

Laminar shell structure of *Antigonambonites planus* (Pander, 1830) (Brachiopoda, Billingsellida)

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Received 5 May 2017, accepted 7 June 2017, available online 16 October 2017

Abstract. The order Billingsellida comprises brachiopods with laminar and fibrous shells, however, the data on their microstructure are scanty and the taxonomic value of differences in their shell structure is uncertain. The shell structure of clitambonitidine *Antigonambonites planus* was found to be laminar, not fibrous as previously considered; possibly this shows that it belongs to the suborder Billingsellidina. The pseudopunctae in the secondary layer normally are formed by deflected laminae and lack taleolae. Possible remains of the tertiary prismatic layer are described and the diagenetic changes are appreciated.

Key words: Brachiopoda, shell microstructure, Billingsellida, Ordovician.

INTRODUCTION

The genus *Antigonambonites* Öpik, 1934 was traditionally referred to the family Gonambonitidae (superfamily Clitambonitoidea), which is characterized by spondylium triplex, i.e. spondylium supported by three septae: one median and two lateral. However, the detailed study of its ventral muscle field revealed that in fact *Antigonambonites* lacks a true spondylium (Vinn & Rubel 2000). This became a reason for Popov et al. (2001) to refer *Antigonambonites* to the superfamily Polytoechioidea, family Polytoechiidae. Later their opinion was confirmed by the study of early ontogenetic stages of *Antigonambonites* Popov et al. (2007) and shared by Benedetto (2009). Finally *Antigonambonites* was formally assigned to Polytoechiidae in Topper et al. (2013).

The SEM study of the shell structure of clitambonitidines was first performed by Williams (1968), who mentioned that *Vellamo*, *Eremotoechia* and *Antigonambonites* were fibrous but he figured only *Vellamo* sp. Later he published a figure of the section through the shell of *Antigonambonites planus* (Pander, 1830) with a thin pseudopuncta noting that it was fibrous, but no regular fibrous mosaic is seen on this picture (Williams 1970, fig. 9). On the contrary, the section through the secondary layer of *Vellamo* shows standard stacking of fibres (Williams 1968, pl. 18, fig. 6). The fibrous secondary layer with a pseudopuncta has been figured for *Estlandia marginata* (Pahlen) (Vinn 2001). The stratiform laminar shell structure of *Billingsella lindströmi* (Linnarsson) from the suborder

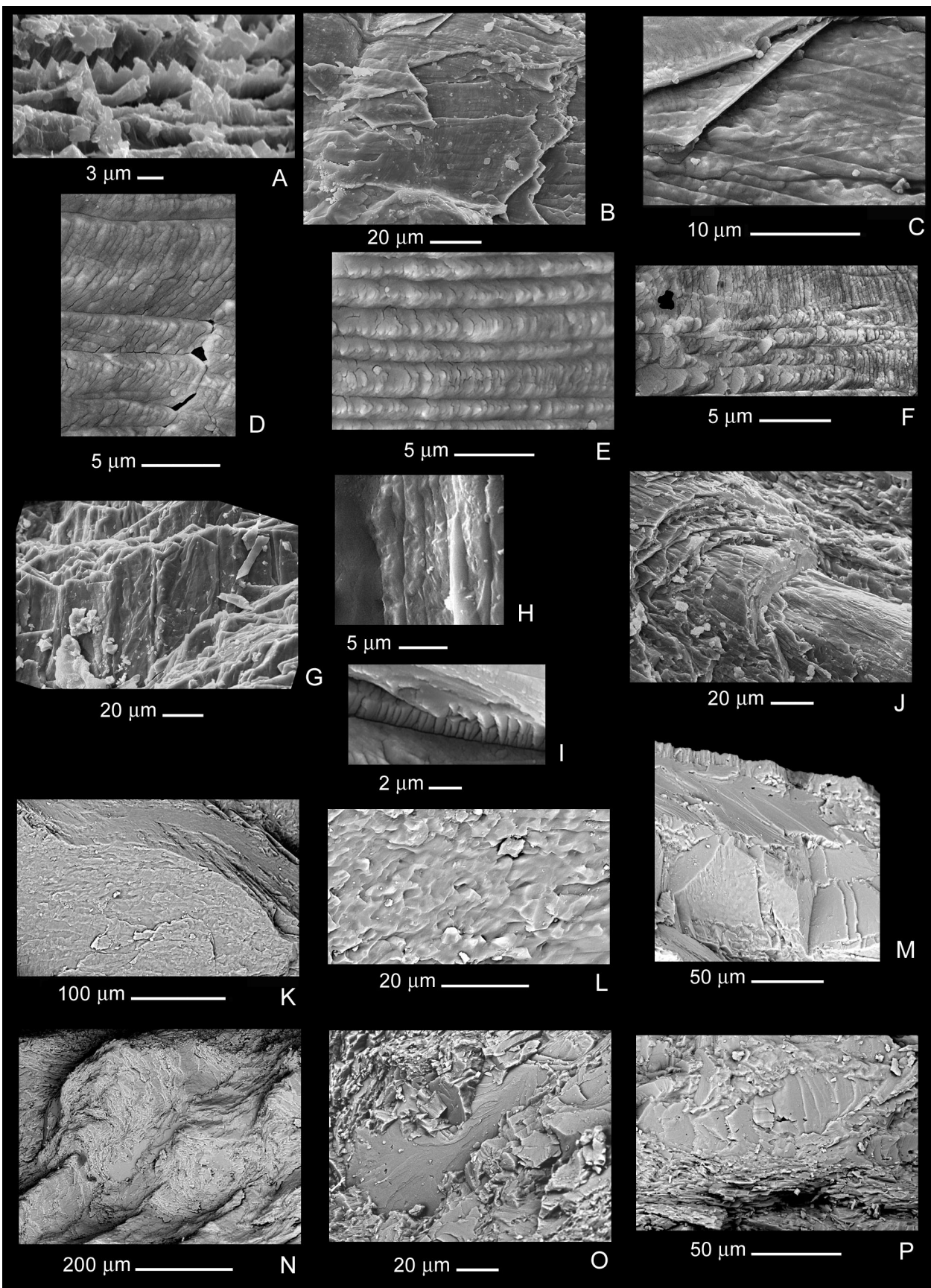
Billingsellidina of the order Billingsellida is well documented (Williams 1970; Williams & Cusack 2007). Thus in literature there are data on the shell structure of only five species of the entire order Billingsellida. Recent publications suggest that the shells of billingsellidines are laminar and the shells of clitambonitidines are fibrous, based on the data on the microstructure of these five species, one of which was not depicted and the photo of another is controversial. The insufficiency of data on shell fabric of this polyphyletic order comprising superfamilies of uncertain origin is obvious.

The present paper deals with the shell structure of *A. planus*, which is described here by the splints of one dorsal and two ventral valves from the upper Volkhovian (BIIγ, Middle Ordovician) of the Leningrad Region, mouth of the Lynna River. The material studied is housed at the Borissiak Paleontological Institute of the Russian Academy of Sciences (PIN RAS), Moscow, coll. No. 4921.

DESCRIPTION OF THE *A. PLANUS* SHELL MICROSTRUCTURE

The shell fabric of *A. planus* is usually strongly recrystallized and the original microstructure is preserved rarely and in small areas. The **primary layer** has not been found but longitudinal rows of vertical fine crystals, possibly altered remains of original capillae, are observed on the umbonal region of one ventral valve (Fig. 1A). The rows are approximately 3 µm high and 0.5–1 µm thick.

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The **secondary layer** of *A. planus* is typically cross-bladed laminar and pseudopunctate. The tabular laminae are best preserved on the rib crests (Fig. 1B, C). The thinnest laminae are about 250–500 nm thick, which possibly is their original thickness. The laminae are up to 20 µm wide and composed of up to 14 laths. The lath thickness is 1–3 µm, rarely 5–6 µm (Fig. 1D–F). The surfaces of laminae show fine growth marks, which are 250–300 nm thick on the longitudinal sections of laminae and possibly correspond to daily deposition.

The umbonal thickening of the ventral valve is usually strongly recrystallized and only its superficial region has remained laminar, though usually these laminae are variously altered. Figure 1G shows a well-ordered set of laminae located closer to the outer surface of the ventral valve. Each lamina in this set is about 25 µm wide but their superficial preservation is different. The surfaces of laminae that underwent early diagenetic stages are uneven and wrinkled but an area with original laths is preserved in one lamina (Fig. 1H). The thinnest laths are 1 µm; thicker laths were possibly formed by fusion in the course of diagenesis. Very narrow (about 3 µm) laminae (or very wide laths?) were found in the umbonal region of specimen 4921/661 but they show excellent cross-bladed mosaic (Fig. 2C).

Possibly the earliest diagenetic stages are shown in Fig. 1F, where the laths are partly slightly altered by the planes of growth. The possible initial stage of vertical fusion of two neighbouring laminae is displayed in Fig. 1I. In the following course of diagenesis the laminae became vertically and horizontally fused and lost their bladed structure; their surfaces turned variously wrinkled (Fig. 1K, L). These strongly thickened and wide diagenetic laminae compose a considerable part of the shell fabric.

The secondary layer may generally be subdivided into two main sublayers: the about 400 µm thick outer sublayer with undular laminae of the ribs (Fig. 1N) and the about 130 µm thick inner sublayer composed of planar but variously altered elements (Figs 1K, 2A, G). Anteriorly the inner sublayer is stratified into variously altered regions, from strongly thickened laminae to small isoform, irregularly shaped elements (Fig. 2G).

It is likely that fig. 9 of Williams (1970) illustrates a similarly altered area of the *A. planus* secondary shell.

The shell wall near the spondylium is composed of three variously altered sublayers: the 55 µm thick inner sublayer of cubical granules (this sublayer also separates lateral septae from the shell wall) (Fig. 2A), the 12–20 µm thick solid interlayer of diagenetic calcite (Fig. 2B) and the about 400 µm thick upper sublayer of cross-bladed laminae (Fig. 2C).

The diagenetic calcite is the next stage of laminae alteration. It is usually developed in the umbonal region and in the rib interspaces (Fig. 1N–P), while the ribs are composed mainly of original or diagenetic laminae (Fig. 1J).

A possible prismatic **tertiary layer** was found in two places on the inner surfaces of ventral valves. In the first case the remains of the tertiary layer are better preserved, 20–30 µm thick, and composed of 9–14 µm high vertical columns, which are densely spaced and sharply bordered from the underlying laminae (Fig. 2D). The possibility that these columns are laminae prolongations as in the case of the tertiary prismatic layer of the fibrous shell is controversial. In the second case the columnar elements possibly became recrystallized and altered into 12 µm high and 4 µm thick vertical crystals (Fig. 2E, F). In both cases these areas of inner valve surface are smooth and lack tubercles; however, these vertical elements could also form in the course of diagenesis.

Other possible remains of the tertiary layer were found on the inner surface of the strongly recrystallized spondylium. Two spondylia studied by longitudinal splits are completely composed of diagenetic calcite (Fig. 1M).

The shell of *A. planus* is pseudopunctate but in most cases the taleolae were not observed and the pseudopunctae are composed only of deflected laminae (propunctae) (Fig. 2I–K). The cones are 30–50 µm wide and irregularly and sometimes very closely (especially near the anterior margin, Fig. 2H) spaced. In few cases possible thin (5–10 µm) taleolae were present (Fig. 2L). The length of the longest observed pseudopuncta is about 50 µm.

Fig. 1. **A**, longitudinal rows of crystals in the umbonal region of the ventral valve. **B**, laminae on the rib crest; furrow on the left is the transverse growth mark. **C**, cross-bladed lamination. **D**, **E**, close up of lamina surfaces. **F**, lamina surface altered by growth lines. **G**, **H**, set of laminae in the umbo of the ventral valve; one lamina (H) is less altered than the others. **I**, possible vertical fusion of two neighbouring laminae. **J**, rib crest composed of variously preserved laminae. **K**, thick diagenetic lamina. **L**, wrinkled surface of the diagenetic lamina. **M**, longitudinal section through the spondylium completely composed of diagenetic calcite; inner surface on the top consists of the vertically hatched crust. **N**, **O**, transversely broken valve showing laminar ribs (N) and diagenetic calcite in the rib interspace (O). **P**, diagenetic calcite lining the bottom of rib interspace and bordering with inner sublayer of planar laminae. **A**, **N–P**, ventral valve PIN 4921/661. **B–D**, **F**, **I**, **J**, dorsal valve PIN 4921/780. **E**, **G**, **H**, ventral valve PIN 4921/781. **K–M**, ventral valve PIN 4921/663.

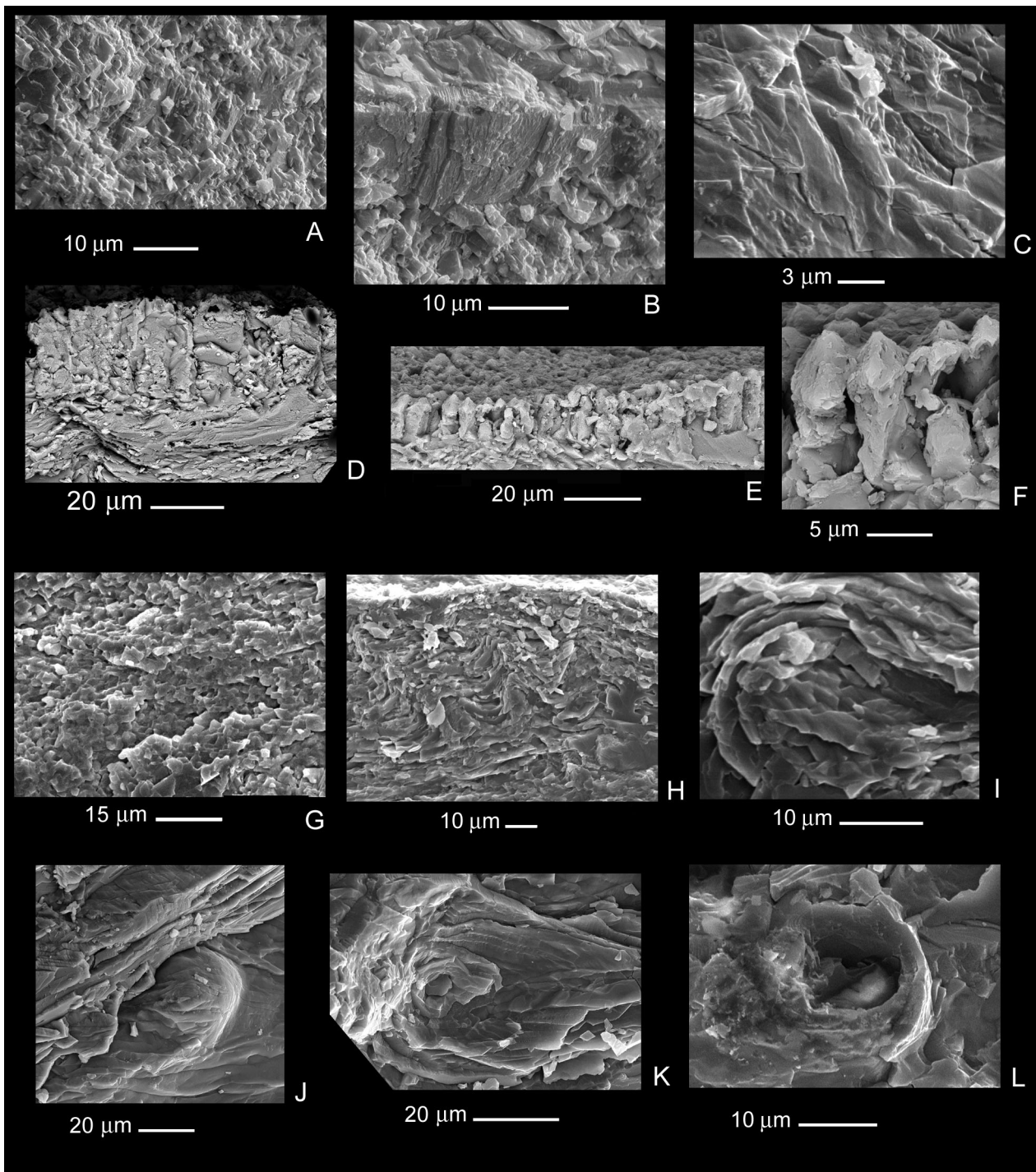


Fig. 2. A–C, three variously altered sublayers of the secondary layer in the umbonal region of the ventral valve: inner sublayer of cubical granules (A), sublayer of solid diagenetic calcite (B), upper sublayer of cross-bladed laminae (C), PIN 4921/661. D, possible tertiary layer of densely spaced thick vertical columns in ventral valve PIN 4921/781. E, F, altered tertiary layer of separate vertical crystals, ventral valve PIN 4921/664. G, longitudinal section of the inner sublayer of the secondary layer with small isoform, irregularly shaped elements. H, three densely spaced pseudopunctae on longitudinal section. I, longitudinal section through a pseudopuncta lacking taleola. J, upper view of a pseudopuncta in the secondary laminae. K, inner view of a pseudopuncta composed of deflected laminae. L, possible thin taleola, dorsal valve PIN 4921/780.

CONCLUSIONS

It has been assumed that Polytoechioidea rather belongs to the suborder Billingsellidina than to Clitambonitidina (Topper et al. 2013). As *A. planus* is considered now to be polytoechioid, its laminar secondary shell is another evidence of close affinity between Polytoechiidae and laminar Billingsellidae. Unfortunately, it is the only polytoechioid species with documented shell microstructure as Williams (1968) did not picture the sections through the shell of *Eremotoechia* but only mentioned it was fibrous. Further investigation of the shell structure of brachiopods of the order Billingsellida probably will tribute to the clarification of their relationships.

Acknowledgements. This study was supported by the Arctic Program of the Presidium of Russian Academy of Sciences, project No. 44 'Paleontological Base for Reconstruction of the Early Paleozoic Paleogeography'. The referee O. Vinn and the anonymous referee are thanked for constructive reviews of the manuscript. The publication costs of this article were covered by the Estonian Academy of Sciences.

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Antigonambonites planus'e (Pander, 1830) (Brachiopoda, Billingsellida) laminaarne koja struktuur

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Antigonambonites planus'e koja struktuur on laminaarne, mitte fibriiline, nagu varem arvati. Laminaarne koja struktuur toetab *Antigonambonites*'e polütehhioidide hulka arvamist. Uuritud Ordoviitsiumi-vanuste kodade struktuuris on näha diageneesist tingitud muutusi. Käsijalgse laminaarne koja struktuur on paremini säilinud rõnnete kohal. Laminaarse koja struktuuri esinemine *A. planus*'el kinnitab polütehhioidide ja billingselliidide lähedast sugulust.