Repaired injuries and shell form in some Palaeozoic pleurotomarioid gastropods

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Pleurotomarioid gastropods typically develop a spiral band called the selenizone in the outer whorl face of the shell that is formed by the closure of an open slit in the apertural margin. The slit and selenizone may be important in controlling the extent to which fractures induced by predatory attacks propagate across the whorl surface. A prominent selenizone can prevent fractures from traversing the entire whorl. Study of six Palaeozoic pleurotomarioid gastropod species with repaired shell injuries shows that repaired injuries are dependent on both the nature of the selenizone and shell form. The species can be divided into three morphological groups (turbiniform, trochiform and planispiral) and show a variety of selenizones with different degrees of prominence. Turbiniform shells show more repaired injuries than planispiral forms, indicating that species in the former group more often survive predatory attacks. The studied material is too sparse for meaningful statistical analysis, but individual case studies suggest that the combined influence of shell form and the nature of the selenizone can make the interpretation complex.

Key words: Gastropoda, Pleurotomarioidea, repaired injuries, shell form, selenizone, Palaeozoic.

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Introduction

The vetigastropod superfamily Pleurotomarioidea includes some of the first gastropods to appear in the fossil record; its members are first known from the Upper Cambrian (Knight et al. 1960; Tracey et al. 1993; Wagner 2002) and persist until the present day. Most described pleurotomarioid species are Palaeozoic in age (Hickman 1984), a time when pleurotomarioids enjoyed a high diversity and formed a prominent part of gastropod faunas worldwide. Pleurotomarioid gastropods display a pairing of internal organs, such as the bipectinate ctenidia, which has later been lost or reduced in most modern gastropod groups (Knight et al. 1960; Hickman 1984; Harasewych 2002) and thus they are generally considered to be "primitive".

Pleurotomarioids are characterised by the presence of a spiral band in the shell called the selenizone that is usually located near its periphery. The selenizone is generated when a slit of varying depth in the apertural margin closes at its adapical margin during shell growth. Traditionally, the slit is considered to be the locus of the exhalant water stream from the mantle cavity, with inhalant streams located on either side (Yonge 1947), but Voltzow et al. (2004) demonstrated that both inhalation and exhalation take place through the slit in two species of living Pleurotomarioidea. This peculiar emargination might be expected to adversely affect the resistance of the gastropod shell aperture to breakage by predation and other means by decreasing the strength of the apertural margin. Lindström (2003) recently discussed the influence of shell morphology of pleurotomarioids, and in particular the presence of the selenizone, on shell breakage patterns in two Carboniferous pleurotomarioids, recognising three main categories of repaired shell injuries.

Injuries to gastropod shells result from a variety of processes in the surrounding environment. Minor chipping of the outer lip can be caused by mode of life or result from life in a turbulent environment. Accidental damage, epibiont scars and epibiont forced changes of growth may also affect the gastropod shell (Bowsher 1955; Nielsen 1975; Savazzi 1991; Horný 1998; Cadée 1999; Alexander and Dietl 2003; Lindström and Peel 2003). It is difficult, particularly in fossil shells, to establish the exact cause of shell breakage but the majority of repaired shell injuries in both fossil and recent faunas are usually attributed to failed predatory attacks (Vermeij 1977, 1987; Zipser and Vermeij 1978; Signor and Brett 1984; Preston et al. 1996; Castell and Sweatman 1997; Ebbestad and Peel 1997; Lindström and Peel 1997, 2003; Dietl and Alexander 1998). Recent reviews of possible predatory groups in Palaeozoic marine environments are given by Brett and Walker (2002) and Brett (2003).

In this study, the distribution of repaired shell injuries relative to shell morphology and the selenizone is discussed in a number of Palaeozoic pleurotomarioid species, based on specimens found in museum collections and described in the literature. Comparisons are made with earlier studies of shell repair distribution in Carboniferous pleurotomarioids (Lindström 2003). The paucity of available material and uncertainties surrounding precise locality information do not allow

Table 1. Shell form, number of repaired specimens and age of the material.

Species	Shell form	Number of specimens with repairs/total number of specimens	Age	Locality
Baylea yvanii	turbiniform	1/4	Early Carboniferous	Belgium
Lophospira gothlandica	turbiniform	9/26	Early Silurian	Sweden
Arjamannia thraivensis	turbiniform	2/12	Late Ordovician	Scotland
Oehlertia gradata	trochiform	2/83	Late Silurian	Sweden
Crenilunula limata	trochiform	2/12	Late Silurian	Sweden
Porcellia woodwardii	planispiral	2/>30	Early Carboniferous	Belgium

meaningful statistical analysis, but some general observations can be made concerning the location of the injuries on the shell and the shape of the fractures relative to shell form.

It should be noted that the superfamily Pleurotomarioidea is employed in a traditional sense (Knight et al. 1960) and that later classifications place some of these described gastropods in other vetigastropodan superfamilies (e.g., Bandel 1993, Frýda 1997; Frýda and Rohr 2004). Indeed, Wagner (2002: 65) quite reasonably commented that use of Pleurotomarioidea in the Palaeozoic has no utility in classification, although his novel classification is controversial. Ponder and Lindberg (1996, 1997) presented a phylogeny of gastropods which recognised patellogastropods as the sister group (termed Eogastropoda) of all other gastropods (collectively termed Orthogastropoda), although recognition of this former group in the Palaeozic fossil record is highly speculative. Undoubted patellogastropods have been recognised in the Triassic (Hedegaard et al. 1997).

Institutional abbreviations.—BMNH, Natural History Museum, London, UK; SMNH, Swedish Museum of Natural History (Naturhistoriska riksmuseet), Stockholm, Sweden.

Material

The specimens in this study range in age from Ordovician to Carboniferous and are arranged into three distinct morphological groups: (a) turbiniform and relatively high spired; (b) trochiform; (c) planispiral. Turbiniform shells are typically higher than wide, and the base is convex and inflated; the spire may have a stepped or conical profile. Shell height in members of the trochiform group is approximately the same as shell width, or less, and the base is flattened rather than inflated. In planispiral shells the whorls are coiled within a single plane rather than the three dimensional coil of the other two groups, and shell width greatly exceeds shell height. All specimens preserve a selenizone but the original depth of the corresponding slit is not known. In some cases, a number of specimens of the individual species is available but, in the general absence of precise collecting information, such samples provide only a weak base for estimation of the frequency of injuries. We are unable to ascertain that specimens currently associated together in old museum collections were actually collected together. The data are summarised in Table 1.

Turbiniform pleurotomarioids.—Specimens of three species of high spired turbiniform pleurotomarioids are placed here: *Baylea yvanii* (Leveillé, 1835) from the Carboniferous of Belgium; *Lophospira gothlandica* Ulrich in Ulrich and Scofield, 1897 from the Silurian of Gotland, Sweden; *Arjamannia thraivensis* (Longstaff, 1924) from the Ordovician of Scotland.

A specimen (BMNH PG 1787) of *Baylea yvanii* (Leveillé, 1835) from the Lower Carboniferous of Tournai, Belgium, the only one of four in the collection with injuries, displays three events of shell breakage (Figs. $1A_1$–A_3, $2A_1$–A_3). It is well preserved, high spired and conspicuously gradate in outline. The upper whorl face is almost horizontal and the outer whorl face almost vertical in standard orientation, giving the shell a stepped appearance. Ornamentation consists of numerous spiral threads of varying thickness. Two of the repaired injuries affect the whole whorl face from suture to suture. The third injury seems to affect only the shell below the selenizone.

Lophospira gothlandica Ulrich in Ulrich and Scofield, 1897 from the Silurian of Gotland, Sweden, also has a gradate, turbinate form, reminiscent of *Baylea yvanii*. Prominent angulations occur at the periphery (carrying the selenizone) and at the junction between the outer whorl face and the base. The shell is crossed by faint growth lines. *Lophospira gothlandica* was originally described by Lindström (1884) from several localities and horizons within the Silurian of Gotland as *Pleurotomaria bicincta* (Hall, 1847) but Ulrich and Scofield (1897: 963) considered it to be quite distinct from *Murchisonia bicincta* Hall, 1847 from the Ordovician Trenton Limestone of New York State, USA, the type species of *Lophospira* Whitfield, 1886 (Knight 1941: 179). Twenty six specimens have been studied from the Slite Beds (Wenlock) at Slite, Gotland (SMNH Mo 16034–16035, Mo 27399–27411, 27412–27414, Mo 27437–27444) and nine of these show repaired injuries; it can not be assumed that these specimens form part of a single sample or association. While some specimens are only a couple of millimeters high, a typical specimen measures some 40 mm in height and 35 mm in width.

Most of the repaired injuries are located below the selenizone with no continuation discernible on the upper whorl surface, although three more severe injuries traverse the entire whorl surface. The distribution of injuries in *Lophospira gothlandica* is much like that described in the Carboniferous *Worthenia tabulata* (Conrad, 1835) by Lindström (2003); most injuries in the sample are found below the selenizone, although some major injuries traverse the whole whorl surface (Figs. 1D–F, 2D–F).

Arjamannia thraivensis (Longstaff, 1924) from the Late Ordovician Drummock Group of Scotland has a turbiniform shell, with a globose base, although the conical spire gives it a trochiform appearance. It is still relatively high spired, some 15–20 mm tall, with the selenizone situated at the prominent angulation separating the upper whorl face from the convex base (Figs. 1B, C, 2B, C). Ornamentation consists of growth lines and spiral threads which form a reticulation on the base. Two specimens from the collection of the Natural History Museum display one repaired injury each; both injuries are situated below the selenizone and stretch all the way down to the umbilicus. These injuries are reminiscent of some injuries below the selenizone seen in *Glabrocingulum grayvillense* (Norwood and Pratten, 1855), as described by (Lindström 2003), a species which has a rounded base similar to that seen in *Arjamannia*.

The specimen of *Arjamannia thraivensis* illustrated as Fig. 1B (BMNH G 25407) is the holotype of *Lophospira thraivensis* Longstaff, 1924 that was referred to the new genus *Arjamannia* by Peel (1975). The specimen was illustrated by Longstaff (1924: pl. 33: 5) from the late Ordovician Starfish Bed, South Threave Formation, Drummock Group at Thraive Glen, Girvan, Ayrshire, Scotland. BMNH G 46232 (Fig. 1C) is from the same locality. Ten other associated fragmentary specimens, usually preserved as partial external moulds, show no preserved trace of repaired injuries.

Trochiform pleurotomarioids.—The turbiniform pleurotomarioids grade morphologically into trochiform species with a relatively flattened base. In these, shell height is typically the same or less than shell width. Repaired injuries are described in *Crenilunula limata* (Lindström, 1884) and *Oehlertia gradata* (Lindström, 1884), both from the Silurian of Gotland, Sweden.

The most high spired of the two species is *Oehlertia gradata*, which is typically trochiform, with a flat base and a conical spire. Growth lines provide the only ornamentation. *Pleurotomaria gradata* Lindström, 1884 was tentatively assigned to *Clathrospira* Ulrich and Scofield, 1897 by Ulrich and Scofield (1897: 1005) but the nature of the selenizone supports assignment to *Oehlertia* Perner, 1907, as proposed by Wagner (2002). Eighty three specimens, generally quite small, are available from different localitites in Gotland; Lye, Sandarve kulle, Etelhem: Tänglingshällar (SMNH Mo 28163–28179, Mo 28081–28096, 28097–28098, Mo 28185–28190, Mo 28034–28063, 28064–28076). The specimens are often incomplete but the ornamentation is well preserved. The two specimens showing repaired injuries are figured (Figs. 1G, H, 2G, H), one with a major injury traversing the whole whorl margin. In the second specimen an injury affects the upper whorl face above the selenizone, but the shell is broken and the continuation of the injury is not seen. The injury follows the suture with the previous whorl for nearly 1/3 of a whorl before the shell is broken, indicating a major fracture, with a large part of shell broken away.

The second species, *Crenilunula limata*, is relatively low spired with the selenizone bordered by a small, lamellose, fringe on each side. The sample of 12 specimens (SMNH Mo 28451–28462) contains two examples showing repaired injuries (Figs. 1I, J, 2I, J). Both injuries are clearly visible on the upper whorl face above the selenizone, but disturbance of the selenizone makes it very likely that they continued onto the umbilical surface. Unfortunately, the umbilical surface is not preserved in any of the available specimens.

Crenilunula limata was originally described by Lindström (1884) as *Pleurotomaria limata* (Lindström 1884: 114–115, pl. 10: 2–17). Ulrich and Scofield (1897: 955) in error considered *P. limata* to be the type species of *Mourlonia* Koninck, 1883, but Knight (1945) designated it type species of his new genus *Crenilunula*. *Crenilunula* was assigned to the pleurotomarioidean family Euomphalopteridae by Knight et al. (1960) but Linsley et al. (1978) disbanded that family, excluding the nominate genus from the Pleurotomarioidea and transferring *Crenilunula* to the pleurotomarioidean family Luciellidae. Wagner (2002) considered *Crenilunula* to be a junior subjective synonym of *Prosolarium* Perner, 1907.

Planispiral pleurotomarioids.—Repaired injuries are described in *Porcellia woodwardii* (Sowerby, 1829) from the Lower Carboniferous of Belgium. While traditionally regarded as a pleurotomarioid (Knight et al. 1960), the genus was placed within the superfamily Cirroidea by Bandel (1993) and Frýda (1997) and within the Porcellioidea by Frýda (2004). Frýda (2004) placed *Porcellia woodwardii* in a new genus, *Martinidiscus*, although the cited type species is not a binomial and hence not valid (see discussion in Batten 1966).

Two specimens of *Porcellia woodwardii* (Sowerby, 1829) from the Lower Carboniferous of Belgium, show repaired shell injuries (BMNH PG 1854, PG 1855). One specimen shows an injury that cuts almost straight across the whorl below the selenizone (Figs. 1L, 2L). The shell directly above the selenizone is broken away so any continuation of the injury cannot be seen. The other specimen shows several injuries, with one major fracture traversing the whorl immediately prior to the aperture and a second one affecting only the whorl below the selenizone (Figs. $1K_1$, K_2, $2K_1$, K_2). The available specimens are small for the species, only around 13–15 mm in diameter. Specimens figured by Koninck (1883) are about twice this size, while Peel (1986) described a specimen some 43 mm in diameter. The widely phaneromphalous specimens appear to be almost bilaterally symmetrical, although the apical and umbilical sides are easily recognised.

Porcellia woodwardii differs from other species assigned to the genus in lacking tubercles along the upper and lower


A1
A3
B
C
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E
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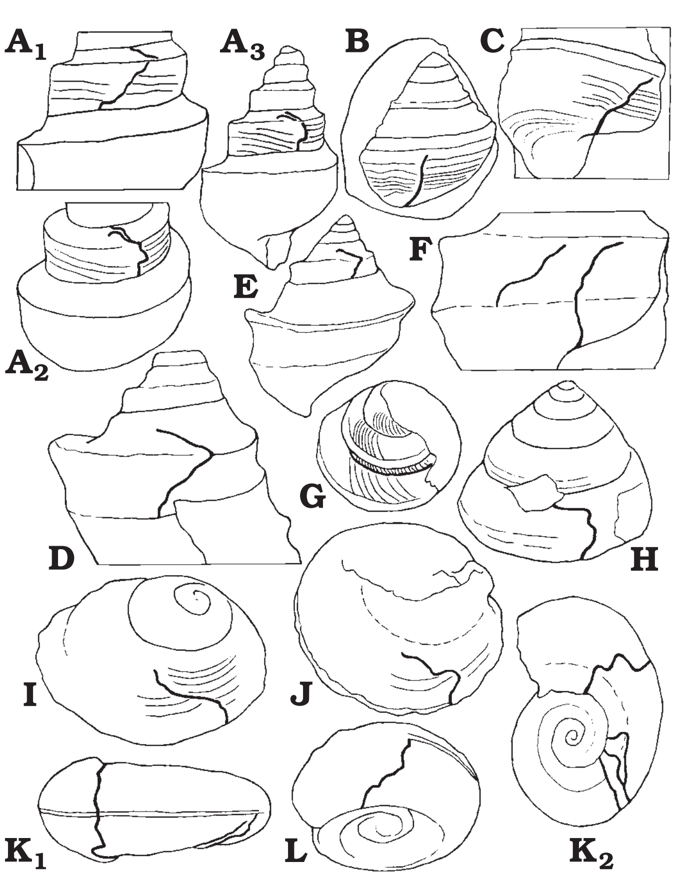

Fig. 2. Schematic drawing of Fig. 1 as a guide to emphasize the location of repaired injuries, here shown in thicker lines. For explanation see Fig. 1 captions and the text. **A**–**F**. Turbiniform shells. **G**–**J**. Trochiform shells. **K**, **L**. Planispiral shells.

surfaces of the whorl (Peel 1986). It shows a reticulate ornamentation from the interference pattern of spiral and collabral lines, and has an extremely narrow selenizone. Several tens of specimens of a strongly tuberculate *Porcellia* species from the Carboniferous of Belgium are also present in the collections of the Natural History Museum, but repaired injuries have not been observed.

Discussion

The morphology of a shell strongly influences its mechanical response to breaking agencies (Vermeij 1977, 1982; Bertness and Cunningham 1981; Savazzi 1991; Alexander and Dietl 2003; Brett 2003; Lindström 2003; Lindström and Peel 2003). Vermeij (1977, 1987) considered that traits such as a thickened outer lip, prominent external sculpture and the development of a narrow aperture evolved within gastropods as means to resist predatory attacks by increasing shell strength. The morphology of a shell, however, may also give clues as to how a shell will break when subjected to attacks. Shells of several Palaeozoic gastropod species displaying repaired injuries are divided in this study into three generalised morphological groups: turbiniform (e.g., *Baylea yvanii*), trochiform (e.g., *Oehlertia gradata*), and planispiral (e.g., *Porcellia woodwardii*). In addition to their overall morphology, these shells also display other morphological traits that might influence shell breaking patterns, such as a strengthened selenizone (e.g., *Arjamannia thraivensis*) or prominent angulations (e.g., *Lophospira gothlandica*). It is recognised that most forms of prominent ornamentation will probably also hamper breakage.

Vermeij (1982) recognised that the turbinate shell form better withstands shell crushing than a planispiral shell. This recognition seems to be confirmed by examination of the museum collections, as a whole, which led to selection of the present material, although this is a subjective observation. More repaired injuries do appear to be present in turbiniform shells than in the available planispiral ones, with the increased abundance of repaired injuries reflecting survival of attacks. However, one of two specimens of *Porcellia woodwardii* figured here (Figs. $1K_1$, K_2, $2K_1$, K_2) atypically preserves several repaired injuries. Schindel et al. (1982) showed that the frequency of shell repair increases with increasing shell height, which means that gastropods with a higher spired shell have a higher survival rate. Slowly expanding planispiral shells such as *Porcellia woodwardii* are considered to be more easily crushed than other pleurotomarioids since forces can be applied to the two opposing

← Fig. 1. Repaired injuries in Palaeozoic pleurotomarioid gastropods. Compare with Fig. 2. **A**. *Baylea yvanii* (Leveillé, 1835), BMNH PG 1787, from the Lower Carboniferous of Tournai, Belgium. A_1. Close up of major repaired shell injury on the penultimate whorl, traversing the whorl from suture to suture. A_2. Close up of a second similar repaired injury on the penultimate whorl. A_3. Lateral view of the same injury visible in (A_2). **B**, **C**. *Arjamannia thraivensis* (Longstaff, 1924), from the Late Ordovician Starfish Bed, South Threave Formation, Drummock Group at Thraive Glen, Girvan, Ayrshire, Scotland. **B**. BMNH G 25407 with a repaired shell injury below the selenizone on the last whorl. **C**. BMNH G 46232 with an injury almost identical to the previous specimen. **D**–**F**. *Lophospira gothlandica* Ulrich in Ulrich and Scofield, 1897, from the Silurian of Gotland, Sweden. **D**. SMNH Mo 27438. Close up of repaired injury. The injury is visible on both sides of the selenizone. **E**. SMNH Mo 160535. Lateral view of specimen with a major repaired injury on the penultimate whorl. **F**. SMNH Mo 27440. Close up of lower whorl surafce of last whorl showing two shell injuries only affecting the area below the selenizone. **G**, **H**. *Oehlertia gradata* (Lindström, 1884) from the Silurian of Gotland, Sweden. **G**. SMNH Mo 28052, small specimen with an injury visible along the suture of the last whorl; only the part above the selenizone is preserved. **H**. SMNH Mo 28185, with a major injury traversing from the suture to the umbilicus. **I**, **J**. *Crenilunula limata* (Lindström, 1884) from the Silurian of Gotland, Sweden. **I**. SMNH Mo 28456, shows a repaired injury above the selenizone. The shell below the selenizone is not preserved. **J**. SMNH Mo 28451 with a similar injury as figured in I, only visible above the selenizone. **K**, **L**. *Porcellia woodwardii* (Sowerby, 1829), from the Lower Carboniferous of Belgium. **K**. BMNH PG 1854. K_1. Lateral view with a major injury traversing the whole whorl. K_2. Umbilical view of the same specimen with three occasions of shell injury close to each other, and with the injury figured in (K_1) near the aperture. **L**. BMNH PG 1855. Oblique lateral view showing a repaired injury below the selenizone. The shell above the selenizone is not well preserved. Scale bars 50 mm.

sides simultaneously. Fewer shells survive and the incidence of repaired injuries is therefore low. However, peeling back of the shell aperture by predators, as distinct from crushing, may produce a different response depending on how the leverage to the apertural margin is applied or how the gastropod is manipulated during the attack by the predator. Schindel et al. (1982) noted that planispiral straparollid (euomphaloidean) gastropods with a low rate of whorl expansion showed a higher shell repair frequency than accompanying, more rapidly expanding, planispiral bellerophontoideans. The latter are globose, with narrow umbilici, and a quite different mode of life to the probably sedentary straparollids. Bellerophontoideans also possess a selenizone, which is lacking in straparollids.

The most common type of injury in planispiral pleurotomarioidean shells is a major fracture that traverses the entire whorl surface, as seen in *Porcellia woodwardii* (Figs. $1K_1$, K_2, $2K_1$, K_2) where a piece of the last whorl has been broken away. While *Crenilunula limata* is trochiform, its low spired and lenticular shell is almost planispiral and repaired injuries also seem to have traversed the entire whorl. However, the umbilical surface is not well preserved in the two specimens of *C. limata* with repaired injuries (Figs. 1I, J, 2I, J).

While shell form can dictate the effectiveness of overall resistance to breakage, other shell features may influence the ease with which fractures are propagated. The characteristic pleurotomarioid slit and selenizone are obvious candidates. The pleurotomarioid selenizone shows a variety of forms, with its surface carrying tubercles, lunulae and spiral striations, and its margins delimited by spiral threads of varying degrees of expression. The generally prominent band divides the shell surface into two halves, above and below the selenizone, and its ability to stop the propagation of fractures has been noted by Lindström (2003). In describing the Carboniferous pleurotomarioids *Worthenia tabulata* and *Glabrocingulum grayvillense*, Lindström (2003) observed that injuries were commonly restricted to only one side of the selenizone, either to the upper whorl surface, or to the lower whorl surface. Major injuries, however, crossed over the selenizone and affected the whole whorl sruface.

The two figured specimens of *Arjamannia thraivensis* (Figs. 1B, C, 2B, C) show repaired injuries only affecting the shell surface below the selenizone. They resemble the Carboniferous species described by Lindström (2003) in shell form and ornamentation, and the repaired injuries are closely similar to repaired injuries in *W. tabulata* and *G. grayvillense* (Lindström 2003). Thus, the more prominent selenizone of *A. thraivensis* also seems to have limited the propagation of fractures.

The selenizone in *Baylea yvanii* has a different form. While lying on the outer edge of the upper whorl face, it is not prominent and blends in among the spiral threads ornamenting the rest of the shell. *Lophospira gothlandica* has a selenizone located on a prominent angulation, but the selenizone itself is inconspicuous in comparison with the angulation. In detail, it resembles the selenizone of *A. thraivensis*, with a median keel and bordering spiral threads but *A. thraivensis* shows stronger delimitation of the selenizone from the whorl. The prominent angulations in both *B. yvanii* and *L. gothlandica* might be expected to inhibit propagation of fractures since they increase the strength of the apertural margin and whorl. However, the limited material available does not support this supposition. Both species show major injuries that cross over the selenizone-bearing angulation (Figs. $1A_1$–A_3, D, E, $2A_1$–A_3, D, E), together with injuries confined to the lower whorl surface (in *L. gothlandica* Fig. 1F, in *B. yvanii* not figured). It is possible that the combination of a prominent strengthening angulation and a weakly expressed selenizone nullifies the limiting effect of the selenizone alone to propagation of fractures.

The trochiform *Oehlertia gradata* has a well-defined selenizone bordered by carinae, but *Crenilunula limata* has lamellar lunulae between marginal frills. The last formed lamella delimits an exhalant notch and, strictly speaking, a selenizone is not developed. In these species the selenizone does not appear to have had a limiting effect on the propagation of fractures, although preservation in critical areas of the shell is poor. However, in a monograph on Early Devonian gastropods from China, Pan and Cook (2003: fig. 4.7) figured a specimen of a trochiform gastropod with a concave base, *Zhusilengospira turbiniformis*, with a major repaired injury on the last preserved whorl. Batten (1966: pl. 4: 3) illustrated a specimen of the trochiform *Spiroscala intricata* from the Lower Carboniferous of England with a fracture on the lower whorl surface apparently terminating at the selenizone.

Porcellia woodwardii has a deep slit and a narrow, sunken, selenizone without bordering ridges. Weak spiral and collabral threads produce a tuberculate, reticulate, ornamentation. The planispiral shell form is susceptible to crushing but one specimen of *P. woodwardii* still shows repaired injuries only affecting the shell below the selenizone (Figs. $1K_1$, K_2, $2K_1$, K_2). Batten (1989: pl. 5: 9) figured a planispiral pleurotomarioid, *Ambozone dictyonema*, with an injury below the selenizone, and *Ambozone* has prominent spiral and collabral ornamentation which forms nodes at intersections on the upper side of the shell. This strong ornament may have strengthened the shell on the upper side above the selenizone. In *P. woodwardii*, the depth of the open slit may have proved the limiting factor. As noted above, repaired injuries have not been observed in strongly tuberculate *Porcellia* from the Carboniferous of Belgium in the collections of the Natural History Museum, London.

The possible influence of the selenizone in controlling fractures is also evident in specimens figured in the literature. A specimen of *Ruedemannia* sp. from the Ordovician of Sweden figured by Ebbestad and Peel (1997) shows a minor repaired injury below the selenizone. Horný (1997) figured an undetermined pleurotomarioid from the Ordovician of the Czech Republic showing three separate repaired injuries. Two of them were traumatic events, where large parts of the shell were peeled away, but the third only affected the lower whorl surface below the selenizone. The difference between these two records concerns shell ornamentation; *Ruedemannia* has prominent spiral threads and collabral growth lines, and the selenizone is clearly visible. The Czech specimen has a smooth, rounded shell with no ornamentation other than fine growth lines. It has a short emargination which actually becomes even shallower in the repaired shell area (Horný 1997: fig. 13).

Batten (1989: pl. 4: 6, 9, 14, 15, 18, pl. 5: 2, 3, 9) figured several Permian turbiniform pleurotomarioids from the USA showing injuries traversing the whole whorl surface or restricted to below the selenizone. In a study of Middle Pennsylvanian gastropods from New Mexico, Kues and Batten (2001: figs. 6.15, 6.21, 6.23, 6.24) illustrated several pleurotomarioids with repaired injuries. One specimen of *Glabrocingulum* (*Ananias*) *talpaensis* shows a major repaired injury across the whole whorl (Kues and Batten 2001: fig. 6.15). Three different specimens of *Worthenia speciosa* show a repaired injury below the selenizone (fig. 6.21), a major injury across the entire whorl (fig. 6.24) and an unusual semicircular injury situated just above the selenizone (fig. 6.23) of a type also seen in *Glabrocingulum grayvillense* and *Worthenia tabulata* (Lindström 2003). Small (height about 10 mm) Carboniferous pleurotomarioids figured by Hoare et al. (1997) include *Abylea*, a turbiniform and rather high spired species with a relatively broad selenizone. Figured repaired injuries either cross the whole whorl or occur only below the selenizone (Hoare et al. 1997: figs. 3.3, 3.14, 3.17, 3.20). A small specimen of *Worthenia parvula* (Hoare et al. 1997: fig. 4.13) has a repaired injury below the selenizone. Size of shell does not seem to have influenced the limiting function of the selenizone, since these tiny specimens of *Abylea* show exactly the same types of injuries as are found in much larger specimens of *L. gothlandica* and *B. yvanii*. Kaim (2004: fig. $136B_2$) observed a high number of attempted attacks on the shells of Late Jurrassic pleurotomarioids from the Russian Platform.

The three categories of repaired injuries recognised by Lindström (2003) were considered to be mainly dependent on the influence of the slit/selenizone, but the present study indicates that shell form also plays a contributory role. However, the extent and form of fractures is also influenced by prominent features of shell ornamentation, and the interaction between these three properties can be complex. Injuries are usually located either above or below the selenizone, but severe injuries cross the entire whorl face and are unaffected by the presence of the selenizone or prominent angulations. It should be stressed, however, that these three morphological characters are only elements in the complex interaction between predators and their prey. Mode of life, shell orientation, environment and the nature and abundance of the predators themselves are certainly key factors steering fracture morphology and distribution.

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