory attacks in endocerids. The high rate of multiple injuries (36 % in *Anthoceras buchi* against a maximum of 20 % in Jurassic ammonoids, Kröger 2002) and the occurrence of severe slit-like repair scars contradict this impression. By contrast, a high rate of repaired scars does not necessarily indicate a low rate of successful attacks that affect the peristomal mantle epithelia. It appears quite likely that the soft body of *Anthoceras buchi* was much more vulnerable against attacks compared with ammonoids. The speculative protective function of the aptycha of some Jurassic ammonoids (Engeser & Keupp 2002) may explain the discrepancy.

Possible predators

The shape of the scars are partly a result of specific modes of attacks (Schäfer 1954). Additionally, the conch form and ornamentation plays an important role for the resulting breakage pattern caused by an attack (Stridsberg 1988; Kröger 2002). Transverse annuli, and constrictions which are common in *Anthoceras buchi* have the potential to redirect the shear power during a bite and eventually spatially constrain fractures and fissures. Fractures parallel to the aperture and distal widenings (Fig. 2A) at the distal rim of the deepest breakages thus can be interpreted as a result of the transverse ornamentation in *Anthoceras buchi*. Similar distal widenings of slit-like breakages are known from annulate ammonoids (e.g. Isakar & Ebbestad 2000, figs 4, 6g; Kröger 2000, figs 17–18, 32, 33a). The rarity of injuries of the *forma verticata* type may indicate that the conch breaking device of the predators were not very sharp or acute, and therefore unable to injure a flexible epithelium. The occasional deep, slit-like breakages can only be explained by predators that were able to fix their prey and to peel the shell in a controlled attack. The concentration of these deep breakages at the ventral part of the prey further indicate 1) either some control over the position of the peeling or 2) a less protected aperture or 3) a combination of both. Similar slit-like breakages are known from modern crustaceans with chelae. Chelae of 10 mm length which could potentially have inflicted larger slit-like breakages preserved in *Anthoceras buchi* are not known in any Middle Ordovician arthropod (see also Kröger 2000; Brett & Walker 2002). Cephalopods with massive beaks and the potential to fix their prey with arms or tentacles are other potential predators. Since not a single pre-Carboniferous unequivocal non-ammonoid cephalopod beak has been found so far, the actual originators of the large slit-like breakages cannot be identified yet (see also Brett & Walker 2002; Kröger 2004).

Conclusion

The high frequency of repaired scars in specimens of *Anthoceras buchi* is striking, with 29 % of the conchs being injured. In average 0.49 repaired scars occur per conch. These frequencies are comparable only with repair scars documented in the Late Ordovician Laurentian gastropod *Trochonemella* sp. (Ebbestad & Stott 2008) of which 36 % are injured. In *Trochonemella* sp. the number of scars per shell is 0.46. Ebbestad & Stott (2008) pointed out that these percentages are in the

range of injury frequencies known from Mesozoic molluscs. They are exceptional in the Ordovician and probably indicate high exposure to durophagous predators. The annulated and constricted conch of *Anthoceras* ex gr. *buchi* can be interpreted as an adaption against conch breaking predators (Vermeij 1977; Brett & Walker 2002; Kröger 2002) and is additional evidence for a high exposure to durophagous predators.

In contrast to *Trochonemella* sp., most injuries in *Anthoceras buchi* did not occur in the larger size classes. Most injuries, as well as the most severe cases occur in medium sized, premature conchs. In large, and mature specimens healed injuries where not only less severe but multiple repair scars are less common (Figs 5–6). This is interpreted as indication for a size limitation of the unknown predator. The large size of endocerids, thus can be interpreted as a size refuge against predator.

The position of the repair scars (often dorsal), their shape (often slit-like), and their depth (sometimes several centimetres behind the anterior margin of the scar) suggest that other cephalopods, most probably other endocerids or even *Anthoceras* ex gr. *buchi* itself were the originators of these injuries. Endocerids were the largest molluscs (Teichert & Kummel 1960) and the largest potential durophagous predators in the Middle and Late Ordovician (see discussion in Frey 1995; Kröger 2004).

Kröger & Landing (2010) detected a trend of increasing body size, conch strength, and mobility in cephalopods of the Early Ordovician platform carbonates of eastern Laurentia. They interpreted the evolutionary trends as a possible result of increasing competition and an escalation among predators. Endocerids are a major component and among the largest taxa in these Laurentian carbonates. In endocerids, the Ordovician trend of size increase was the strongest.

The size limitation of the predators of *Anthoceras* ex gr. *buchi* and as a conseqence a size refuge of the prey may have been an important factor in the excessive size evolution of endocerids in general and are another argument for predatory escalation as driving evolutionary factor among Ordovician cephalopods. However, a rigorous quantitative testing of this hypothesis is needed for further evaluation of the driving evolutionary factors of endocerids.

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