Deltidial Coverings of Middle Ordovician Clitambonitidines (Clitambonitidina, Brachiopoda) and Their Significance for Attachment to the Substrate

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Abstract—The growth and microstructure of deltidial covering plates of Lower and Middle Ordovician Clitambonitidines from Estonia and Leningrad Region are reviewed. In the genera *Anchigonites, Antigonambonites, Vellamo,* and *Estlandia,* the fusion of deltidial plates was followed by the formation of both the symphytium and the tube covering the pedicle. Subsequently, the end of the tube was sealed with the apical disc, which supposedly provided cementation to the substrate.

*Key words*: Clitambonitidina, Ordovician, deltidium, symphytium, cementation.

In the new edition of *Treatise…* (2000), the order Billingselida comprising the suborders Billingselidina Schuchert, 1893 and Clitambonitidina Öpik, 1934 (Williams and Harper, 2000) was established in the class Strophomenata. The diagnosis of this order includes a high interarea with a convex deltidium that is continued by the chilidium, the apical foramen, and the absence of pedicle muscles, or adjustors (Wright and Rubel, 2000). On the threshold of the publication of the new Treatise, clitambonitidines were studied by Wright and Rubel (1996), who supposed that the clitambonitidines had a deltidium (a plate formed by the fusion of two deltidial plates with a visible junction trace) rather than a pseudodeltidium (a single convex plate without a junction trace that forms the apical foramen). The junction trace is usually clearly seen in young shells; however, no such material was studied, and the authors questioned this assumption.

At the early development stages, the clitambonitidines are assumed to have used their pedicle for attachment. Subsequently, the delthyrium may have remained open, as in the genus *Oslogonites* Öpik, 1939, or was partially closed as in *Apomatella* Schuchert et Cooper, 1931. In this case, the apical foramen is retained, which also suggests an attached mode of life. In the genus *Kullervo* Öpik, 1932, the pseudodeltidium may have formed a distorted, collarlike tube with the foramen at its end (so-called foramen with a lip). In many genera (*Clitambonites* Pander, 1830, *Clinambon* Schuchert et Cooper, 1932, *Estlandia* Schuchert et Cooper, 1931), the foramen was sealed or became filled with the sec-

ondary shell substance, which may serve as evidence of transition to a free-lying mode of life (Wright and Rubel, 2000). Öpik (1934) described a specimen of *Antigonambonites planus* (Pander, 1830) with a cork plugging the foramen that had a scar formed, in the opinion of the author, as the result of attachment to the substrate. This specimen was figured by Williams (1965, text-figs. 225, 4d). The present paper is based to a large extent on the work of Sir Alwyn Williams, whose death on April 4, 2004 was a great loss to Paleontology.

Considerable attention has always been given to the study of the formation of the structures framing the pedicle opening in brachiopods; however, only with the use of scanning electron microscopy (SEM) did it become possible to reveal the mechanism of the formation of such structures and to appreciate their value for systematics. Williams and Hewitt (1977) demonstrated with modern terebratulids and rhynchonellids the presence of two types of epithelium (pedicle and outer epithelium) and showed that the formation of the deltidial plates was a result of a secretory activity of ventral and dorsal mantle lobes fused in the posterior part of the shell.

In the course of the growth, the position of the junction migrates into the delthyrial cavity across the secondary fibers, which became realigned. This surface is usually covered with a thin layer of microcrystalline calcite. This entire structure is called the pedicle collar. The paired ends of the ventral lobe of the mantle continue growing mediodorsally from the place of their

Plate 6

1a

1b

1c

1d

300 μm

100 μm

2a

2b

2c

2d

300 μm

300 μm

300 μm

300 μm
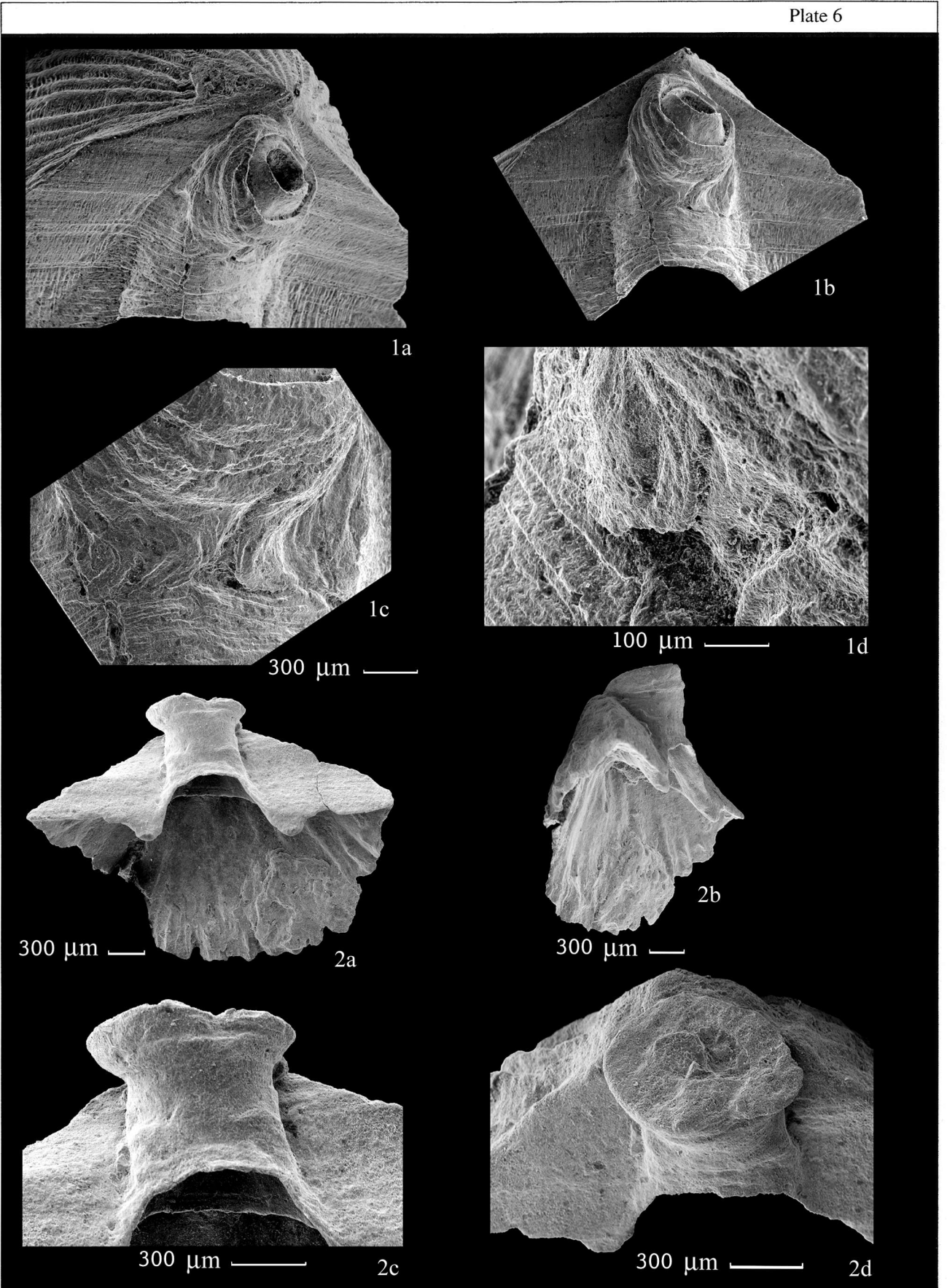
intersection with the dorsal lobe and, in the process of growth, secrete a pair of trihedral structures, the deltidial plates. Each plate is externally composed of the primary shell layer, while internally, it is formed by fibers and, laterally, bounded by the pedicle collar. As the deltidial plates grow dorsally above the umbo of the ventral valve, they can extend to the middle of the delthyrium and, in the case of further junction, the deltidium retains traces of fusion between the plates. The further junction of the two mantle lobes leads to the formation of a united secretory system that secretes periostracum and carbonate shell. The resulting structure, the symphytium, continues the deltidium and lacks any sign of fusion between plates (Williams and Hewitt, 1977).

The pseudodeltidium was formed in quite a different way. At the early developmental stages, the junction between the mantle and pedicle epithelia was presumably restricted to the ventral valve. The pedicle opening in strophomenids is the supraapical foramen, that is, it is situated on the ventral valve umbo beyond the interarea and is not on the top of the delthyrium. The pseudodeltidium is a part of the interarea and does not stand out in relief (Williams *et al.*, 1997a).

We obtained interesting material of clitambonitids from the Leningrad Region and Estonia that may supplement and illustrate previous suppositions. The first is a specimen of unique preservation of *Vellamo praeemarginata* (Alichova, 1953) (Pl. 6, figs. 1a, 1b) from the Middle Ordovician of the Leningrad Region. The deltidial plates, deltidium, and symphytium are preserved simultaneously in this specimen. The apical part of the deltidium forms a tube with the foramen and well-preserved pedicle collar. Two small tongues, embracing the convex deltidium on the edges, are placed immediately under the tube. Since these tongues lie on the outer deltidial surface, they are the first layer secreted by the mantle in the process of structure formation (Pl. 6, figs. 1c, 1d). These plates are undoubtedly deltidial plates. Between them is situated the median part of the deltidium with a scar in the middle that marks the fusion between the ends of the ventral lobes of the mantle. Consequently, the whole scarless structure situated below is the symphytium. A tubelike projection located above also lacks any sign of a junction (Pl. 6, fig. 1c); this is evidence that the fused mantle

ends continued their secretory activity in two directions: towards the ventral umbo, forming a tube, and towards the dorsal valve, forming the symphytium.

However, it is not improbable that the ends of the mantle lobes could become merged before the beginning of secretion of the shell substance. If this were the case, the entire delthyrial cover would be represented by a single plate, the symphytium.

Apparently, this is the case in some other specimens in our collection. After treatment of washed clays from the Lower Ordovician of the Leningrad Region, we obtained 15 specimens of *Anchigonites conulus* Öpik, 1939 ranging in size from 0.2 to 0.5 cm. About 15 smaller specimens have unusual delthyrial covers that differ from other covers of this species from the same layer. This is a scarless structure that resembles in shape the pedicle of modern terebratulids (Pl. 6, figs. 2a–2d). The apical foramen is absent. We also received remains of such "pedicles," which also belonged to small individuals, judging from their size. The majority of specimens have a closed deltidium, and the thickness of the plug closing the pedicle is up to 300 μm, while the deltidium itself is only about 60 μm thick (Figs. 1a, 1b).

The preparations of longitudinal and cross sections of complete valves and also of isolated deltidial structures were studied with the aid of a scanning electron microscope (SEM) at the Paleontological Institute of the Russian Academy of Sciences. During preparation, the samples were embedded in epoxy resin and, then, ground down to the level needed. Unfortunately, air bubbles often remained in the delthyrial cavity of the shells, which caused the shells with the maximum wall thickness 300–400 μm to be destroyed during grounding. Therefore, most of the photographs show isolated fragments rather than complete shells.

Subsequent examination has shown that the delthyrium of *Anchigonites* Öpik, 1939 is covered by a single plate that lacks any sign of a junction in the middle part or in the place of transition into the interarea (Figs. 2a–2d). Consequently, this plate is a symphytium formed by the ends of the ventral lobe of the mantle, which fused at early developmental stages. It is visible in transverse sections that the structure is made up of fibers 40–50 μm long and 10–15 μm wide (Fig. 1c). Large iso-

Explanation of Plate 6

Fig. 1. *Vellamo praeemarginata* (Alichova, 1953), specimen PIN, no. 4921/4: (1a) left side view of the posterior margin, pedicle collar in the apical part of tubelike symphytium is well seen, ×13.5; (1b) the same, strict posterior view, ×11; (1c) symphytium fragment immediately under the foramen, deltidial plates with the median trace of junction between them are well seen, ×35; and (1d) right side view on the left deltidial plate, ×130; Leningrad Region, village of Klyasino, screes on the opposite to the village slope of neglected quarry; Middle Ordovician, Kukruse Regional Stage.

Fig. 2. *Anchigonites conulus* Öpik, 1939, juvenile form, ventral valve, specimen PIN, no. 4921/5: (2a) inside view, ×23; (2b) side lateral view, ×23; (2c) inside of the symphytium, ×47; and (2d) view from the posterior margin, ×47; Leningrad Region, Lynna River, steep, sloping bank, 0.5 km from the inflow into the Syas' River; Middle Ordovician Substage, upper substage of the Volkhov Regional Stage.
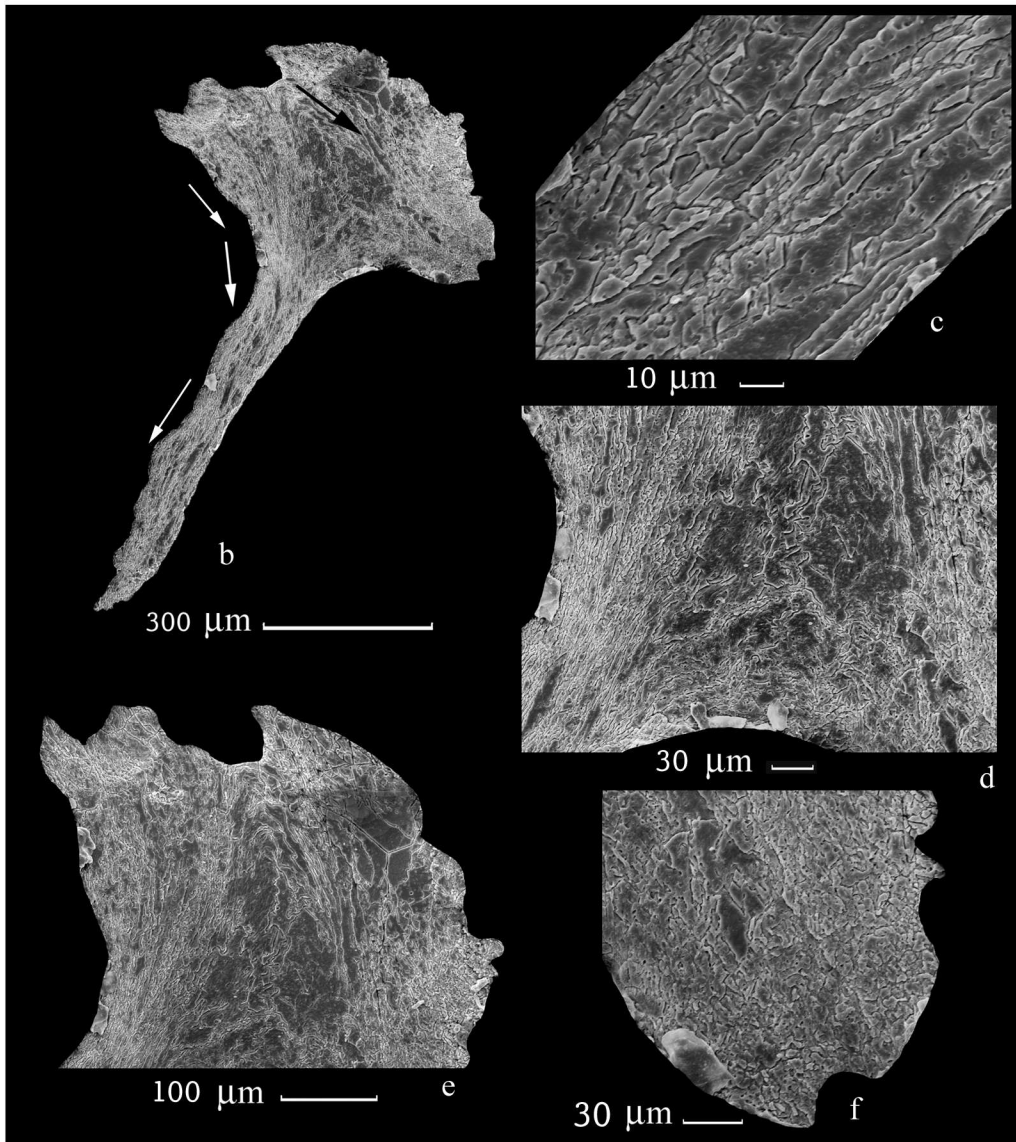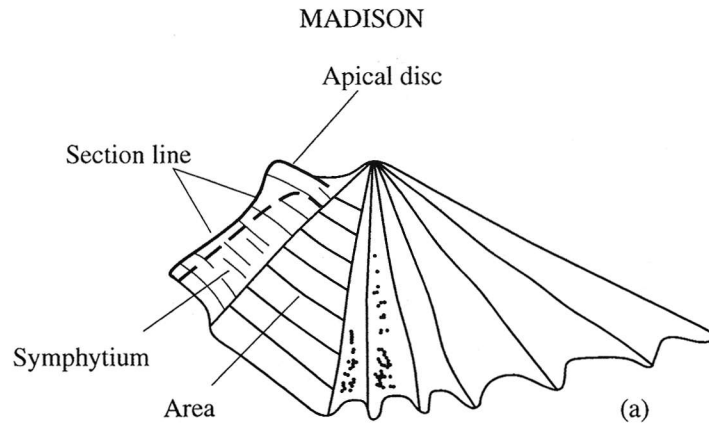
Fig. 1. Longitudinal section through the anterior wall of the symphytium and apical disc of *Anchigonites conulus* Öpik, 1939; specimen PIN, no. 4921/1: (a) position of the section line in the shell; (b) general view of the longitudinal section of the symphytium, ×53; (c) magnified fragment of the symphytium wall, ×500; (d) magnified fragment of the lowermost part of the apical disc, ×170; (e) magnified fragment of the apical disc, a segment remote from the umbo, ×110; and (f) magnified fragment of the part of the apical disc adjacent to the umbo, ×230; Russia, Leningrad Region, Lynna River, steep, sloping bank, 0.5 km from the inflow into the Syas' River; Middle Ordovician Substage, upper substage of the Volkhov Regional Stage.
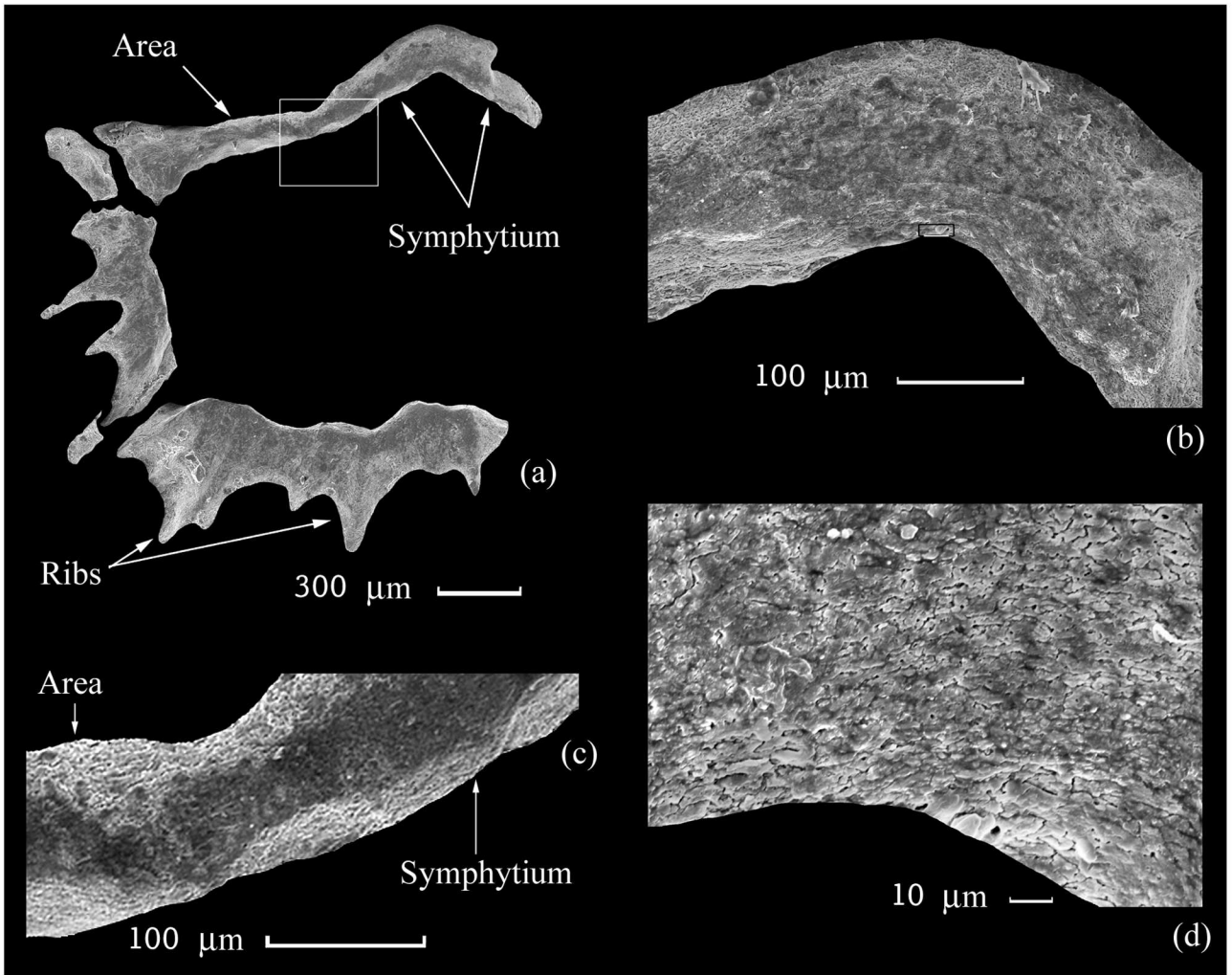
Fig. 2. Transverse section through the shell of *Anchigonites conulus* Öpik, 1939; specimen PIN, no. 4921/2: (a) general view, square marks the segment given with magnification in Fig. 2c, ×30; (b) symphytium, rectangle marks the segment given with magnification in Fig. 2d, ×160; (c) magnified segment of transition of the symphytium into the area, ×120; and (d) magnified segment of bend of the symphytium, ×400; Leningrad Region, Lynna River, steep, sloping bank, 0.5 km from the inflow into the Syas' River; Middle Ordovician Substage, upper substage of the Volkhov Regional Stage.

metric fibers of size 30–40 μm in transverse section are located in the central part of the plug (apical disc). Magnified individual areas of the transverse section are shown in Figs. 1d–1f.

Arrows in Fig. 1b show the assumed directions of growth that can be reconstructed by longitudinally extended fibers. They correspond to the outer wall of the symphytium and the apical disc, i.e., having sealed the pedicle, the mantle was displaced dorsally. Simultaneously the apical disc thickened.

In general, the fibers of the umbo are substantially larger than those of the symphytium. In the left part of Fig. 3, the fibers of the umbo are dorsally directed and reach 100 μm in length and 40 μm in width, while the fibers of the symphytium that radiate in a fan shape are

up to 40 μm long and 10 μm wide. A strip of longitudinally extended front fibers visible in this figure probably corresponds to the secretion of the posterior mantle margin at the earliest developmental stages.

Similar structures were recognized for three more genera of the suborder Clitambonitidina (although they have not been examined in detail): *Antigonambonites* Öpik, 1934 (several dozen specimens from the Leningrad Region and Estonia), *Estlandia* (one specimen from the collection of Karpinskii All-Russia Geological Research Institute), and *Vellamo* Öpik, 1930 (two specimens from the Leningrad Region). Some variants of tubelike symphytium with the apical disc are shown on Pl. 7, figs. 2–4.

Plate 7

1a

1000 μm

1b

500 μm

2

300 μm

3

100 μm

4a

4b

4c

300 μm

4d

10 μm
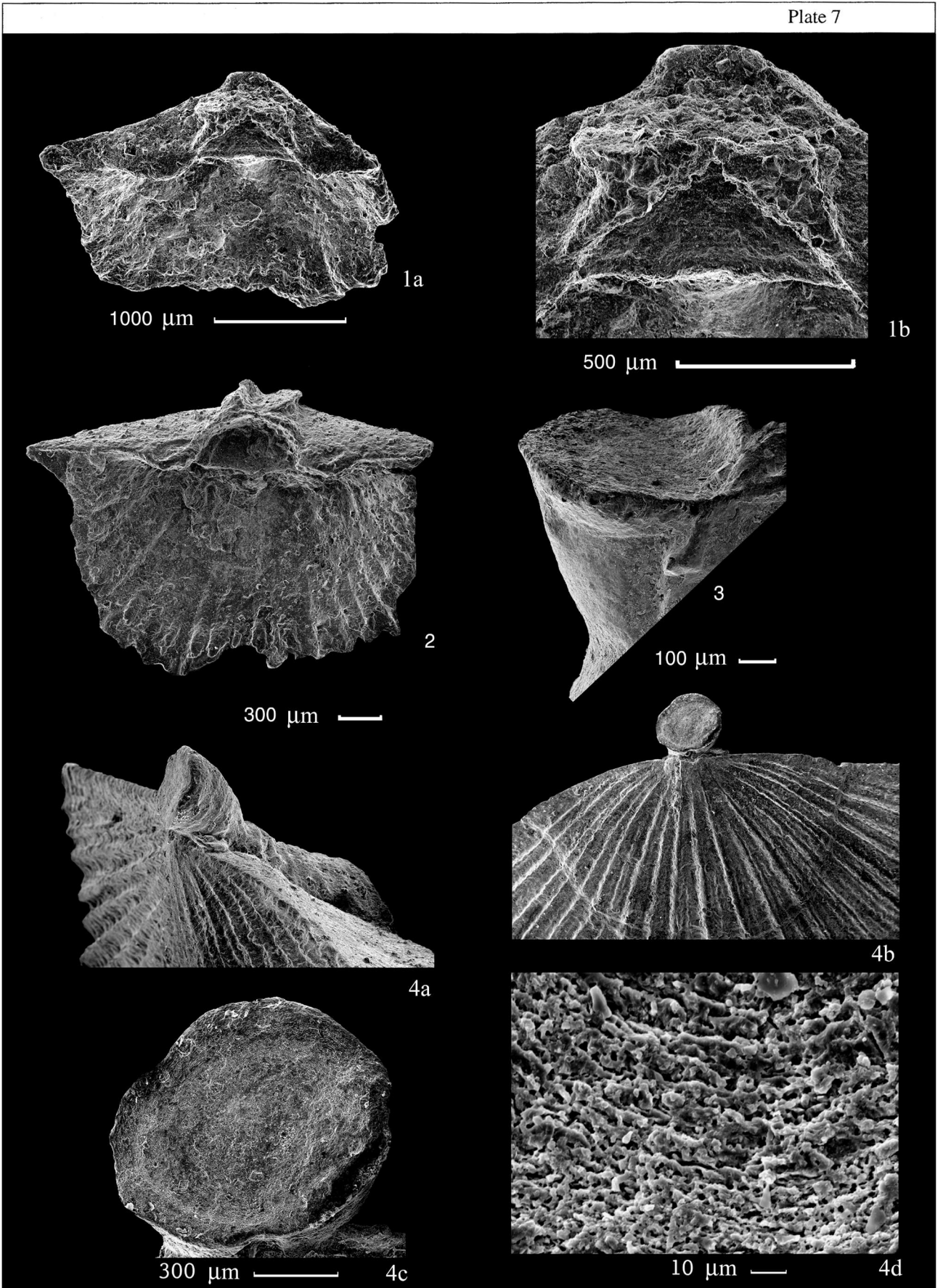
A variant type of development that may be assumed on histological data is observed in a series of juvenile *Anchigonites conulus*. Only one specimen has a foramen in the process of being plugged (Pl. 7, figs. 1a, 1b). This shell is 3 mm wide and 2 mm long and has an oval thickening of size 1.4 mm at the top of the deltidium. The apical disc is not completely formed, and the deltidial plates have not come into contact, so that the distance between their ends is 0.05 mm. The pedicle opening is closed except in the central part and has a diameter of 0.15 mm. Thus, at the stage when the pedicle could function, the size ratio of the shell and the apical disc is about 1 : 4. Subsequently, the growth rate of the shell considerably exceeds that of the pseudodeltidium; as a result, when the foramen is completely sealed, the ratio is 1 : 7. The case in point is specimen PIN, no. 4921/166 with the symphytium at the initial stage of growth. It may be assumed that *Anchigonites conulus* was only attached by its pedicle at early developmental stages, after metamorphosis and almost immediately after settlement, the pedicle opening became sealed.

A possible interpretation of the sealing of the foramen and expansion of the apical part of the symphytium is cementation by the apical disc. It is probable that, soon after settlement, when the shell had adopted a position convenient for filtration, the symphytium began to grow in the following manner. The mantle grew over around the circumference of the pedicle and, having reached the place of attachment, it separated the pedicle from the substrate with the simultaneous secretion of a cementing substance. After complete sealing of the pedicle, the secretion of shell continued towards the apical disc, i.e., the apical disc became thickened and strengthened as was shown above. Such a growth scheme provides an explanation for the diverse orientation of the apical disc with reference to the area (compare Pl. 7, figs. 2, 3) and also for the presence of this structure and rare complete preservation of shells. The cementation was probably rather durable, so that, when the individual reached adult size (clitambonitids are large brachiopods with a massive shell), the apical disc together with part of the symphytium was broken of by the force of gravity. Thus, only the foramina with a lip or eroded edges remained; such structures are often
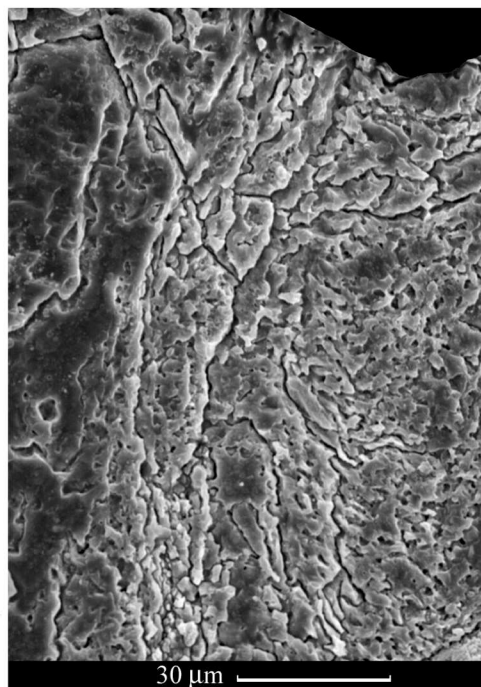

Fig. 3. Fragment of the longitudinal section through the shell of *Anchigonites conulus* Öpik, 1939; specimen PIN, no. 4921/3, on the left are large fibers of the umbo, on the right are fibers of the symphytium which radiate in a fan shape, separated from the symphytium by a strip of longitudinally extended front fibers, ×300; Leningrad Region, Lynna River, steep, sloping bank, 0.5 km from the inflow into the Syas' River; Middle Ordovician Substage, upper substage of the Volkhov Regional Stage.

described in *Kullervo, Vellamo, Antigonambonites, Estlandia*, and some other clitambonitid genera.

Cementation in brachiopods with a carbonate shell is known in craniids, productids, and thecideidines. Cementation in productids presumably followed the same pattern as in the ventral valve of craniids: the outer epithelial cells that secreted fibers, the primary layer, and the periostracum, also secreted large quantities of adhesive mucus, which provided firm cementation of the shell to the substrate (Williams *et al.*, 1997b). The same scheme was probably characteristic of the clitambonitids discussed above, whose position during life is here reconstructed (Fig. 4).

Explanation of Plate 7

Fig. 1. *Anchigonites conulus* Öpik, 1939, juvenile form, ventral valve, specimen PIN, no. 4921/167: (1a) inside view, ×24; and (1b) fusing deltidial plates, ×65; Leningrad Region, Lynna River, steep, sloping bank, 0.5 km from the inflow into the Syas' River; Middle Ordovician Substage, upper substage of the Volkhov Regional Stage.

Fig. 2. *Anchigonites conulus* Öpik, 1939, juvenile form, ventral valve, specimen PIN, no. 4921/166, ×27; completely formed apical disc and the newly forming symphytium are seen; Leningrad Region, Lynna River, steep, sloping bank, 0.5 km from the inflow into the Syas' River; Middle Ordovician Substage, upper substage of the Volkhov Regional Stage.

Fig. 3. *Antigonambonites planus* (Pander, 1830), specimen PIN, no. 4921/6, ×70; side lateral view of the apical disc and tubelike upper part of the deltidium; Estonia, Väke-Pakri Island; Middle Ordovician Substage, Volkhov Regional Stage.

Fig. 4. *Antigonambonites planus* (Pander, 1830); specimen PIN, no. 4921/7, ventral valve: (4a) side lateral view of the umbonal part of the valve, ×18; (4b) external view of the umbonal part of the valve, ×12; (4c) apical disc, ×50; and (4d) fibers from the middle of the radius of the apical disc, ×700; Estonia, Väke-Pakri Island; Middle Ordovician Substage, Volkhov Regional Stage.
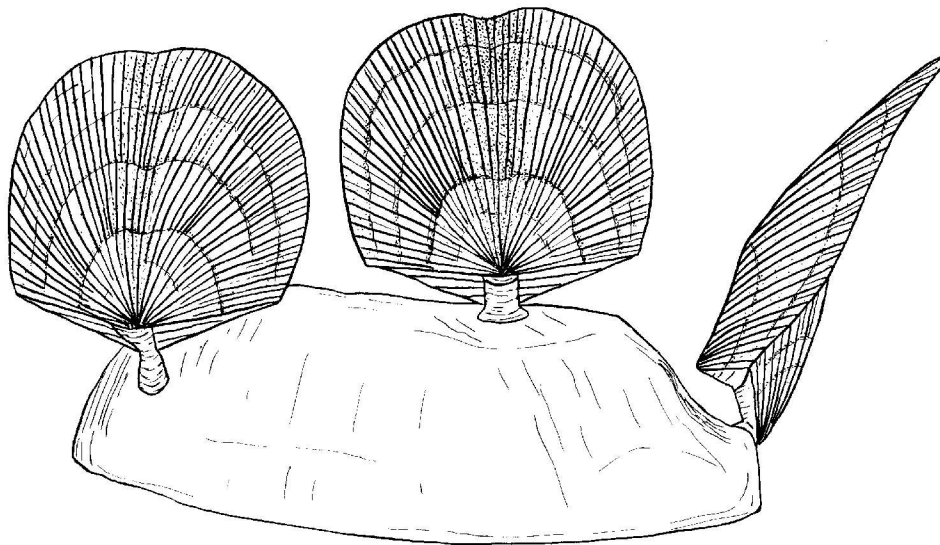
Fig. 4. Reconstructed position of some clitambonitids during life (drawing by S.V. Moloshnikov).

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