

# Evolution of the embryonic development in lingulid brachiopods

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The style of embryonic development in the lingulids has changed through time; that of Recent lingulids is not primitive for the group. The shell of Devonian lingulids consists of two valves already at the embryonic stage, whereas in Recent lingulids the protegulum originates as a single plate, subsequently folded in two. The protegulum of the Devonian lingulids is a cup-shaped, subcircular plate, usually with a characteristic radial sculpture suggesting the presence of marginal setae, similar to those occurring in early juvenile stages of Recent discinids. Devonian protegula are 81 to 100  $\mu\text{m}$  in width and thus are three times smaller than protegula of the Recent *Lingula* and *Glottidia*, and twice as small as those of the Late Cretaceous *Lingula* sp. The embryonic development of lingulids underwent important modification during last 370 Ma.

**Key words:** Lingulidae, protegulum, ontogenetic development, Late Devonian.

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## Introduction

Our knowledge of the embryonic development of lingulid brachiopods is based exclusively on extant species. Although some brachiopods secrete their first exoskeleton as early as the embryonic stage, findings of truly embryonic fossil shells are usually questionable. Most records actually correspond to the postembryonic stages of growth (Popov *et al.* 1982: pp. 102–103; Rowell 1986: p. 1056; Holmer 1989: p. 52). The supposed protegulum, in a strict sense, was recorded in the Ordovician discinid *Trematis elliptopora* Cooper, 1956 (Chuang 1971b) and in the Middle Ordovician acrotretid *Eoconulus* cf. *semiregularis* Biernat, 1973 (Holmer 1989). On the other hand, fossilized larval (postembryonic) shell has been frequently recorded in different stocks of inarticulate brachiopods. Several papers have been published describing details and peculiarities of the larval shells (e.g., Biernat & Williams 1970; Ludwigsen 1974; Popov *et al.* 1982; Holmer 1989).

The larval shell is easily recognizable in the studied Late Devonian lingulids (Figs 1A, B, 2A, B, D). It is clearly delineated from the rest of the valve (postlarval) especially at its posterior margin, where conspicuous growth disturbance is seen, caused by an interruption of the shell deposition (e.g., Figs 1B–F, 2E, F). This change in the secretional regime undoubtedly reflects a change from free-swimming (larval) to sedentary (postlarval) modes of life. The length of the larval shell in studied lingulids ranges from 320 to 560  $\mu\text{m}$  and closely corresponds to the dimensions of larval shells in many fossil lingulaceans (Holmer 1989: p. 59).

Most intriguing, however, is the apical part of the larval shell where a tiny, uniquely structured, cup-shaped subcircular plate developed (Figs 1–3). The plate is interpreted here as the embryonic shell, i.e. protegulum, as defined by Beecher (1891) and Chuang (1971a, b). Most probably it was secreted by the embryo just prior to hatching from the vitelline membrane. The major difference in topography between the protegulum and larval shell may reflect a change from embryonic lecithotrophic to larval planktotrophic mode of life. This is the first record of embryonic shell in fossil lingulids.

## Material

The protegular stage of the shell has been studied in lingulid brachiopods from several horizons of the Upper Devonian of the Dębnik anticline (southern Poland) and Holy Cross Mountains (central Poland). Thirteen well-preserved dorsal protegula have been revealed among those specimens (Tables 1, 2). Additional 23 dorsal and 10 ventral protegula, although not so well preserved, have provided an important contribution to the present research. All specimens are from samples dissolved in acetic acid. The specific or even generic identification of the studied specimens has not been possible because all are crushed. Fortunately, the posterior parts of both valves, which are thick and resistant are most frequent in samples. Several specimens reveal a distinctly punctate shell substance – the feature characteristic of the genus *Lingulipora* (Baliński 1985; Table 1). Non-punctate specimens were identified as *Lingula* s.l., and are referred to '*Lingula*' below (Table 2). Seven specimens of *Lingula* sp. from the Late Cretaceous of Mielnik (eastern Poland) have been studied for comparative purposes (Table 3). 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.

## Description of embryonic shell

**Dorsal protegulum.** — Dorsal protegulum of the Late Devonian '*Lingula*' and *Lingulipora* is a subcircular structure with slightly blunt and expanded posterior margin (Figs 1, 2, 5). The width of protegulum ranges from 81 to 100  $\mu\text{m}$ . Its maximum length is less than its width and ranges from 64 to 89  $\mu\text{m}$ . Thus, the index of length is 79 to 97% (mean = 86%; see Tables 1–3). The protegulum is a convex structure, but its central region is frequently concave or flattened (Figs 1B–E, 2B–E). This region is usually seen as a circular central depression bordered at its periphery by a rounded and very weak rim (Fig. 1C–F). The height of the protegulum reaches 25  $\mu\text{m}$ . The most

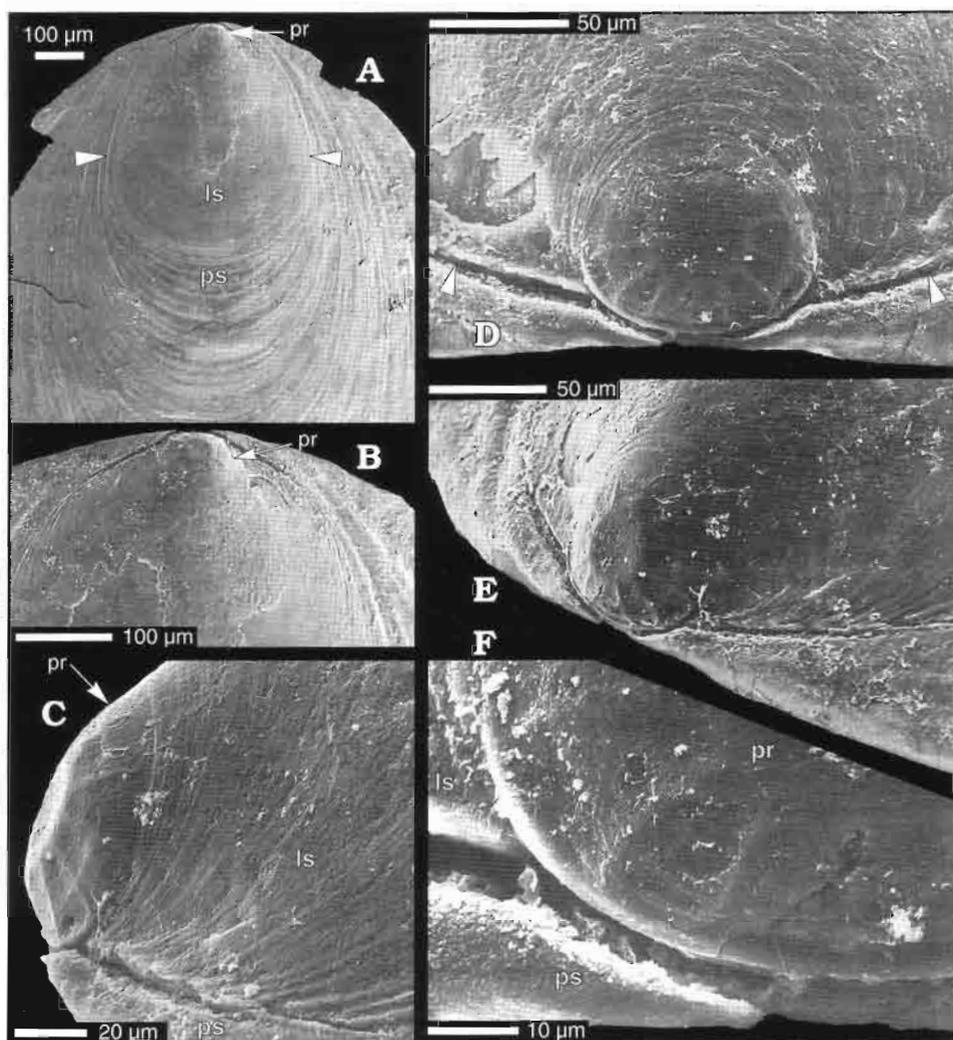


Fig. 1. A–F. Brachial valve of *Lingulipora* sp., Late Devonian, southern Poland, Dębnik, trench Z-6, ZPAL Bp MsI/25-6. A. General exterior view of the valve showing protegulum, larval and post-larval shell; periphery of the larval shell marked with white triangles. B. More detailed view showing location of protegulum. C–E. Lateral, posterior, and postero-lateral view of the protegulum showing radial ribs, central depression, and marginal rim; note also a distinct boundary between posterior margin of the larval shell and the post-larval shell (marked with white triangles in D). F. Detailed view of posterior part of the protegulum showing the thickened marginal rim. *ls* – larval shell, *pr* – protegulum, *ps* – post-larval shell.

striking character of these dorsal protegula is their distinct radial sculpture. It consists of thick, rounded radial ribs which start at the rim of the central depression and extend almost to the margin of the protegulum, where they reach a thickened marginal rim (Figs 1C–F, 2B–E). The marginal rim is especially well exposed at the posterior part of the protegulum. In the anterior part, the marginal rim is gradually embedded in

post-embryonic shell. The radial ribs are distributed more or less symmetrically on both sides of the protegulum. They are best delineated in lateral and posterior parts of the protegulum. Those in anterior part are very weak and usually difficult to trace. In exceptional cases, well preserved protegula do not reveal any radial ribs (Fig. 2G, H). Their number varies from five to six pairs.

Table 1. Dimensions of dorsal protegula of *Lingulipora* sp. from the Late Devonian of the Dębnik anticline (southern Poland) and Holy Cross Mountains (central Poland). SD – standard deviation.

Cat. No ZPAL Bp	XLI/1-2	XLI/6-10	MsI/25-6	XLI/6-1	XLI/6-2	XLI/4-20	mean	SD
Length (µm)	64	65	73	80	88	89	76.5	4.9
Width (µm)	81	81	83	94	100	92	88.5	3.6
Length : Width (%)	79	81	88	85	88	97	86.3	3.1

Table 2. Dimensions of dorsal protegula in '*Lingula*' from Late Devonian of the Dębnik anticline (southern Poland) and Holy Cross Mountains (central Poland).

Cat. No ZPAL Bp	XLI/2-4	MsI/1-4	XLI/2-2	XLI/4-10	XLI/4-5	XLI/4-8	XLI/6-8	mean	SD
Length (µm)	70	72	75	78	80	80	88	77.6	6.7
Width (µm)	86	85	85	90	90	100	100	90.1	5.6
Length : Width (%)	81	85	88	87	89	80	88	85.4	3.3

Table 3. Dimensions of dorsal protegula in *Lingula* sp. from the Late Cretaceous of Mielnik (eastern Poland).

Cat. No ZPAL Bp	XLI/5-21	XLI/6-15	XLI/5-13	XLI/5-18	XLI/5-17	mean	SD
Length (µm)	130	130	(130)	140	160	138	6.5
Width (µm)	170	200	210	210	200	198	8.2
Length : Width (%)	76	65	62	67	80	70	3.8

Apart from the sculpture described above, the external surface of the studied protegula is usually smooth. Some of exceptionally well-preserved specimens show original microtopographic features, such as densely packed depressions or pits up to 3.5 µm in diameter (Fig. 2G, H). These can be interpreted as an imprint of a disintegrated periostracum and may reflect traces of intercellular boundaries. Some protegula show characteristic arched drapes (Fig. 2F). Similar structures were described on the shell surface of the Carboniferous *Lingula squamiformis* Phillips, 1841 and were interpreted as deformation formed by stress couples between periostracum, primary layer and underlying outer mantle lobe (Cusack & Williams 1996).

**Ventral protegulum.** — The ventral protegula of the studied specimens are less well preserved than the dorsal ones. Apparently during life of the animal the ventral protegulum was exposed to more intense mechanical wear. Whereas the dorsal protegulum could be well protected by the thickened and frequently elevated margin of the valve (Fig. 2G), the ventral protegulum occupied the most apical position and was gradually worn out. In effect, posterior margins of the ventral protegula are never preserved in pedicle valves studied; instead, they show distinct traces of mechanical abrasion (Fig. 3A–D). This may be explained, at least in part, by the infaunal mode of life of Devonian lingulids.

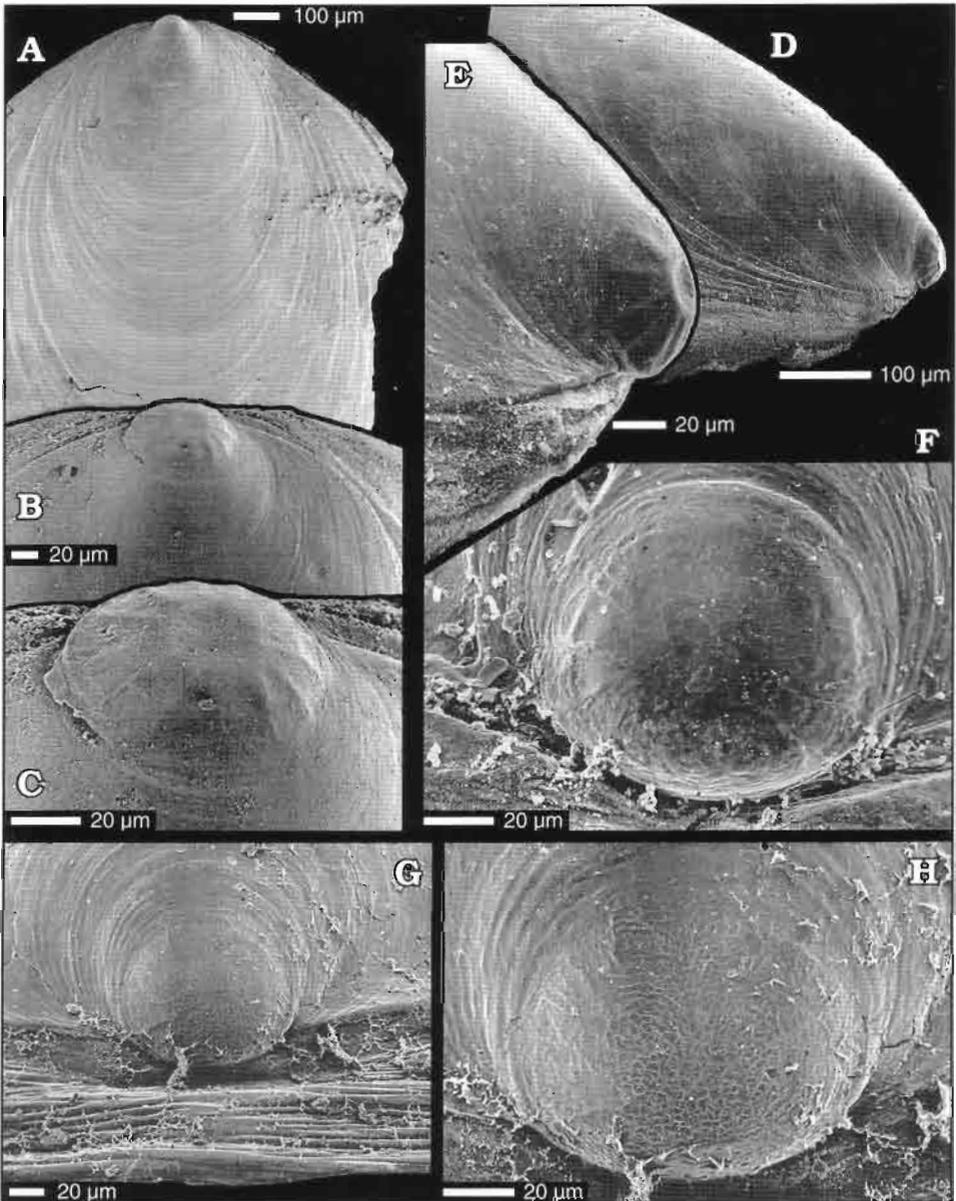


Fig. 2. A–E. Brachial valve of '*Lingula*', Late Devonian, southern Poland, Dębnik, locality PG (see Baliński 1995), ZPAL Bp Msl/12-4. A–C. General view and two close-ups of the posterior part of the valve showing location of protegulum and its morphological details. D, E. Postero-lateral views of the same specimen showing well-developed radial ribbing and central depression of the protegulum; note also a distinct boundary between the larval and post-larval shells. F. Dorsal protegulum of *Lingulipora* sp., Late Devonian, Holy Cross Mts, Jabłonna, ZPAL Bp XLJ/4-20; note a weakly-developed radial ribbing and strong concentrically disposed arched drapes, the most probably formed by stress couples between periostracum, primary layer, and underlying outer mantle lobe. G, H. General and detailed view of the protegulum of *Lingulipora* sp., age and locality as in F, ZPAL Msl/21-8. Note a thickened posterior margin of the post-larval shell protecting protegulum from mechanical abrasion and well-preserved surface of the protegular shell with imprints of the intercellular boundaries.

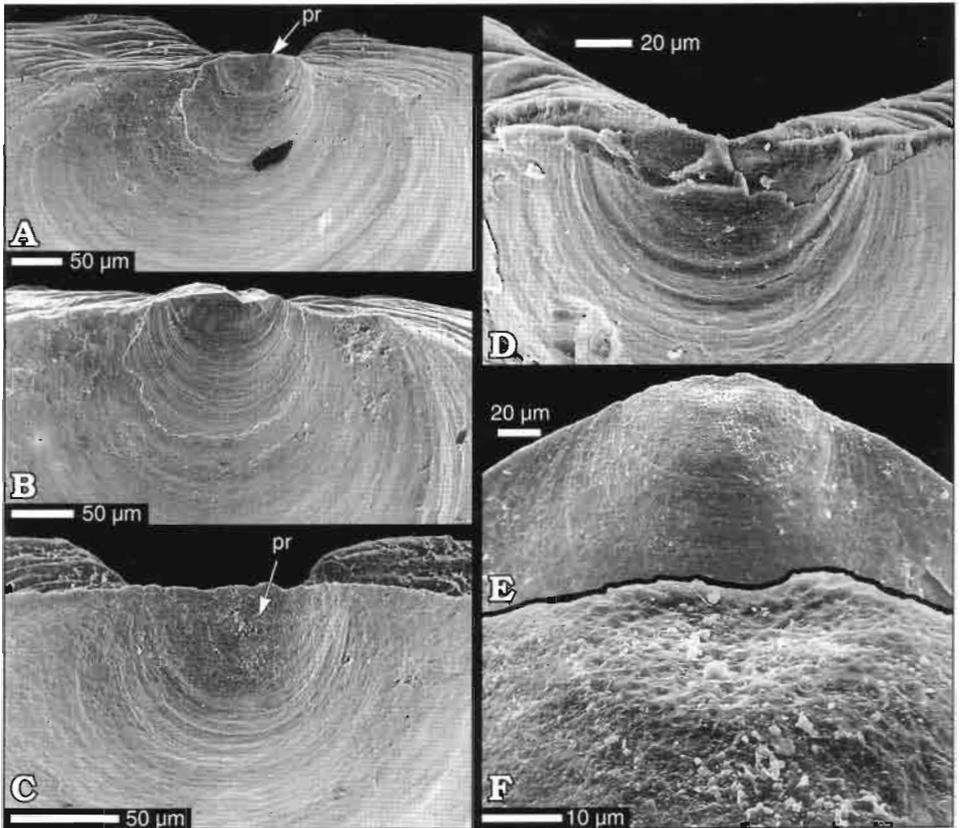


Fig. 3. A–D. Postero-ventral view of the ventral protegula of *Lingulipora* sp. showing different degree of their mechanical abrasion, ZPAL Bp XLI/3-2, 5-23, 5-24, and 4-14. E, F. General and more detailed ventral views of the ventral protegulum of *Lingulipora* sp. (same as in C) showing poorly preserved, supposed traces of imprints of the intercellular boundaries. Late Devonian, Holy Cross Mts, Jabłonna. *pr* – protegulum.

The preserved antero-lateral margin of ventral protegula is regularly arched. Characteristic radial ribs, similar to those from dorsal protegula are seen in one fragmentarily preserved ventral protegulum of *Lingulipora* sp. Other features characteristic for the dorsal protegulum (central depression and pitted surface) have been sporadically observed in ventral protegula (Fig. 3E, F).

The maximum width (80 to 98  $\mu\text{m}$ ) as well as convexity (25  $\mu\text{m}$ ) of the available ventral protegula precisely corresponds to the measurements of the dorsal protegula.

## Discussion

It is generally accepted that lingulid brachiopods are extreme evolutionary conservatives and the genus *Lingula* is traditionally quoted as an example of a 'living fossil'.

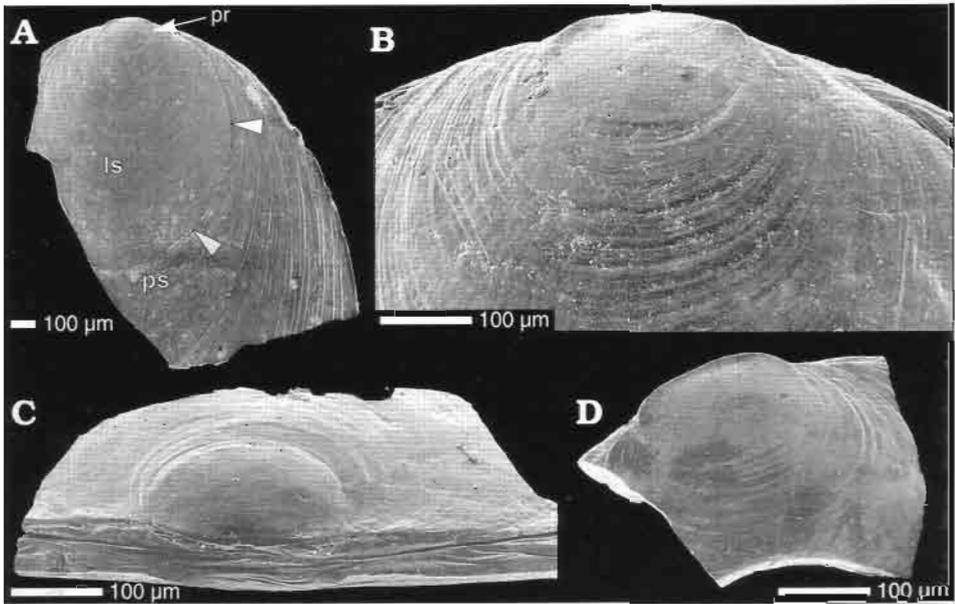


Fig. 4. A–D. *Lingula* sp., Late Cretaceous, eastern Poland, Mielnik. A, B. General and more detailed views of a fragment of the brachial valve showing well delimited larval shell (marked with white triangles) and the protegium, ZPAL Bp XLI/5-13. C. Posterior view of a fragment of the brachial valve with preserved protegium, ZPAL Bp XLI/5-17. D. Dorso-lateral view of a small fragment of the brachial valve with protegium. ZPAL Bp XLI/5-21. *ls* – larval shell, *pr* – protegium, *ps* – post-larval shell.

One might thus expect, that the structure of protegium of Devonian lingulids would not differ from those of Recent taxa. This, however, is clearly not the case.

The protegula of the Late Devonian '*Lingula*' and *Lingulipora* show some fundamental differences in comparison to the embryonic shell of living *Lingula* and *Glottidia*. In his statistical study, Chuang (1962) found that the width of protegium in *Lingula unguis* from the coasts of Singapore Island ranges from 232 to 300 µm. Yatsu (1902: p. 36) measured the maximum width of the protegium of *Lingula anatina* along its posterior straight edge and obtained 280 µm on average. These data demonstrate that the embryonic shell in the studied Late Devonian lingulids was as much as three times smaller than that in the extant relatives. The Late Cretaceous lingulids from Mielnik (eastern Poland; see Bitner & Pisera 1979) reveal intermediate dimensions of protegium; they are illustrated here for comparison in Fig. 4. In these brachiopods, the protegium ranges from 170 to 210 µm in width, i.e. it is twice as large as that in the Late Devonian lingulids.

Even more important is the difference between the studied Late Devonian and Recent lingulid protegula in the details of their morphology. As noted by Yatsu (1902: pp. 32, 33), the first embryonic shell in *Lingula anatina* is secreted as a single circular lamella which is folded over along one of its diameters and is then divided to form a dorsal and a ventral half. In consequence, the dorsal and ventral protegula are semicircular in outline and have straight posterior edge (Fig. 5; Yatsu 1902: pl. 5: 73, 77; Ashworth 1915: pl. 4: 1–6; Paine 1963: fig. 5). In contrast, the dorsal protegula of

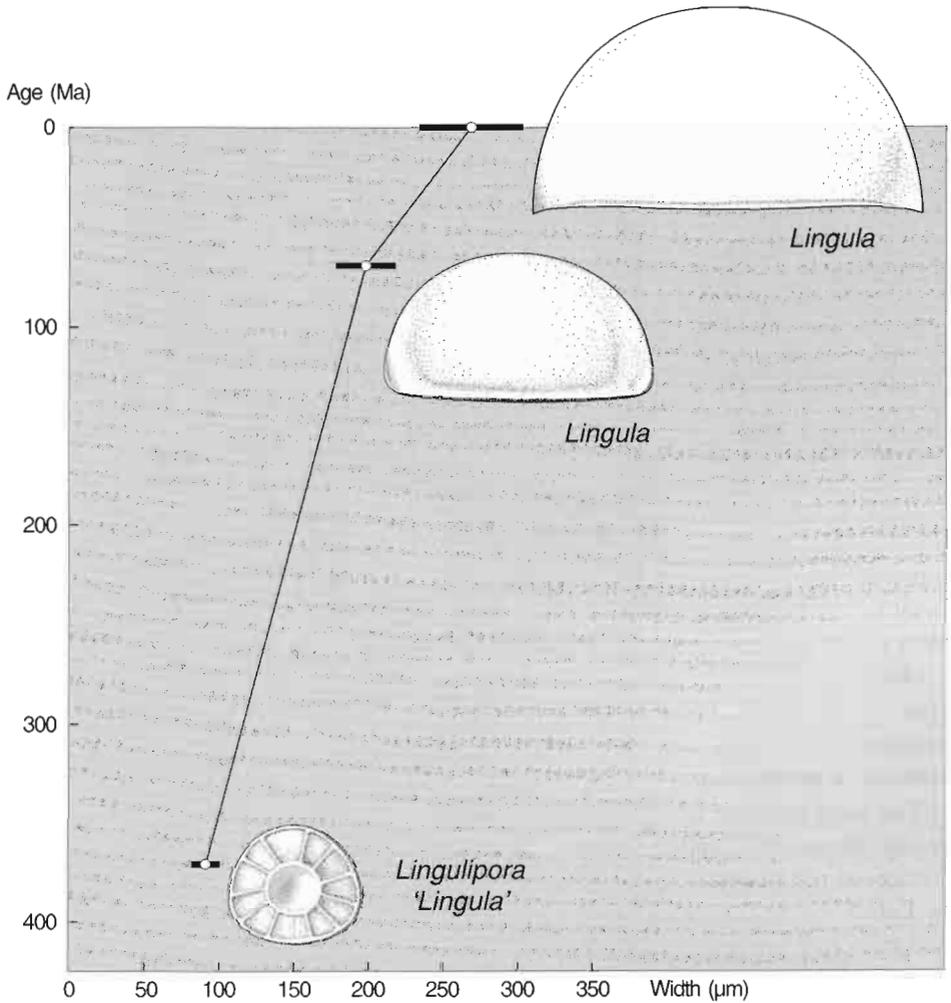


Fig. 5. Comparison of the general morphology of the protegula of the Late Devonian, Late Cretaceous, and Recent lingulid brachiopods. Morphology of Recent protegulum mainly after Yatsu (1902), Paine (1963), and Chuang (1983).

the Late Devonian lingulids are subcircular, with broadly arched posterior margins. As noted above, the studied ventral protegula lack the posterior region because it has been progressively abraded during life of the animals. There is no reason to believe that they were of basically different shape than dorsal protegula. Thus, immediately after hatching, the larvae of Devonian lingulids possessed certainly two separate, ventral and dorsal, protegula. This basic difference between fossil and Recent protegula suggests that during 370 Ma since the Devonian Period, the embryonic development of these brachiopods has undergone an important gradual change (Fig. 5).

The subcircular outline and very well developed posterior and marginal rim in the Late Devonian protegula suggest that there were two separate secretional areas of the

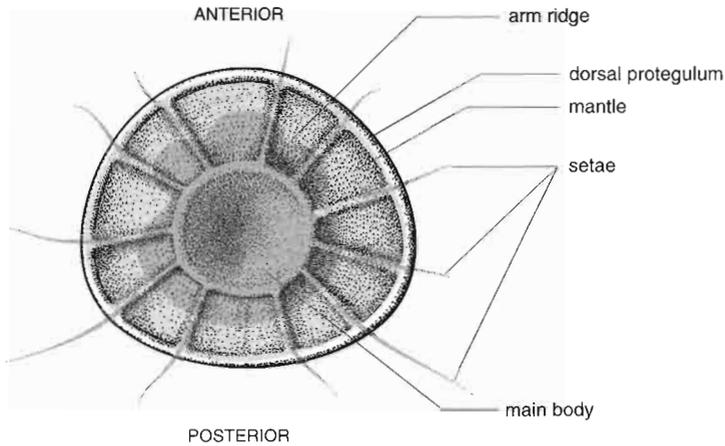


Fig. 6. Hypothetical reconstruction of the main anatomical features of the embryo of the Late Devonian lingulids; dorsal view.

embryonic shell. These areas reflect an early mantle differentiation into ventral and dorsal lobes. In the course of evolution, the shell secretional areas have been unified into a single area, as it is exemplified by Recent *Lingula*. Later in ontogeny, this area is folded into two parts and a furrow develops separating dorsal and ventral mantle lobes (Yatsu 1902: p. 31–33, pl. 4: 60–64). In other words, during the course of evolution, the formation of the mantle lobes underwent retardation in relation to the secretion of protegulum.

The most peculiar feature of the Late Devonian protegula is their surface topography. The central depression and radial ribs have no equivalents in neither the Late Cretaceous nor Recent lingulid protegula. The different topography of the protegula in the Late Devonian lingulids most probably reflects some anatomical differences of their embryos. Perhaps the radial sculpture of protegulum is related to disposition of setae similar to those occurring in embryonic and larval stages of Recent *Pelagodiscus* and *Discinisca* (Blochmann 1880; Ashworth 1915; Chuang 1977; Hammond 1980; Long & Stricker 1991). The radial ribs may reflect internal grooves which accommodated the embryonic setae. Williams & Holmer (1992: p. 680, pl. 7: 6) noted that periostracum of Recent *Discinisca striata* (Schumacher) may be indented on its inner surface by radial grooves accommodating the outer surfaces of adpressed setae. The radial ribs of the Late Devonian protegula may also indicate a disposition of radially arranged muscles serving the setal follicles. The arrangement of these muscles is well-known in post-embryonic stages of Recent *Lingula* (Williams & Holmer 1992: pp. 687–689, fig. 12). The more or less constant number of radial ribs on Late Devonian protegula suggests that there were five or six pairs of long embryonic setae (Fig. 6). The first setae and the protegulum were formed by the embryo probably at the end of the embryonic stage, just before hatching from its vitelline membrane. The arrangement of setae is reminiscent of the condition in Recent discinids. Juvenile stage of discinids is characterized by a succession of several kinds of more or less radially disposed long setae (Ashworth 1915: p. 60, pl. 5: 11; Hammond 1980: pp. 650–652,

figs 1–3; Chuang 1983: p. 231, figs 12, 13). If the presence of the early juvenile setae in discinids is a plesiomorphic feature, then the proposed presence of embryonic setae in the Devonian lingulids suggests that in the Paleozoic the earliest ontogenetic stages of these two brachiopod stocks were much more similar than they are now.

In Recent lingulids, however, setae of this kind are absent. According to Yatsu (1902) and Paine (1963) the first setae in *Lingula* and *Glottidia* appear as late as at the end of larval stage, i.e. just prior to settlement. They appear along the entire mantle margin. These very short and very densely distributed mantle setae certainly cannot explain the radial sculpture of the embryonic shell in the Devonian lingulids.

The function of hypothetical embryonic setae in the Devonian lingulids, as well as of those in Recent discinids, remains unclear. It is possible that they may help in keeping the proper orientation of a newly hatched swimming larva, although their sensory function cannot be excluded.

## Conclusions

The uniquely structured fossil protogula revealed evident morphological differences between them and those in Recent *Lingula* and *Glottidia*. This suggests fundamental anatomical difference between the embryonic stages of Late Devonian and Recent lingulids. So basic evolutionary modification of their embryos contradicts the common opinion that the lingulid brachiopods are extremely conservative evolutionarily. It thus supports Bassett (1986) and Biernat & Emig (1993) who questioned the long stratigraphic range of the genus *Lingula* (but see Williams 1977).

It seems obvious that more paleontological data are needed to trace the process of gradual morphological modification of lingulid embryonic shell. Especially valuable would be information on the lingulid protogula from the post-Devonian to Late Cretaceous interval.

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## Ewolucja rozwoju zarodkowego u lingulidów

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### Streszczenie

Na kilkudziesięciu okazach lingulidów z późnego dewonu antykliny Dębnika i Gór Świętokrzyskich stwierdzono występowanie okrągławej, wypukłej tarczki o szeroko-

ści 81–100  $\mu\text{m}$  usytuowanej w najbardziej apikalnej części obu skorup. Tarczka ta jest wyraźnie odgraniczona od muszli larwalnej. Brak jest na niej koncentrycznych linii przyrostowych charakterystycznych dla muszli larwalnej i postlarwalnej. Nie ulega wątpliwości, że tarczka ta odpowiada muszli zarodkowej, czyli protegulum. Jest to pierwszy przypadek tak dobrego zachowania protegulum u kopalnych lingulidów. W porównaniu z protegulum współczesnej linguli i glotidii jest ono trzy razy mniejsze, a ponadto charakteryzuje się szczególną morfologią, na którą składają się promieniste fałdki, centralnie usytuowana wklęsłość oraz wałeczkowato zgrubione brzegi. Również protegula późnokredowych lingul odbiegają znacznie od muszli zarodkowej form późnodewońskich (Fig. 5). Można przypuszczać, że różnice w budowie muszli zarodkowej odzwierciedlają różnice w szczegółach anatomicznych stadium embrionalnego późnodewońskich, późnokredowych i współczesnych lingulidów. Zapewne więc w czasie ostatnich 370 milionów lat rozwój zarodkowy lingulidów uległ znacznej modyfikacji, co podważa dość powszechnie przyjmowany pogląd o wyjątkowym konserwatywnie ewolucyjnym tej grupy ramienionogów.