Shell repair and shell form in Jurassic pleurotomarioid gastropods from England

ANNA LINDSTRÖM & JOHN S. PEEL

Specimens of the vetigastropods *Pleurotomaria* Defrance, 1826 and *Pyrgotrochus* Fischer, 1885, from the Jurassic of England were separated into three morphological groups and surveyed for traces of shell repair. Two measures of shell repair frequencies were calculated: 1) ratio of the number of specimens with at least one repaired injury to the total number of specimens; 2) ratio of the total number of injuries to the total number of specimens in the sample. The *Pleurotomaria anglica* (Sowerby, 1818) group containing large, high spired trochiform shells showed the lowest repair frequency with 28.8% and 75.3%, respectively. The shell repair frequency in the low spired trochiform *Pleurotomaria actinomphala* Deslongchamps, 1848 group was 44.4% and 81.0%, respectively. Lastly, the *Pyrgotrochus* group containing conoidal trochiform shells showed the highest frequency calculated by both methods, 46.2% and 92.3%. Three types of injuries were found in all morphological groups, although in different proportions. Breaks across the entire whorl constitute the majority of repaired injuries in shells of the *Pleurotomaria anglica* group; in the *P. actinomphala* group the figure is about 50% and in *Pyrgotrochus* only 35%. The coniodal shell form and a deep slit in the aperture margin probably proved to be a defensive strategy for *Pyrgotrochus*, with many fractures terminating at the margin of the slit, whereas *Pleurotomaria anglica* was protected by its size. • Key words: Pleurotomarioidea, Gastropoda, shell repair, slit/selenizone, Jurassic.

LINDSTRÖM, A. & PEEL, J.S. 2010. Shell repair and shell form in Jurassic pleurotomarioid gastropods from England. *Bulletin of Geosciences 85(4)*, 541–550 (2 figures, 1 table). Czech Geological Survey, Prague. ISSN 1214-1119. Manuscript received June 21, 2010; accepted in revised form August 25, 2010; published online October 20, 2010; issued December 20, 2010.

Anna Lindström, Department of Earth Sciences (Palaeobiology), Uppsala University, Villavägen 16, SE-752 36 Uppsala, Sweden; current address: Naturhistoriska riksmuseet, Box 50007, SE-104 05 Stockholm, Sweden; anna.lindstrom@nrm.se • John S. Peel (corresponding author), Department of Earth Sciences (Palaeobiology), Uppsala University, Villavägen 16, SE-752 36 Uppsala, Sweden; john.peel@pal.uu.se

The gastropod shell accumulates a record of most of the life history of the individual animal since interaction with its environment is often preserved in the calcareous shell as scars and repaired injuries. Such injuries are common in fossil and recent gastropod shells and can be interpreted in the ancient world by comparison to the present day (Vermeij 1987, Alexander & Dietl 2003). Injuries to the shell may be caused by a variety of agents. Life in a turbulent environment may cause minor chipping of the apertural margin, while accidental damage and the effects of epibionts may also cause injuries or malformation (Bowsher 1955, Nielsen 1975, Savazzi 1991, Horný 1998, Alexander & Dietl 2003, Lindström & Peel 2003). Most fractures, however, are attributed to the action of failed predatory attacks, where the snail survived to repair its shell. This is certainly true in Recent faunas where predator-prey interaction can be studied live (*e.g.* Shoup 1968, Zipser & Vermeij 1978, Elner & Raffaelli 1980, Bertness & Cunningham 1981, Preston *et al*. 1996, Castell & Sweatman 1997). It is also believed to be true in fossil faunas even if the identity of the predator often remains obscure (Vermeij 1977, 1987; Signor & Brett 1984; Ebbestad & Peel 1997; Lindström & Peel 1997, 2003, 2005; Ebbestad & Stott 2008; Ebbestad *et al*. 2009). However, a timely reminder to consider the mode of life of the animal when interpreting the cause of shell injuries is provided by Alexander & Dietl (2005) in their analysis of non-predatory shell damage in deep-burrowing bivalves (see also Checa 1993).

In this study we examine repaired shell injuries within three morphological groups of pleurotomarioid gastropods from the Jurassic of England, as a sequel to an earlier study of related Palaeozoic gastropods (Lindström & Peel 2005). Pleurotomarioid gastropods have a geological record extending from the upper Cambrian to the present day (Knight *et al.* 1960, Tracey *et al.* 1993); their current classification is reviewed by Bouchet *et al.* (2005). They enjoyed a high diversity during the Palaeozoic, with approximately 1500 described species (Hickman 1984), but after the Permian extinction event their diversity decreased to just a few genera during the Mesozoic. Amongst these is the eponymous *Pleurotomaria* Defrance, 1826 which, despite many published records to the contrary, is not known from either the Palaeozoic or modern seas. About 30 species of pleurotomarioids live in present day oceans at depths of several hundred metres (Anseeuw & Goto 1996, Harasewych 2002, Anseeuw & Poppe 2005), but it is evident that Palaeozoic and Mesozoic pleurotomarioids inhabited a broad range of shallow marine environments.

Pleurotomarioid gastropods have a characteristic v-shaped sinus or slit in the aperture margin like the isostrophically coiled Palaeozoic–earliest Mesozoic bellerophontiform gastropods (*cf.* Ebbestad *et al.* 2009). The slit is usually considered to be the point of exit of the exhalant water current from the mantle cavity (Yonge 1947, Knight 1952) but it may also be the location for the inhalant water current in at least some living species (Voltzow *et al.* 2004). This observation contradicts the general assumption that separate inhalant currents are present in pleurotomarioid gastropods which have paired gills, and that these currents unite prior to expulsion medially. It is uncertain, however, if the important observation of Voltzow *et al.* (2004) can be applied uncritically to ancient pleurotomarioids living in other environments. In bellerophontoids, at least, the presence of well-developed dorso-lateral emarginations is consistent with separation of inhalant currents (Knight 1952, Peel 1974).

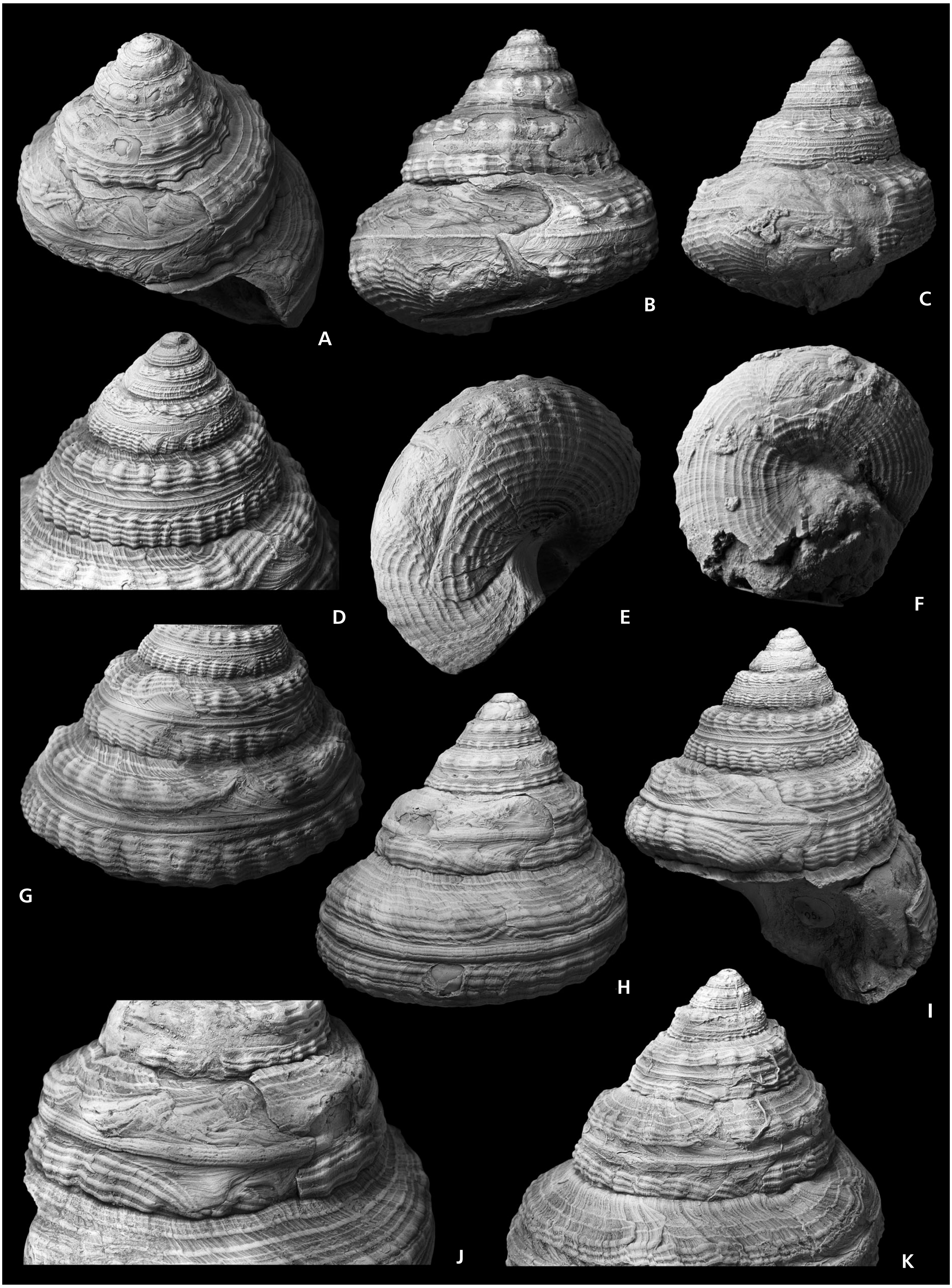
Whatever its function, the emargination in the apertural margin of pleurotomarioids might be expected to negatively affect the resistance of the gastropod shell to breakage by predation and other means by decreasing shell strength in the apertural region, particularily if the slit is deep. Lindström (2003) studied two well known species from North America, *Worthenia tabulata* (Conrad, 1835) and *Glabrocingulum grayvillense* (Norwood & Pratten, 1855), focusing on the relation between the repaired injuries and slit length. The frequency of shell repair was much higher in the form with a short slit, *Worthenia tabulata,* than in *Glabrocingulum grayvillense* with a longer slit, contrary to what might be expected. It is likely, however, that *Glabrocingulum* succumbed more easily to predatory attacks, leaving fewer individuals to repair the broken shell. In contrast, more specimens of *Worthenia* survived attacks, with the result that shell repairs are more frequent.

Our study discusses the location of the repaired injuries in the Jurassic pleurotomarioideans relative to shell form and the slit in the apertural margin and compares the frequency of repaired injuries with shell repair frequencies in the two Carboniferous species described by Lindström (2003). We examine the prediction by Vermeij (1977, 1987) that the frequency of shell repairs increases with time. The Jurassic pleurotomarioid gastropods retain the same general shell morphology (*i.e.* trochiform with a slit) as their Palaeozoic relatives, making them well suited for study of the form and abundance of shell repairs with time.

Material

This study is based on Jurassic pleurotomarioid gastropods within the collections of the Natural History Museum, London, U.K. While these collections give access to well preserved specimens suitable for the study of repaired shell injuries, they provide no information concerning the abundance of specimens with shell repair on outcrop. Given the diverse origins, ages and taxonomy of the specimens, it is not meaningful to recognize size categories within the available material, although it is acknowledged that such information provides an invaluable tool to the analysis of predation within individual taxa (Ebbestad & Stott 2008). Thus, all numerical observations are based solely on the specimens within the museum collections. On account of the scarcity of material the specimens are grouped into three arbitrary morphological categories, each containing a number of species, with full awareness that specimens from a variety of stratigraphic horizons and environmental settings are placed together (*cf.* Ebbestad *et al.* 2009):

Figure 1. Jurassic pleurotomarioid gastropods from England. • A, B, E – *Pleurotomaria* sp., BMNH G 16631, Lower Lias, Honeybourne, Worcester, × 1. A – oblique apical view showing a major repaired injury on last whorl. B, E – lateral and oblique umbilical view of another major repaired injury on last whorl. • C, F – *Pleurotomaria* sp., BMNH G 22552, Middle Lias, Day's Shell Bed, Margaritus Zone, Stokesi sub-zone, 200–300 yds E of Seatown, Ridge Cliff, Dorset. C – lateral view of a major repaired injury on last whorl, × 1.8. F – umbilical view of the same injury shown in C, × 2. • D, G, I – *Pleurotomaria* sp., BMNH G 10542, Lower Lias, Bengeworth, Gloucestershire. D – oblique apical view with two repaired whole shell injuries right after one another. At the lower right corner another repaired injury is visible, × 1.4. G – lateral view of the lower whorls with four instances of repaired shell damage visible. On the last whorl there is a repaired injury affecting only the shell above the selenizone. On the whorl above there are two injuries; the one to the left is clearly seen above the selenizone with a possible continuation below (also figured in D). The one to the right is an injury below the selenizone with a small portion of shell above the selenizone broken away at the same time. On the uppermost whorl in the photo a repaired injury is visible only affecting the shell below the selenizone, × 1. I – lateral view with a major repaired injury on last whorl, × 0.8. • H, J – *Pleurotomaria anglica* (Sowerby, 1818). BMNH G 632b, Lower Lias, Gloucestershire. H – close up of penultimate whorl with a major repaired injury affecting the whole whorl. In the newly formed shell after the injury a repaired injury is visible below the selenizone, × 1. J – lateral view with another major repaired injury on the penultimate whorl. An injury affecting only the shell above the selenizone is visible on the last whorl. An injury affecting the whole whorl is visible near the apex, × 0.6. • K – *Pleurotomaria anglica* (Sowerby, 1818). BMNH G 632a, Lower Lias, Gloucestershire. Lateral view of apical part showing two smaller scallops close to each other on the last whorl above the selenizone. On the whorl above two repaired injuries are visible below the selenizone and one above the selenizone, × 0.8.


A
B
C
D
E
F
G
H
I
J
K

(1) the *Pleurotomaria anglica* (Sowerby, 1818) group contains rather large high spired trochiform shells, where height and width are typically equal (see Fig. 1); (2) the *Pleurotomaria actinomphala* Deslongchamps, 1848 group consists of less high spired trochiform shells (height less than width), often with prominent tubercles (see Fig. 2A, B, H); (3) the *Pyrgotrochus* Fischer, 1885 group contains conoidal trochiform shells with a flat base (Fig. 2C, E, G).

No attempt has been made to revise the specimen identifications given on museum labels, although it is likely that many of these date back to the studies of Mesozoic pleurotomarioids made by L.R. Cox within the Natural History Museum (*e.g.* Cox 1960). Specimens are grouped after the division made at the Natural History Museum. The *Pleurotomaria anglica* group, for example, also includes single specimens of *P. rustica*, *P. subradians*, *P. cognata*, *P. multicincta*, *P. amathei*, *P. araneosa*, *P. undosa* and *P. hettangiensis*. The *P. actinomphala* group also includes specimens labelled *P. ornata*, *P. armata*, *P. granulata* and *P. paucistriata*. Many of the 39 nicely preserved *Pyrgotrochus* specimens are not assigned to species but some single specimens are named *P. bitorquata*, *P. punctata*, *P. princeps*, *P. agatha*, *P. elongata*, *P. subfasciata*, *P. conoidea* and *P. ornata*.

A total of 73 specimens of *Pleurotomaria anglica* and similar forms, 64 specimens of *Pleurotomaria actinomphala* and similar forms, and 39 specimens of *Pyrgotrochus* were examined. The material is from Jurassic localities in England. Specimens of the *P. anglica* group were collected from a variety of Lower Jurassic (Lower Lias–Middle Lias) localities, commonly in Somerset, Dorset, Gloucestershire and Worcestershire. Many of the specimens come from Bengeworth, Worcestershire (27 of 73). The majority of specimens in the *P. actinomphala* group (35 of 64) come from the Middle Jurassic Inferior Oolite at Bradford Abbas, Dorset. The rest were collected from other localities in Dorset, Somerset and Gloucestershire, with two collections from Yeovil, Somerset (9) and Dundry, Somerset (9). Specimens of *Pyrgotrochus* are also mainly from the Inferior Oolite at Dundry, Somerset (20 of 39), and other single localities in Dorset and Somerset.

Shell repair frequency

Measuring the frequency of repaired injuries within an assemblage of gastropods is the simplest way to gain an estimate of the interaction between gastropods and their presumed predators, although interpretation is fraught with difficulties. A low incidence of injuries can either mean that predators were scarce or ineffective, or that the predators were so abundant and successful that most prey succumbed with few individuals surviving to repair the shell. A high incidence of shell repair probably demonstrates a greater abundance of predators and the figure then reflects the ability of the gastropod to withstand shell crushing or peeling or some other defensive strategy (Vermeij 1982, 1987; Leighton 2002; Alexander & Dietl 2003).

There are two simple ways to calculate shell repair frequency. In the first method, shell repair frequency is calculated as the number of specimens with at least one repaired injury divided by the total number of specimens. This method gives a clue as to how many individuals are affected in a sample and has been widely used (Raffaelli 1978, Elner & Raffaelli 1980, Vale & Rex 1988, Cadée *et al*. 1997, Lindström 2003). At the same time, it can give a somewhat skewed picture since some specimens can have several injuries.

In the second method, shell repair frequency is measured as the total number of injuries divided by the total number of specimens in the sample, as used by Schindel *et al*. (1982), Vermeij & Dudley (1982), and Vermeij *et al*. (1982). This method gives an estimate of the 'intensity' of predatory attacks on a sample of gastropods, a relationship between the effectivness of the predator and the gastropod's ability to withstand it. Even here, the figure can deceive. For example, if one specimen in a sample of ten had all five recorded injuries, the shell repair frequency calculated by the second method is 50%, in contrast to 10% calculated with the first method. A thorough discussion of these, and other ways of calculating repaired frequency and prey effectiveness is given by Alexander & Dietl (2003).

Neither method is sufficient in itself and the best approach is to use both. The first method provides the overall

Figure 2. Jurassic pleurotomarioid gastropods from England. • A – *Pleurotomaria armata* (Münster, 1844). BMNH G 66467, Halfway House, Yeovil, Somerset. Oblique lateral view with two repaired injuries near the aperture. To the right, an injury only affects the upper whorl surface of the final whorl, while a later injury (lower centre) only affects the area below the selenizone, × 2.2. • B, D, F – *Pleurotomaria actinomphala* Deslongchamps, 1848. BMNH G 52112, Inferior Oolite, Yeovil, Somerset. B – oblique lateral view with two repaired injuries on the last whorl, both of them are affecting the whole whorl surface on both sides of the selenizone, × 2.8. D – lateral view showing two repaired injuries near the aperture only affecting the whorl above the selenizone, plus one of the more severe injuries figured in Fig. 2 to the right, × 2.6. F – umbilical view with the continuation of the most severe injury figured in B and D, × 2.2. • C – *Pyrgotrochus elongata* (Sowerby, 1818). BMNH G 18579, Inferior Oolite, Dundry, Somerset. Lateral view showing a major repaired injury near apex tracing back for ¼ of a whorl, × 1.6. • E, G – *Pyrgotrochus* sp. Fischer, 1885. BMNH G 66405, Inferior Oolite, Dundry, Somerset. E – oblique lateral view with a major repaired injury in the centre of the photograph, × 2.2. G – oblique lateral view showing a severe injury at the final preserved growth stage. Two whorls earlier there is another major repaired injury affecting the whole whorl surface, × 2.4. • H – *Pleurotomaria granulata* (Sowerby, 1818). BMNH G 83767, Inferior Oolite, Bradford Abbas, Dorset. Lateral view with a repaired injury affecting the whorl on both sides of the selenizone on last whorl, × 2.8.

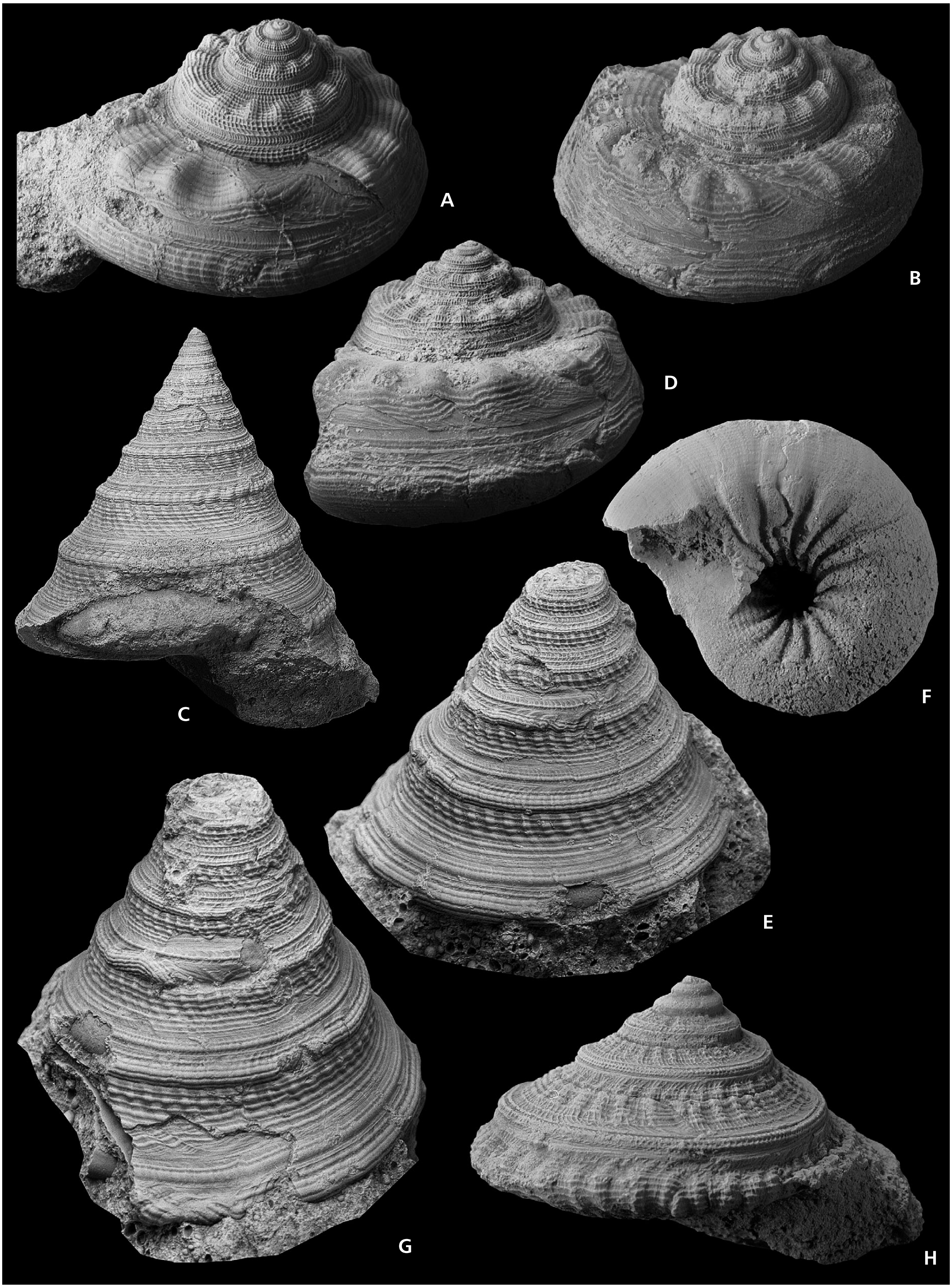

A
B
D
C
F
E
G
H

Table 1. Shell repair frequency in three Jurassic pleurotomarioid gastropod groups calculated in two ways, and the proportion of three types of injuries. 1 – the total number of specimens with repaired injuries divided by the total number of specimens. 2 – the total number of repaired injuries divided by the total number of specimens.

	Number of specimens	Repair Frequency 1	Repair Frequency 2	Whole whorl injuries	Above the selenizone	Below the selenizone
Pleurotomaria anglica group	73	0.288	0.753	0.608	0.235	0.157
Pleurotomaria actinomphala group	63	0.444	0.810	0.500	0.238	0.262
Pyrgotrochus sp. group	39	0.462	0.923	0.353	0.412	0.235

picture concerning how many specimens with repaired injuries are present in a sample, while the second method gives a measurement of the encounter rate between predators and their prey.

Calculated by the first method, the shell repair frequency for the *P. anglica* group is 28.8%. For the *P. actinomphala* group it is 44.4% and for the *Pyrgotrochus* group it is 46.2%. Shell repair frequencies calculated by the second method are always higher; for *P. anglica* 75.3%, *P. actinomphala* 81.0%, and *Pyrgotrochus* 92.3% respectively (see Table 1).

The *Pleurotomaria anglica* group consistently shows a lower incidence of shell repairs than the *P. actinomphala* group and *Pyrgotrochus* group. The difference is greatest using the first method (proportion of specimens with injuries) and much less when the second method is considered (proportion of all repaired injuries to the number of specimens). Thus, fewer specimens within the *P. anglica* group show repaired shell injuries, but those specimens that do often have several injuries. Indeed, one specimen has 11 repaired shell injuries (some of these injuries are shown in Fig. 1D, G, I). Specimens in the *P. anglica* group are often large, with many of the specimens between 50 and 100 mm in shell height. The mean number of injuries per specimen with repaired injuries is: *P. anglica* group 2.6, for *P. actinomphala* group 1.8 and for *Pyrgotrochus* group 2.0.

Location and type of injuries

The selenizone effectively divides the outer shell surface in two halves, above or below, in standard orientation with the apex up and the aperture facing the viewer. Lindström (2003) discussed the effect of a selenizone on the patterns of repaired injuries, discriminating three main types of repaired injuries that are also recognized in the present Jurassic material.

The first type of fracture crosses the selenizone and affects all the outer shell surface from the suture with the previous whorl to the umbilical surface, or at least to the angulation at the base. These major injuries often result in the loss of a large piece of the shell (*e.g.* Figs 1A, B, E, J; 2B, C, G, H). The other two types of injuries are perhaps no less severe in terms of the degree to which the shell is broken back, adapically, from the aperture, but they are restricted to either above or below the selenizone (*e.g.* Figs 1G, H, K; 2A, D). They probably occurred in the most adapertural part of the shell, where the slit was present, with the slit preventing extension of the fracture. However, it is also possible that the band of shell material forming the selenizone was a line of weakness which might also have prevented propagation of the break.

It can be difficult to establish if an injury results from one single attack or perhaps two, for example, when injuries above and below the selenizone are separated by a short distance along the selenizone as seen in Fig. 2A. The two injuries might result from a single attack if the transverse fracture is displaced by the slit or the selenizone. Since such relationships are difficult to confirm, this type of injury is considered as two separate events throughout.

In the *Pleurotomaria anglica* group 60.8% of the injuries traverse the entire outer shell surface, from suture to the umbilical side; only 23.5% affect the shell above and 15.7% the shell below the selenizone, respectively (see Table 1). In the *P. actinomphala* group, injuries affecting the entire outer whorl surface are still the most common (50%), but there is a larger proportion of injuries below the selenizone (26.2%). In the *Pyrgotrochus* group, injuries above the selenizone are the most common (41.2%), with the percentage of injuries (35.3%) affecting the entire outer whorl surface is substantially lower than in the other two groups.

The abundance of injuries below the selenizone may be biased negatively on account of whorl overlap in the trochiform shells. In whorls prior to the final whorl much of the umbilical surface is covered by the following whorl, and injuries occurring within this area are not visible. However, a significant portion of the lower whorl surface is exposed between the selenizone and the suture with the following whorl in members of the *P. anglica* group (Fig. 1I, J), enabling recognition of injuries which extend to the slit/selenizone. This area is less well exposed in the spire of members of the *P. actinomphala* and *Pyrgotrochus* groups, although injuries reaching the selenizone will still be detected.

Repaired injuries found above the selenizone the *Pleurotomaria anglica* group usually terminate at the selenizone and normally start at the suture with the previous whorl (Fig. 1G, H, K). Some smaller scallops show no connection with the selenizone or the suture (Fig. 1K on the last whorl) but these are quite uncommon. A single example of a similar scallop found on the umbilical side had no connection with the selenizone. In the *P. actinomphala* and *Pyrgotrochus* groups many injuries on the upper whorl surface seem to start below the suture with the previous whorl (*e.g*. Fig. 2B–D, G). If they start at the suture the fracture quickly bends adapically to follow a spiral thread some distance below the suture, as noted in *Pyrgotrochus*. *P. actinomphala* has a row of protruding knobs on the upper shell surface which may hamper the propagation of breaks. Adpression of whorls resulting from the conical profile of *Pyrgotrochus* probably strengthens the sutural area, with the result that fractures develop somewhat below the sutural line.

Discussion

We know of no specific study of shell repair in Jurassic pleurotomariids but repaired injuries of the type described herein are visible in illustrated specimens in published systematic studies (*e.g*., Das *et al*. 2005, Harasewych & Kiel 2007, Schubert *et al*. 2008).

The division into three loosely defined morphological types was proposed to facilitate investigation of the relationship between shell repair frequency and shell shape, using the two ways of calculating shell repair frequency mentioned above. Differences in shell repair frequency between the groups were found to be greater with the first method (proportion of specimens with at least one repaired injury) than with the second method (total number of injuries divided by the total number of specimens; see Table 1). The *P. anglica* group stands out, with a much lower repair frequency (28.8%) calculated by the first method than for the *P. actinomphala* (44.4%) and *Pyrgotrochus* groups (46.2%). The *P. anglica* group also shows a lower figure when the second method is used but the difference is less pronounced: 75.3% compared to 81.0% for the *P. actinomphala* group and 92.3% for the *Pyrgotrochus* group. Thus, members of the *Pleurotomaria anglica* group have the lowest frequency of repairs in both cases, while members of the *Pyrgotrochus* group show the highest frequency of shell repairs.

The incidence of repaired injuries in gastropods usually increases with increasing size of the shell as the individual gastropods have been exposed to shell breaking agents for a longer time. Furthermore, small (or juvenile) shells might have a higher fatality rate than large (adult) shells. Larger specimens are also likely to be more resistant to lethal breakage than smaller shells, as confirmed by Vermeij & Dudley (1982) and Vermeij *et al*. (1982). Schindel *et al*. (1982) demonstrated that higher spired species tend to show a higher shell repair frequency than species of lesser shell height. While the shells in this study differ in size and relative height, they cannot be directly compared in these terms. Shells of the *P. anglica* group are always much larger than those of the *P. actinomphala* and *Pyrgotrochus* groups, and shell size within the three groups is relatively consistent. *P. anglica* group specimens are most frequently between 50 and 100 mm high, whereas shells in the *P. actinomphala* and *Pyrgotrochus* groups were generally much smaller, 15–30 mm and 30–40 mm in shell height, respectively. Despite this, it cannot be shown that shells of a greater size (*i.e*. *P. anglica* group) show more repaired injuries and thus a higher shell repair frequency than the smaller shells. Perhaps shells of the *P. anglica* group were too large for most contemporary predators, were attacked less often and therefore show lower figures of shell repair as they grew into a size refuge (Schindel *et al.* 1982, Vermeij 1987, Schmidt 1989). Such a refuge might show two aspects: one with large shells in which a growth stage shows many repaired injuries, and a second where injuries are absent as the shell simply becomes too large to attack (Leighton 2002). The mean number of injuries per specimen with repaired injuries in the *P. anglica* group is the highest value recorded, at 2.6 injuries per repaired specimen even though fewer specimens show repaired injuries.

Schindel *et al*. (1982, table 4) noted a direct correlation between spire height and shell repair frequency in six trochiform taxa and the studied material conforms well with that general scenario if only shell form is concerned. Collectively, members of all three groups show high frequencies of shell repair in agreement with published figures from several works containing both low and high spired species (Schindel *et al*. 1982, Vermeij & Dudley 1982, Vermeij *et al*. 1982). Members of the *P. anglica* group, however, show a lower frequency of injuries than gastropods in the *P. actinomphala* group in spite of being higher spired. The shell in the *Pyrgotrochus* group is almost perfectly conoidal (Fig. 2C), with the highest spire and smallest pleural angle, and shows the highest frequency of repaired injuries. This high frequency may be a combination of the greater resistance of the conoidal form but also reflect the higher number of whorls present in members of this group.

Many individual injuries appear substantial on account of the highly disturbed growth of the newly formed shell (*e.g*. Fig. 1A, B, I, J). However, the gastropod still retains a large part of undisturbed original shell around the aperture in those cases where the slit or selenizone restricts the fracture to one sector of the outer whorl surface. Injuries of this type are clearly traumatic but probably not often lethal. Injuries which cross the entire outer face are potentially more of a threat to the gastropod and probably result in death in many cases. If only these most extensive injuries are considered, members of the *P. anglica* group show a repair frequency of 42.5%, compared to 33.3% in the *P. actinomphala* group and 35.9% in the *Pyrgotrochus* group, calculated by method two. Assuming that the higher number reflects a greater rate of survival, there is support for the notion that larger shells are more resistant to lethal predatory attacks.

The characteristic pleurotomarioidean slit in the apertural margin delimits two free apertural lips of shell material, one above and one below, which potentially may be easily broken off by either a predator or perhaps even by accidental non-biological damage. This type of breakage could create the separate injuries found either above or below the selenizone (*e.g.* Fig. 1G, K; Fig. 2A, D). It is probable that the force required to break these free lips is substantially less than that required to peel the shell backwards from the aperture to produce a major injury across the entire outer whorl surface (*e.g.* Fig. 1A–C, J). If substantially less force is needed to break the individual free lips this type of injury should be relatively common. In the *P. anglica* group such injuries comprise about 40% of all injuries and in the *P. actinomphala* group the figure is 50%. Members of the *Pyrgotrochus* group, however, show a much higher relative incidence of this type of injury, about 64%. This higher value probably reflects the greater depth of the open slit, and its greater effectiveness in stopping the propagation of fractures, thus inhibiting lethal injury. Moreover, the most common type of injury in the *Pyrgotrochus* group only affects the shell surface above the selenizone. This is probably due to the conical shell shape, with the slit/selenizone being located low on the body whorl. The base is relatively reduced, leaving the upper whorl surface, which lacks a shoulder, more susceptible to attack. In life position, the shell was probably oriented with the axis of coiling at a high angle to the substrate, further protecting the flattened base.

Specimens of *Pleurotomaria*, on the other hand, have a shorter slit and a more rounded whorl profile with a convex base. The umbilical surface was almost as susceptible to attack as the upper whorl surface. The shorter slit was probably less effective in limiting propagation of fractures such that injuries traversing the entire outer whorl surface should be more frequent. In the *P. anglica* group, such injuries crossing the entire outer whorl surface make up the majority (about 60%) of repaired injuries.

The length of the slit seems to be positively correlated with the number of individual injuries in the specimens of *Pleurotomaria* and *Pyrgotrochus* considered here. *Pyrgotrochus*, with the deepest slit, shows the highest frequency overall of shell repair. It was just this relationship that Lindström (2003) tested in the Carboniferous *Worthenia tabulata* and *Glabrocingulum grayvillense*. The hypothesis was that more repaired injuries would be expected in *Glabrocingulum grayvillense* with a deeper slit since the aperture would be weakened by the presence of the deep slit. Nevertheless, it was the short-slitted *Worthenia tabulata* that showed the higher figure of shell repair frequency; apparently it adopted a better defensive strategy, resulting in greater survivorship. The deeper slit of *Glabrocingulum* rendered it more susceptible to lethal attacks with the result that shell repair frequency was low (Lindström 2003).

Following this argumentation, the abundance of non-lethal injuries in members of the *Pyrgotrochus* group is not a simple reflection of the weakening effect of greater slit depth, but an indication of some kind of effective defensive strategy. Members of this group show a lower frequency of injuries crossing the entire outer whorl surface than in the *Pleurotomaria anglica* group, which may suggest that they were less effective in surviving this type of attack than members of that group or that there were fewer attacks. The first alternative is not unlikely if it reflects the aperture being peeled back beyond the culmination of the deep slit since a substantial amount of shell material will have been removed. The high abundance of attacks on the upper whorl surface in the *Pyrgotrochus* group indicates successful resistance, many attacks were apparently contained to this stage. It may well be that a better interpretation of the protective influence of a deep slit in members of the *Pyrgotrochus* group lies in the abundance of repaired injuries on the upper whorl surface as fractures are constrained by the slit. Once a predator had penetrated beyond the culmination of the open slit, the chances of survival of the gastropod were much reduced.

The dominance of whole whorl repaired injuries in two of the three pleurotomarioid groups (Fig. 3) can be compared with the similar dominance of medial repairs in bellerophontiform molluscs with a deep slit (Ebbestad *et al.* 2009). Given the bilateral symmetry of the latter group, the distinction between repaired injuries on the upper and lower whorl surfaces is not relevant. Bellerophontiform molluscs with a shallow median slit or sinus showed a near equal distribution of medial and lateral injuries, confirming the potentially limiting effect of the deep slit in Jurassic pleurotomarioids seen herein.

Vermeij (1977, 1987) predicted that the incidence of shell repair would increase with time because of an arms-race between prey and predator. The currently described Jurassic specimens are derived from the early stages of this 'Marine Mesozoic Revolution' (MMR; Vermeij 1977, Harper 2003), at least as depicted in the classic Sepkoski curves of diversity (*cf.* Huntley & Kowalewski 2007, fig. 1). Harper (2003) implied that this late appearance of the MMR (in the Cretaceous) may be a result of a lack of information from the Triassic and Jurassic, as is also apparent from sampling data presented by Huntley & Kowalewski (2007, fig. 1) in their investigation of the coupling between diversity and predation in the Phanerozoic. Our data may help resolve this deficit.

Overall, the frequency of shell repair for all three pleurotomarioid groups is high when compared to

Palaeozoic gastropods (Schindel *et al*. 1982; Lindström 2003; Lindström & Peel 2003, 2005) but Ebbestad & Stott (2008) have demonstrated that shell repair frequencies in Ordovician gastropods can be significantly higher than is often assumed for the Lower Palaeozoic. Their data support the observations of Huntley and Kowalewski (2007) that predation intensity increased already at that time, rather than 60–70 m.y. later, during the 'mid-Palaeozoic Marine Revolution' of Signor & Brett (1984). Lindström (2003) noted an injury frequency of 46.5% for *Worthenia tabulata* and 5.4% for *Glabrocingulum grayvillense* from the Carboniferous, while Schindel *et al.* (1982) noted 79% and 12%, respectively, in assemblages of the same species. Values in this study range between 75.3% and 92.3%. (All figures are method two, total number of injuries divided by the total number of specimens). This trend may indicate that there were more predators in the Mesozoic and therefore more traces of their durophagous activities in the pleurotomarioid shells. Alternatively, or additionally, it can reflect some new adaptation resulting in fewer lethal attacks. The Jurassic pleurotomarioids described herein are profoundly larger than most of their Palaeozoic relatives, suggesting that size increase may be the strategy they adopted for survival in the Mesozoic.

Acknowledgements

It is a pleasure to acknowledge the help of the staff at the Palaeontology Department, Natural History Museum, London during a visit partly funded by a stipend to A.L. from The Royal Society of Sciences and Letters (*Kungliga Vetenskapsakademien*) Stockholm, and partly through grants to J.S.P. from the Swedish Research Council (Vetenskapsrådet). Comments from J.O.R. Ebbestad and G. J. Vermeij are gratefully acknowledged, as well as the reviews for the journal by A.J. Boucot and R.J. Horný.

References

Alexander, R.R. & Dietl, G.P. 2003. The fossil record of shell-breaking predation on marine bivalves and gastropods, 141–176. *In* Kelley, P.H., Kowalewski, M. & Hansen, T.A (eds) *Predator-prey interactions in the fossil record. Topics in Geobiology 20*. Kluwer Academic/Plenum Publishers, New York, Boston, Dordrecht, London, Moscow.

Alexander, R.R. & Dietl, G.P. 2005. Non predatory shell damage in Neogene western Atlantic deep-burrowing bivalves. *Palaios 20,* 280–295. DOI 10.2110/palo.2004.p04\|[ndash]\|29

Anseeuw, P. & Goto, Y. 1996. *The living Pleurotomariidae*. 202 pp. Elle Scientific Publications, Osaka, Japan.

Anseeuw, P. & Poppe, G.T. 2005. *Pleurotomariidae. Visaya, supplement 1*, 1–37.

Bertness, M.D. & Cunningham, C. 1981. Crab shell-crushing predation and gastropod defense. *Journal of Experimental Marine Biology and Ecology 50*, 213–230. DOI 10.1016/0022-0981(81)90051-4

Bouchet, P., Rocroi, J.P., Frýda, J., Hausdorf, B., Ponder, W., Valdes, A. & Warén, A. 2005. Classification and nomenclator of gastropod families. *Malacologia 47(1–2)*, 1–397.

Bowsher, A.L. 1955. Origin and adaptation of platyceratid gastropods. *University of Kansas Paleontological Contributions, Mollusca Article 5*, 1–11.

Cadée, G.C., Walker, S.E. & Flessa, K.W. 1997. Gastropod shell repair in the intertidal of Bahia la Choya (N. Gulf of California). *Palaeogeography, Palaeoclimatology, Palaeoecology 136*, 67–78. DOI 10.1016/S0031-0182(97)00041-2

Castell, L.L. & Sweatman, H.P.A. 1997. Predator-prey interactions among some intertidal gastropods on the Great Barrier Reef. *Journal of Zoology London 241*, 145–159. DOI 10.1111/j.1469-7998.1997.tb05505.x

Checa, A. 1993. Non-predatory shell damage in Recent deep-endobenthic bivalves from Spain. *Palaeogeography, Palaeoclimatology, Palaeoecology 100,* 301–301. DOI 10.1016/0031-0182(93)90061-M

Conrad, T.A. 1835. Descriptions of five new species of fossil shells in the collections presented by Mr Edward Miller to the Geological Society. *Transactions of the Geological Society of Pennsylvania 1*, 267–270.

Cox, L.R. 1960. The British Cretaceous Pleurotomariidae. *Bulletin of the British Museum (Natural History), Geology 4*, 387–423.

Das, S.S., Bardhan, S. & Kase, T. 2005. A new pleurotomatiid gastropod assemblage from the Jurassic sequence of Kutch, western India. *Paleontological Research 9,* 329–346.

Defrance, M.J.L. 1826. Genus *Pleurotomaria*, 381. *In* Cuvier, G. (ed.) *Dictionnaire des Sciences Naturelles, dans lequel on Traite Méthodiquement des Differens Êtres de la Nature, Considérés Soit en Eux-mêmes d'Après l'État Actuel de nos Connoissances, soit Relativement à l'Utilité qu'en Peuvent Retirer la Medicine, l'Agriculture, le Commerce et les Artes: suivi d'une Biographie des plus Célèbres Naturalists, par Plusieurs Professeurs du Muséum National d'Histoire Naturelle et des Autres Principales de Écoles de Paris, Volume 41.* Paris & Strasbourg.

Deslongchamps, J.A. 1848. Mémoire sur les Pleurotomaires des terrains secondaires du Calvados, suivi d'une note sur une espèce d'oscabrion fossile des mêmes terraines, et de suppléments aux mémoires sur les genres Ombrelle, Bulle, Tornatelle et Cone. *Mémoires de la Société Linnéenne de Normandie 8*, 1–166.

Ebbestad, J.O.R. & Peel, J.S. 1997. Attempted predation and shell repair in Middle and Upper Ordovician gastropods from Sweden. *Journal of Paleontology 71*, 1007–1019.

Ebbestad, J.O.R. & Stott, C.A. 2008. Failed predation in Late Ordovician gastropods (Mollusca) from Manitoulin Island, Ontario, Canada. *Canadian Journal of Earth Sciences 45,* 231–241.

Ebbestad, J.O.R., Lindström, A. & Peel, J.S. 2009. Predation on bellerophontiform molluscs in the Palaeozoic. *Lethaia 42*, 469–485.

Elner, R.W. & Raffaelli, D.G. 1980. Interactions between two marine snails, *Littorina rudis* Maton and *Littorina nigrolineata* Gray, a predator, *Carcinus maenas* (L.), and a parasite *Microphallus similis* Jägerskiöld. *Journal of Experimental Marine Biology and Ecology 43*, 151–160.

Fischer, P. 1885. *Manuel de conchyliologie et de paléontologie conchyliologique. Histoire naturelle des mollusques vivants et fossiles*. *Fasc. 9*, 785–896. Libraire F. Savy, Paris.

Harasewych, M.G. 2002. Pleurotomarioidean gastropods, 237–294. *In* Southward, A.J., Tyler, P.A., Young, C.M. & Fuiman, L.A. (eds) *Molluscan radiation – lesser known branches. Advances in Marine Biology 42*. Academic Press, London.

Harasewych, M.G. & Kiel, S. 2007. Upper Jurassic Pleurotomariidae (Gastropoda) from southwestern Madagascar. *The Nautilus 121*, 76–89.

Harper, E.M. 2003. The Mesozoic marine revolution, 433–455. *In* Kelley, P.H., Kowalewski, M. & Hansen, T.A. (eds) *Predator-prey interactions in the fossil record. Topics in Geobiology 20*. Kluwer Academic/Plenum Publishers, New York, Boston, Dordrecht, London, Moscow.

Hickman, C.S. 1984. *Pleurotomaria*: Pedigreed perseverance?, 225–231. *In* Eldredge, N. & Stanley, S.M. (eds) *Living fossils*. Springer Verlag, New York, Berlin, Heidelberg, Tokyo.

Horný, R.J. 1998. A large injury and shell repair in *Boiotremus incipiens* (Mollusca, Gastropoda) from the Silurian of Bohemia. *Bulletin of the Czech Geological Survey 73*, 343–345.

Huntley, J.W. & Kowalewski, M. 2007. Strong coupling of predation intensity and diversity in the Phanerozoic fossil record. *Proceedings of the National Academy of Science 104*, 15006–15010. DOI 10.1073/pnas.0704960104

Knight, J.B. 1952. Primitive fossil gastropods and their bearing on gastropod classification. *Smithsonian Miscellaneous Collections 117(13)*, 1–56.

Knight, J.B., Cox, L.R., Keen, A.M., Batten, R.L., Yochelson, E.L. & Robertson, R. 1960. Systematic descriptions, I169–I310. *In* Moore, R.C. (ed.) *Treatise on invertebrate paleontology, Part I. Mollusca 1(6)*. Geological Society of America, Boulder and University of Kansas Press, Lawrence.

Leighton, L.R. 2002. Inferring predation intensity in the marine fossil record. *Paleobiology 28*, 328–342. DOI 10.1666/0094-8373(2002)028<0328:IPIITM>2.0.CO;2

Lindström, A. 2003. Shell breakage in two pleurotomarioid gastropods from the Upper Carboniferous of Texas, and its relation to shell morphology. *GFF 125*, 39–46.

Lindström, A. & Peel, J.S. 1997. Failed predation and shell repair in the gastropod *Poleumita* from the Silurian of Gotland. *Bulletin of the Czech Geological Survey 72*, 115–126.

Lindström, A. & Peel, J.S. 2003. Shell repair and mode of life of *Praenatica gregaria* (Gastropoda) from the Devonian of Bohemia (Czech Republic). *Palaeontology 46*, 623–633. DOI 10.1111/1475-4983.00312

Lindström, A. & Peel, J.S. 2005. Repaired injuries and shell form in some Palaeozoic pleurotomarioid gastropods. *Acta Palaeontologica Polonica 50,* 697–704.

Münster, G. zu 1839–1846. *Beiträge zur Petrefakten-Kunde*. 7 heft mitt 142 tafeln. Bayreuth.

Nielsen, C. 1975. Observations on *Buccinum undatum* L. attacking bivalves and on prey responses, with a short review of attack methods of other prosobranchs. *Ophelia 13*, 87–108.

Norwood, J.G. & Pratten, H. 1855. Notice of fossils from the Carboniferous series of the western states, belonging to the genera *Spirifer, Bellerophon, Pleurotomaria, Macrocheilus, Natica* and *Loxonema* with descriptions of eight new characteristic species. *Journal of the Academy of Natural Sciences of Philadelphia, series 2, 3,* 711–78.

Peel, J.S. 1974. Systematics, ontogeny and functional morphology of Silurian trilobed bellerophontacean gastropods. *Bulletin of the Geological Society of Demnark 23*, 231–264.

Preston, S.J., Roberts, D. & Montgomery, W.I. 1996. Crab predation as a selective agent on shelled gastropods: a case study of *Calliostoma zizyphinum* (Prosobranchia: Trochidae), 313–325. *In* Taylor, J. (ed.) *Origin and evolutionary radiation of the Mollusca*. Oxford University Press, Oxford.

Raffaelli, D.G. 1978. The relationship between shell injuries, shell thickness, and habitat characteristics of the intertidal snail *Littorina rudis* Maton. *Journal of Molluscan Studies 44*, 166–170.

Savazzi, E. 1991. Constructional morphology of strombid gastropods. *Lethaia 24*, 311–331. DOI 10.1111/j.1502-3931.1991.tb01482.x

Schindel, D.E., Vermeij, G.J. & Zipser, E. 1982. Frequencies of repaired shell fractures among the Pennsylvanian gastropods of north-central Texas. *Journal of Paleontology 56*, 729–740.

Schmidt, N. 1989. Paleobiological implications of shell repair in recent marine gastropods from the northern Gulf of California. *Historical Biology 3*, 127–139. DOI 10.1080/08912968909386517

Schubert, S., Gründel, J. & Nützel, A. 2008. Early Jurassic (Upper Pliensbachian) gastropods from Herforder Liasmulde (Bielefeld, Northwest Germany). *Paläontologische Zeitschrift 82*, 17–30.

Shoup, J.B. 1968. Shell opening by crabs of the genus *Calappa*. *Science 160*, 887–888. DOI 10.1126/science.160.3830.887

Signor, P.W., III & Brett, C.E. 1984. The mid-Paleozoic precursor to the Mesozoic marine revolution. *Paleobiology 10*, 229–245.

Sowerby, J. de C. 1812–1845. *The Mineral Conchology of Great Britain*. Vols 1–7, 648 plates. London.

Tracey, S., Todd, J.A. & Erwin, D.H. 1993. Mollusca: Gastropoda, 131–167. *In* Benton, M.J. (ed.) *The Fossil Record*. 845 pp. Chapman & Hall, London.

Vale, F.K. & Rex, M. A. 1988. Repaired shell damage in deep-sea prosobranch gastropods from the western north Atlantic. *Malacologia 28*, 65–79.

Vermeij, G.J. 1977. The Mesozoic marine revolution: evidence from snails, predators and grazers. *Paleobiology 3*, 245–258.

Vermeij, G.J. 1982. Gastropod shell form, breakage, and repair in relation to predation by the crab *Calappa*. *Malacologia 23*, 1–12.

Vermeij, G.J. 1987. *Evolution and escalation. An ecological history of life*. 527 pp. Princeton University Press, Princeton & New Jersey.

Vermeij, G.J. & Dudley, E.C. 1982. Shell repair and drilling in some gastropods from the Ripley Formation (Upper Cretaceous) of the south-eastern U.S.A. *Cretaceous Research 3*, 397–403. DOI 10.1016/0195-6671(82)90041-6

Vermeij, G.J., Zipser, E. & Zardini, R. 1982. Breakage-induced shell repair in some gastropods from the Upper Triassic of Italy. *Journal of Paleontology 56*, 233–235.

Voltzow, J., Morris, P J. & Linsley, R.M. 2004. Anatomy of and patterns of water currents through the mantle cavities of Pleurotomariid gastropods. *Journal of Morphology 262*, 659–666. DOI 10.1002/jmor.10267

Yonge, C.M. 1947. The pallial organs in the aspidobranch Gastropoda and their evolution throughout the Mollusca. *Philosophical Transactions of the Royal Society of London, Series B 233*, 443–418. DOI 10.1098/rstb.1947.0003

Zipser, E. & Vermeij, G.J. 1978. Crushing behavior of tropical and temperate crabs. *Journal of Experimental Marine Biology and Ecology 31*, 155–172. DOI 10.1016/0022-0981(78)90127-2