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ABSTRACT—A dorsal valve of an Upper Cambrian lingulate brachiopod exhibits a repair scar on the anterior lateral edge of its larval shell. This species is characterized by an abrupt change in ornamentation from larval to postlarval growth. Shell material secreted in the injured area after the damage occurred exhibits ornamentation that is characteristic of postlarval growth, although equivalent growth exhibits characteristics of the larval stage. A break in the edge of the shell is visible, and the growth lines of the larval and postlarval shell were distorted until the broken area was filled in. Damage to the surface of the shell is interpreted to have been caused by the same event. Modern lingulate brachiopod larvae are planktotrophic and are interpreted to have been so throughout their long geologic history. Therefore, an environmental cause of shell damage seems unlikely and the injuries are interpreted to have been caused by an unknown durophagous predator. This specimen offers evidence that lingulate brachiopod larvae were able to survive shell breakage and repair their shells.

INTRODUCTION

CAMBRIAN PREDATOR/PREY relationships are most easily understood through fossil evidence of their interactions which is infrequently preserved. Evidence of predation may be of apparently successful attacks, such as boreholes, or more rarely, lethal shell breakage (Pratt, 1998). Shell repair scars attributed to sublethal predation provide evidence of unsuccessful attacks but may also provide important evidence of interactions between predators and their prey.

Cambrian injury scars attributed to sublethal predation are most often reported from trilobites (see Babcock [2003] for a review). Other reports of Cambrian repair scars include the benthic Lower Cambrian possible mollusc, *Marocella* Geyer, 1986 (Evans, 1992; Skovsted et al., 2007), the enigmatic Lower Cambrian *Mobergella* Bengtson, 1968 (Bengtson, 1968; Conway Morris and Bengtson, 1994), also interpreted as a benthic mollusc (Conway Morris and Chapman, 1997), as well as the problematic Lower Cambrian fossil *Estoniadiscus* Peel, 2003. Peel (2003) interpreted *Estoniadiscus discinoides* (Schmidt, 1888) as a possible stem-group brachiopod, but Babcock and Robison (1988) and Yochelson and Gil Cid (1984) interpreted as it as a chondrophore. If the interpretation of *Estoniadiscus* as a chondrophore is accepted, it is the only previous record of a repair scar on a Cambrian planktic organism, and if it is accepted as a brachiopod, it is a rare record of a repair scar on a Cambrian brachiopod.

Direct evidence of Cambrian brachiopod predation is usually in the form of boreholes or punctures (Miller and Sundberg, 1984; Conway Morris and Bengtson, 1994; Robson and Pratt, 2007). Boreholes are relatively easy to distinguish from post-mortem breakage or sample preparation damage. Breakage to the edge of the shell that may be the result of predation is usually identifiable in the event that the attack is unsuccessful and the injury is repaired. Williams and Holmer (1992) described a Cambrian acrotretid brachiopod dorsal valve with a repaired fracture in postlarval growth. Evidence of Cambrian predation on brachiopods also comes from preserved gut contents (Conway Morris and Whittington, 1979; Bruton, 2001) and coprolites (Conway Morris and Robison, 1988; Babcock, 2003).

It is clear that predation was established in the Cambrian benthic realm and that mature brachiopods were victims of predation. Brachiopod larvae were part of the Cambrian pelagic realm, an ecosystem that is less well understood. Brett and Walker (2002) characterized the Cambrian as a time when pelagic predator-prey relationships were not yet developed. Hu et al. (2007) argued that the pelagic ecosystem, including predators, was established during the Cambrian. Vannier and Chen (2000) reported possible Early Cambrian pelagic organisms, and the same authors (2005) reported Middle Cambrian mid-water predators. Vannier et al. (2007) also reported Early Cambrian chaetognaths, a group which is carnivorous and abundant in the modern pelagic realm (Terazaki, 2000). However, little direct fossil evidence exists for predation on planktic organisms during the early part of the Paleozoic. One of the earliest records came much later, as repaired shell injuries on Devonian dacryoconarid tentaculites (Berkyová et al. 2007). A planktic larval stage or adult existence has been suggested as a refuge from predation that was largely unexploited until the Late Cambrian (Signor and Vermeij, 1994).

If brachiopod larvae were under predation pressure, and particularly if they sometimes survived the attack, then evolutionary pressure may facilitate the development of antipredatory adaptations specific to the larval stage. This mechanism was suggested for the gastropods, for example (Garstang, 1928). If predation is a driving force behind evolution (Vermeij, 1987) then it follows that this should be true for larvae as well as for adult forms.

GEOLOGIC SETTING

The specimen was discovered in a large collection of lingulate brachiopods from the Upper Cambrian Hellnmaria Member of the Notch Peak Formation in Millard County, western Utah (Sunwaptan Stage of Millardan Series). The specimen is from the East Shoreline Butte measured section (Fig. 1) described by Miller et al. (2003). It was found 251.5 m above the base of the section, 27.7 m below the base of the *Proconodontus tenuiserratus* conodont Zone, the oldest conodont zone recognized in North America. The area is within the House Range Embayment, interpreted by Rees (1986) as a

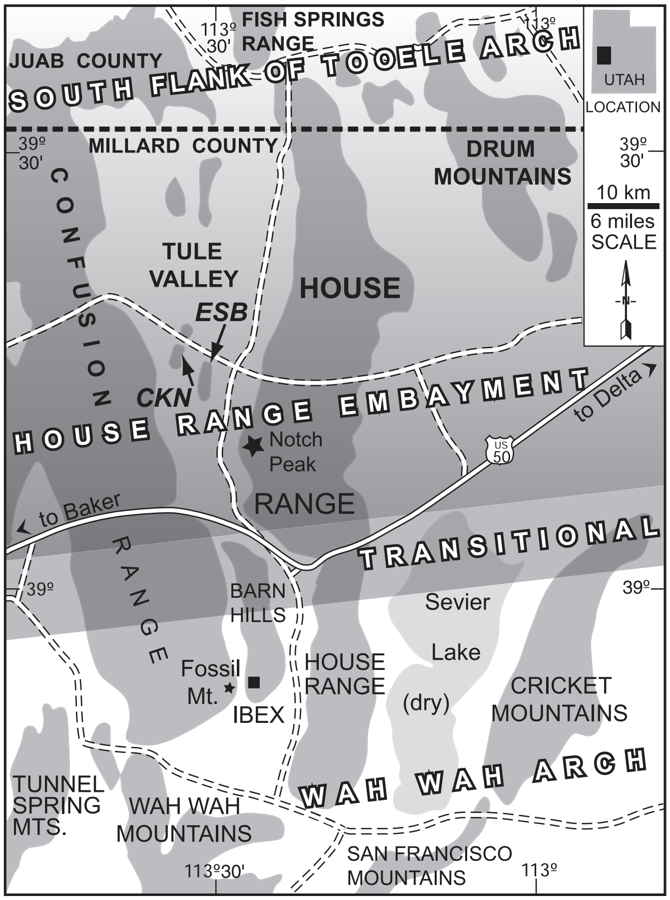

FIGURE *1*—Map showing location of East Shoreline Butte (ESB) and Chalk Knolls North (CKN) sections of Miller et al. (2003). Wah Wah Arch, House Range Embayment, and Tooele Arch are regional tectonic features discussed by Miller et al. (2003). Transitional area is inferred location of a Cambrian growth fault at the south edge of the down-faulted House Range Embayment. Figure modified after Miller et al. (2003, fig. 1).

fault-controlled, deep-water basin on the carbonate platform. Additional specimens of this species have been found throughout the upper parts of the Hellnmaria Member in this section and in the nearby Chalk Knolls North measured section (Miller et al., 2003; see CKN on Fig. 1). The species is scarce in both sections.

SYSTEMATIC PALEONTOLOGY

All specimens illustrated are reposited in the National Museum of Natural History (USNM), Washington DC, U.S.A.

Order LINGULIDA Waagen, 1885
Superfamily LINGULOIDEA Menke, 1828
Family OBOLIDAE King, 1846
Subfamily OBOLINAE King, 1846
Genus and species indeterminate
Figures 2, 3

Description.—Nearly equally biconvex valves, suboval in outline, with prominent larval shell. Larval shell with fine growth lines and subtle radial ornamentation. Larval shell boundary prominent, generally marked by slightly raised rim on latest larval growth, followed by marked growth disruption. Mature growth ornamentation of concentric, raised, transverse ridges, evenly spaced approximately 40–55 µm apart, and with slightly irregular margins. Transverse ridge lines truncate against larval shell laterally and cross growth lines. Ridges deflect towards posterior at midwidth of valve.

Dorsal pseudointerarea with prominent elongated median groove, rounded in transverse profile. Reduced dorsal propareas with lateral grooves along posterior edge.

Ventral valve with subacuminate posterior margin. Ventral pseudointerarea with orthocline propareas slightly elevated above floor of valve. Flexure lines barely discernible. Narrow, shallow pedicle groove bounded by low ridges along edges of propareas. Visceral area slightly thickened with median tongue extending towards anterior to approximately one-third the length of the valve. Faintly impressed furrows bounding central part of visceral area.

Material examined.—Four ventral valves and 31 dorsal valves, all fragmental.

Occurrence.—In the Upper Cambrian (Millardan, Sunwaptan) Hellnmaria Member of the Notch Peak Formation, Millard County, western Utah.

Discussion.—The material does not fit within described species or genera. The material is neither abundant nor well-preserved. Therefore the brachiopod is left in open nomenclature. The systematic treatment of the lingulates of the Hellnmaria Member is the subject of research in progress.

The elongate outline and ornamentation of terrace-like transverse ridges exhibited by this brachiopod is similar to the obolid genera *Westonia* Walcott, 1908 and *Libecoviella* Mergl, 1997. Externally it differs in having a smooth shell during early growth (Fig. 2.1, 2.4–2.7). Internally, it differs in having an elongated median groove on the dorsal valve, as well as transverse grooves along the posterolateral edges of the dorsal propareas (Fig. 2.3, 2.6).

No complete valves of the species were recovered. The most nearly complete valves were juveniles. Fragments of much larger individuals were also found. The elongated median groove on the dorsal valve was especially prominent on these fragments (Fig. 2.6).

LARVAL SHELL IDENTIFICATION

The term larval shell has been applied inconsistently in the literature, but we follow the usage of Freeman and Lundelius (1999) to indicate a shell that is secreted after embryogenesis, when the embryo forms, but before settlement when the larva transforms into an adult. Because lingulate brachiopod larvae feed and grow in the water column before settlement, the larval shell exhibits growth lines, but the embryonic shell does not. The coincidence of settlement with the commencement of postlarval shell growth was demonstrated in the modern lingulate *Glottidia* by Paine (1963), who collected larvae out of the water column in two field areas. In both locations the largest larvae collected were equivalent in size to the larval shell measured on postlarval shells of individuals collected from the same area.

One of the key characteristics used to differentiate larval and postlarval growth is a pronounced shell discontinuity (Freeman and Lundelius, 1999). Morphologic changes which occur in shell growth after settlement may also be used to distinguish the larval shell. Many lingulate species exhibit changes in shell ornamentation coinciding with the pronounced growth disruption. These changes in shell ornamentation may also be used as a criterion to distinguish the larval shell (Holmer, 1989). More indirectly, a change in the shape of the shell may indicate a shift of habitat from pelagic to benthic.

If a pronounced disruption in shell secretion is used as the sole criterion to distinguish the margin of the larval shell, then interpretation of this specimen is ambiguous. Strong growth

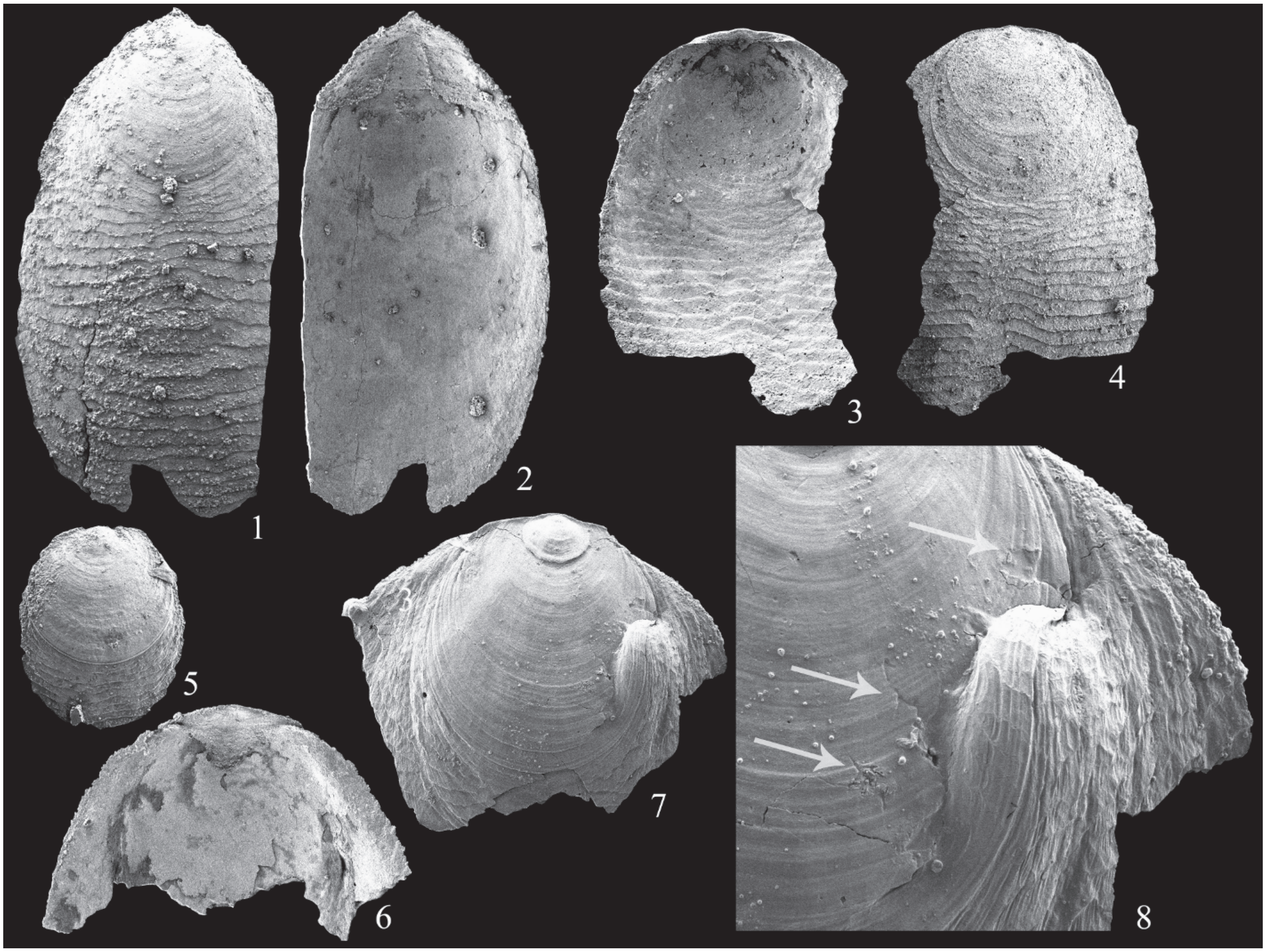

FIGURE 2—Lingulate brachiopod (genus and species indeterminate) from the Hellnmaria Member of the Notch Peak Formation, Millard County, Utah. *1, 2*, ventral valve exterior and interior from 75.6 m above the base of CKN section, ×38, USNM 542983; *3, 4*, dorsal valve interior and exterior from 278 m above the base of East Shoreline Butte section, ×38, USNM 542978; *5*, juvenile dorsal valve exterior, from 48.8 m above the base of CKN section, ×38, USNM 542981; *6*, dorsal valve fragment from 86.3 m above the base of CKN section, USNM 542980; *7, 8*, dorsal valve exterior exhibiting repair scar from 251.5 m above the base of ESB sections, ×38 and ×100, with arrows indicating three areas of shell damage, USNM 543037.

discontinuities are seen at about 200 μm, 900 μm, and 1 mm from the apex of the valve. The discontinuity at 900 μm appears to have occurred at the time of the injury. The growth discontinuity at 200 μm is extremely pronounced, but discontinuities at this position are not seen on other dorsal valves of the same species (Fig. 2.4, 2.5). A larval/postlarval shell boundary should be detected at approximately the same position on both the dorsal and ventral valve, and a strong discontinuity at approximately 200 μm on the ventral valve of this species (Fig. 2.1) is not detected.

Therefore, the discontinuity at 200 μm is interpreted to be unique to this individual, and the discontinuity at 1 mm is interpreted as the larval/postlarval shell boundary. The growth discontinuity that occurs on this specimen at 1 mm is bounded by a slightly raised rim with a groove-like depressed area to the anterior, a feature observed on all four illustrated exteriors (Fig. 2.1, 2.4, 2.5, 2.7), although the groove-like discontinuity occurs at varying distances from the apex, 600 μm (Fig. 2.5), 800 μm (Fig. 2.1), and 825 μm (Fig. 2.4).

The growth disruption at 1 mm coincides with both a change in ornamentation and a change in the shape of the shell from being almost equidimensional to more elongate. The elongate shape may be an adaptation to burrowing, which began after settlement of the shell to the substrate. The type of postlarval ornamentation seen on this brachiopod is interpreted as an adaptation to burrowing (Seilacher, 1973b; Savazzi, 1986; Mergl, 1997). This ornamentation supports the interpretation of this growth line as the larval/postlarval boundary, as well as a boundary between the shell material secreted during the planktic stage and the shell material secreted during the benthic (and possibly infaunal) stage. The modern lingulate *Glottidia* Dall, 1870, which also has a relatively large larval shell, develops its pedicle while still planktotrophic and immediately extends it and starts burrowing upon settlement (Paine, 1963).

The interpreted larval shell is approximately 850 μm at its widest point (900 μm, if the missing part of the larval shell is restored) and 1 mm long. This fits into the larger end of the range of larval shell sizes reported by Freeman and Lundelius (1999) for obolid brachiopod fossils and is smaller than the dimensions of the larval shell of the morphologically similar obolid *Westonia pinegensis* Popov and Gorjansky,

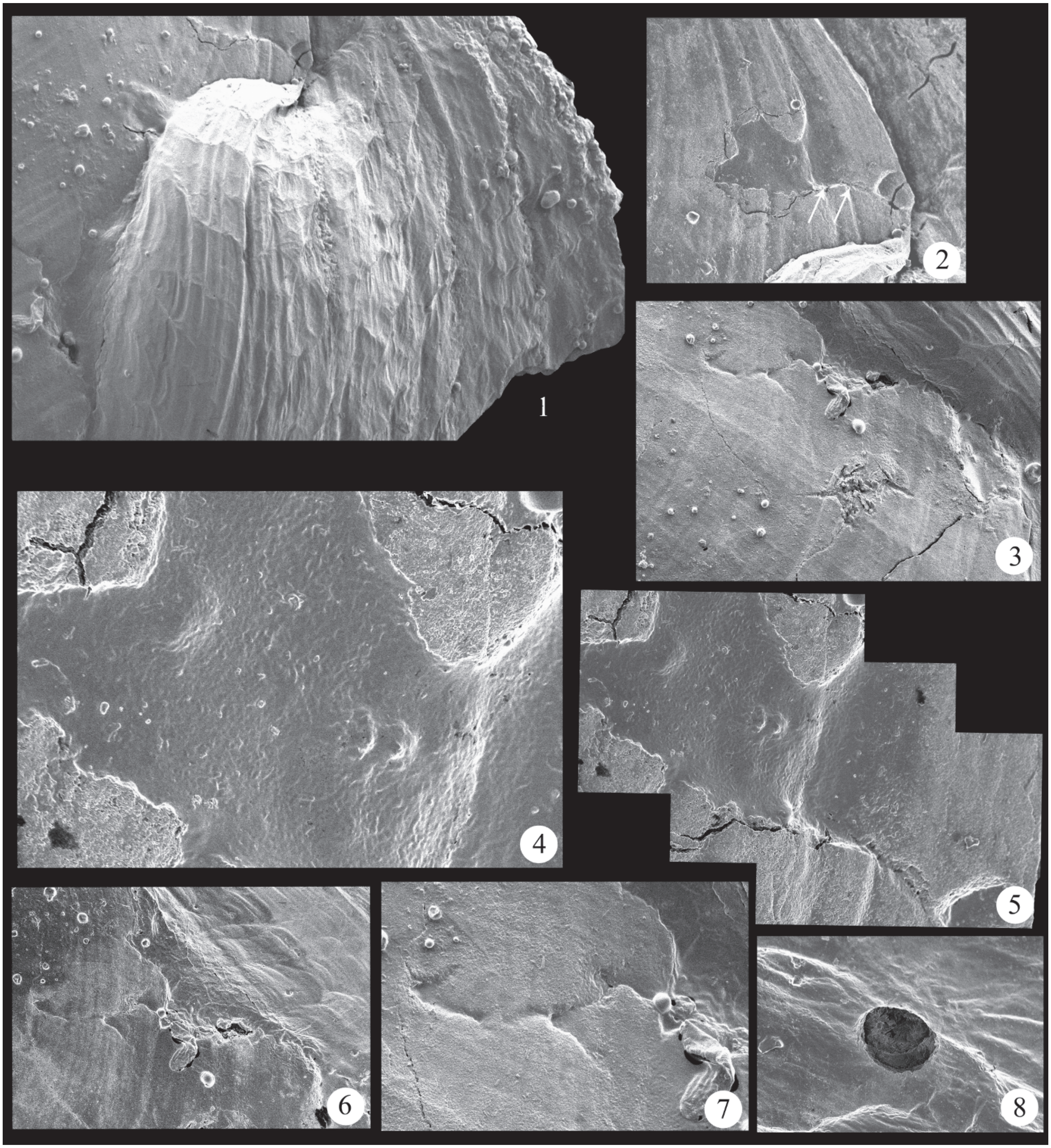

FIGURE 3—*1–8*, dorsal valve of a lingulate brachiopod from the Hellnmaria Member of the Notch Peak Formation, Millard County, Utah from 251.5 m above the base of the East Shoreline Butte section of Miller et al., 2003, USNM 543037. *1*, detail of repair scar shown in Figure *2.7* and *2.8*, ×219; *2*, *4*, *5*, details of area of scalloped-shaped area of shell damage indicated with top arrow in Figure 2.8, ×310, ×1660, ×860, respectively; *2,* left arrow indicates growth line which appears to match break along growth line on posterior side of the scalloped damaged shell area and right arrow indicates growth line which is not continuous on posterior side of scalloped damaged shell area; *3,* detail of shell damage indicated by lower two arrows in Figure *2.8*, ×195; *6–7,* detail of shell damage indicated by middle arrow in Figure *2.8*, ×214, ×430, respectively; *8*, detail of possible borehole seen in Figure *2.7*, ×610.

1994 (900 µm wide and 1.5 mm long). Other Early Paleozoic obolid species have been reported with relatively large larval shells, such as *Libecoviella divaricata* Brock and Holmer, 2004 (fig. 3K), with a width of 800 µm, and *Wahwahlingula*? *emanuelensis* Brock and Holmer, 2004 (fig. 4K) with a diameter of approximately 500 µm. The modern lingulate *Glottidia* has a larval shell as much as 1.1 mm in length (Paine, 1963).

CHARACTER OF INJURY AND REPAIR

The injury was apparently sustained during a late stage of larval growth, and the disruption in growth-line orientation indicates that abnormal secretion of the shell continued into postlarval growth until the missing area was filled in, at which time normal postlarval growth continued. At the time of the injury, the shell was 900 μm long and 825 μm wide, with approximately 5.5 percent of the area of the shell being removed by the injury.

The edge of the breakage is visible along the anterior one-third to one-half of the length of the break (Fig. 2.7, 2.8). Growth of new shell material over the broken edge obscures the break towards the posterior. The break is jagged, with some segments paralleling growth lines and some shorter segments cross-cutting them. The break extends along the margin of the shell for at least 550 μm, approximately one-fifth the circumference of the shell margin at the time of the injury. The maximum embayment of the broken margin was approximately 75 μm, measured perpendicular to the reconstructed original edge of the shell. This damage is similar to damage described as "scalloped" by Alexander (1986) for Ordovician rhynchonelliform brachiopods.

In addition to the visibly broken shell edge and fractures, three areas of additional shell damage are present. A section of outer shell layers appears to have flaked away directly posterior to the main repair scar (Figs. 2.7, 3.2, 3.4, 3.5), exposing a micro-pitted shell layer that is not observed anywhere else on the specimen (Fig. 3.4, 3.5). This damage could be post mortem, but the fact that the rest of the larval shell is well preserved and does not show this type of exfoliation supports the idea that this is an injury to the shell that was caused by the same shell-breaking event. The stepped lateral margin of the micro-pitted area is interpreted as a break in the edge of the shell that occurred at the same time as the larger break. Additionally, the edge of the shell posterior to this break appears to have broken off along a growth line (Fig. 3.2). Growth lines anterior to the chipped and broken area cannot be matched to growth lines posterior to that area (Fig. 3.2, right arrow). Another area (Fig. 3.3, 3.6, 3.7) consists of three indentations in the shell, each triangular in shape, and each with concave sides in outline. Each indention is oriented perpendicular to growth lines and deepens away from the shell margin, with a maximum width of approximately 25 μm. A similar notch occurs along the visibly broken edge. A third area (Fig. 3.3) consists of a series of scratches or shell excavations, some of which are V-shaped. It is unclear whether they were caused by the same event or might represent postmortem colonization of the shell by an encrusting organism.

The anterior end of the main broken area was healed with new layers of shell material added beneath the edge of the break, at an orientation that is nearly parallel to the pre-existing growth lines. At approximately one-third to one-half of the length of the break towards the posterior, the new growth was added over the edge of the break. This type of growth continues to the inferred posterior end of the primary break. To the posterior, the new growth is curved dorsally and cuts across pre-existing growth lines, forming a raised, swollen area on the shell.

INTERPRETED CAUSE OF REPAIRED INJURY

Possible causes of shell malformation include encrustation by an epibiont or a pathological condition. Pathologic causes seem to be eliminated by the eventual normal secretion of the postlarval shell. The visibly broken shell edge eliminates a reaction to an encrustation of the shell as a cause of the injury.

Damage to the edge of a shell could be caused by environmental conditions. Burrowing brachiopods often have small healed injuries to the anterior edge of the shell (Savazzi, 1986). Modern linguliform brachiopods are planktotrophic as larvae, a mode of life which would not appear to present an opportunity for accidental shell breakage under normal circumstances. Cambrian lingulate brachiopods are also assumed to have been planktotrophic, an interpretation supported by their generally widespread geographic distribution (Ushatinskaya, 2001), as well as by their relatively large larval shells (Freeman and Lundelius, 1999).

Although the planktic nature of lingulate brachiopod larvae appears to rule out routine environmental damage, it is possible that larvae could be swept into a hazardous shallow-water environment during a storm. Studies dealing with the effects of storms on shell fragmentation or breakage generally have focused on benthic organisms (e.g., Boyajian and Thayer, 1995; Cadée et al., 1997; Cadée, 1999). Seilacher (1973a) suggested that breakage due to pounding would generally occur along concentric and radial ornamentation and that rolling of a shell would be more likely to affect the edge. Boyajian and Thayer (1995) documented damage to infaunal clams exhumed during a storm. They found that larger clams, rather than smaller ones, were more likely to have small chips along the edge of the shell from pounding against other shells during transport, and these chips were concentrated along the posterior.

The breakage on this shell occurs along the anterior lateral edge which would be consistent with rolling rather than pounding. However, the extremely small size of the brachiopod at the time of the injury, as well as its planktic habitat, makes it unlikely that it would have been subjected to rolling during a storm. The seemingly non-random placement of what is interpreted to be multiple point injuries is also not suggestive of rolling. Rolling along the seafloor during a storm would probably cause abrasion as well as point injuries (Zuschin et al., 2003), and no abrasion of the edge of this specimen is observed. It seems likely that such a small organism (less than 1 mm at the time of the injury) would be cushioned by the viscosity of water from any type of accidental chipping or rolling.

Shell breakage by a durophagous predator is the most likely cause of this injury. The shape of the injury and the possibility that there are three to four areas of shell damage suggest a predator chipping away at the edge of the shell, possibly by grasping the shell with an appendage, because durophagous predation on a planktic organism in the water column would require some method of securing the prey. Criteria set forth for recognizing sublethal predation on trilobites versus injuries of uncertain origin (Babcock, 2003) can be applied to the interpretation of this specimen. The first criterion is that the injury occurs in an area that is unlikely to have been damaged accidentally. As outlined above, it is unlikely that a minute planktic organism would sustain accidental damage, although the possibility cannot be ruled out. Additionally, the injury should be developed over a fairly extensive area of the body. The area of missing shell on this specimen fits this criterion. The third aspect of this interpretation is the shape of the injury, which should be complex rather than simple, indicating deliberate rather than accidental breakage. If the areas of missing and damaged layers on the shell surface are accepted as being related to the shell break, then this injury does seem to have been made deliberately by a predator.

The attempt to identify a possible predator which would be capable of inflicting such an injury to this brachiopod is a highly speculative endeavor by nature and is particularly so because so few pelagic predators are known from the Late Cambrian. Most literature concerning Cambrian predation focuses on relatively large predators, but the small size of the injury and of the brachiopod itself at the time of attack makes it likely that the predator was quite small. Hansen et al. (1994) attempted to quantify predator/prey size ratios for a wide range of modern predatory planktic predators. Many of the studied groups were filter feeders, but of more active feeders ("'raptorial interceptors"), cladocerans had a predator/prey size ratio ranging from 1:1 to 17:1. Size in this case was calculated as dry weight, which was converted to carbon and then to body volume. This methodology cannot be directly applied to Cambrian predators, but it seems clear that many groups that were potentially pelagic predators were too large to have been likely predators of brachiopod larvae.

The shape and orientation of the three V-shaped indentations along the edge of the break (Fig. 3.3, 3.6, 3.7) seems especially consistent with a very small organism grasping and chipping at the edge of the brachiopod shell. Chaetognaths have been documented from the Cambrian (Vannier et al., 2007), and if protoconodonts are interpreted as the grasping spines of chaetognaths or an organism closely related to them (Szaniawski, 2002), there is an excellent record of their abundance throughout the Cambrian. Miller et al. (2003, figs. 4, 5) showed that the protoconodont *Phakelodus elongatus* (An et al., 1983) occurs through the stratigraphic interval where these brachiopods were collected. Modern pelagic chaetognaths are documented to prey on diverse small organisms in the water column with the prey generally in the range of 0.4–1.8 mm, with a mean of 0.8 mm for *Sagitta inflata* Grassi 1881 (Terazaki, 2000), consistent with the size range of the brachiopod larval shell.

The search for a potential predator need not focus on adult forms only. Hickman (2001) documented larval shell injuries and repair in modern gastropods when the breakage occurred in the presence of crustacean larvae. Perhaps larvae preyed on larvae in the Cambrian pelagic ecosystem as well. The Upper Cambrian orsten fauna preserves various small arthropods and arthropod-like organisms which may be pelagic larval forms, but it is not clear that they were predatory (e.g., Waloszek, 2003). Collette and Hagadorn (2010) documented Cambrian phyllocarids, a crustacean group which Signor and Brett (1984) considered to be potential durophages during the middle Paleozoic. It is not clear whether Cambrian phyllocarids, especially their larvae, had this capability.

If the injury to this specimen is accepted as direct fossil evidence of failed predation on a lingulate brachiopod larva, then a question is raised about the lack of previous reports of this type of repair scar in the fossil record. One issue may well have to do with the minute size of brachiopod larval shells and the difficulty in detecting this type of injury with light microscopy. The maximum dimension of most linguliform brachiopod larval shells is often much less than 1 mm (Freeman and Lundelius, 1999). This specimen falls in the range of the larger larval shells reported and the injury is quite pronounced, yet it is barely visible under the light microscope. Another issue is that this species had an unusually large larval shell and was perhaps more likely to be selected and attacked by a durophagous predator than smaller brachiopod larvae. The large size may have also increased its chances of surviving an attack, and thus exhibiting a repair scar. The many growth lines seen on the larval shell may also indicate that this brachiopod spent a prolonged time in the water column before settlement, perhaps increasing its chance of being exposed to pelagic predators.

Shell secretion in the malformed area includes transverse ornamentation characteristic of postlarval growth (Figs. 2.8, 3.1), although the brachiopod was apparently at a late larval stage at the time of injury. The pronounced growth disruption interpreted to mark the transition from larval to postlarval growth is as pronounced in the area undergoing regeneration as it is throughout the rest of the shell. The growth disruption is assumed to correlate to metamorphosis after the larva settled to the substrate. Apparently, changes in mantle tissue trigger the secretion of different shell material in the postlarval stage of life, and such changes may have taken place in the injured area before occurring in the rest of the mantle. This change in shell structure may indicate that the mantle tissue in the injured area regenerated as a somewhat different cell type. If so, this specimen is rare evidence of metaplasia (Purtilo, 1978; Babcock, 1993) in the fossil record.

In addition to the repaired shell breakage, this specimen also has a small (approximately 20 μm in diameter), nearly perfectly circular hole (Figs. 2.7, 3.8) that appears to be a borehole. The hole is located near the larval/post-larval boundary and is situated between two of the raised transverse lines of ornamentation that are characteristic of the post-larval shell. It is within the size range of similar holes interpreted by Robson and Pratt (2007) as non-predatory, although it differs in being a single hole, rather than the multiple holes observed on their specimens. A single hole is more often interpreted as predatory. The hole is smaller than the size range of borings for Late Cambrian acrotretids (50–200 μm) that Miller and Sundberg (1984) reported from Nevada, and it is within the small end of the range of sizes of Cambrian borings (10–240 μm) discussed by Conway Morris and Bengtson (1994). The latter authors noted that the majority of borings reported in Cambrian phosphatic-shelled brachiopods are in acrotretids, although approximately one-fourth of the specimens reported as perforated by Robson and Pratt (2007) were lingulids, with circular holes in both the lingulids and actrotretids ranging from 66–130 μm.

CONCLUSIONS

This unusual brachiopod specimen offers direct fossil evidence that at least some lingulate brachiopod larvae were able to survive shell breakage and to repair the broken shell. The shape and location of the shell breakage seems most consistent with durophagous predation as the cause of the injury. This conclusion suggests that durophagy was established within the pelagic realm by the Late Cambrian and that lingulate brachiopod larvae were under at least some measure of predation pressure, possibly from chaetognaths or from the larvae of other organisms. Such predation would indicate that the Cambrian pelagic ecosystem was more modern in its structure than previously documented. It also raises the question as to whether the interaction between larvae and their predators, previously undocumented in the fossil record, should be considered for other larval-shell bearing organisms as well as for the evolution of linguliform brachiopods.

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