A recovery from sublethal damage to the shell of a Devonian spiriferoid brachiopod

ANDRZEJ BALIŃSKI

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A shell of the Famennian spiriferoid brachiopod *Cyrtiorina* sp., from the Dębnik anticline in southern Poland. displays a severe damage, probably the result of a bite by a jawed or clawed predator. The injury comprises several indentations on the pedicle valve and partial disarticulation of the shell exposing large areas of soft tissue in living animal. The brachiopod successfully repaired the damage, demonstrating its ability to recover from sublethal injuries. It is suggested that the attacker may have been repelled of the brachiopod's soft tissues, as has been observed in some Recent articulates.

Key words: spiriferoid brachiopod, Devonian, shell damage, predation.

Andrzej *Baliński, Instytut Paleobiologii* PAN, Aleja *Żwirki* i Wiguy 93, 02–089 *Warszawa*, Poland.

Introduction

In Recent times predation plays a major role in determining taxonomic abundances and distribution. It is quite reasonable to expect a similar biotic phenomenon in the past (Sheehan & Lesperance 1978: p. 812) although fossil evidences of predation is not common. Nevertheless, predation evidences in fossil brachiopods has been documented in several papers.

Recently Ruggiero (1990) classified all traces of damage on living brachiopods into four categories, namely Praedichnia (predation structures), Domichnia (dwelling structures), Cubichnia (resting structures) and traces of penetrative Thallophyta. The most fully documented of these is the first category in which the structures may be of two different types – breakage and borings. Borings in brachiopod shells are the commonest evidence of predation activity and have been described and illustrated in several papers (see Ruggiero 1990 for review). These drillings are usually attributed to carnivorous gastropods (eg. Sheehan & Lesparence 1978; Brunton 1966; Boucot 1981; Ruggiero 1990) although some authors discussed also an alternative interpretation of the markings, i.e. as being of non predatory origin (Rodriguez & Gutschick 1970; Rohr 1976).

Another type of Praedichnia discussed by Ruggiero (1990) are different sorts of breakages of brachiopod valves (Tash 1973; Alexander 1981; Boucot 1981). Those breakages which include evidences of crushing or bites may be situated at the valve margins or may affect large portions of the shell. This type of damage was attributed to attacks by fish (e.g. Alexander 1981), decapods (e.g. Ruggiero 1990), reptiles (Tchoumatchenko 1987) or even to abiotic mechanism (Sarytcheva 1949; Małkowski 1976).

In this paper an unusual type of Praedichnia is described in one shell of a spiriferoid *Cyrtiorina* sp. Severe sublethal damages of its shell and the later successful recovery may throw some light on the early history of predator–prey interactions.

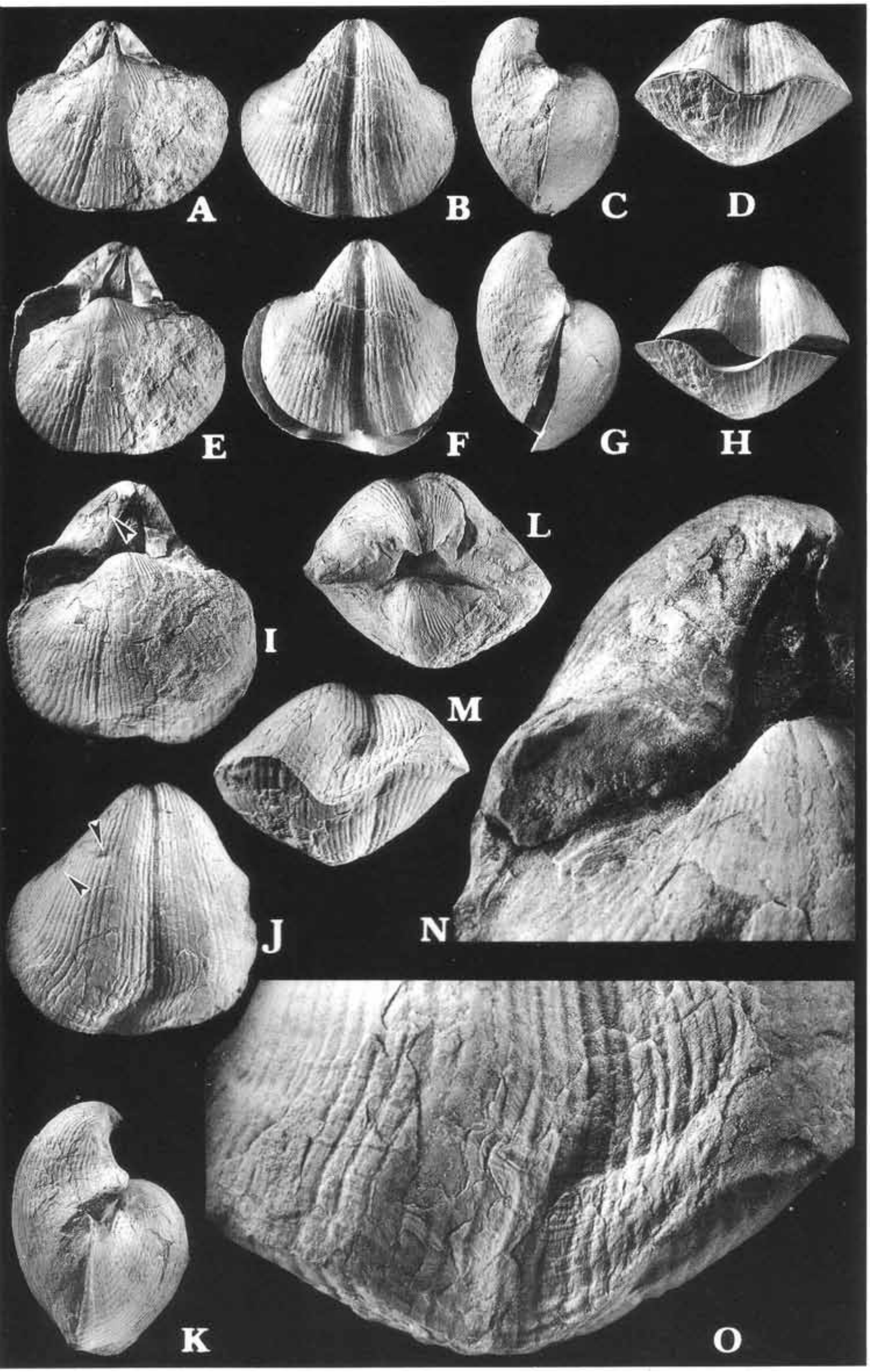
Material

The specimen of *Cyrtiorina* sp. considered in this report comes from the Late Devonian (Famennian) deposits of the Dębnik anticline (southern Poland, 23 km west of Krakow). It was found in a small pit (locality ZS–2) situated ca. 0.7 km south–west of Dębnik village (see Baliński 1979, Fig. 1), together with other brachiopods represented by *Leioproductus* cf. *pauperculus*, *Cyrtospirifer wesgensis* and *Mesoplica* sp. Associated fauna includes scarce gastropods, ostracods, crinoids and laminar stromatoporoids. Conodonts are represented by *Palmatolepis rhornboidea*, *Polygnathus semicostatus*, *P. glaber glaber* and *P. szulczewskii* They define the age of the limestone as the Early to Late *P. rhomboidea* Zone. These layers represent lower parts of the Grained and Micritic Limestone unit (Narkiewicz & Racki 1987).

Description of damaged shell

The described shell is 37.6 mm long, with a maximum width of 37.2 mm. The brachial valve is comparatively less damaged and deformed than the pedicle one. At a distance of 23 mm from umbo there occurs an apparent temporary constraint of the growth in the form of a concentric undulation

Fig. 1. ❑A–O. Cyrtiorina sp., Famennian, Dębnik anticline (trench ZS–2), Poland. A–D. Plaster cast reconstruction of the shell prior to damage caused by the predator's attack. E–H. Reconstruction of the shell immediately after the attack showing the damage (partial disarticulation). I–O. The original shell showing complete recovery from its injuries; indentation arrowed, ZPAL Bp XXIII/123e. A–M, x 1; N–O, x **3.**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of the external surface of the valve. Anteriorly from this undulation the valve displays a distinct change of direction and growth acceleration on the right half of the valve (Fig. 11). Thus the newly secreted section of shell is 2.5 mm long on its left half and up to 5 mm long on its right.

The pedicle valve shows much more deformation than the brachial one described above. At a distance of 29 mm from umbo there can be observed an abrupt change in the direction of shell accretion manifested by deviation of radial ornamentation and by condensed growth lines (Fig. 1J). This change is best seen in the median part of the valve, where the ribs show a deviation of up to 30° (Fig. 1O). At a distance of 32.5 mm from umbo there is the second stage of constraint in shell growth, expressed as an undulation corresponding to that observed on the brachial valve. Both valves show a distinct acceleration of growth on their left halves. An abnormal growth of the valve is manifested also by extensive development of scar tissue just below the hinge margin on left side of the interarea (Fig. 1I, N, 2D). This additionally secreted area of shell forms a flat semicircular surface measuring 12.5 by 6 mm. It is a prolongation of the commissure plane and forms a right angle with the ventral interarea. On the left side of the valve there are a few (at last three) shallow indentations measuring from ca. 10 to 24 square milimeters (Fig. 1J). The largest one shows a disturbed radial ornamentation. A few other indentations occur in the opposite side of the valve, i.e. near the lateral margin of the interarea (Fig. 1I, 2C).

Discussion

The described damage to the shell indicates that the living animal suffered severe sublethal wounds. The indentations observed on the surface of the pedicle valve were probably caused by a jawed or clawed, durophagous (shell-crushing) predator with crushing elements that were bluntly rounded (arthrodirans or chondrichtyan fish cannot be excluded). The brachiopod was attacked in its adult stage, when ca. 30 mm long (Fig. 1A–D, 2A, B). It was bitten by the predator causing several superficial injuries to the pedicle valve which were later repaired and sealed by the shell–secreting mantle. The brachiopod was not ingested but abandoned by the predator. As a result of the attack, however, a severe damage was inflicted to the hinge mechanism: one side of the shell lost its hinge capability. Furthermore, the tension of muscles and other soft tissue of the animal caused a rotation of 30° by the brachial valve around the remaining, undamaged tooth and socket. This movement exposed vast area of soft tissue (Figs 1E–H, 2C) to the external environment.

Despite these injuries, the brachiopod remained alive and started the process of repair by secreting new shell material. In order to restore a tight closure of the valves, which is an important feature of brachiopod shells (Brunton 1990), the mantle epithelium posteriorly secreted a new element

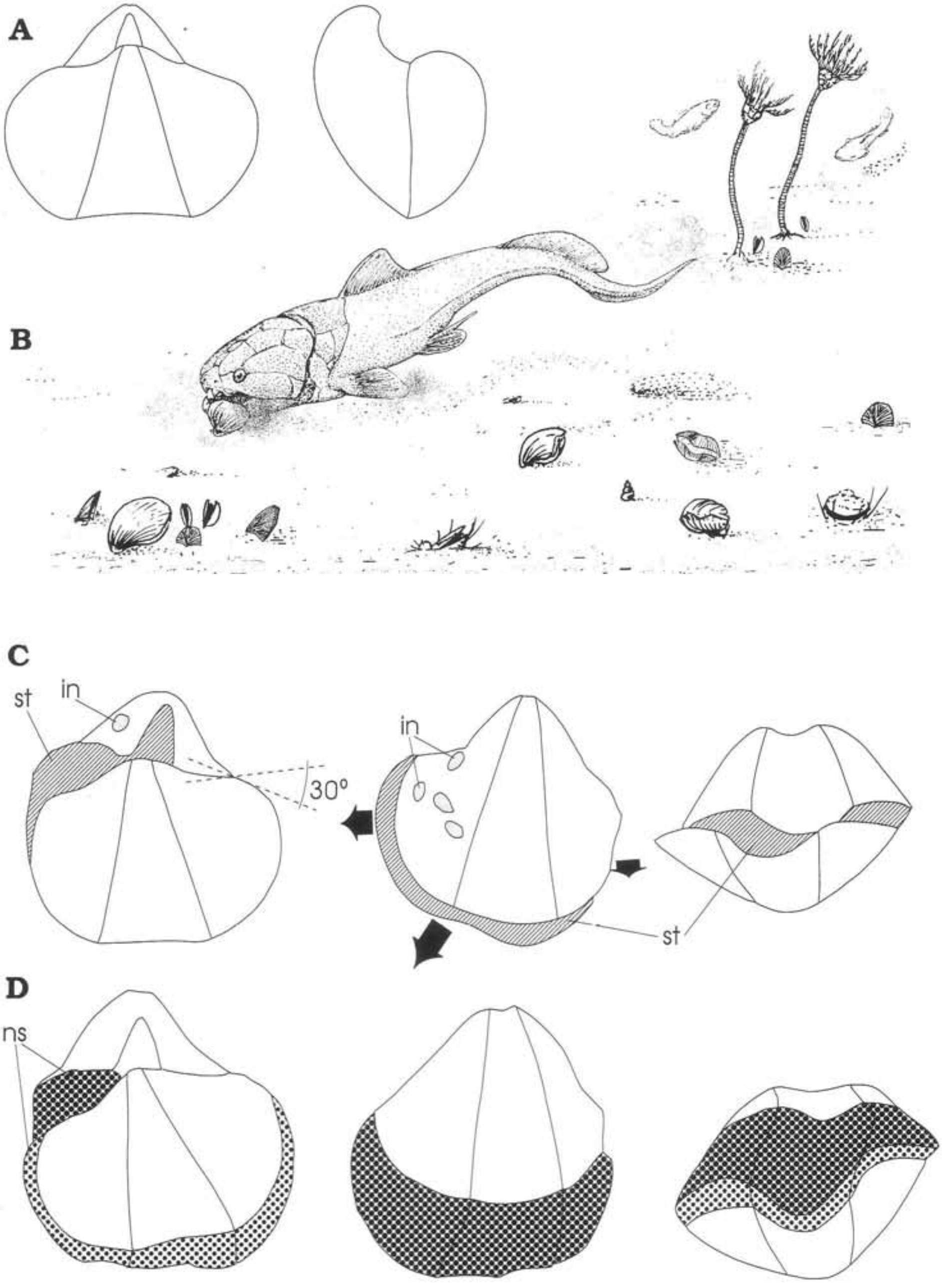

Fig. 2. A diagram showing consecutive stages of damage and repair of the shell of *Cyrtiorina* sp. ❑A. Shell before damage. OB. A hypothetical representation of the attack. OC. Shell after damage, showing rotated brachial valve and exposed soft body (dashed). OD. Shell showing repaired damages; in – indentations, ns – new shell secreted after damage, st – exposed soft body. Arrows indicate direction and rate of shell accretion by the pedicle valve.

of the shell (scar tissue) which protected the exposed soft body and reestablished a good fit between valves along the hinge margin (Fig. 1N). Although not destroyed during attack, the lateral and anterior margins no longer fitted, resulting in the presence of a constant gape (Figs 1G, H, 2C). In order to restore a tight closure of the valves the mantle had to differentiate between direction and rates of shell growth (see Fig. 2C). Finally the brachiopod recovered from its injuries and its valves once again formed a tight seal at the commissure (Figs 1I–M, 2D).

Why was the brachiopod abandoned by the attacker although the prey was seriously damaged? A possible explanation is a loss of interest by the predator caused, for example, by difficulties in crushing further the brachiopod shell. Crushing experiments on brachiopod shells conducted by Alexander (1990) revealed that shell thickness and ribbing and to a lesser extent biconvexity of the valves and relief of the central fold, serve to strengthen the shell against compressional forces. It is evident, that shell morphology of the spiriferoid here described represents rather good adaptation against jawed or chelate durophagous predators. Its main morphologic features are shell biconvexity, thick valves (especially in the posterior part where it was crushed), ribbing and the presence of a fold and sulcus.

One may offer also another explanation for the abandoned attack. It is known that, unlike other shelly marine invertebrates, modern articulate brachiopods are repellent to predators (Thayer 1985: p. 1527). In Thayer's laboratory experiments invertebrate and vertebrate predators showed a statistically significant preference for bivalves rather than articulates. They often convulsed and regurgitated the unpalatable brachiopod pray (Thayer 1985: p. 1527). According to the cited author repellants may have been evolved in Paleozoic articulates, although Alexander (1989: p. 170) suggests that it is very unlikely to be detected in fossil shells. The fact that the articulate *Cyrtiorina* sp. was attacked but discarded by the predator, can readily be explained by a repellent in the brachiopod body. The developed skill to emit (secrete) a repellent by the spiriferoid might be the main reason why the predator found it distasteful and retreated. Thus, the described specimen illustrates not only the great ability of the group to recovery from injuries but also it may suggest that some characteristic interaction between articulates and predators evolved as early as in the Late Devonian.

Frequency of repaired brachiopod specimens through geologic time indicates that sublethal damage is nonrandomly distributed among articulate orders (Alexander 1986a, b, 1992). Paleozoic strophomenids had capability to repair severe shell damage (Brunton 1966; Alexander 1986b, 1989), while experiments on living terebratulids showed that severe damage of shell in *Terebmtulina retusa* apparently cannot be repaired (Alexander 1992). This inability to repair certain severe shell damage in Recent terebratulids is in contrast with the ability to recover in strophomenids and *Cyrtiorina* sp. Besides the shell–structure difference, a possible explanation of the phenomenon may be a change of pray responses to predators during the course of evolution. Thus, the reparability of severe shell damage among early Paleozoic articulates could have been replaced later by a repellent in their soft tissues. This process might have taken place as early as the Devonian, when there appeared several new groups of well equipped and effective, jawed or clawed predators.

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Streszczenie

Ślady drapieżnictwa w stanie kopalnym nie należą do znalezisk częstych. Tym niemniej zostały one opisane u ramienionogow w szeregu publikacjach. Najczesciej występującymi sladami dzialalnosci drapieżników na muszlach ramienionogow są niewielkie wywiercone otworki zwykle przypisywane drapieżnym slimakom (Sheehan & Lasparence 1978; Brunton 1966; Boucot 1981; Rugierro 1990). Inną kategorią uszkodzen muszli ramienionogow spowodowanych przez drapieżniki są slady ugryzień i zlaman (Tasch 1973; Alexander 1981; Boucot 1981). W pracy opisano muszlę spirifera *Cyrtiorina* sp. z uszkodzeniami w postaci płytkich wgnieceń na skorupce nóżkowej (spowodowanyrni zapewne przez drapieżnika wyposażonego w szczęki lub szczypce) oraz wyłamanym częściowo mechanizmem zawiasowym muszli, co spowodowalo zsunięcie się lewej strony skorupki ramieniowej o ok. 30^{o}. Spowodowalo to odsłonięcie na czynniki zewnętrzne dużych powierzchni ciała miękkiego. Mimo znacznych, prawie śmiertelnych uszkodzen ramienionog został porzucony przez drapieżnika i po pewnym czasie zdołał całkowicie zregenerować muszlę przywracając zdolnosd do szczelnego zamknięcia skorup. Samo porzucenie przez drapieżnika poranionego rarnienionoga może wskazywać na fakt, że jui dewonskie zawiasowce miały zdolnosd emisji substancji odstraszających, podobnie jak czynią to współcześni przedstawiciele tych ramienionogow (Thayer 1985).