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GEOLOGY

The First Finds of Larval Shells in Ordovician Orthids

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The paper considers the first discovered larval shells of Rhynchonelliformea brachiopods from the Lower Ordovician of the Leningrad region. Casts of larval shells on the pedicle and brachial valves are characterized by a different relief, probably representing the cast of a soft larva body. Early Paleozoic Rhynchonelliformea presumably had planktotrophic long-floating larvae.

The following three subtypes are recognized in the recent brachiopod classification: Linguliformea, Craniiformea, and Rhynchonelliformea (see [1]). The modern representatives of all three subtypes have larvae that substantially differ in morphology and life mode. When a Linguliformea larva hatches from the envelope, it has all the features typical of the adult animal and an embryonic shell (or protegulum). During prolonged (approximately 1-month) evolution in the water column, the newly formed larval shell grows somewhat obliquely relative to the protegulum. The embryonic shell is separated from the its larval counterpart in a growth ring that is related to the change in life mode. Both shells are organic formations. After settling on the basin floor, the larva forms an adult mineral shell that is usually separated from the larval one by conspicuous growth rings (halos). Thus, Linguliformea demonstrate three types of shell, corresponding to the embryonic (or protegulum), larval, and adult stages. The adult shell also grows beneath the soft larval shell. If the shell retains structural features of the larval morphology, the mineral shell can become its internal cast. The embryonic and larval shells of modern brachiopods are usually up to 100 and approximately 300–400 μm across, respectively [1].

Larvae of the Craniiformea and Rhynchonelliformea subtypes are lecithotrophic formations with a planktonic period of approximately 1 day. They are metamorphosed after settlement. Although the larvae of these subtypes have several substantial morphological differences, both are characterized by the presence of a gullet, absence of a mouth, and formation of a calcareous shell only after metamorphism. Thus, recent forms of Craniiformea and Rhynchonelliformea have only shells of the adult type.

Recent craniids lack even prerequisites for the formation of larval shell in ontogenesis. Nevertheless, indications of a larval shell have been discovered in fossil Paleozoic and Mesozoic craniids [2]. This suggests that representatives of all three brachiopod subtypes had larvae that had a prolonged planktonic existence and were protected by a shell at least, in the Paleozoic [2]. However, it should be noted that such observations have been made only for craniids and that the morphology of recent Rhynchonelliformea larvae rules out the formation of an external larval shell.

The casts of orthid larval shells confirming the possibility of changes in the morphology of Rhynchonelliformea larvae since the Paleozoic were first found in the Middle Ordovician of the Leningrad and Pskov regions. Juvenile orthid and clitambonitid forms with a minimal size of 0.5 mm have been obtained from clays of the Volkhov and Kundas stratigraphic units. In some orthid (five pedicle and approximately one hundred brachial valves) and clitambonitid (three pedicle valves) shells, the apical area is located obliquely relative to the rest of the shell. This area, which is approximately 400 μm across, bears no growth lines and is separated by halo rings from the main shell. The location, dimensions, and characteristic relief of the area, as well as the presence of halos, suggest that the apical area is an internal cast of the organic larval shell. The juvenile shell is characterized by a fibrous microstructure (Fig. 1h). The visible length and width of fibers are approximately 50 and 10 μm, respectively. Despite insignificant variations in dimension and shape, the structures of the larval shell in the pedicle and brachial valves of orthid and clitambonitid shells are generally similar.

Pedicle shells of orthids have a smooth slightly elevated apical area, approximately 400 μm wide and up to 200 μm long, separated by one or two halo rings from the main shell (Figs. 1a, 1b). The apex, in some species, can be shaped as a thin tube up to 100 μm long that surrounds a pedicle foramen (Fig. 1a). The insignificant

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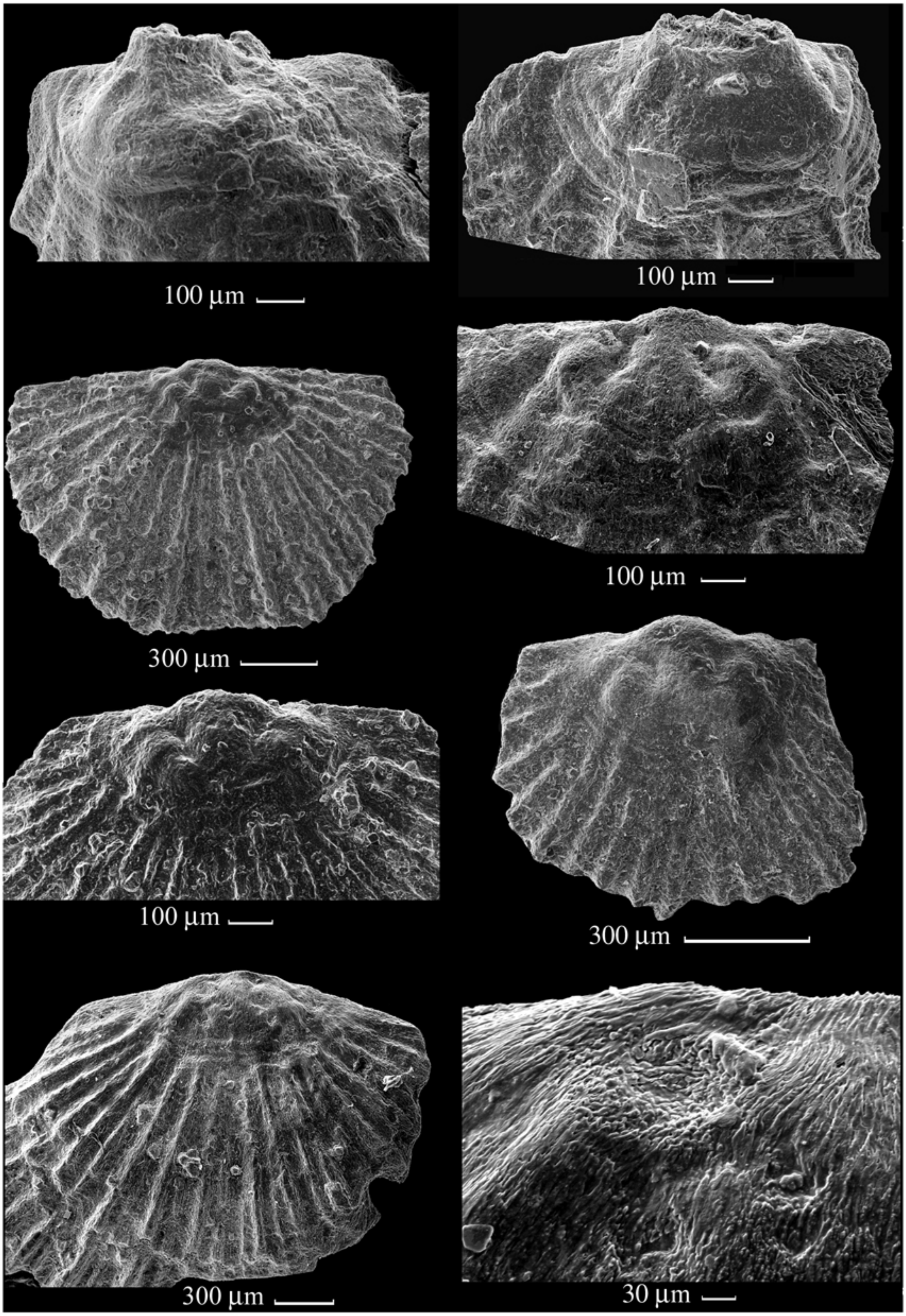

Fig. 1. Structure of orthid larval shells. (a) *Orthis* sp. Specimen 4921/40. Hereinafter, Lynna River, riverside precipice 0.5 km away from the river inflow into the Syas River; Lower Ordovician, lower subunit of the Kundas stratigraphic unit. (b) Pedicle valve (suborder Clitambonitidina). A notch in the anterior part of the shell is visible. Specimen 4921/49. (c) *Notorthis penetrabilis* Rubel, brachial valve. Specimen 4921/41. (d) *Orthis* sp., brachial valve. Specimen 4921/42. (e) *Notorthis* sp., brachial valve. Specimen 4921/43. (f) *Orthis* sp., brachial valve. Specimen 4921/44. (g) *Orthis* sp. A fragment of the larval shell cast surface on a brachial valve with small tubercles. Specimen 4921/46. (h) *Orthis* sp., brachial valve. A fragment of the central elevation with separating depression. Specimen 4921/45.

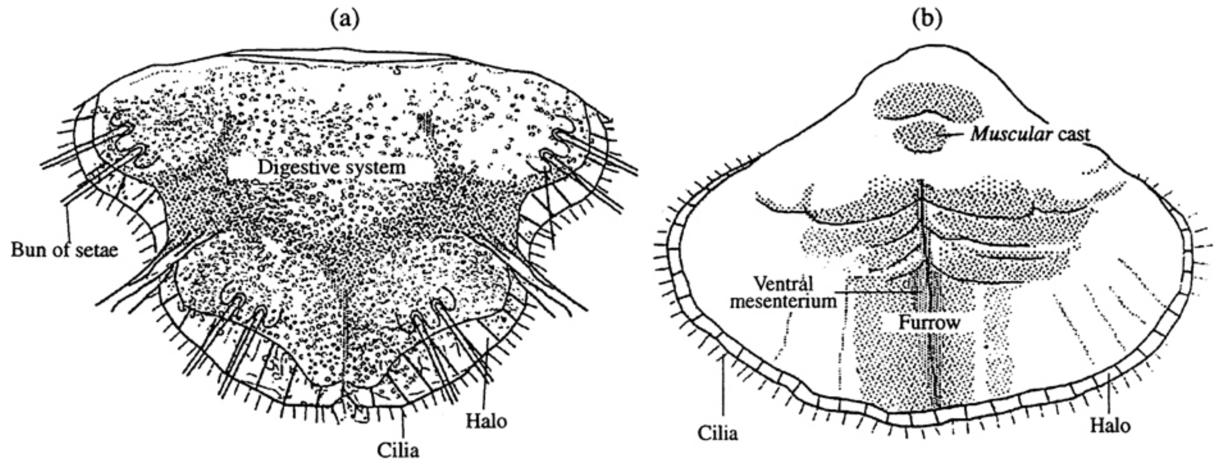

Fig. 2. Probable reconstruction of the soft body structure in *Micromitra* cf. *ornatella* larva based on casts of the larval shell: (a) brachial valve, (b) pedicle valve (after Williams *et al.*, 1998).

number of pedicle valves is most likely explained by a grinding of their back parts related to the growth peculiarities of the curved beak-shaped apex.

The structures of larval shells in the brachial valves of all species are similar (Figs. 1c–1e). The middle part of the shell includes a wide and low T-shaped ridge, with the short segment having the form of an apex. The anterior edge of the ridge widens in some species and narrows in others. The ridge is bordered on both sides by two (*Orthis* sp.) or three (*Nothorthis penetrabilis*) tubercles separated by pits or furrows, depending on their degree of development. The tubercles can merge near the anterior edge of the ridge. The apical area can rise above the shell surface as high as 20 to 50 μm. Halo rings are sometimes missing. The surface of some well-preserved larval shells is entirely or partly covered by small tubercles approximately 5 μm high (Fig. 1g). G.T. Ushatinskaya interpreted similar tubercles as being negative casts of a destroyed organic shell with a reticular internal surface [3]. Other authors have interpreted a similar relief in the apical parts of juvenile shells of recent terebratulids as an artifact [4].

Although larval shells probably represent real casts of their soft bodies, reconstructing them is difficult because of the absence of features shared with the larvae of recent brachiopods. It is most similar to a reconstruction proposed for the larval soft body of paterinids [5]. The anterior part of the pedicle valve in the paterinid larval shell bears a notch that is identical to that observed in Specimen 4921/49 (Fig. 1b), whereas brachial shells in both types of larval shells are characterized by similar systems of convexity (Fig. 2) [5]. If both groups had similar larvae in the Early Paleozoic, the above observation can serve as an additional argument in favor of a monophyletic origin for brachiopods with phosphate and carbonate shells. It is worth noting that the only known fossil lingulid embryonic shells also differ from their recent counterparts [6], probably suggesting coenogenetic transformations in lingulid phylogenesis.

The finds of casts of orthid and clitambonitid larval shells suggest that Early Paleozoic Rhynchonelliformea had feeding larvae that floated, like the larvae of recent lingulids, using lophophore cilia. Light one-layer larval shells protected the larvae and were not burdensome when floating. It is probable that the pits and furrows at the external surface of the shell correspond to muscle-attachment areas, whereas the tubercles correspond to the digestive system and paired coeloms. Thus, the muscular system could include both diductors and adductors. However, one can confidently make assumptions about only the metameric structure of larvae. The structure of the orthid ventral shell implies the presence of pedicle segments in their larvae. The existence of planktotrophic larvae in Rhynchonelliformea is also indirectly confirmed by the presence of nerve plates and a digestive tract in the larvae of recent forms. Such structures are unnecessary for lecithotrophic larva, and their presence can most likely be explained by the inheritance of some features from larvae of a different type (V.V. Malakhov, 2001, private communication). It is also important that the ontogenesis of recent Linguliformea and Craniiformea is characterized by an embryo that is folded in two, with subsequent formation of a shell (this stage is lacking in the development of Rhynchonelliformea). Based on the position of some structures, Malakhov [7] assumed that the Rhynchonelliformea ontogenesis lacks a folding stage and that this is responsible for development of the third segment (a mantle in recent larvae); i.e., the development of recent brachiopods shows signs of coenogenetic transformations.

All three subtypes of Early Paleozoic brachiopods probably underwent the ontogenetic stage of floating larva, which was subsequently lost by forms with carbonate shells. This is probably because of migration of these forms to deeper habitat environments. The planktotrophic larva has more advantages in shallow-water environments, in which most brachiopods were embossed by bivalves. In any case, brachiopods with carbonate shells were forced to develop lecithotrophic larvae of the current type under unfavorable conditions. Thus, the transition to lecithotrophic larvae represents embryonic adaptation.

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