The Late Devonian trematid lingulate brachiopod Schizobolus from Poland

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Baliński, A. & Holmer, L.E. 1999. The Late Devonian trematid lingulate brachiopod *Schizobolus* from Poland. — *Acta Palaeontologica Polonica* **44**, 3, 335–346.

A new species of the poorly known lingulate brachiopod *Schizobolus* is described from the Famennian (Upper Devonian) of Poland. *S. polonicus* sp. n. has a triangular pedicle notch and a small listrium, indicating that it belongs to the Trematidae within the superfamily Discinoidea. *S. polonicus* retains some linguloid features, such as a linguloid-like 'pedicle groove' and a V-shaped imprint of the pedicle nerve. The disturbance band, which occurs in the apical part of the larval shell, probably delimits two stages of growth, namely pre-larval (embryonic?) and larval, or, early-larval and late-larval. *S. polonicus* is the youngest member of the genus, and of the family Trematidae. Five incompletely preserved discinids from the Famennian of Łagów are described as Trematidae gen. et sp. indet.

Key words: Brachiopoda, Discinoidea, systematics, larval shell, Late Devonian, Poland.

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Introduction

The Devonian lingulate brachiopod *Schizobolus* Ulrich, 1886 has remained a poorly known genus mainly due to the fact that the type species *S. concentricus* (Vanuxem, 1842) is invariably represented by poorly preserved material from black shales. *Schizobolus* has commonly been included within the Discinoidea Gray, 1840 and compared with the Trematidae Schuchert, 1893, whereas Rowell (1965) considered it more doubtfully related to the Discinacea. This paper describes etched material of a new species of *Schizobolus* from the Late Devonian of Poland. The new material indicates that it is best regarded as a genus of the Trematidae. The new occurrence is also the

youngest record of *Schizobolus*. A few specimens regarded here as Trematidae gen. et sp. indet. are also described from the Famennian of Łagów.

Material

All studied material is from samples which were collected in two regions of Poland, i.e. the Holy Cross Mts (central Poland) and Dębnik anticline (southern Poland, Silesia-Cracow region) (Fig. 1). Of all the nine samples which contained studied brachiopods (see Table 1), one (PG) is from micritic, fossiliferous limestone at locality Pałkowa Góra near village of Dębnik (southern Poland; see Baliński 1995). The limestone contains a relatively rich brachiopod fauna, which was studied by Baliński (1995). The associated fauna comprises remains of holothuroids, crinoids, ostracodes, conodonts, and fish. The limestone represents the *Cavatisinurostrum longilinguis* interval, which can be correlated with the Middle *Palmatolepis crepida* conodont Zone.



Fig. 1. Devonian palaeogeographic map of Poland (after Racki & Baliński 1998, modified) showing locations of the studied collecting sites.

The section at Łagów where the second sample (Ł.09) containing the studied brachiopods was collected is not so well studied. The sampled part of the section is within the *Prolobites* Zone, which is characterized by the occurrence of marly shales with limestone intercalations crowded with trilobite exoskeletons (Osmólska 1962: p. 64).

At Jablonna the studied brachiopods were recovered from six samples (see Table 1) in different horizons of the lower and middle part of the Famennian. This part of the section is developed as organic detrital limestones with cephalopods, brachiopods,

STANDARD STAGES southern Poland Holy Cross Mts CONODONT Debnik Łagów Jabłonna ZONES praesulcata expansa postera z trachytera < Ī [Ł.09] z marginifera (J.54) ш Σ ∢ rhomboidea ш J.08 (PG) crepida triangularis linguiformis FRASNIAN rhenana

Table 1. Stratigraphic and geographic distribution of samples with trematid lingulate brachiopods studied in this paper. Numbers of samples from Jabłonna and Łagów after J. Dzik, unpublished.

trilobites, and conodonts and sporadically with gastropods, bivalves, and corals (Wolska 1967).

All samples were etched in dilute acetic acid. Conodonts and phosphatic brachiopods were the most common fossil groups in processed residua. The first were used in determining the stratigraphic age of the samples, as summarized in Table 1. The total brachiopod material comprises some thirty specimens, of wich two-thirds are dorsal valves and one-third are ventral valves. The specimens are generally well preserved revealing fine details of their morphology, but they are generally fragmented.

The described specimens are housed in the Institute of Palaeobiology of the Polish Academy of Sciences in Warsaw, for which the abbreviation ZPAL is used.

Systematic palaeontology

Superfamily Discinoidea Gray, 1840

Remarks. — The Discinoidea have traditionally been regarded as a superfamily within the Acrotretida (Rowell 1965). However, cladistic analysis by Holmer & Popov (1996) indicated that the discinoideans belong within the Lingulida (see also Williams



Fig. 2. Schizobolus concentricus (Vanuxem, 1842); Middle Devonian, Poor Valley, Tennessee, USA, all × 5. A. Ventral internal mould, USNM459685c. B. Dorsal internal mould, USNM459685b. C. Ventral internal mould, USNM459685a.

et al. 1998a). *Schizobolus polonicus* sp. n. described below appears to retain some linguloid features, including a small listrium with a lingulid-like 'pedicle groove', in addition to a lingulid-like V-shaped imprint of the pedicle nerve. The linguloid-like features of some discinoideans are also evident from the new discovery by Südkamp (1997) that some Devonian discinoids from the Hunsrückschiefer had a long linguloid-like pedicle.

Family Trematidae Schuchert, 1893

Diagnosis. — Shell usually ornamented with large, superficial pits; beak of dorsal valve usually marginal and protruding beyond ventral valve; pedicle opening extending to posterior margin of ventral valve in all growth stages.

Discussion. — The family Trematidae is not a well-defined family which is probably not monophyletic. It differs from the Discinidae in a combination of features, including the presence of postlarval ornamentation of superficial pits (lacking in *Schizocrania* and *Schizobolus*) and a posteriorly unrestricted pedicle opening. Both *Schizocrania* and *Trematis* have a marginal, re-curved beak, whereas in *Schizobolus* the beak is posteriorly placed. Up to now, the genus *Schizobolus* has been reported only from the Early–Middle Devonian strata; thus, *S. polonicus* sp. n. extends the range of the genus and the family into the Late Devonian (Famennian).

Fig. 3. A–N. Schizobolus polonicus sp. n., Famennian of Poland. A, C–G, I. Seven fragmentarily preserved dorsal valves from the exterior. A – ZPAL Bp 45/1, Jabłonna J.08, \times 30; C – ZPAL Bp 45/2, Jabłonna J.60, \times 50; D – ZPAL Bp 45/3, Jabłonna J.60, \times 30; E – ZPAL Bp 45/4, Jabłonna J.60, \times 25; F – holotype ZPAL Bp 45/5, Jabłonna J.57, \times 45; G – ZPAL Bp 45/6, Dębnik, Pałkowa Góra (PG), \times 40; I – ZPAL Bp 45/7, Jabłonna J.57, \times 40. B. Internal view of fragmentarily preserved dorsal valve, ZPAL Bp 45/8, Jabłonna J.54, \times 50. H. Enlarged fragment of E showing distinct boundary between larval (ls) and postlarval (ps) shell, \times 300. J, K. Internal view of incomplete dorsal valve, ZPAL Bp 45/9, Jabłonna J.30, \times 30 (J) and \times 100 (K). L–N. Three enlargements of apical part of F showing peeled-off external shell layer (L) and pitted ornamentation (M, N), \times 225 (L), \times 300 (M), and \times 1000 (N). O–Q. Pelagodiscus atlanticus (King);



northeastern Pacific Ocean, USNM 384198. **O**. Dorsal larval shell, \times 1100. **P**. Detail of dorsal larval showing pitted ornamentation (imprint of siliceous tablets), \times 2200. **Q**. Detail of juvenile section of dorsal shell, showing siliceous tablets in place, \times 8000.

Genus Schizobolus Ulrich, 1886

Type species: Original designation by Hall (1863: p. 28): Discina truncata Hall, 1863 (= Lingula concentrica Vanuxem, 1842); see Fig. 2.

Diagnosis. — Shell elongate oval, weakly biconvex; both valves with beak placed posteriorly, not marginal; pedicle opening forming triangular notch extending from beak to posterior margin, sometimes, when preserved, with small listrium.

Remarks. — Material of the type species *S. concentricus* (Vanuxem, 1842), from the Middle Devonian of Tennessee, is illustrated here (Fig. 2) for comparison with *S. polonicus* sp. n.

Schizobolus polonicus sp. n.

Figs 3A-N, 4, 5A-C, E, G.

Holotype: ZPAL Bp 45/5, figured on Fig. 3F, L-N.

Type locality: Section at Jabłonna, Holy Cross Mountains.

Type horizon: Organic detrital limestones, sample J.57 (Table 1), middle part of the Famennian. Etymology: After its occurrence in Poland.

Diagnosis. — Pedicle notch widely triangular and short, with small listrium and lingulid-like 'pedicle groove'; dorsal valve with rounded posterior margin; ventral interior with V-shaped imprint of the pedicle nerve.

Material. — Total of 27 mostly fragmentary valves, of which 16 are dorsal. One specimen is from the Famennian of Dębnik (southern Poland, Silesia-Cracow region, sample PG), whereas the rest of the collection is from the lower and middle parts od the Famennian of Jabłonna section (central Poland, Holly Cross Mts, samples J.03, J.08, J.38, J.54, J.57, and J.60; see Table 1). Illustrated paratypes: ZPAL Bp 45/1–4 and 45/6–16, 18.

Description. — The complete outline of the adult shell is not known, due to the fragmentary nature of the material, but judging from earlier growth stages it is elongately suboval, and weakly biconvex. Both valves with beak in posterior 1/3 of the shell. Ornamentation consists of low, rather irregularly spaced concentric lamellae, interspersed with fine growth lines (Figs 3, 5).

Ventral valve with rounded posterior margin. Pedicle notch widely triangular and short, occupying about 20% of total valve width, with small listrium and narrow lingulid-like 'pedicle groove', occupying up to about 20% of width of pedicle notch, and extending for less than half the length of the listrium (Fig 4A–E, H). Ventral interior with two raised muscle scars directly anterior to pedicle notch, bisected by V-shaped impression of pedicle nerve (Fig. 4F, G).

Dorsal valve with rounded posterior margin. Dorsal interior characters poorly impressed (Fig. 3B, J, K).

Discussion. — Schizobolus polonicus differs from the type species in having a shorter and more widely triangular pedicle notch, in addition to a small listrium. However, it is possible that the listrium is not visible in *S. concentricus* due to the poor preservation in black shales (Fig. 2). The dorsal valve of *S. polonicus* has a rounded posterior margin, whilst that of the type species is short and straight, and the new species lacks all traces of a dorsal median ridge. The ventral interior of *S. polonicus* has a well-defined V-shaped imprint of the pedicle nerve. The ventral interior of *S. concentricus* is not well known,



Fig. 4. Schizobolus polonicus sp. n., Famennian of Poland. A–E, H. Three fragmentary preserved ventral valves viewed externally; a general (A–C) and more detailed (D, E, H) views showing pedicle notch and imperfectly preserved listrium. A, D – ZPAL Bp 45/10, Jabłonna J.60, \times 50 and \times 150; B, H – ZPAL Bp 45/11, Jabłonna J.03, \times 25 and \times 50; C, E – ZPAL Bp 45/12, Jabłonna J.60, \times 50 and \times 150. F, G. General (G) and more detailed (F) views of incomplete ventral valve showing V-shaped impression of pedicle nerve, ZPAL Bp 45/13, Jabłonna J.60, \times 100 (F) and \times 50 (G).

but it has some kind of median septum, which bifurcates at the posterior end. The muscle scars of neither species are preserved in enough detail to merit a detailed analysis.

Ontogeny. — *Larval shell.* The larval stage of growth is clearly marked in all studied ventral and dorsal valves. The outline of the larval shell is transversely oval to subpentagonal with slightly flattened lateral and posterior margins (e.g., Figs 3A, D, 4H, 5E, G). A very weak median indentation may be developed in the posterior margin in some ventral and dorsal larval shell (e.g. Fig. 4D, E). The larval shell is sharply delimited posteriorly and laterally (Fig. 3H), whereas anteriorly it is bounded by only a slightly more accentuated growth ring. The external surface of the larval shell is generally smooth but with evenly distributed hemiperipheral growth lines. In one dorsal larval shell a characteristic pitted ornamentation is developed (Fig. 3L–N). The pits are shallow, partly obliterated, densely packed, and attain a diameter of 1 to 2 μ m. They resemble the external shell ornamentation of Recent *Pelagodiscus* (Fig. 3O–P), where these types of pits are caused by imprints of siliceous tables in a vesicular periostracum (Fig. 3Q) (Williams *et al.* 1998a, b).

The earliest (?embryonic) stage of growth. All larval valves studied possess a weak disturbance band which delimits their most apical part. This part of the valve is transversely oval in outline and reaches 0.15 to 0.20 mm in width. Its surface is smooth except for subtle concentric growth lines. In one of the studied specimens these growth



Fig. 5.A–C, E, G. Schizobolus polonicus sp. n., Famennian of Poland. A–C. Three valve exteriors showing details of ornamentation. A – ZPAL Bp 45/14, Jabłonna J.38, × 220; B – ZPAL Bp 45/15, Jabłonna J.60, × 70; C – ZPAL Bp 45/16, Jabłonna J.08, × 220. G. Exterior of dorsal valve, ZPAL Bp 45/18, Jabłonna J.38, × 50. E. Apical part of dorsal valve showing posterior border of postlarval shell (ps), early larval or embryonic (?) shell (es), and late larval shell (lls); same as C, × 150. D, F. Trematid gen. et sp. indet., Famennian of Poland. Exterior of ventral valve in general (D) and more detailed (F) view showing ornamentation of postlarval shell (ps), late larval shell (lls), and early larval or embryonic (?) shell (es); note also imperfectly preserved listrium (li) and pedicle groove (g) in F; ZPAL Bp 45/17, Łagów Ł.09, × 40 (D) and × 350 (F).

lines are exceptionally well preserved (Fig. 5E), their total number can be approximately determined as 23. Each of them is about 5 μ m thick. Very similar structured apical part of the larval valve is seen also in trematid gen. et sp. indet. (Fig. 5F).

The consistent occurrence of a disturbance ring in the apical part of larval valves probably delimits two stages of growth, namely pre-larval and larval, or, early-larval and late-larval. However, there is no important growth differentiation during the larval stage of Recent discinoids. Although it is difficult to speculate whether such differentiation occurred in Palaeozoic discinoids, it seems possible that the earliest growth stage observed in our material represents a pre-larval or embryonic stage. If that is so, the disturbance in shell growth could be associated with hatching of the embryo from the vitelline membrane and the transition to a free-swimming larval mode of life. Contrary to Recent and fossil lingulid brachiopods, in which protegulum is formed as a single plate (e.g., Yatsu 1902; Ashworth 1915; Chuang 1962; Baliński 1997), the supposed

embryonic shell (or early-larval) of the Devonian discinoids may have been secreted gradually, which resulted in the formation of growth lines.

The presence of a pre-larval (or early-larval) shell in Devonian discinoids is supported by the presence of the similarly structured apical part of shell in the Ordovician discinoid *Trematis elliptopora* Cooper, 1956 (Chuang 1971). The youngest stage in the shell development of *T. elliptopora* was recognized by Chuang (1971: p. 98, pl. 1) as a protegulum. This embryonic shell was described as transversely oval in outline and measuring 0.145 mm in length and 0.183 mm in width on average. This is in striking accordance with measurements of the Devonian specimens from Poland (0.14 and 0.18 mm respectively). Also, the average dimensions of the larval shell of *T. elliptopora* (0.412 long and 0.471 mm wide) are very close to these described here for *S. polonicus* (0.42 and 0.46 mm, respectively).

The disturbance of growth in the apical part of larval shell of some Ordovician discinoids is also identifiable from the illustrations of Holmer (1989). This youngest part of shell delimited in the dorsal valves of *Schizotreta* sp. a is 0.30 mm wide (Holmer 1989: fig 112: G, I, J). It is also marked in two ventral valves of *Orbiculoidea*? sp. c (Holmer 1989: fig. 113A, B).

Recent representatives of discinoid brachiopods have a shell-less embryonic stage (Chuang 1977). Their first shell is secreted in early, but not the earliest, larval free--swimming stage of growth. If the apical part of the larval shell in Palaeozoic discinoids was secreted during the embryonic stage of growth, it would suggest a very important difference in the secretory regime between the Palaeozoic taxa and their extant relatives. As noted above, it seems plausible that the disturbance in growth recorded in fossil discinoids took place during the larval growth stage. Although we do not know the cause of the disturbance band on the surface of the larval shell, we assume that it could be related to a change in behaviour, metabolism or organogenesis of the larva.

Trematid gen. et sp. indet.

Figs 5D, F, 6.

Remarks. — Four almost complete dorsal valves and one ventral valve have been retrieved from sample Łagów Ł.09 (Holy Cross Mts); one dorsal valve is from sample Jabłonna J.55 (Famennian, see Table 1). They are rather small (dimensions of two specimens: 1.27 and 1.32 mm in length, 1.04 and 1.10 mm in width, respectively). Their larval shell is 0.44 mm wide and smooth except for very delicate concentric growth lines. Outside the larval shell the valves are ornamented by strongly developed and more or less evenly spaced lamellae, up to 0.03 mm thick. Some of the lamellae decrease in height in the posterolateral part of valve or may even disappear in the median region of the valve (Fig. 6D). The post-larval shell also bears fine, impersistent, more or less radially disposed striae, which can be traced also on top of the lamellae (Fig. 6H). Where well developed, the radial striae attain 3 μ m in width. They are spaced at intervals averaging from 5 to 30 μ m. The striae are most likely identical to the radial disturbances described by Williams & Holmer (1992), and might be related to stresses at the mantle edge caused by the movement of the setal muscles.

These dorsal valves differ clearly from *S. polonicus* in having strong concentric lamellae and radially disposed striae. They probably represent a new genus but the material is too scarce to propose a new taxon.



Fig. 6. Trematid gen. et sp. indet., Famennian of Poland. A, D, F, H. Four views of dorsal valve exterior ZPAL Bp 45/19, Łagów Ł.09, \times 25 (A), \times 85 (D), \times 100 (F), and \times 300 (H). B, C. Two dorsal valve exteriors. B – ZPAL Bp 45/20, Jabłonna J.55, \times 50; C – ZPAL Bp 45/21, Łagów Ł.09, \times 100. E, G. Two views of dorsal valve exterior showing repaired shell injury, ZPAL Bp 45/22, Łagów Ł.09, \times 25.

One dorsal valve bears a trace of a very serious damage (Fig. 6E, G). A predator equipped with some sort of claws probably caused it. The injury affected almost a half of the whole valve length at the time of the attack. After injury the brachiopod sealed in the destroyed area of the valve and successfully recovered. It is worth noting that in the Recent brachiopods, the injury at such a scale usually causes infection and death of the animal (Thayer 1985).

Acknowledgements

We would like to thank Dr. C.H.C. Brunton and an anonymous referee for constructive reviews of the manuscript and providing useful comments. Special thanks are due to Professor J. Dzik who donated specimens from the Holy Cross Mts. Grants (to LH) from the Swedish Natural Science Research Council (NFR) supported the work. The visit to Sweden by AB has been funded within the exchange programme of the Polish and Swedish Academies of Sciences.

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Późnodewoński trematid Schizobolus (Brachiopoda) z Polski

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Streszczenie

Bezzawiasowy ramienionóg *Schizobolus* jest niedostatecznie znanym rodzajem głównie ze względu na zły stan zachowania typowego gaunku *S. concentricus* z środ-

kowego dewonu Tennessee (USA). Opisane w niniejszej pracy okazy z famenu (górny dewon) Dębnika (region krakowski) i Jabłonnej (Góry Świętokrzyskie) zostały zaliczone do nowego gatunku *Schizobolus polonicus* sp. n. Gatunek ten charakteryzuje trójkątne wycięcie na nóżkę w skorupce brzusznej, które jest częściowo zakryte słabo zachowującą się, delikatną płytką (*listrium*). U *S. polonicus* występuje też – charakterystyczny dla linguloidów – rowek nóżkowy oraz V-kształtny odcisk nerwu nóżkowego w skorupce brzusznej. Okazy z Polski charakteryzuje ponadto występowanie dobrze wykształconego stadium larwalnego muszli. Jest on nieco poprzecznie owalny w zarysie i osiąga przeciętnie 0,42 mm długości. Muszla larwalna jest wyraźnie wyodrębniona z tyłu i z boków, natomiast w części przedniej oddziela ją od reszty muszli jedynie silniej zaznaczona linia przyrostowa. Z zewnątrz muszla larwalna pokryta jest delikatnymi koncentrycznymi liniami przyrostowymi, choć w wyjątkowych przypadkach zachowuje się również odcisk struktury periostrakum (Fig. 3M, N).

W części apikalnej muszli larwalnej daje się zaobserwować występowanie koncentrycznego pierścienia przyrostowego (zaburzenie wzrostowe), które wyodrębnia w rezultacie najwcześniejsze stadium wzrostowe muszli. Ten region muszli larwalnej osiąga 0,15–0,20 mm szerokości. Świadczy on, że w rozwoju ontogenetycznym dewońskich trematidów występowało zróżnicowanie na stadium wczesno- i późnolarwalne, lub też na stadium emrionalne (*protegulum*) i larwalne (u współczesnych dyscinidów takie zróżnicowanie w obrębie muszli larwalnej nie występuje).

Z famenu Łagowa opisano też pięć silnie ornamentowanych koncentrycznie skorupek reprezentujących zapewne nowy rodzaj z rodziny Trematidae; zbyt skąpy materiał nie pozwala jednak na pełne zdefiniowanie taksonomiczne tej formy.