

Attempted predation and shell repair in *Euomphalopterus* (Gastropoda) from the Silurian of Gotland

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Two cases of shell breakage and subsequent repair are described in *Euomphalopterus* Roemer, 1876 from the Silurian of Gotland, Sweden. One specimen shows a single repaired injury. The second specimen shows repeated breakage and repair, with eventual loss of the prominent peripheral frill which is considered characteristic of the genus. Scalloped fracture margins comparable to those produced by the living cuttlefish *Sepia* suggest that the Silurian predators may also have been cephalopods.

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Tertiary and Recent gastropod shells often show the results of predation in the form of drilled holes, broken apertural margins or decapitated spires. Attempted, unsuccessful predation is witnessed by shell repair. In the Mesozoic, signs of predation or attempted predation on gastropod shells are less frequent, with Vermeij (1977), for example, observing a lower incidence of repaired injuries in collections of Cretaceous gastropods than in their present-day counterparts. Evidence of shell repair in Palaeozoic gastropods is rare and there are only a few reported cases, for example Pennsylvanian gastropods from Texas studied by Schindel, Vermeij & Zipser (1982). Better documentation of repaired injuries exists in more intensively studied groups, such as trilobites and brachiopods, with case histories extending back to the Cambrian (summaries by Alexander 1981; Ludvigsen 1977; Vermeij 1983). Repair in the coral *Phaulactis* from the Silurian of Gotland has been described by Flügel (1979). The cumulative evidence is insubstantial, however, confirming Vermeij's (1977, 1983) thesis that the rise in importance of shell breaking predators is largely a Mesozoic phenomenon.

The present paper describes two examples of shell breakage and subsequent repair, interpreted as unsuccessful attempts at predation, in the gastropod *Euomphalopterus* Roemer, 1876 from the Silurian of Gotland. One specimen was

first illustrated a century ago by Lindström (1884, pl. 10, fig. 20) without reference to the injury, and shows a single episode of shell repair (Fig. 1). The second example shows repeated major breakage and repair (Figs. 2, 3). One of these attacks was sufficiently violent to cause loss in subsequent growth stages of the pronounced spiral frill around the whorl periphery, which is the principal morphological characteristic of the genus. The scalloped nature of some of the fractures in this specimen may indicate attack by a cephalopod, by analogy to scars produced on arthropod prey by living *Sepia* (Hewitt & Watkins 1980).

Euomphalopterus from Gotland

Euomphalopterus Roemer, 1876 is one of the most common gastropods in collections from the Silurian of Gotland. Lindström (1884) included ten species and varieties within his "Division VI. Alatae" of the genus *Pleurotomaria*. He equated the division with *Euomphalopterus*, although he did not employ this generic name. The ten taxa have not been collectively revised since Lindström's day and it is unlikely that all would now be retained within *Euomphalopterus*. Knight (1941) redescribed the type species, *Euomphalopterus alatus* (Wahlenberg 1821), which is the

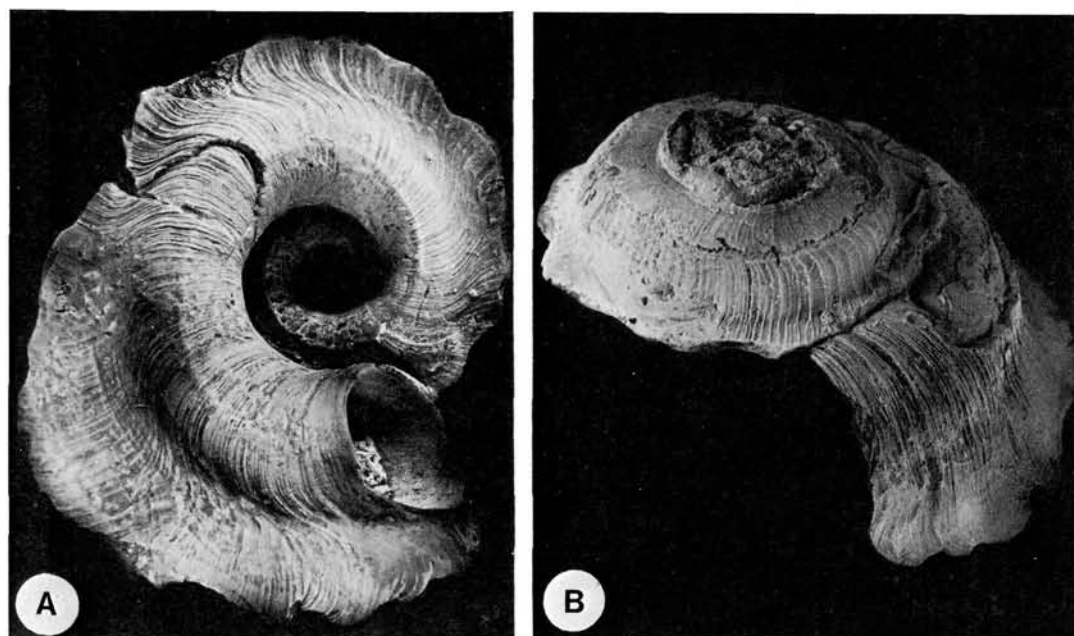


Fig. 1. *Euomphalopterus alatus* (Wahlenberg 1821), Naturhistoriska Riksmuseet, Paleozoologiska Avdelning, specimen Mo 27021, Höglint Beds, Visby, Gotland, $\times 1.5$. A, umbilical view showing the broad frill characteristic of the genus and the deep, notch-like fracture (upper left) occurring about one third of a whorl prior to the aperture. B, oblique lateral view.

most well known of the Gotland species. Linsley, Yochelson & Rohr (1978) recently discussed the mode of life of *E. alatus* from Gotland, noting a comment from Anders Martinsson (Uppsala) that the species ranges through strata of late Llandovery and Wenlock ages.

The characteristic frill around the whorl periphery in *Euomphalopterus* may be as wide as the whorl diameter (Fig. 1). The frill has previously been considered analogous to the pleurotomarian selenizone, resulting in the assignment of the family Euomphalopteridae to the superfamily Pleurotomariacea (Knight et al. 1960). Linsley, Yochelson & Rohr (1978) reinterpreted the frill on the basis of the morphological description given by Lindström (1884), and concluded that it served the function of propping the shell aperture above the substratum. Contrary to the exhalant function inferred from interpreting the frill as a modified selenizone, Linsley, Yochelson & Rohr (1978) suggested that the frill was deposited by a small mantle fold which may have served an inhalant function. As a result of this reinterpretation, they transferred the Euomphalopteridae from the Pleurotomariacea to the Euomphalacea.

Shell damage and repair in *Euomphalopterus*

Lindström (1884, pl. 10, fig. 20) illustrated without comment the lower (= umbilical) surface of one specimen of *Euomphalopterus alatus* from Visby, refigured by Knight (1941, pl. 78, fig. 1f), which shows breakage and subsequent repair of the apertural margin almost half a whorl previous to the preserved, seemingly undamaged, aperture. The disruption of growth ornamentation is distinct, with a deep, adaperturally concave scar visible on the umbilical surface (Fig. 1A). Subsequent shell growth occurred on the interior surface of the fractured margin, i.e. from below the damaged layer, as viewed in Fig. 1A. A transverse fracture immediately adapertural of the repaired fracture (below in Fig. 1A) is of post depositional origin.

The specimen described below is much less well preserved than the example figured by Lindström (1884) and Knight (1940). Indeed, it can not be identified with certainty at the level of species, although the narrowness of the umbilicus (Fig. 2D) suggests that it is not referable to the

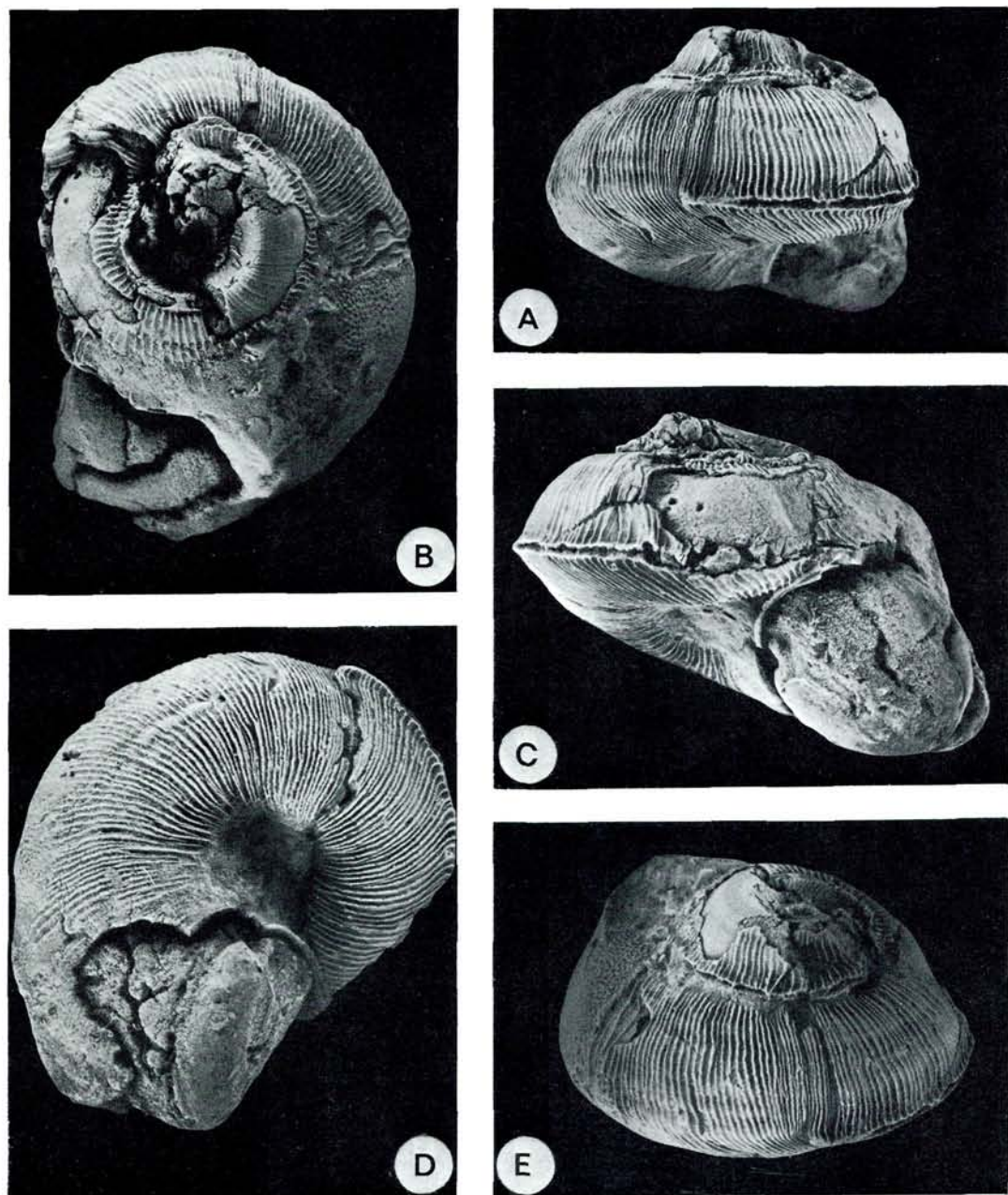


Fig. 2. *Euomphalopterus* sp., U.S. National Museum of Natural History, specimen USNM 311767, Klinteberg Beds, Klintehamn, Gotland, $\times 3$. A, lateral view showing loss of the peripheral flange subsequent to fracture d (Fig. 3). B, apical view showing bryozoan overgrowth (lower right) located adaperturally of the pronounced notch-like fracture (h in Fig. 3A). The angular fracture d (compare Fig. 3A) is visible at the top of the figure. C, apertural view showing a fragment of the inner lip. D, umbilical view showing the prominent fracture d (upper right) and post burial breakage of the aperture, exposing the internal mould. E, oblique lateral view locating fractures c, d, and e (lower centre) and the deep notch of fracture h (lower left).

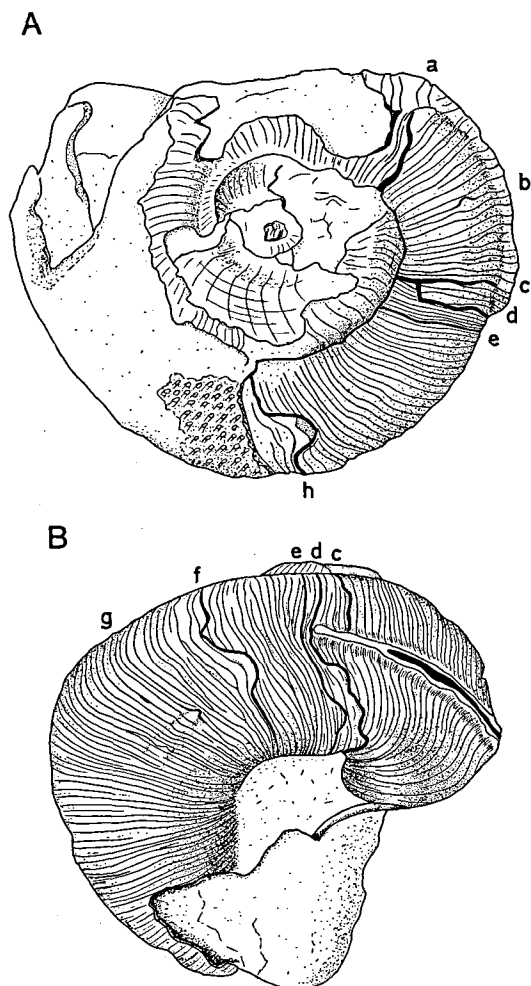


Fig. 3. *Euomphalopterus* sp. Camera lucida drawings of USNM 311767 locating fractures described in the text and illustrated in Fig. 2A–E. A, apical view. B, oblique lateral view.

type species *E. alatus*. The specimen is labelled “Klintehamn, Gotland” and was possibly derived from the Klinteberg Beds of Wenlock age at Klintehamn (Anders Martinsson personal communication, 1981). Maximum preserved length is about 24 mm, height 18.5 mm. The apex has been broken away such that only about one and a half whorls are preserved. The aperture has been broken since burial since the mudstone internal mould is retained with the impression of encrusting organisms from the shell interior; part of the columellar lip is preserved (Fig. 2C). Flattening of the most adapical part preserved suggests that the apex was not sediment infilled and was

crushed during diagenesis. A small encrusting bryozoan is present mainly on the upper whorl surface during the last fifth of a whorl (Figs. 2B, E).

The series of repaired breaks or irregularities in growth lamellae in the specimen from Klintehamn are lettered a–h in Fig. 3. The earliest episode (a) follows an exfoliated part of the whorl, with the internal mould visible. The break appears to be substantial but exfoliation of individual shell layers makes evaluation difficult. A minor dislocation of growth lamellae is visible on the upper whorl surface at this point and fractures are present on the upper and lower surfaces. The frill is unaffected.

A minor invagination (b) on the upper surface can only be traced for a short distance along the affected growth lamella. An almost identical structure is present on the lower whorl surface at g, at a later growth stage.

A rather linear fracture (c), roughly parallel to the growth lamellae, is present only on the upper whorl surface and can not be traced across the frill (Fig. 3B). The new growth area, immediately adapertural of the fracture, is sunken relative to the pre-fracture surface. Its ornamentation of abundant, fine growth lamellae suggests rapid shell formation.

A major break (d) is characterised by its irregular shape. Near the suture with the previous whorl (Fig. 3A), the break takes the form of an angular notch penetrating adapically as far as the previous plane of fracture (c). At the whorl periphery, the plane of fracture swings slightly forward, adaperturally, as it crosses the frill, presumably reflecting the strengthening influence of the frill on the aperture. On the lower whorl surface (Figs. 2D; 3B), the fracture is scalloped with three or possibly four concave re-entrants. The frill terminates at the fracture. The new growth area developed adapertural of the fracture is again characterised by relatively abundant, fine growth lamellae. The half whorl of shell growth subsequent to fracture d lacks any indication of the frill, the whorl periphery being instead rather uniformly convex (Fig. 2A).

Fracture e can be traced on both the upper and lower whorl surfaces, but is generally inconspicuous on account of its parallelism to growth ornamentation. A single deep invagination is present on the lower surface (Fig. 3B). In

similar fashion to fractures c and d, growth lamellae immediately after the break are relatively fine. Fracture f is principally evident on the lower whorl surface (Fig. 3B) where a deep notch penetrates back (adapically) through four previous growth lamellae. In contrast to earlier fractures, f is not followed by a growth period with fine growth ornamentation.

Fracture h is a major structure visible on the upper whorl surface (Figs. 2B, E; 3A) with the deep invagination penetrating six previous growth lamellae. The new shell growth in the notch is largely covered with fine growth lines. The final quarter of a whorl, preserved only on the lower whorl surface, shows no further fractures other than a minor dislocation at g (Fig. 3B).

The predator

Vermeij (1977) drew parallels between increase in the sturdiness of gastropod shells and the marked rise in the number of shell-destroying predators which occurred during the late Mesozoic. He observed that several structurally weak morphological features occur commonly in Palaeozoic gastropods, but are notably less frequent in Tertiary and Recent gastropods. The latter often develop features such as thickened and restricted apertures, varices and the ability to withdraw deep into the shell, aimed at strengthening the shell against potential crushers and at frustrating the 'peeling' activity of crabs.

Euomphalopterus displays several of the structurally weak characters enumerated by Vermeij (1977, 1983). Coiling is loose and, in *E. alatus* (Fig. 1), the umbilicus is widely open. In the specifically unassigned specimen of *Euomphalopterus* (Fig. 2) the umbilicus is somewhat narrower but this, and *E. alatus* (Fig. 1A), possess simple rounded apertures without thickened margins.

Low incidence of cases of shell repair indicates that shell-breaking predators are rare, or that they are usually successful in causing fatal damage (Vermeij 1982). A high frequency of repairs implies that most individuals in the gastropod population are the subject of unsuccessful predatory attack. The low success rate of the predator in such circumstances can be attributed to many causes, ranging from shell characteristics

through defensive behavioural patterns to inaccurate evaluation of potential prey by the predator.

The high failure rate of living molluscivores (Vermeij 1983) and the absence of strengthening, predation resistant shell features in Silurian gastropods strongly suggest that the general rarity of repaired shells in the Silurian should be attributed to a lack of shell-destroying molluscivores relative to the present day, rather than to the existence of highly efficient predators. The present description clearly indicates that predation existed during the Silurian, but the lack of other published accounts is itself a measure of the rarity of shell crushers. Indirect evidence of the existence of predators is presented by the development of a strongly calcified operculum in *Oriostoma* Munier-Chalmas, 1876. Records of preserved fossil opercula in the Lower Palaeozoic are few, with several notable exceptions reviewed by Yochelson (1979). Opercula in Silurian *Oriostoma* are well known (Whiteaves 1895; Lindström 1884) and specimens of several species of the genus occur widely in Gotland, often in great numbers (Lindström 1884).

Two groups of Recent molluscivores also existed in the Palaeozoic (Vermeij 1977). One of these, the asteroides, do not crush or break their prey but have employed extraoral and intraoral digestion since the Ordovician (Carter 1968). Dipnoans arose during the Devonian and together with co-existent, but now extinct, groups of fishes they developed pavement-like jaw dentitions well suited to crushing molluscs.

Vermeij (1978) figured examples of present-day gastropods which had been crushed or 'peeled' by crabs or lobsters. Peeling back of the apertural margins, commonly the outer lip, can produce scars reminiscent of the type seen here in Fig. 1A, although fatal attacks often require peeling of a whorl or more (Vermeij 1978, Fig. 2.13). Crabs and lobsters originated during the Jurassic, but other groups of arthropods, e.g. eurypterids may have employed similar techniques.

Vermeij (1977) also pointed out that cephalopods may have been molluscivores in the earlier Palaeozoic, but he could not document their activity. A feature of the major fractures described above is their scalloped form (Fig. 1A; fracture h in Figs. 2B; 3A; fracture d in Figs. 2D; 3B). Hewitt & Watkins (1980, fig. 5) illustrated

similar scars in the dorsal carapace of the crab *Carcinus maenas* produced as a result of predation by the cuttlefish *Sepia*. A notable difference between *Carcinus* and *Euomphalopterus* is the presumed ability of the latter to withdraw into its shell. With even modest withdrawal, successful predation would probably require a degree of peeling considerably greater than that evidenced by the present examples of *Euomphalopterus*, although predation in these two specimens was not successful. It is not possible to deduce with certainty how much shell has been broken away with each attack, but several fractures can only be traced over part of the whorl, suggesting minor loss.

Hewitt & Watkins (1980) noted reports that only cephalopods with a body weight of 40–100 g are strong enough to break or disarticulate large bivalves or crustaceans. The often common occurrence of orthocones up to several tens of centimetres long in the Silurian of Gotland and other areas suggests that the described specimens of *Euomphalopterus* could well have been attainable prey for molluscivorous cephalopods.

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Dansk Sammendrag

To tilfælde af itugåede og senere reparerede snegleskaller af slægten *Euomphalopterus* Roemer, 1876 fra Gotlands silur bliver beskrevet og afbildet.

Det ene eksemplar er blevet skadet en gang, mens det andet eksemplar viser gentagne skader. Dette har medført tab af den perifere fure, der ellers er karakteristisk for slægten. Kanterne på bruddene minder om de mærker, der opstår efter angreb af den nutidige blæksprutte *Sepia* og det foreslås derfor, at bruddene hos de silure former er lavet af cephalopoder.

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