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Columnar shell structures in early linguloid brachiopods – new data from the Middle Cambrian of Sweden

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ABSTRACT: The records of columnar shell structures of linguloid brachiopods (Class Lingulata, Order Lingulida, Superfamily Linguloidea) are reviewed in the light of the discovery of two new taxa from the Middle Cambrian Forsemölla Limestone Bed of southern Sweden. The linguloid taxa, described here as *Eoobolus*? sp. aff. *E. priscus* (Poulsen) and *Canalilatus*? *simplex* sp. nov., are both characterised by a columnar shell structure, a structural type that is representative for acrotretoid brachiopods and that has previously only rarely been reported from the linguloids. Though the two taxa are superficially similar to known genera, i.e., *Eoobolus* and *Canalilatus*, their shell structure challenges such affiliations, as the shell structure of the type species of these genera is previously unknown. Linguloid families whose morphological characteristics agree the most with those of the new taxa, i.e., the Zhanatellidae and the Eoobolidae, and from which columnar shell structures have been reported, i.e., the Lingulellotretidae and the Kyrshabaktellidae, are reviewed briefly. Many taxa assigned to these families completely lack shell structure data and are in need of restudy in order to elucidate their systematic position. Knowledge of the representative type of shell structure of the various suprageneric taxa within the Linguloidea is considered crucial, in order to unravel their currently poorly resolved phylogenetic relationships.

KEY WORDS: Eoobolidae, Forsemölla Limestone Bed, Lingulata, Linguloidea, new taxa, phylogeny, Scania, Zhanatellidae

Organophosphatic brachiopods (subphylum Linguliformea) are currently divided into two classes, i.e., the Paterinata and the Lingulata (Williams *et al.* 2000). Recent phylogenetic analyses suggest a monophyletic origin of the class Lingulata (Holmer *et al.* 1995; Holmer & Popov 2000), but the relationships among the various groups recognised within the class are still poorly resolved. This is especially true within the Lingulida and Linguloidea which themselves cannot be resolved as monophyletic groups (Holmer & Popov 2000). An effective way to unravel phylogenetic relationships within the linguliformean brachiopods is the study and comparison of the structure of the shell (e.g. Williams & Cusack 1999; Streng & Holmer 2005; Holmer *et al.* 2008). Several types of shell structure can be distinguished that are considered to be representative for major taxonomic groupings within the Linguliformea (e.g., Williams & Holmer 1992, 2004; Williams *et al.* 1998a, b; see below). Unfortunately, investigation of the shell structure has often either been neglected in taxonomic studies, or the preservation of the described material has not allowed the study of shell structural details. For these reasons, the shell structure of many genera, especially within the Linguloidea, is still unknown or assumed by comparison with putative related genera. This lack of information hampers phylogenetic analyses. The present study shows how important an accurate identification of the shell structure is, as superficially similar genera may have different types of shell structure and should be classified in different suprageneric taxa. In addition, it is shown that the so called columnar shell structure type, characteristic for the Acrotretoidea, is more common within the Linguloidea than previously assumed, potentially providing a tool to resolve phylogenetic relationships within this group.

1. Shell structure types within the early Lingulata

In general, two basal types of shell structure can be distinguished within the early Paleozoic lingulates: the columnar and the baculate type. From these basal types, various derived types such as the septate and the camerate type, and the orthogonal baculate type, have evolved (see below).

1.1. The columnar type

Holmer *et al.* (2008) recently reviewed and described several columnar-like structures within the stem and crown groups of the organophosphatic brachiopods. They showed that various ‘columnar structures’ are present which are, however not necessarily related; many of them still require formal description. The columnar structure *sensu stricto* as used in this paper is the acrotretoid columnar structure as originally defined by Holmer (1989). This structure is characterised by discrete apatitic lamellae connected by perpendicular columns. The columns are 1·5–5 μm in diameter and bear a central canal that may penetrate successive sets of laminae (Figs 1.1, 4.2) (see Holmer 1989, p. 31 for definitions of lamina and lamella).

The term septate shell structure was introduced by Ushatinskaya (1994) to describe a shell structure in which radially arranged septa connect the lamellae. This type is

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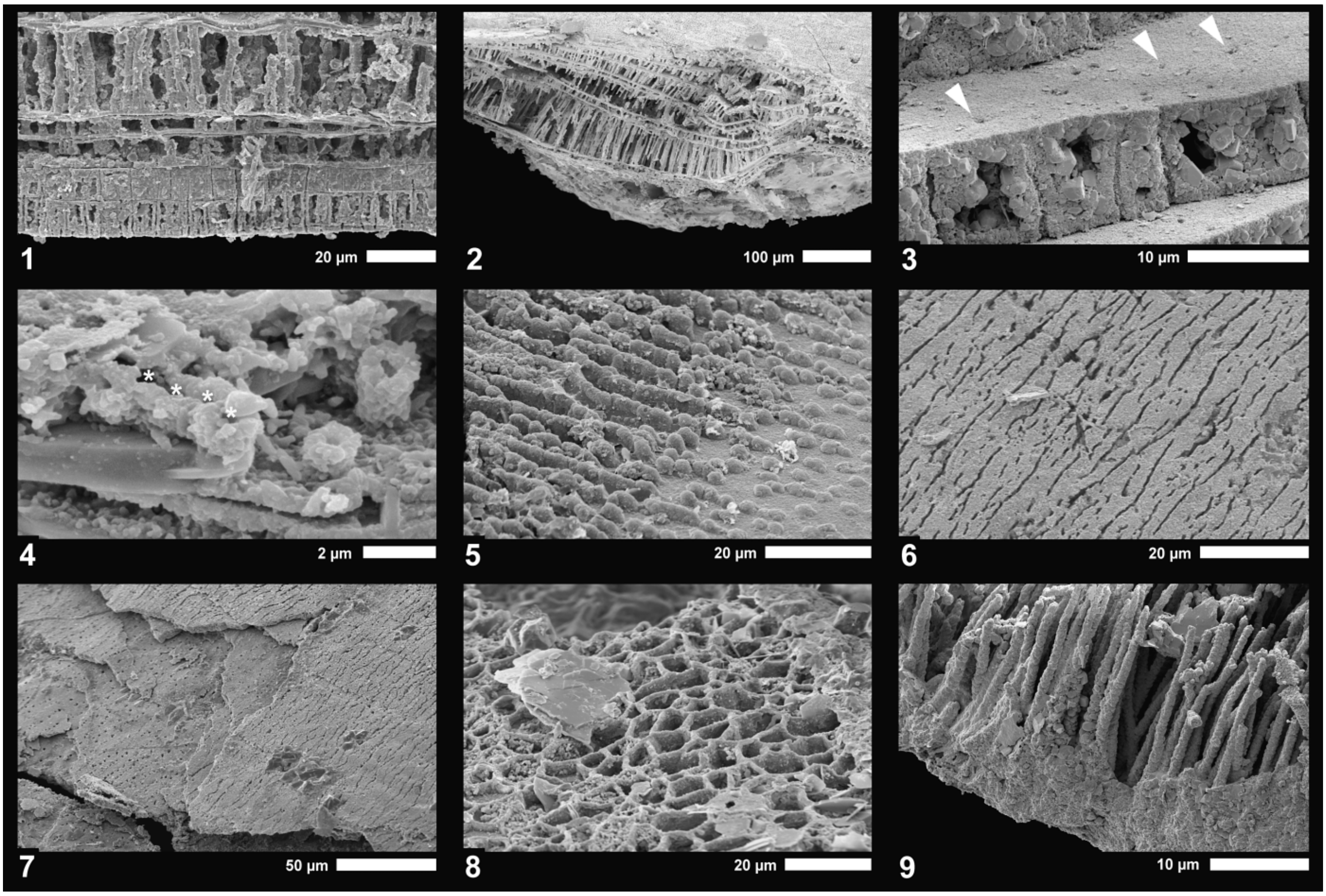

Figure 1 Shell structural details of various species: (1) *Hadrotreta primaeva* (Walcott), Lower Cambrian, Pioche Shale, Nevada: succession of five laminae. Note that individual laminae are differentially altered by diagenesis; (2) *Hadrotreta primaeva* (Walcott), Lower Cambrian, Pioche Shale, Nevada: cross section through apical process showing columnar laminae of up to 80 µm in thickness; (3) *Vandalotreta* sp., Middle Cambrian, Forsemölla Limestone Bed, southern Sweden: columnar lamina with intralaminar space partly filled by diagenetic apatite crystals; columnar nature of lamina also shown by perforated interlaminar surfaces (arrows); (4) *Hadrotreta primaeva* (Walcott), Lower Cambrian, Pioche Shale, Nevada: amalgamated columns (asterisks) forming a septum but still showing outline of individual columns; (5) *Canthylotreta crista* Streng & Holmer, late Middle Cambrian, Lincoln Peak Formation, Nevada: radially aligned domes partly amalgamated to form septa; (6) *Hadrotreta primaeva* (Walcott), Lower Cambrian, Pioche Shale, Nevada: an exterior lamina close to the margin of the shell with a septate shell structure; (7) *Canthylotreta crista* Streng & Holmer, late Middle Cambrian, Lincoln Peak Formation, Nevada: exfoliated exterior surface showing three different outer interlamellar surfaces; note radially aligned perforations on innermost interlaminar surface (left side of picture) indicating a columnar structure of lamina and parallel grooves on outermost interlaminar surface (right side of picture) attesting a septate shell structure, lamina in-between shows a transitional structure; (8) *Anabolotreta mogota* Streng & Holmer, late Middle Cambrian, Shafter Formation, Nevada: camerate lamina; (9) *Curticia*? *pattersonensis* Streng & Holmer, late Middle Cambrian, Orr Formation, Utah: orthogonal baculate lamina.

similar to the camerate type of Holmer (1989) in which the discrete lamellae are connected by perpendicular walls that form irregular polygonal chambers (Fig. 1.8). In fact, both structures might be considered as homologues because in both types lamellae are connected by walls which form discrete chambers. The only difference is in the outline of these chambers, which are elongated, often rectangular in outline, and radially arranged in the septate type (Figs 1.6, 4.5), and irregular polygonal in the camerate type (Fig. 1.8). Recent and ongoing studies have shown that the septate and camerate structure can directly be derived from a columnar structure by the alignment and fusion of columns to form walls and septa (Streng & Holmer 2006; Figs 1.4, 1.5, 4.7). This transition can be seen in the ontogeny of several species (Williams & Holmer 1992: pl. 7, fig. 3; Streng & Holmer 2006; Streng, unpublished data; Fig. 1.7) and is also reflected in the phylogeny of the Acrotretoidea. Early and Mid Cambrian acrotretid genera typically have a columnar structure, whereas in the late Mid Cambrian septate structures become more common; the presence of camerate structures is typical for many Ordovician genera and families. However, first septate structures are already realised in the Early Cambrian *Hadrotreta primaeva* (Walcott) (Fig. 1.4, 1.6) and typical camerate structures are already known from the Middle Cambrian (e.g., Ushatinskaya 1994; Streng & Holmer 2006; Fig. 1.8). Thus, an increase in complexity of the shell structure, which might also convey increased stability or strength, is evident in the phylogeny and ontogeny of the Acrotretoidea. As the septate structure *sensu* Ushatinskaya (1994) seems in an evolutionary sense to be intermediate between the columnar and the typical camerate structure (in the narrow definition of Holmer 1989), and also distinctive for certain genera, it is emphasised in the present paper that both terms should be used when describing the shell structure of organophosphatic brachiopods.

The columnar state, with the derived septate and camerate structure, was considered to be typical for the Acrotretoidea only, until Cusack *et al*. (1999) identified indubitable acrotretid columnar structures in the Lower Cambrian linguloid *Lingulellotreta*. However, Kruse (1991, 1998) already depicted columnar structures for an Australian species of the Lower

Cambrian linguloid *Kyrshabaktella*, but interpreted them as diagenetically formed pseudocolumns. Ushatinskaya (1995) also illustrated shell structural details of *Kyrshabaktella tatjanae* and *Clivosilingula* sp. showing clear columnar structures. More recently, Skovsted & Holmer (2006) described columnar structures in *Kyrshabaktella* from the Lower Cambrian of Nevada. With the two linguloid taxa described below, also showing unequivocal acrotretid columnar structures, it becomes evident that the columnar shell structure is considerably more widespread within the Lingulata than previously assumed. In fact several families presently accommodated within the Linguloidea might include taxa characterised by a columnar shell structure (see Systematic Palaeontology below). Future phylogenetic analysis might show that such 'columnar linguloids' might represent a sister group to either the Acrotretoidea or the 'baculate linguloids'. However, a broader data set on the shell structures of many genera and species is needed, especially of nominate genera and type species, to perform a meaningful analysis.

The presence of columnar and septate structures in the Middle Cambrian lingulid *Canalilatus*? *simplex* sp. nov. and to some extent in *Eoobolus*? sp. aff. *E. priscus* (see Systematic Palaeontology below) suggests a shell structural development from columnar to septate in the 'columnar lingulids' analogous to that in the Acrotretoidea. This might be supported by the development of ″a variant of the camerate condition″ (Cusack *et al*. 1999, p. 835) in the Upper Cambrian genus *Experilingula* although baculate structures were also described from the same genus (Cusack *et al.* 1999).

1.2. The baculate type

The term baculate structure was introduced by Holmer (1989), who first extensively described shell structures within fossil linguliforms. More recently, Williams & Cusack (1999) gave a detailed classification of this structural type, encompassing its variability within the Lingulida. Generally, the baculate shell structure is characterised by rhythmic sets of laminae whose intralaminar spaces are filled by minute apatitic rods, so-called bacula, forming a criss-cross array in an organic matrix. [Note: the term baculate is derived from the Latin noun baculum (Holmer 1989) meaning small rod; the plural form is bacula not baculae or baculi as previously used.] The baculate type is restricted to the Lingulida, but, as outlined above, not the only structural type for this taxon.

Streng & Holmer (2005) recently described the coexistence of columnar and baculate laminae within *Curticia*? *pattersonensis* Streng & Holmer. With this discovery, they not only made the phylogenetic position of this particular taxon problematic, but also seriously questioned the significance of the shell structure for distinguishing suprageneric taxa, as shell structures assumed to be distinctive for major taxonomic groupings were found in a single species. Reinvestigation of the material of *C.*? *pattersonensis* herein shows that the 'columnar structures' in *C.*? *pattersonensis* are different from those of the acrotretids. The individual 'columns' (1) are thinner than in a typical acrotretid columnar structure (diameters do not exceed 1 µm); (2) might bifurcate; and (3) have a massive ultrastructure lacking the diagnostic central canal (Fig. 1.9). Such columns are better compared with *bacula* of the baculate structure, differing from those in being slightly thicker and being arranged perpendicular to the compact lamellae enclosing the 'columnar' sets. Accordingly, as in the baculate type, the interlaminar surfaces of these compact lamellae remain imperforated. Such 'columnar structures' were first mentioned by Cusack *et al*. (1999), who described the disposition of the *bacula* in *Dysoristus orientalis* as orthogonal. Subsequently, Holmer *et al*. (2008) introduced the term 'orthogonal baculate' for such a shell structure. The orthogonal baculate type is so far only known from four genera of Mid and Late Cambrian age, i.e., *Dysoristus* Bell (see Cusack *et al*. 1999), *Vaculina* Koneva and *Aboriginella* Koneva (see Holmer *et al*. 2008), and *Curticia* Walcott (Streng & Holmer 2005, reinterpreted herein). Analogous to the evolution of the columnar type developing septate and camerate structures, the orthogonal baculate structure might be interpreted as having evolved from the typical baculate structure during the Mid Cambrian, also to increase shell stability or strength. The derived origin of the orthogonal baculate from the baculate structure is supported by the co-existence of both types in *C.*? *pattersonensis* (Streng & Holmer 2005). But in contrast to the Acrotretoidea where new structural types, the septate and camerate type, are restricted to the secondary layer, no restriction of the orthogonal baculate layer to the secondary layer is evident. The coexistence of genera with a columnar and genera with a orthogonal baculate shell structure within the family Lingulellotretidae Koneva & Popov, 1983 needs, as outlined in Holmer *et al*. (2008), further examination which might demonstrate the lingulellotretids to be paraphyletic.

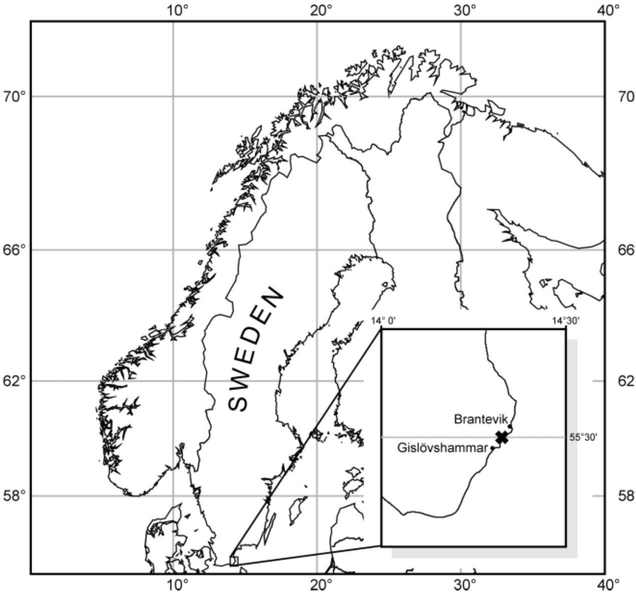

Figure 2 Sample locality (x) on the shore between Brantevik and Gislövshammar, Scania, southern Sweden.

2. Material and methods

The specimens described below are derived from a single limestone block, about 10 kg in weight, which was collected in Summer 2005 by GEB on the shore between Gislövshammar and Brantevik, south-eastern Scania, Sweden (55°30′N/ 14°19.6′E; Fig. 2). The block is a greenish-grey, glauconite- and pyrite-bearing biocalcarenite with phosphorite nodules, and is lithologically equivalent to the nearby outcropping Forsemölla Limestone Bed (a.k.a. the 'fragment limestone') (S. Bengtson, pers. comm. 2005). This affiliation has been confirmed by the study of its faunal content that matches the one described by Bengtson (1976) and Bergström & Ahlberg (1981).

All faunal elements were obtained by etching of about two thirds of the calcarenite block in 10% acetic acid and subsequent picking of the residue under a stereomicroscope. Selected specimens were gold-coated and studied under a scanning electron microscope (Leo Supra 35VP). Specimens are deposited in the collection of the Paleontological Museum, Uppsala (acronym PMU).

2.1. Fossil content

The following taxa have been identified from the acid residue: the protoconodonts *Amphigeisina danica* (Poulsen) and *Gapparodus bisulcatus* (Müller), the problematica *Lapworthella bornholmiensis* (Poulsen) and *Hyolithellus* cf. *micans* Billings, the organophosphatic brachiopods *Acrothele* cf. *granulata* Linnarsson, *Vandalotreta* sp., *Linnarssonia* sp., *Kotylotreta*? sp., *Canalilatus simplex* sp. nov. and *Eoobolus*? sp. aff. *E. priscus* (Poulsen), disarticulated paleoscolecid sclerites (*Hadimopanella* spp.), fragments of sclerites of *Microdictyon* sp., and bivalved arthropod shells (phosphatocopids?). Fresh unetched surfaces of the original rock sample showed in addition trilobite fragments, which were too poorly preserved to allow determination.

2.2. Age

The Forsemölla Limestone Bed in south-eastern Scania is a 4–20 cm-thick limestone layer which is part of the Middle Cambrian Alum Shale Formation. It is generally considered as early Mid Cambrian in age because of the presence of *Paradoxides paradoxissimus* (for more information see Bengtson 1976, p. 186–187; Bergström & Ahlberg 1981, p. 200; Nielsen & Schovsbo 2007, p. 84–85).

3. Systematic palaeontology

Class Lingulata Gorjansky & Popov, 1985
Order Lingulida Waagen, 1885
Superfamily Linguloidea Menke, 1828
Family indet.

Discussion. The two lingulid taxa described below as *Canalilatus*? *simplex* sp. nov. and *Eoobolus*? sp. aff. *E. priscus* (Poulsen) are both characterised by a columnar shell structure. Within the linguloids, such structures are so far only known from the Lingulellotretidae and the Kyrshabaktellidae Ushatinskaya, 1992. The Lingulellotretidae are, however, characterised by a ventral pedicle foramen and an internal pedicle tube, and the Kyrshabaktellidae by a smooth external shell surface, features regarded as taxonomically important (see below) but not present in the two described taxa excluding an affiliation with these two families. For this reason the systematic position of the two taxa is problematic, although shape, outline and additional features would suggest an affiliation of *C.*? *simplex* with the Zhanatellidae Koneva, 1986 and of *Eoobolus*? sp. aff. *E. priscus* (Poulsen) to the Eoobolidae Holmer, Popov & Wrona, 1996.

Comparison with the Zhanatellidae and Kyrshabaktellidae. The family Zhanatellidae was originally established by Koneva (1986) to include her two new linguloid genera *Zhanatella* and *Kyrshabaktella*, characterised by a deep pedicle groove and a semicircular emarginature. Popov & Ushatinskaya (1992) recognised a pitted microornamentation on the larval and post-larval shell of *Zhanatella*, a feature which they considered to be characteristic for the family and emended it accordingly. As a consequence, (1) *Kyrshabaktella* was excluded from the Zhanatellidae because of the absence of microornamentation and accommodated in its own newly-erected family (Ushatinskaya 1992); and (2) *Rowellella* Wright and the new genus *Fossuliella* were included because of similarities in ornamentation and the presence of a deep emarginature (Popov & Ushatinskaya 1992). Koneva (1992) also accommodated the new genus *Aksarinaia* Koneva within the Zhanatellidae, which was not followed in subsequent publications (Popov & Holmer 1994; Holmer & Popov 2000), as the genus lacks the typical ornamentation (Holmer *et al.* 2001). Based on the presence of microornamentation, Holmer & Popov (2000) assigned several other genera to the Zhanatellidae, i.e., *Hyperobolus* Havlíček, *Paldiskia* Gorjansky, *Rosobolus* Havlíček, *Thysanotos* Mickwitz, *Tropidoglossa* Rowell, and *Canalilatus* Pelman. For the same reasons, Popov *et al.* (2002) recently referred *Lingula antiquissima* Jeremejew to the Zhanatellidae as the type species of the new genus *Wahwahlingula*. The family Kyrshabaktellidae with its single genus *Kyrshabaktella* was rejected by Holmer & Popov (2000), who accommodated the genus within the Obolidae. The family was, however, retained subsequently by Skovsted & Holmer (2006), because of the observation of a columnar shell structure within their *Kyrshabaktella* sp. from the Lower Cambrian of Nevada.

With the new assignment of the various genera listed above to the Zhanatellidae by Holmer & Popov (2000) and Popov *et al.* (2002), the emended diagnosis of the family by Popov & Ushatinskaya (1992), which stresses the presence of microornamentation on the larval and post-larval shell as well as a semicircular aperture became imprecise, as now genera lacking the typical emarginature were also included in the family, as well as those bearing different types of microornamentation. This was considered to a certain extent by Holmer & Popov (2000), who gave a more general definition for the family. However, the definition of the Zhanatellidae is currently very weak, as it is mainly based on the presence of microornamentation and a gently biconvex shell. The latter feature distinguishes the Zhanatellidae from the Elkaniidae Walcott & Schuchert *in* Walcott 1908, a family also typified by an ornamented larval and postlarval shell, whose shell is strongly biconvex and in addition has raised muscle platforms and/or thickened visceral areas. A feature which would strengthen the diagnosis of the Zhanatellidae is a shell structure consistent throughout the family. However, knowledge of zhanatellid shell structure is incomplete. Shell fabrics have been illustrated and described for only a few species so far, i.e., *Rowellella* cf. *lamellosa* Popov and *Rosobolus*? sp. nov. a (see Holmer 1989); *Zhanatella rotunda* Koneva (see Popov & Holmer 1994; Ushatinskaya 1995); and *Zhanatella* sp. (see Ushatinskaya 1995). In every case, a baculate shell structure is either described or is most probable when judging from the illustrations provided. As *Zhanatella rotunda* is the type species of *Zhanatella*, which is in turn the type genus of the Zhanatellidae, a baculate shell structure must be implied as a plesiomorphic feature for the family.

Comparison with the Eoobolidae. Similar to the family Zhanatellidae, the family Eoobolidae Holmer, Popov & Wrona, 1996 is also typified by a distinctive microornamentation of the shell, but in contrast to the Zhanatellidae, the postlarval shell of the Eoobolidae is finely pustulose rather than pitted. Apart from that, eoobolids look quite similar to typical obolids in having a well developed ventral pseudointerareas with deep pedicle groove, propareas with distinct flexure lines, and a dorsal valve with a tongue-like, median projection. In fact, taxa whose exterior ornamentation is unknown and which are currently accommodated within the Obolidae might also represent eoobolids. Currently, only two genera are included within the Eoobolidae, i.e., *Eoobolus* Matthew (=*Clivosilingula* Ushatinskaya) and *Vassilkovia* Popov & Khazanovitch *in* Popov *et al.* 1989. Shell structural details reported from the Eoobolidae are scarce and contradictory. Ushatinskaya (1995) depicted shell cross sections of two specimens from the Middle Cambrian of the

Siberian Platform both identified as *Clivosilingula* sp. The first specimen of Amgan age has an indisputable baculate shell structure (Ushatinskaya 1995: photo 16), and the second one from the Mayan stage shows clear columnar structures (Ushatinskaya 1995: photo 168). Skovsted & Holmer (2005) described a baculate shell structure for *Eoobolus priscus* (Poulsen, 1932) from the Lower Cambrian of north-east Greenland, but depicted shell cross sections are recrystallised and identification of the structure type is not unambiguous (Skovsted & Holmer 2005, pl. 3, fig. 3). Nevertheless, a baculate structure seems to be more likely. Further studies on well determined eoobolid species are needed to decide on the shell structure type characteristic for the Eoobolidae (see also discussion on *Eoobolus*? sp. aff. *Eoobolus priscus* below).

Genus *Canalilatus* Pelman, 1983
[=*Pelmania* Koneva, 1992, p. 89]

Type species. *Canalilatus paulus* Pelman, 1983, 126–127 by original designation; Middle Cambrian, upper Amgan, north-central Siberia.

Diagnosis (Holmer & Popov 2000, p. 64). Shell small, subcircular; ventral pseudointerarea small; pedicle groove wide, shallow; dorsal pseudointerarea vestigial, undivided; ventral visceral field slightly thickened posteromedially, not extending to midlength; dorsal visceral field slightly thickened posteriorly with broad anterior projection, extending anteriorly beyond midlength, bounded laterally by ridges and bisected by fine median ridge.

Occurrence. Middle Cambrian (upper Amgan) of Russia (Siberia) and Kazakhstan (Malyi Karatau); ?Middle Cambrian of Sweden.

Species included. *Canalilatus paulus* Pelman, 1983; *Pelmania perrara* Koneva, 1992; *Canalilatus*? *major* Holmer, Popov, Koneva & Bassett, 2001; *Canalilatus*? *simplex* sp. nov.

Discussion. *Canalilatus*? *major* has questionably been assigned to *Canalilatus* as it differs from the type species and *C. perrarus* in size and in the distinctness of the dorsal and ventral pseudointerareas. *C.*? *major* reaches sizes of up to 7 mm in length and shows well developed pseudointerareas on both valves, which is in contrast to *C. paulus* and *C. perrarus*, which are smaller than 1 mm and have poorly differentiated posterior margins. This discrepancy has been explained by considering the latter two species as immature forms inhabiting near-shore environments (Holmer *et al*. 2001). The discovery of *C.*? *simplex* sp. nov. described below, which is also characterised by a relatively small size and vestigial pseudointerareas, suggests that such features may represent a generic feature and *C.*? *major* should consequently be excluded from the genus. However, as the affiliation of *C.*? *simplex* sp. nov. itself to the genus *Canalilatus* is uncertain (see discussion of *C.*? *simplex* sp. nov.), we retain *C.*? *major* questionable within the genus.

The genus *Canalilatus* is currently accommodated within the Zhanatellidae, hence a baculate shell structure should be characteristic for the genus (see above). However, for none of the species previously assigned to *Canalilatus* has any shell structural details been described. The columnar structures found in *Canalilatus*? *simplex* sp. nov. described below makes the systematic position of the new taxon and the genus itself intricate. The new species matches the characteristics of the genus, however, as the shell structure of the type species *C. paulus* is not known the affiliation of the new taxon to *Canalilatus* must be regarded as tentative pending restudy of the type species. Accordingly, the accommodation of the genus *Canalilatus* within the Zhanatellidae will demand reconsideration if a columnar ultrastructure will be shown for the type species.

Canalilatus? *simplex* sp. nov.
Figures 3, 4

Holotype. PMU-Sk-353, ventral valve, Figs 3.3, 3.5, 3.7, 4.4.

Type locality. Shore southwest of Brantevik, Scania, southern Sweden (Fig. 2).

Type horizon Forsemölla Limestone Bed, lower Alum Shale Formation, *Paradoxides paradoxissimus* stage, *Ptychagnostus gibbus* Zone?, Middle Cambrian.

Etymology. After the Latin *simplex*, meaning simple.

Material. Seven ventral and seven dorsal valves.

Diagnosis. Shell small, biconvex, slightly longer than wide; outline evenly rounded with the posterior margin somewhat more pointed than anterior. Larval and postlarval shell ornamented by hemispherical imprints of about the same size. Ventral valve with shallow, rudimentary pedicle groove; propareas of dorsal valve vestigial showing flexure lines. Shell structure columnar to septate.

Description. Shell equivalved, biconvex, relatively small, 0·9–1·2 mm in length (N=7); maximum width of shell at midlength, measuring about 90% of total length. Larval and postlarval shell ornamented by small hemispherical pits of about the same size; pits of larval shell range from 1·0 µm to 1·5 µm and those of the postlarval shell from 1·1 µm to 1·4 µm, with the postlarval pits less discrete (compare Fig. 4.3 and Fig. 4.10). Transition from larval to postlarval shell smooth and indistinct, but the latter with smooth, concentric filae (Fig. 3.10). Internal surface of both valves even, without any discernable characteristics. Ventral valve with shallow, semicircular emarginature and rudimentary pedicle groove; propareas not observed, probably owing to poor preservation, but shell thickened lateral to pedicle groove (Fig. 3.3). Dorsal valve bears vestigial pseudointerarea, characterised by tiny propareas divided by the posterior margin of the larval shell; no median groove developed; propareas ornamented by relatively distinct ridges (flexure lines?) (Fig. 3.8).

Shell structure. The shell structure of *Canalilatus*? *simplex* includes both a columnar and a septate fabric, as well as a fabric intermediate between these two. The columnar fabric is the typical acrotretid columnar structure, with sets of columnar laminae separated by interlaminar gaps and individual columns extending through multiple laminae (e.g., Fig. 4.2). The maximal measured thickness of a lamina is 15 µm, columns are 1·5–2 µm in diameter and bear a central canal. The septate shell fabric is best seen on slightly exfoliated and diagenetically altered areas of outer shell surfaces. Here, radially arranged grooves, which coincide with former septa, delineate a radial arrangement of elongated rectangular, chambers (camerae) which are now filled by secondary apatite (Fig. 4.5). Occasionally, the original septa and unfilled camerae are preserved. In such cases the ultrastructure of a septum can be seen that is characterised by two distinct phosphatic walls separated by a narrow gap (Fig. 4.4). Individual septa are 1·5–2·5 µm wide, with the gap measuring about 500 nm, matching the measured diameters of the columns and the central canals, respectively. The intermediate fabric shows accordingly features of both, the columnar and the camerate fabric. It is characterised by laminae with radially arranged columns and domes that are to some extend already amalgamated. Thus, fused domes, e.g., form short radial ridges on intralaminar surfaces (Fig. 4.7). In total the shell structure of *Canalilatus*? *simplex* is interpreted as consisting of three layers: the primary layer, a thin granular sheet bearing a pitted microornamentation, the secondary layer, characterised by septate laminae which become columnar internally, and a

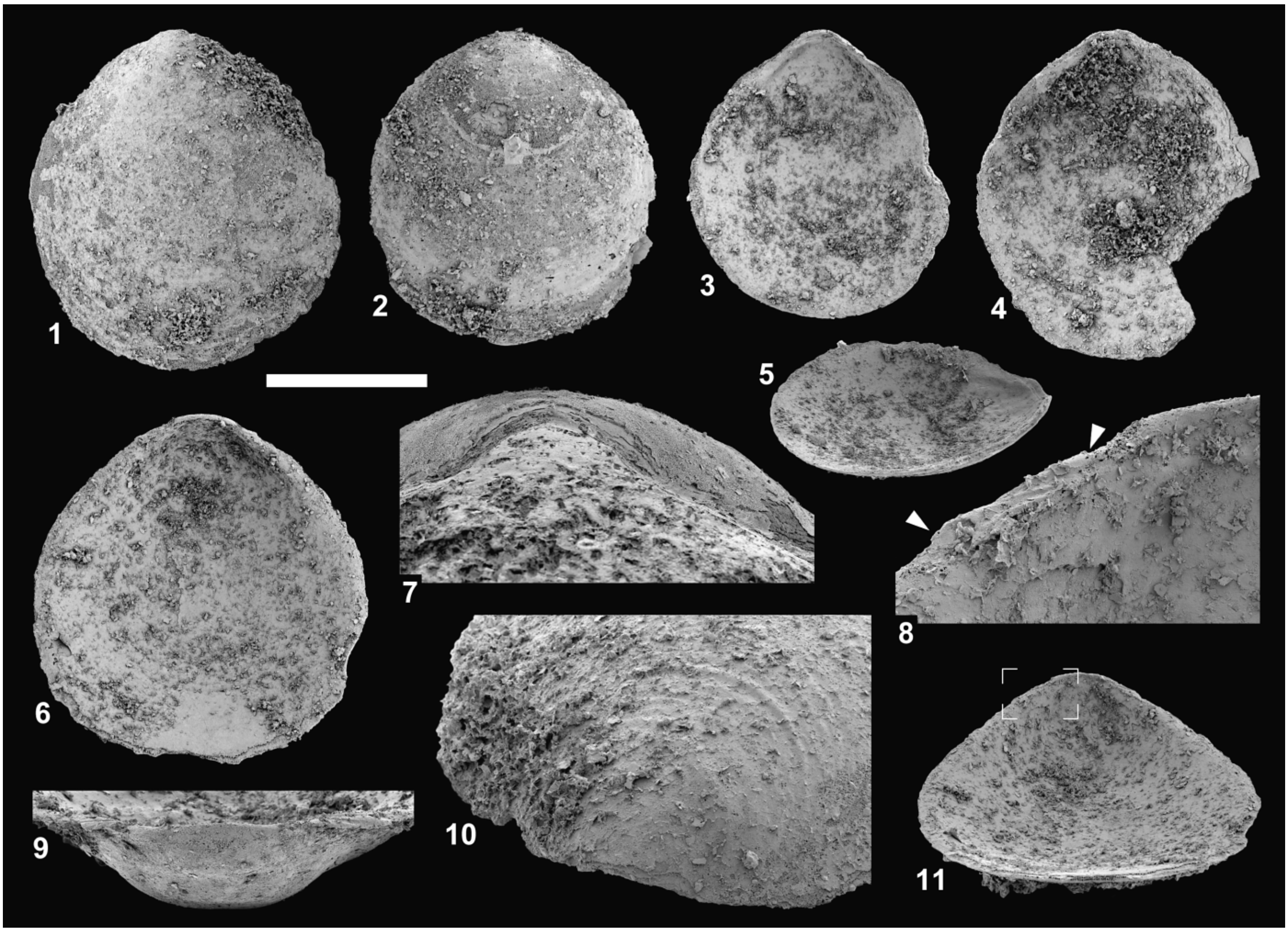

Figure 3 *Canalilatus*? *simplex* sp. nov.: (1) External view of ventral valve (PMU-Sk-354); (2) external view of dorsal valve (PMU-Sk-351); (3) internal view of ventral valve (holotype, PMU-Sk-353); (4) internal view of ventral valve (PMU-Sk-355); (5) lateral view of (3) (holotype); (6) internal view of dorsal valve (PMU-Sk-352); (7) apical view of (3) showing semicircular emarginature (holotype); (8) detail of (11) showing part of dorsal pseudointerarea with vestigial proparea (proparea framed by arrows); (9) apical view of (6); (10) lateral apical view of (1) showing concentric fila; emarginature not obvious as posterior shell margin is worn; (11) oblique anterior view of (6) (location of enlargement as seen in (8) indicated). Scale bar: (1)–(6), (11)=500 µm; (7), (8) =100 µm; (9), (10)=200 µm.

tertiary layer, which is entirely columnar and whose laminae are added interior to the secondary layer to stabilise the shell.

Discussion. *C.*? *simplex* sp. nov. is quite similar to the type of the genus, *C. paululus*, in outline, size, and the development of the ventral and dorsal pseudointerarea. They are distinguished in the development of the ventral and dorsal visceral areas, which are thickened in *C. paululus*, and of the dorsal median ridge, which is absent in *C.*? *simplex*. *C. perrarus* is circular in outline, slightly broader than long, and also has thickened visceral areas. *Canalilatus*? *major* is distinguished from all other species of *Canalilatus* by it size, which is up to eight times larger, and its well developed dorsal and ventral pseudointerareas (see also Discussion of *Canalilatus* above).

Genus *Eoobolus* Matthew, 1902

Type species. *Obolus* (*Eoobolus*) *triparilis* Matthew, 1902; Middle Cambrian, Cape Brenton, Canada (selected by Rowell 1965, p. H263)

Diagnosis. See Holmer *et al*. (1996)

Other species included. *Lingulella wanniecki* Redlich, 1899; ?*Lingulella viridis* Cobbold, 1921; *Lingulella prisca* Poulsen, 1932 (=?*Lingulella elata* Pelman according to Skovsted & Holmer 2005); *Lingulella clivosa* Pelman, 1983; *Lingulella elata* Pelman *in* Pelman & Pereladov 1986 (=*Clivosilingula dilatata* Ushatinskaya); *Eoobolus* aff. *viridis* (Cobbold) of Ushatinskaya & Holmer (2001) and Li & Holmer (2004). Tentatively assigned to *Eoobolus* are *Eobolus*? *shaanxiensis* Li & Holmer, 2004 and *Eoobolus*? sp. aff. *Eoobolus priscus* (Poulsen, 1932) described below.

Eoobolus? sp. aff. *Eoobolus priscus* (Poulsen, 1932)
Figures 5–7

Locality. Shore southwest of Brantevik, Scania, southern Sweden (Fig. 2).

Age. Middle Cambrian, *Paradoxides paradoxissimus* Stage, *Ptychagnostus gibbus* Zone?

Material. 39 ventral and 55 dorsal valves, all fragmentary.

Description. Complete outline of neither valve well-preserved as all specimens are fragmentary; the better preserved specimens suggest a biconvex, slightly inequivalved shell with evenly rounded anterior margin (Fig. 5.1). External surface of post-larval shell covered by a fine pustulose ornamentation; individual pustules are about 10 µm in diameter, often arranged in radiating rows (Fig. 6.2); surface of early formed shell smooth; shell structure columnar.

Ventral valve evenly convex, acuminate with straight posterolateral margins enclosing an apical angle of 84–93°; raised pseudointerarea triangular in outline, medially divided

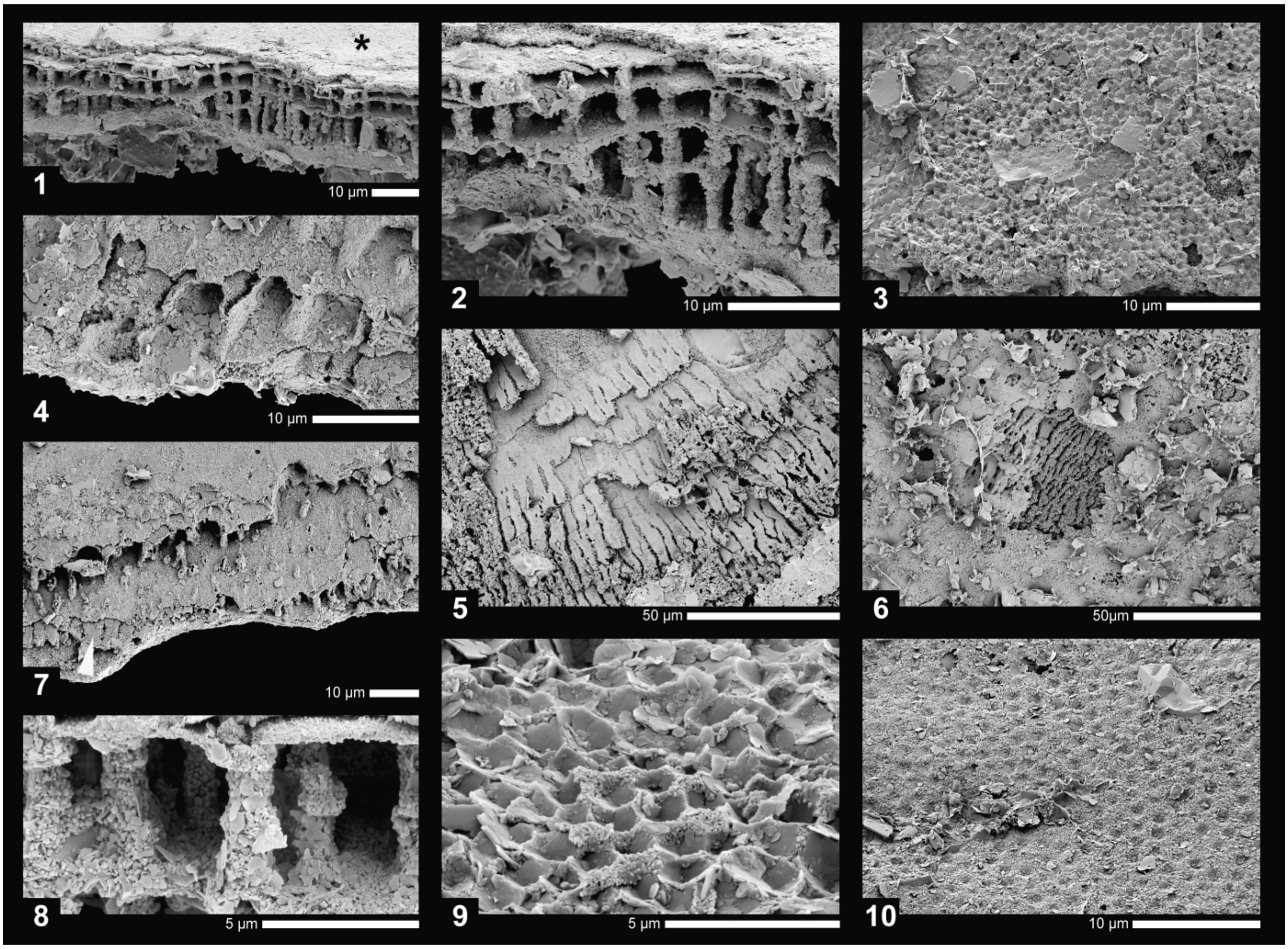

Figure 4 Shell structure and ornamentation of *Canalilatus*? *simplex* sp. nov.: (1) Set of three laminae at the anterior margin of a dorsal shell revealing columnar shell structure; asterisk marks inner shell surface (PMU-Sk-352; same specimen as in Fig. 3.6, 3.9, 3.11); (2) detail of (1) showing an increase in lamina thickness towards the exterior; (3) pitting of a ventral larval shell (PMU-Sk-354; same specimen as in Fig. 3.1, 3.10); (4) broken lateral margin of a ventral valve showing radially arranged septa (PMU-Sk-353; same specimen as in Fig. 3.3; holotype); (5) exfoliated outer surface of a dorsal valve revealing diagenetically altered septate shell structure (PMU-Sk-351; same specimen as in Fig. 3.2); (6) exfoliated area on a ventral valve showing septate structures (same specimen as (3) and as in Fig. 3.1); (7) close-up of anterior shell margin showing (a) the smooth inner shell surface (upper part of picture), (b) an intralaminar surface with radially aligned and partly amalgamated columns and domes (lower part of picture), and (c) an interlaminar surface with radially aligned, intercamerate gaps indicating septate structure of respective lamina (lower left corner of picture; arrow) (same specimen as (1) and (2); (8) close-up of columns; detail of (1); (9) pitting of dorsal larval shell, surface recrystallised (same specimen as (7)); (10) pitting of postlarval outer surface of a dorsal valve (same specimen as (5)).

by deep pedicle groove; lateral margins of pedicle groove typically taper posteriorly in small specimens and are almost parallel in larger specimens; anacline propareas overhang valve floor (Fig. 5.10), divided medially by distinct flexure lines which enclose an angle of about 60–65°. Visceral area faintly discernable by thickened shell in some valves, bisected by faint, anteriorly expanding depression marked laterally by v-shaped scars of pedicle nerve (Fig. 5.12, 5.15); muscle scars generally poorly marked, only anterior and posterolateral muscle scars occasionally visible, marked by exfoliated shell layers (Fig. 5.9). First formed shell smooth but on lateral flanks with delicate radiating ridges, 50–70 μm in length (Fig. 6.11, 6.12).

Dorsal valve convex, evenly ovoid in outline with posterior margin slightly more pointed than anterior one; apsacline pseudointerarea slightly raised above valve floor, anteriorly undercut (Figs 5.11, 5.16, 7.1), with broad and long median groove which is weakly defined laterally; no flexure lines seen on propareas; visceral area distinct, thickened, extending anteriorly as long median tongue; median ridge poorly developed accompanied laterally by indistinct anteriorly diverging ridges bearing central muscle scars (Fig. 5.4); median tongue extends beyond midlength of shell; no vascula lateralia or media observed.

Due to the fragmentary preservation of almost all specimens no measurements could be performed. Evaluation and reconstruction of some better-preserved specimens suggest a length-width ratio of the ventral valve of about 1.45 and a maximum shell length of at least 3 mm.

Shell structure. Three layers can be distinguished in the shell of *Eoobolus*? sp. aff. *Eoobolus priscus*. The outermost primary layer seems to be a thin sheet that accentuates the pustulose ornamentation of the outer shell surface. However, because of the generally poor preservation of the material, the primary layer is only occasionally preserved and no further features, such as potential filae with nick points, could be observed. The secondary layer varies in thickness and is made up of wedge-shaped laminae showing a columnar shell structure. The individual columns bear a central canal and measure about 1·5–2·2 μm in diameter. Columns may be aligned in radiating rows indicating a transition to a septate shell

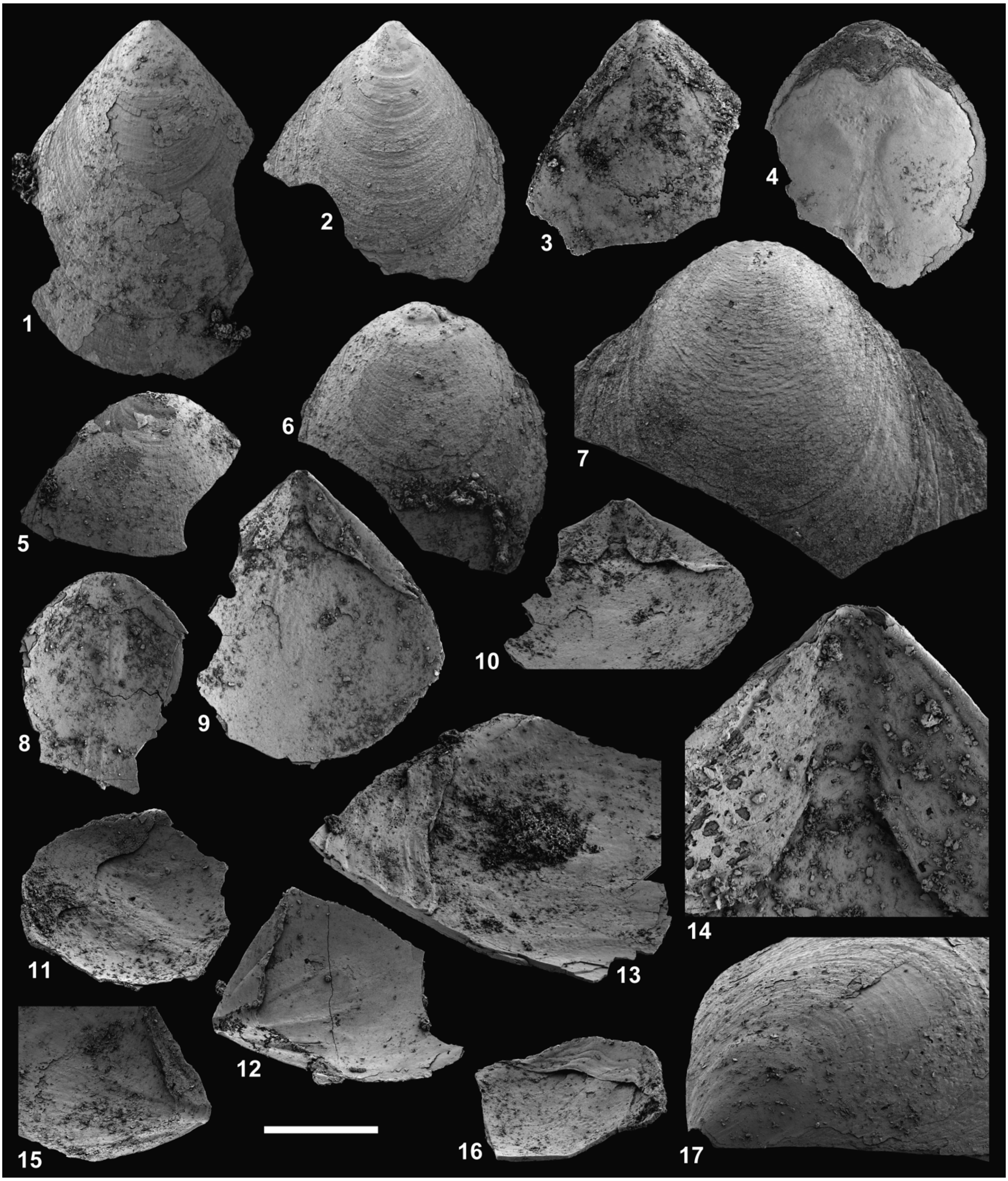

Figure 5 *Eoobolus*? sp. aff. *E. priscus* (Poulsen, 1932): (1) exterior of ventral valve (PMU-Sk-37); (2) exterior of ventral valve (PMU-Sk-365); (3) interior of ventral valve (PMU-Sk-374); (4) interior of dorsal valve with elevated visceral area, median ridge and central muscle scars (PMU-Sk-367); (5) exterior of dorsal valves (PMU-Sk-370); (6) exterior of dorsal valve (PMU-Sk-373); (7) exterior of dorsal valve (PMU-Sk-372); (8) interior of dorsal valve (PMU-Sk-364); (9) interior of ventral valve with well developed pseudointerarea showing flexure lines (PMU-Sk-366); (10) anterior view of (9) showing undercut pseudointerarea; (11) lateral view of dorsal valve (PMU-Sk-378); (12) posterolateral view of ventral valve with v-shaped impressions of pedicle nerve and well developed pseudointerarea (PMU-Sk-382); (13) lateral view of large dorsal valve (PMU-Sk-384); (14) close-up of pseudointerarea of (9) showing pedicle groove; (15) posterolateral view of (3) faintly showing pedicle nerve impressions; (16) anterolateral view of dorsal valve with undercut pseudointerarea (PMU-Sk-388); (17) posterolateral view of (1). Scale bar: (1)–(13), (15), (16) = 500 µm; (14) = 125 µm; (17) = 250 µm.

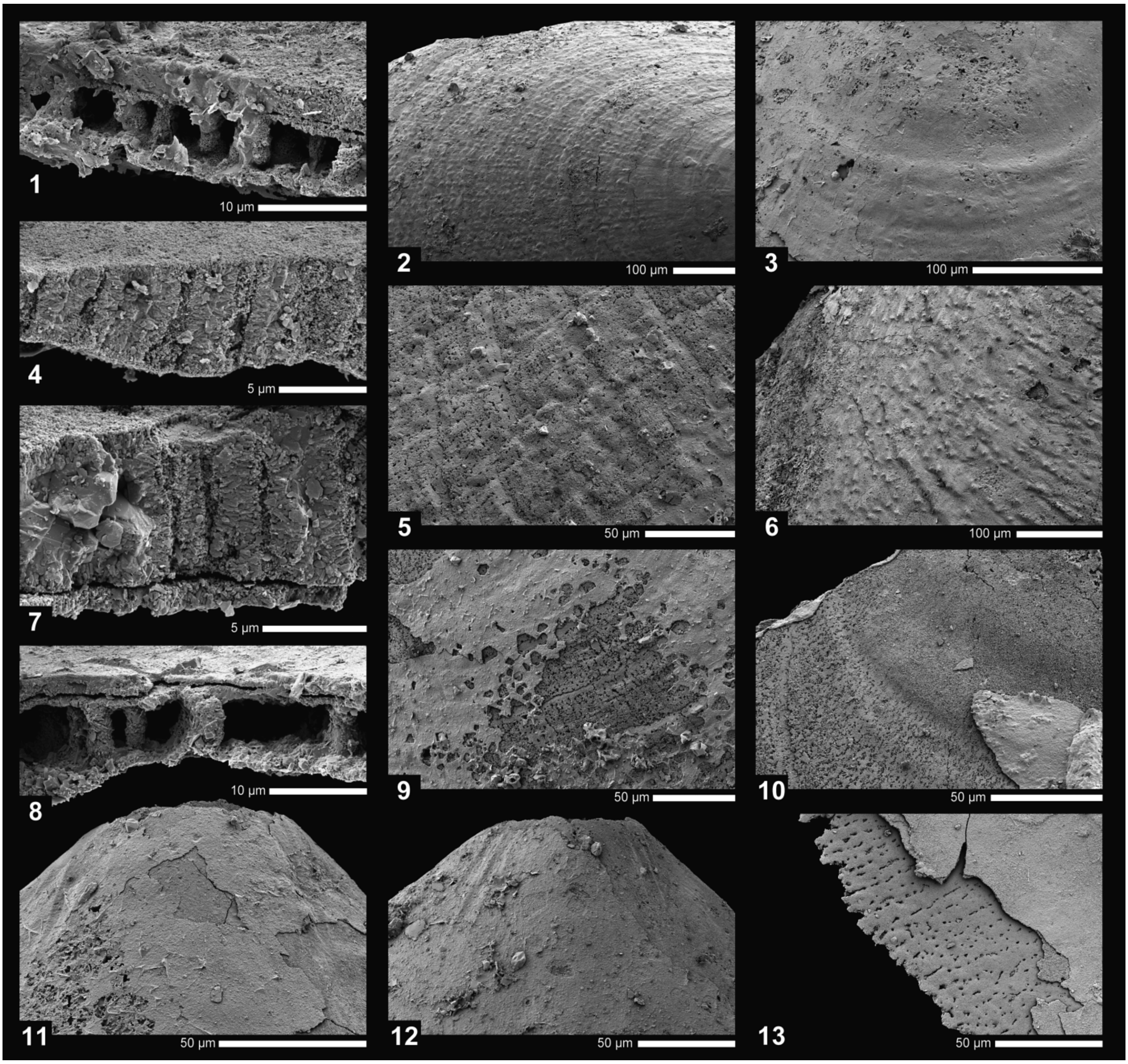

Figure 6 Shell structure and ornamentation of *Eoobolus*? sp. aff. *E. priscus* (Poulsen 1932): (1) lamina with columnar structure in a dorsal valve (PMU-Sk-364; same specimen as in Fig. 5.8); (2) pustulose ornamentation of exterior surface of a ventral valve; note individual pustules are arranged in radially running rows (PMU-Sk-365; close-up of Fig. 5.2); (3) transition from smoother 'juvenile' shell to more ornamented 'adult' shell (same specimen as (2)); (4) recrystallised lamina showing remnants of a columnar structure an a dorsal and a ventral valve (PMU-Sk-369); (5) exfoliated dorsal valve showing the interlaminar surface of outermost lamina; note that the interlaminar surface faintly records the pustulose ornamentation of the missing primary layer (PMU-Sk-373; same specimen as in Fig. 5.6); (6) less organised pustulose surface than in (2) (PMU-Sk-372; detail of Fig. 5.7); (7) recrystallised lamina showing remnants of a columnar structure an a dorsal and a ventral valve (PMU-Sk-368); (8) lamina with columnar structure in a ventral valve (PMU-Sk-374; same specimen as in Figs 5.3, 5.15); (9), (10) partly exfoliated dorsal valve (PMU-Sk-370; close-ups of Fig. 5.5); (11) close-up of apical part of ventral valve showing faint ridges anterolateral to pedicle opening (PMU-Sk-365; same specimen as in Fig. 5.2); (12) close-up of apical part of ventral valve showing faint ridges anterolateral to pedicle opening (PMU-Sk-371; same specimen as in Fig. 5.1); (13) interlaminar surface of inner lamellae close to the margin of a dorsal valve showing radially arranged and partly fused canal openings of a columnar lamina (PMU-Sk-367; same specimen as in Fig. 5.4).

structure (Fig. 6.13). Individual laminae appear to be relatively thin with a maximum observed thickness of about 10 µm. The tertiary layer is distinguished from the secondary layer by an unconformity in the shell laminae, changing from wedge shape to more or less parallelly arranged lamellae and laminae (Fig. 7.9). In addition, the individual laminae have a more massive appearance with a columnar structure only occasionally preserved/developed (see below).

The individual laminae and lamellae of the secondary and tertiary layer show three types of appearances according to varying preservational stages: (1) laminae with distinct intralaminar space and three-dimensionally preserved columns connecting the outer and inner lamella (Figs 6.1, 6.8, 7.9); (2) laminae with intralaminar space filled by secondary apatite; inner and outer lamellae are indistinguishable from intralaminar fillings; laminae pierced by numerous canals of about

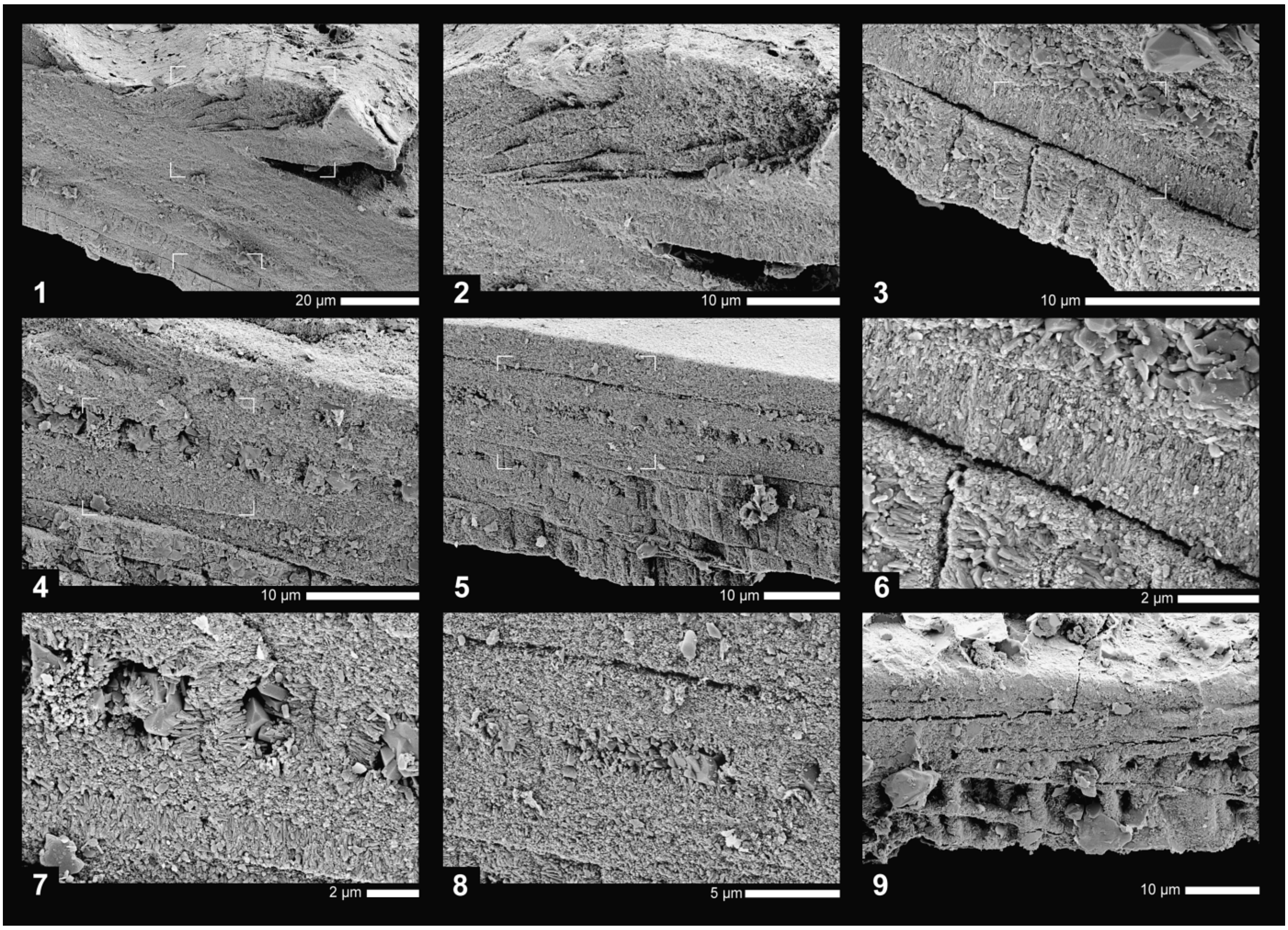

Figure 7 Shell structure of *Eoobolus*? sp. aff. *E. priscus* (Poulsen 1932). (1)–(8) Details of a longitudinal cross section through the posterior part of the dorsal valve seen in Fig. 5.13 (PMU-Sk-384): (1) detail showing undercut pseudointerarea and multi-laminar shell (location of enlargements as seen in (2) and (3) indicated); (2) detail of (1) with unconformable contact between regular shell laminae and laminae forming the pseudointerarea; (3) detail of (1) with an outer lamina showing remnants of a columnar shell structure (only canals of former columns preserved) followed by completely recrystallised laminae; (4) succession of laminae showing different states of recrystallisation and wedging in of additional laminae; (5) succession of laminae with different states of preserved columnar structures; (6) contact between two recrystallised laminae, one of which shows vestiges of a columnar fabric (detail of (3)); (7) detail of (4) showing a partly recrystallised lamina with intralaminar space filled by bulky crystals; (8) almost completely recrystallised lamina showing remnants of intralaminar space; detail of (5). (9) Cross section through the shell of a dorsal valve (PMU-Sk-385) showing the unconformity between wedge-shaped laminae of the secondary layer and horizontally arranged laminae of the tertiary layer.

1 µm in diameter running perpendicular to the interlaminar surfaces; and (3) homogeneous laminae and lamellae of granular apatite. The first type is identical to the typical columnar shell structures of acrotretids (see, e.g., Holmer 1989). The second type represents the columnar type, with the intralaminar spaces filled by secondary diagenetic apatite. The perpendicular canals represent the central canal of former columns whose walls fused with the intralaminar filling. The diagenetic origin of the intralaminar fillings is indicated by the relatively large size of the phosphatic crystallites when compared to less-affected shell areas. Also indicative for a secondary origin of the fillings is the fact that the intralaminar space is successively filled by rod- or needle-shaped crystals, starting from the intralaminar surfaces of the individual laminae and either filling intralaminar space completely (Fig. 7.8), or leaving a cavity in the center of the laminae (Fig. 7.7). These cavities may subsequently be filled by a third generation of apatite crystals that are irregular and larger in size than the rod-shaped crystallites (Fig. 7.7). The homogenous laminae and lamellae observed especially within the tertiary layer are hard to interpret. Some of them are likely to have represented columnar layers, but a primary homogenous or even a baculate appearance cannot be excluded. A diagenetic overprint for most of these laminae and lamellae is analogous to the columnar laminae indicated by the crystal size and an often ordered, parallel arrangement of the enlarged crystals perpendicular to the surfaces of the respective lamellae.

Discussion. Specimens of *Eoobolus*? sp. aff. *E. priscus* are similar to *Eoobolus priscus* regarding outline of shell, features of the pseudointerareas as well as other internal features, such as the dorsal visceral field with the tongue-like anterior extension. *Eoobolus priscus* slightly differs in the impression of the pedicle nerve that reaches more anteriorly, and in the presence of a dorsal median sulcus. Whereas these difference may be interpreted as intraspecific or intrageneric variation, the presence of two different shell structures, baculate in *E. priscus* (Skovsted & Holmer 2005; but see discussion of Family indet. above) and columnar in *Eoobolus*? sp. aff. *E. priscus*, excludes a common accommodation within the same species or genus, even within the same family. Furthermore, the combination of a pustulose post-larval and a smooth larval shell as present in *Eoobolus*? sp. aff. *E. priscus* additionally contradicts an assignment to the Eoobolidae. *Eoobolus*? sp. aff. *E. priscus* might be close to *Eoobolus*? *shaanxiensis* from the Lower Cambrian of

China or the genus *Vassilkovia* Popov & Khazanovitch from the Upper Cambrian of Ingria, Russia. The pustulose ornamentation of *E.*? *shaanxiensis* suggests affinity with the Eoobolidae but as in *Eoobolus*? sp. aff. *E. priscus* the larval shell is smooth rather than pitted. For this reason, *E.*? *shaanxiensis* has only been tentatively assigned to *Eoobolus* and the Eoobolidae by Li & Holmer (2004). Both taxa might represent a new genus, but as the shell structure of *E.*? *shaanxiensis* is not known, no conclusive decision can be made. The genus *Vassilkovia* has been assigned to the Eoobolidae by Holmer *et al*. (1996) based on the pustulose ornamentation of the post-larval shell. However, as noted by Holmer *et al*. (1996), morphology of the larval shell of *Vassilkovia* is unknown; the same is true for the shell structure, leaving the possibility for a relationship with *E.*? *shaanxiensis* and *Eoobolus*? sp. aff. *E. priscus*. The family Eoobolidae needs urgent restudy concerning (1) the shell structure of the type species of the nominate genus *Eoobolus*, i.e. *Eoobolus triparilis*; and (2) the shell structure and ornamentation of the larval shell of *Vassilkovia*, to strengthen its diagnosis and justification as a family.

4. Conclusions

1. Two basal shell fabrics are distinguished in the early linguloid brachiopods, i.e., the columnar and the baculate fabric, from which additional fabrics evolved: the septate and the camerate from the columnar and the orthogonal baculate from the baculate fabric. The columnar shell structure with its derived forms (septate and camerate) is here summarised as the 'columnar group' and the baculate structure with the orthogonal baculate fabric as the 'baculate group'.
2. The columnar group is characteristic for the Acrotretoidea, but is also present in the Linguloidea, where it is most likely more common than previously assumed.
3. The same shell structural evolution recognised within the Acrotretoidea which is characterised by the fusion of the columns to form septa and walls, leading to the septate and the camerate shell structure type, is observed within 'columnar linguloids'.
4. Shell structural development during the Cambrian of both the columnar and the baculate group appears to reflect an increase in shell stability or strength.
5. The family Zhanatellidae Koneva, 1986 is characterised by a baculate and the family Kyrshabaktellidae Ushatinskaya, 1992 by a columnar shell structure. The shell structure within taxa of the family Lingulellotretidae Koneva & Popov, 1983 is inconsistent and needs further study. A baculate shell structure for the family Eoobolidae Holmer, Popov & Wrona, 1996 is likely but needs confirmation.
6. A columnar shell structure within the Linguloidea is so far only known from four Early and Middle Cambrian taxa, i.e., *Lingulellotreta* Koneva, *Kyrshabaktella* Koneva, *Canalilatus*? *simplex* sp. nov. and *Eoobolus*? sp. aff. *E. priscus* (Poulsen). Morphological differences between the taxa are substantial suggesting that the four taxa should be accommodated in four suprageneric taxa.
7. Restudy and reevaluation on the basis of newly attained data on shell structural details of many taxa currently accommodated within the Zhanatellidae, Eoobolidae and Elkaniidae as well as within the Obolidae, is required to more precisely state their diagnoses and to confirm or revise their status as families.

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