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Shell injuries, repair and malformation in the early Cambrian mollusc *Helcionella antiqua* from Scania, Sweden

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ABSTRACT

Three cases of repaired injuries and malformation in specimens of the helcionelloid mollusc *Helcionella antiqua* (Kiær, 1917) from the lower Cambrian (Cambrian Series 2, Stage 4) Gislöv Formation of southern Sweden document some of the oldest known durophagous attacks on Palaeozoic molluscs. Two of the injuries are developed as clefts, of which one had a severe effect on the continued growth of the shell. The third example is a large embayment removing large portions of the supra-apical part of the shell. A similar repaired injury is known in the slightly older mollusc *Marocella mira* Geyer, 1986, from Antarctica and Australia. The morphology of the injuries and the hydrodynamically quiet depositional setting suggests that the shell damage was caused by failed predatory attacks. The location of the repaired injuries suggests that the attacks may have targeted the head region of the molluscs, thus supporting an endogastrically coiled orientation of the shell in *Helcionella*. Only three repaired injuries in 252 *Helcionella* specimens were found, giving a shell repair frequency of 1.2%. All three examples occur in the larger size classes. The size-frequency distribution ($N = 182$) is strongly right skewed, which could suggest high input of juvenile specimens into the assemblage. The assemblage is interpreted as a time averaged and mixed death assemblage, albeit with good correspondence with the living shelly assemblage, due to a relatively thin, homogenous unit that may suggest within-habitat time averaging.

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Introduction



Repaired injuries are a recurrent theme in shells and exoskeletons of marine organisms. They are frequently observed in groups such as molluscs where the entire ontogeny is preserved in the valves or conchs, and less conspicuous in ecdysozoan taxa where the exoskeleton is moulted. Non-lethal damage may result from abiotic circumstances, such as tumbling in strong currents or storms, or from biotic agents such as failed predation, but deducing the cause in fossil organisms may be challenging. An understanding of the causality of repaired damages is vital, especially in the case of failed predation, because an understanding of predator–prey interactions through Earth history may provide insight into the development and evolution of marine ecosystems, ecology, and faunas (Kelly et al., 2003; Sperling et al., 2013; Bicknell & Paterson, 2018; Klompmaker et al., 2019; Wood et al., 2019 and references therein).

Repaired, durophagous injuries from failed predation, along with predation by drilling (Kelly & Hansen, 2003) and coprolites (Bicknell & Paterson, 2018), are tangible evidence for predator–prey interactions in the fossil record. Macropredation may have been in effect already in the late Ediacaran (Wood et al., 2019 and references therein) but physical records of predator–prey interactions in the late Ediacaran and early Cambrian are in fact exceedingly rare (Skovsted 2004; Bicknell

& Paterson, 2018; Klompmaker et al., 2019). The current paper documents three cases of repaired injuries and malformation in a large collection of the helcionelloid mollusc *Helcionella antiqua* (Kiær, 1917) from the lower Cambrian (Cambrian Series 2, Stage 4) of southern Sweden. Bicknell & Paterson (2018, table 2) documented repaired damages in only two other molluscan taxa of this age; together these constitute the oldest records of failed predation in molluscs. Vendrasco et al. (2011) documented high frequencies of healed damages in slightly younger molluscs from Cambrian Series 3 in Siberia and Australia.

Material and methods

Helcionella antiqua (Kiær, 1917) is a Cambrian mollusc with a low, recurved patelliform shell (height:length ratio is c. 0.3), where the apex is placed near the margin, but not overhanging it. The shell is thin, with fine and dense comarginal growth lines crossed by densely spaced but narrow and rounded radial lirae giving the impression of a reticulate pattern. Typically, the entire shell surface also has weakly convex comarginal folds or rugae. *Helcionella* has been discussed recently by Jacquet & Brock (2016) and Geyer et al. (2019), while the type material and a few other specimens of *Helcionella antiqua* from the Evjevik Member of the Ringstrand Formation were described from

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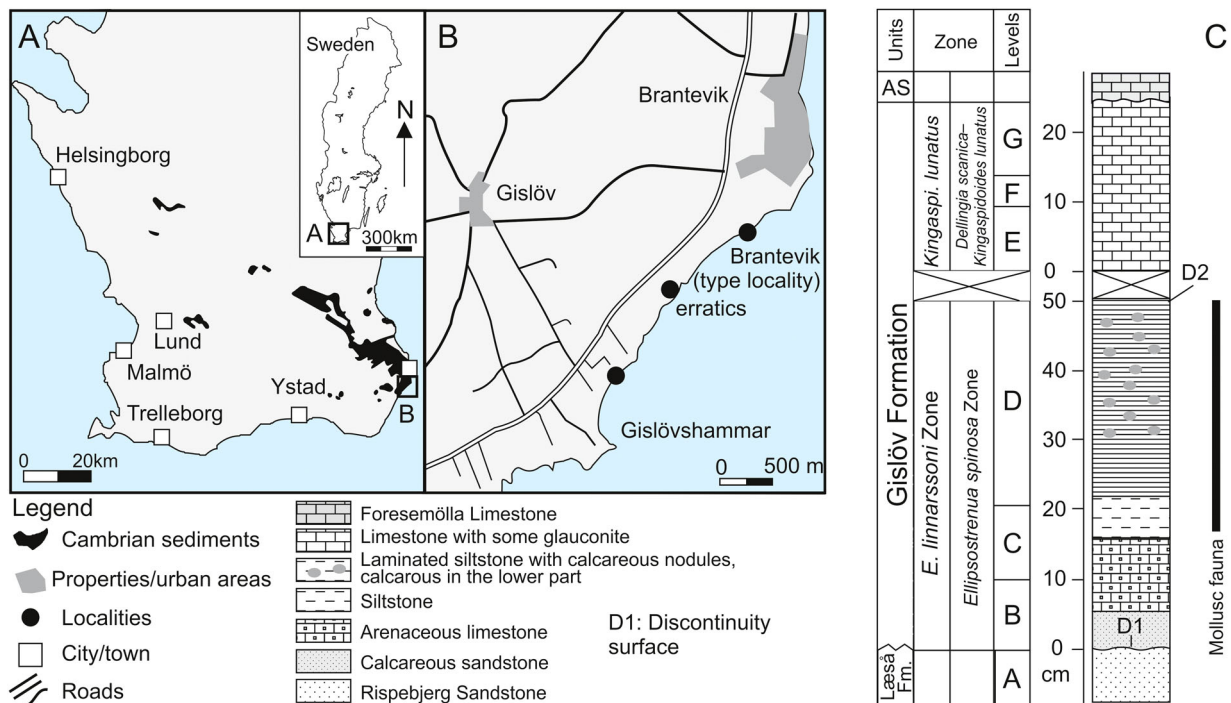


Figure 1. Maps and stratigraphy. **A.** Southern Sweden with main distribution of Cambrian sediments. The position of the area in B is indicated. **B.** Main localities along the coast at Brantevik. **C.** Stratigraphy of the Gislöv Formation, including previous and current trilobite zonation and the levels used by Bergström & Ahlberg (1981) (modified from Cederström et al. 2022, fig. 7). The Gislövshammar section is placed at WGS coordinates 55°29'35"N, 14°19'7.5"E. AS = Alum Shale Formation.

the Lake Mjøsa area in Norway by Høyberget et al. (2015). The abundant material from Gislövshammar in southern Sweden discussed herein adds further details but deviates little morphologically from the type material and is considered conspecific.

The position of *Helcionella* and other helcionellids in molluscan systematics is unresolved, with a summary given recently by Peel & Kouchinsky (2022).

The collection consists of 252 specimens of *Helcionella antiqua*, collected from the Gislöv Formation largely at the costal outcrop at Gislövshammar in southeastern Scania in southern Sweden through many years by PC and colleagues. A few specimens are also registered from the Hardeberga quarry just east of the city of Lund in western Scania. Fossils typically occur as densely packed accumulations in calcareous nodules in a c. 30 cm interval of laminated siltstone and small intercalated calcareous nodules (Fig. 1C). This interval corresponds to bed D of Bergström & Ahlberg (1981, fig. 8) and the *Ellipsostrenua spinosa* Zone of Cambrian Series 2, Stage 4 (Cederström et al., 2022). A diverse fauna of trilobites, several helcionelloid molluscs and sclerites of other fossils is present in these beds (Cederström et al., 2009, 2022; Álvaro et al., 2010). Trilobites in the calcareous nodules are commonly articulated or enrolled, and represent autochthonous assemblages in a low energy depositional setting (Cederström et al., 2009, 2022; Álvaro et al., 2010).

Helcionella specimens are generally preserved as internal moulds but often with shell ornamentation and growth lines superimposed. Recrystallized shell is only rarely preserved. Severely deformed or flattened specimens as well as seemingly undistorted specimens occur in the material. Several specimens are to a various degree dorso-ventrally compressed,

with the older portions of the shell telescoped into the shell. In such cases, one or several of the comarginal rings can be accentuated. Specimens range in size from probable protoconchs with a length of about 0.8 mm, to the largest complete specimen measuring just over 30 mm in length. Despite detailed examination, only three specimens of *Helcionella antiqua* with clear repaired injuries were observed. The lengths of 182 specimens were measured for size–frequency distribution, with 2-mm size classes, to allow assessment of population structure and taphonomic influences.

All specimens are housed in the palaeontological collections at the Museum of Evolution, Uppsala University, Sweden (PMU). Terminology of injuries follows that of Alexander & Dietl (2001, 2003) and Ebbestad et al. (2009), while descriptive morphology of the conchs follows Jacquet & Brock (2016).

Repaired injuries

PMU 37566

The shell is here oriented with the apex in a posterior position with the convex supra-apical margin interpreted as anterior (Fig. 2). The specimen is well-preserved, without evidence of compaction, but the right half of the shell is mainly lacking. Preserved length is approximately 15.5 mm and estimated maximum width is 11 mm. A deep cleft in the shell is developed on the antero-lateral flank, forming a broad and shallow V that is 1.5 mm wide and extends 0.65 mm into the shell from the preserved margin. The broken edges of the shell are visible along the margins of the V (arrows in Fig. 2D). The anterior margin of the injury seems to stop at the ventral edge of the scar while the posterior part trails

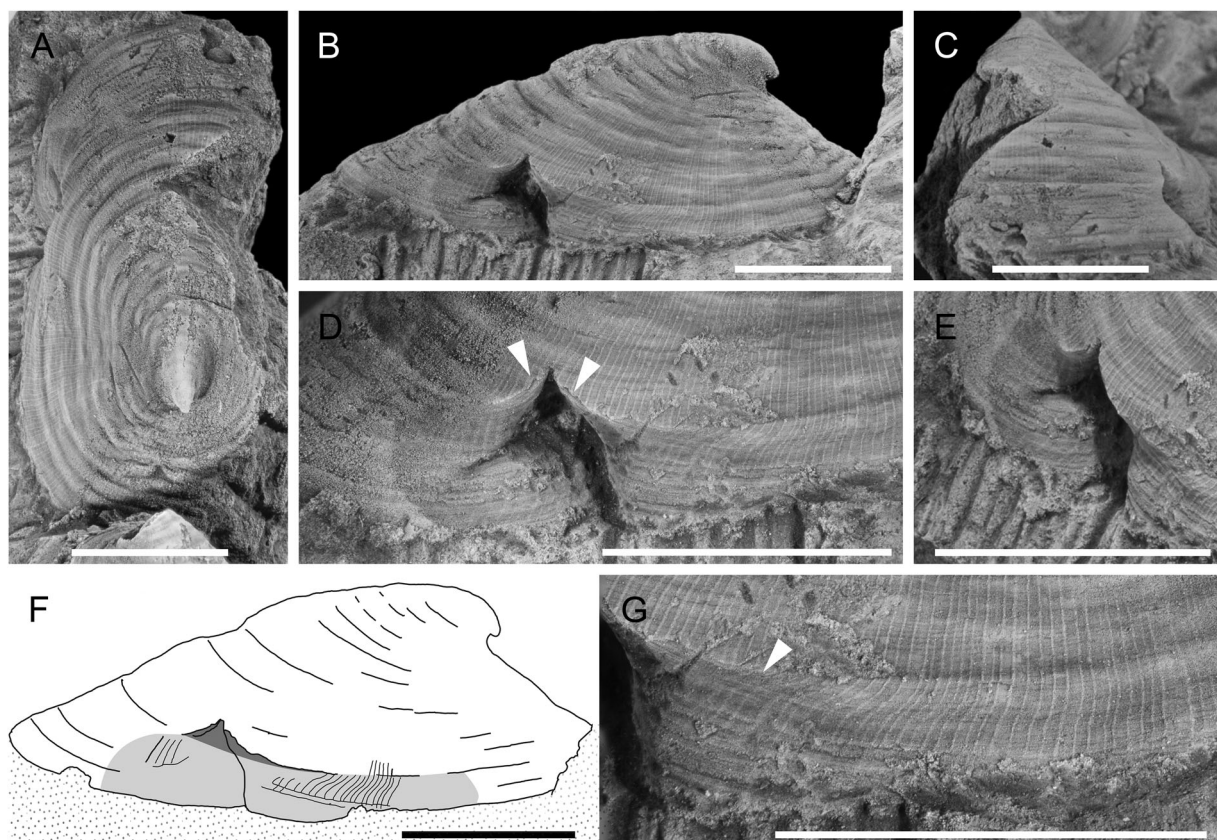


Figure 2. Specimen PMU 37566. **A–C.** Dorsal, left lateral and anterior views. **D.** Detail of cleft, with arrows pointing to edge of scar at the time of the injury. **E.** dorsal oblique view showing how the repaired shell curves deeply into the scar area. **F.** Interpretive drawing. The dark area indicates the injury at the time of attack, whereas the light grey area represents disturbed new shell. **G.** The posterior side of the repaired shell. The white arrow indicates the position of the apertural margin at the time of the attack. Scale bars = 0.5 cm.

posterior for at least 2.0 mm (arrow in Fig. 2G). Further back, the growth lines at the level of the lower scar edge are undisturbed (see dark grey area in the interpretive Fig. 2F). Anteriorly, the growth lines are worn and not discernible. Below the inferred scar edge, and inside the cleft, the repaired shell is deformed (see light grey area in the interpretive Fig. 2F), with the growth following the overall shape of the original injury. The repaired shell curves deeply into the scar area; its inner parts are obscured, but a tracked cleft is likely developed. The growth trajectory of the radial shell ornamentation below the scar line is disturbed posteriorly for at least 5 mm (Fig. 2A, G), while the ornamentation is largely eroded anteriorly and the extent of the repair is difficult to estimate. In anterior view it is also evident that the lateral curvature of the repaired shell posterior to the scar is affected, as the side is nearly vertical (Fig. 2C). The spiral component is nearly missing on the repaired shell in the vicinity of the cleft (Fig. 2D, E, G).

PMU 37567

Only the posterior part of the shell is preserved (Fig. 3), but comparison with other complete specimens suggests a length of little more than 20 mm. A small but distinct cleft is seen on the left lateral side, close to the apertural margin. Its

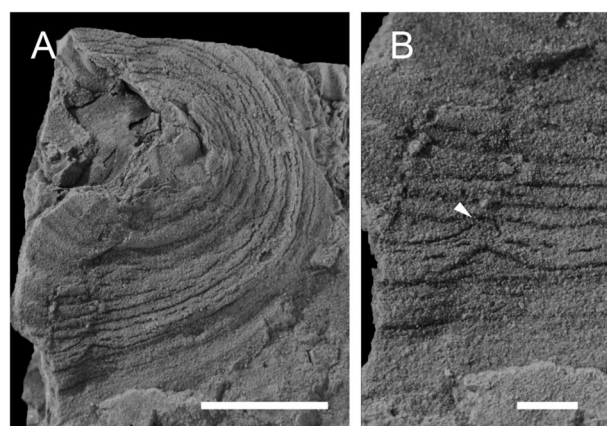


Figure 3. Specimen PMU 37567. **A.** Dorsal view, posterior to the right. **B.** Detail of small cleft on the left lateral side of the shell, close to the apertural margin. Arrow marks the apex of the cleft. Scale bar in A = 0.5 cm, scale bar in B = 0.1 cm.

apex is marked by the arrow in Fig. 3B. Aberrant shell growth is developed, but normal growth was resumed relatively soon.

PMU 37568

The shell is oriented with the apex in a posterior position (Fig. 4). The specimen is dorso-ventrally flattened, with most of the

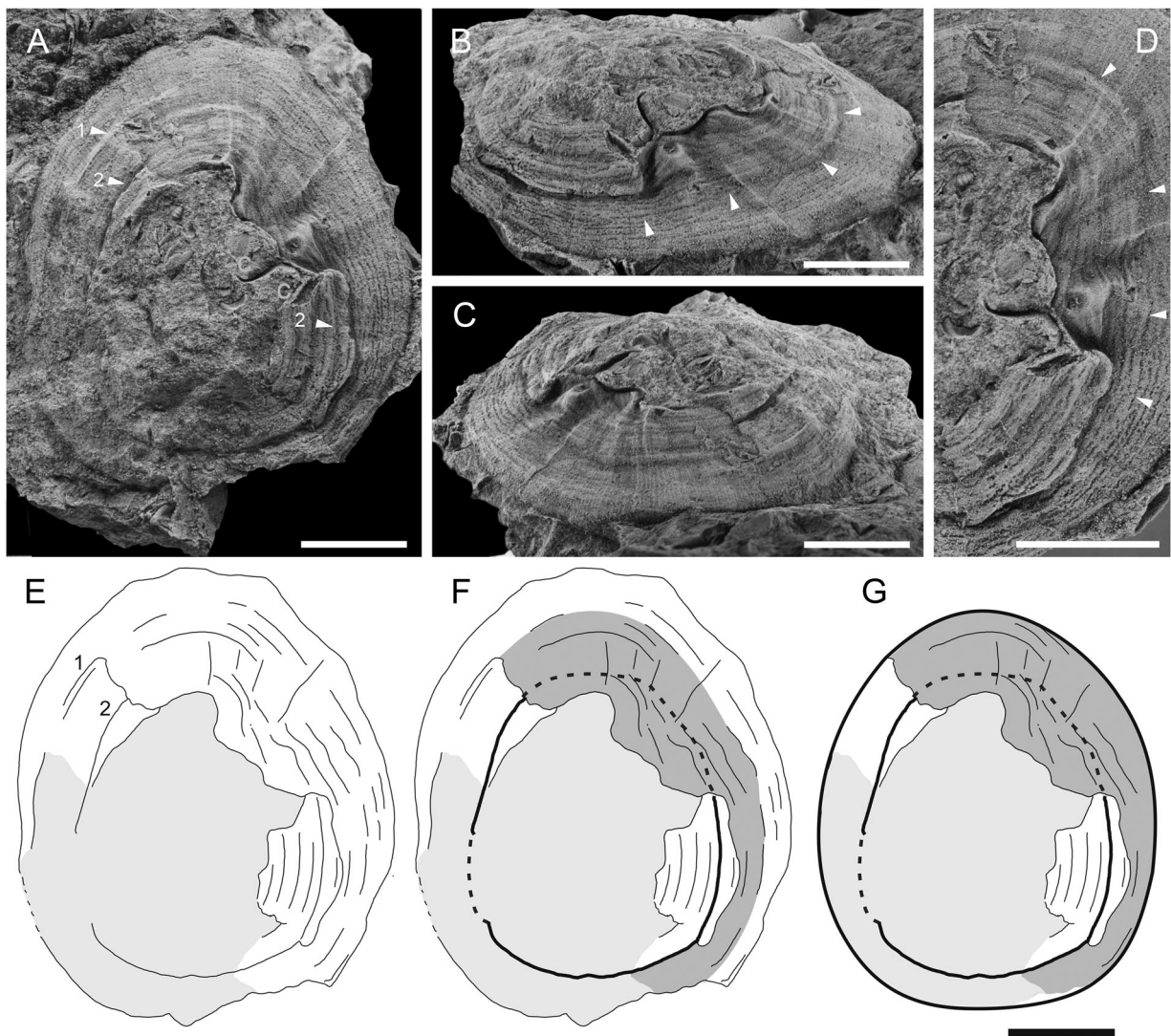


Figure 4. Specimen PMU 37568. **A–C.** Dorsal, anterior oblique and oblique right lateral views. White number 1 indicates the left anterior-lateral flank, whereas numbers 2 mark the impressed comarginal line that circle the shell. The white letters c mark the two cuts immediately on the apical side of the main scar. In Fig. B, the white arrows mark a comarginal line which would approximately delimit the extent of the original damage. **D.** Dorsal view, with detail of embayment. White arrows as in Fig. B. **E–G.** Interpretive drawings. **E.** An outline of the shell and scar (numbers as in Fig. A). **F.** Shell removed during the attacks is indicated in dark grey. Black solid and dotted line indicates the impressed comarginal line that circle the shell (number 2 in Fig. A). **G.** The shell at the time of the attack, with same features as in Fig. F outlined. Scale bars = 0.5 cm.

apex and left posterior flank eroded (light grey area in interpretive Fig. 4E–G). The specimen is one of the largest in the available material, 22.5 mm long with a maximum width of 18.5 mm. An extensive embayment is developed from the left antero-lateral flank near the apertural margin (marked 1 in Fig. 4A), cutting diagonally and slightly adapically across to the right flank, then trailing posteriorly parallel to the margin of the shell. The posterior margin of the scar is difficult to establish as the specimen is eroded. Just adapically of the right lateral scar edge an impressed comarginal line circles the shell to the left anterior margin of the scar (marked 2 in Fig. 4A, B). This comarginal line is outlined by a thick black line in interpretive Fig. 4(F, G) and is interpreted as a line developed subsequently through compaction and telescoping, a feature commonly seen also in other specimens. The arrows in Fig. 4(B, D) show a comarginal line circling towards the right from near the antero-lateral edge of the scar on the left side (marked 1 in Fig. 4A), which would approximately delimit

the extent of the original damage (dark grey area in interpretive Fig. 4E–G). Fig. 4G shows the estimated size of the specimen at that time, revealing the extensive damage inflicted upon the shell.

Discussion

The repaired injuries documented in the three specimens of *Helcionella antiqua* from Gislövshammar consist of two smaller clefts and one embayment with large proportions of the shell removed. In the first example (PMU 37566, Fig. 2) the cleft is restricted, but with a prolonged effect on the continued growth near the scar seen as malformation of the shell and ornamentation. The shell was about 15 mm long at the time of the damage. The cleft in the second specimen (PMU 37567, Fig. 3) is small with only limited effect on the growth. The shell was slightly less than 20 mm long when the damage occurred. In the third specimen (PMU 37568, Fig. 4), the

injury is extensive and severe, with nearly a third of the shell removed. The conch was about 18 mm when damaged. Similar injuries and shell repair morphologies are seen in mollusc shells throughout the geological record. Cadée et al. (2000) for instance illustrated a shell of a recent *Patella*, similar in shell-shape, nearly identical in size and with a strikingly similar type of scar as in PMU 37568; the high-energy habitat of the recent form meant that the injury could have been caused by either mechanical forces or by predation by birds. A search of the literature has not yielded further modern examples.

Failed predation is considered to be the likely cause of the damage observed in *Helcionella antiqua* from Gislövshammar, owing to the shape and form of the injuries combined with the depositional facies. The assemblage occurs in a thin, homogenous unit that suggests quite open marine shelf conditions with limited or no effects by destructive hydrodynamic forces. It may also indicate a within-habitat time averaging of the preserved death assemblage (*sensu* Kidwell & Boscence, 1991), which has implications for the interpretation of the shell repair intensity.

The preservation of many of the 252 available specimens hindered the discovery of repairs. Also, the effect of successful predation is unknown. Since the mollusc taxa are generally small it is likely that individuals could have been ingested whole, e.g. by infaunal worms (Hu et al., 2021), and may have been totally destroyed or even passed through the digestive tract without damage. However, the observed shell repair frequency is still very low, with only about 1.2% repairs (measured by the individuals with scars method, see discussions in Ebbestad & Stott, 2008 and Lindström & Peel, 2010 on shell repair criteria). Generally, this low rate would indicate either very successful predators or alternatively that the predation pressure was low (Vermeij, 1982, 1987; Leighton, 2002). Furthermore, the repaired injuries occur in the higher size classes (based on the shell size at the time of the injury), which could indicate a size refuge as larger individuals are better able to withstand predation attempts (Vermeij et al., 1980; Leighton, 2002; Ebbestad & Stott, 2008).

The size distribution of *Helcionella* shells is right (positively) skewed (Fig. 5), with the mean being in the 10–

12 mm size class. There may be a slight hint of a bimodal distribution with a second peak at the 10–12 mm size class but this is equivocal. The positively skewed size-frequency distribution among the *Helcionella* specimens may suggest that a high proportion of juvenile shells contributed to the fossil assemblage (high natural mortality among young individuals). A right skewed distribution may also be understood as an *in situ* sample or a living assemblage which is in line with a within-habitat time assemblage. Regardless, taphonomic sorting and mixing, diagenesis, as well as time averaging modify any death assemblage (Kidwell & Boscence, 1991; Kidwell, 1998), and the larger shells are most likely underrepresented in the sample. A study of the size frequency in the minute trilobite *Calodiscus* from the same beds in Gislövshammar was interpreted to demonstrate post mortem transport and sorting (Cederström et al., 2009). The size-frequency counts of other minute helcionelloid molluscs found together with *H. antiqua* generally show a normal distribution (Ebbestad et al., 2023), which also supports the presence of post mortem transport and sorting. However, larger specimens may not have been much affected by sorting. The trilobite *Calodiscus* and most of the helcionelloid molluscs found in the Gislöv Formation are minute, less than 3 mm in length or width, and thus were easily subjected to winnowing even by weak currents. Some specimens of *Helcionella*, on the other hand, are among the largest fossils preserved, with the largest individuals being 10 times larger than that of the other helcionellid mollusc species and *Calodiscus* specimens in the same assemblage. Large robust mollusc shells in modern environments tend to break down rapidly and fragment due to a varied set of processes. At the same time, taxa with less robust shells tend to be preserved more locally while larger more robust shells are prone to transport and therefore have a broader spatial and temporal mixing in the sediment (Kidwell & Boscence, 1991; Kowalewski, 1997). In the case of the Gislöv Formation, interpretation as a mixed death assemblage seems appropriate, and sorting by weak hydrodynamic forces before deposition, largely affecting the minute specimens only, and a selective loss of large specimens could explain the right skewed distribution.

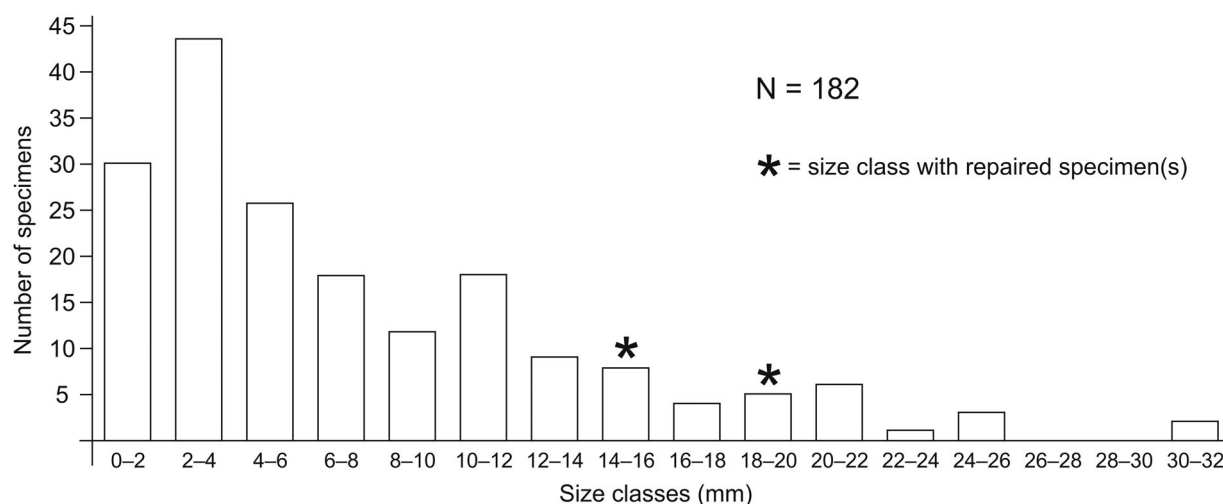


Figure 5. Size-frequency distributions of *Helcionella antiqua* with 2 mm size bins, showing a right (positively) skewed distribution.

If the sample distribution reflects taphonomic loss of large specimens, the repair frequency could be underestimated. However, shell repairs in *Marocella mira* are also rare, and found in the larger size classes (Evans, 1992; Skovsted et al., 2007). On the other hand, shell damage intensity recorded by Vendrasco et al. (2011) in slightly younger Siberian and Australian molluscs was high but with injuries present in minute, up to ~3 mm specimens. The reasons for this discrepancy are uncertain, but may include taphonomic and preservational bias, or true differences in ecological signals.

The injury in PMU 37568 shows several scallops within the major scar on the antero-lateral surface (upper right side in Fig. 4A, see also 4D) that probably represent separate breakage events in the overall attack. Additionally, the pre-attack surface lying immediately on the apical side of the main scar preserves two deep cuts into its upper surface inflicted by the predator. The lowest of these shows depression of the shell surface towards the shell interior. Sharply V-shaped fractures in accounts of failed predation in younger Palaeozoic molluscs have been attributed to the action of the beak in hunting nautiloids (Vermeij, 1977, 1978; Peel, 1984; Bicknell & Paterson, 2018). The absence of nautiloids in the early Cambrian suggests instead that the deep cuts may have been inflicted by the action of arthropod appendages (see discussion on Palaeozoic predators in Bicknell & Paterson, 2018).

Comparison with *Marocella mira*

Shell repairs were recorded in specimens of the mollusc *Marocella mira* Geyer, 1986, from Cambrian Series 2, Stage 4 sediments in Antarctica (Evans, 1992) and Australia (Skovsted et al., 2007). *Marocella mira* occurs in the *Pararaia bunyer-ooensis* Trilobite Zone, which is slightly older than the *Ellipsostrenua spinosa* Zone in Baltica (Geyer, 2019). Its shell is broadly similar in form to that of *Helcionella*, but possesses a unique reticulate structure on the internal shell surface. It is a common and widespread taxon in Morocco, Australia, China, Siberia and Antarctica, with specimens generally smaller than 12 mm (Parkhaev, 2001; Topper et al., 2009). However, the damaged specimens from Australia were between 10 and 18 mm when the damage was inflicted. All injuries are embayments, minor in the small Antarctic specimen but substantial in the Australian specimens and cutting larger, irregular pieces along the apertural margins. As such, these injuries are directly comparable to that seen in PMU 37568. One of the Australian specimens displays a second, much smaller embayment, afflicting the already repaired shell area (Skovsted et al., 2007, fig. 1).

Skovsted et al. (2007) noted that injuries in *Marocella mira* occur in the supra-apical margin of the shell, here treated as anterior, which would be the head region in an endogastrically coiled helcionellid mollusc (Peel, 1991). This is also the case in PMU 37568 (Fig. 4). Such extensive damage to the visceral mass in this region would likely prove fatal in most cases, suggesting that the head region, rather than the posterior mantle cavity (sub-apical surface), would be the favoured target for attacks. This may contribute to the observed rarity of specimens with repaired injuries as a high proportion of attacks in this region may have been successful. Equally, however, it may then be expected that such repaired injuries would be

more common in the sub-apical region as they would be less likely to be fatal. However, the attack strategy of predators may have been based on other behavioural traits. Thus, predators that followed a chemical signal in the exhalant current from the mantle cavity of the prey may have focused their attacks on that area of the shell (Kohn, 1961; Sakata, 1989; Ferner & Weisburg, 2005; Peel, 2020). This would correspond to the sub-apical margin, located posteriorly in shells restored in the endogastric orientation preferred here. This sub-apical surface would be anterior in an exogastric reconstruction, although the mantle cavity would likely be located posteriorly, under the supra-apical surface. It is evident that the small number of shells with observed repaired injuries or open fractures precludes resolution of this discussion.

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Disclosure statement

No potential conflict of interest was reported by the author(s).

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