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Morphology, shell structure and affinities of *Pelmanotreta* gen. nov. from the lower Cambrian of Siberia

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The new genus *Pelmanotreta* is proposed under the provisions of the ICZN to replace *Cryptotreta* Pelman, 1977 (Brachiopoda), a junior homonym of *Cryptotreta* Blanc & Foote, 1961 (Arthropoda). This poorly known brachiopod genus and its type and only species, *Pelmanotreta neguertchensis* (Pelman, 1977), from the early Cambrian of Siberia is redescribed. The Family Cryptotretidae Pelman, 1979, originally based on *Cryptotreta* Pelman, 1977 is invalid and *Pelmanotreta* is tentatively referred to the Salanygolinae Holmer et al. 2009. In *Pelmanotreta*, dorsal valves vastly outnumber ventral valves in all collections but new specimens of the poorly known ventral valve reveal a septate and possibly poorly mineralized apical region. A prismatic hexagonal shell ultra-structure comparable to that of *Salanygolina* is described. *Pelmanotreta neguertchensis* preserve the earliest known record of a larval shell in brachiopods.

Key words: Early Cambrian, Brachiopoda, Siberia, Systematics, Ultra-structure

Introduction:

The first group of brachiopods to appear in the early Cambrian fossil record is the paterinates (Class Paterinata Williams et al., 1996), a Cambrian to Ordovician group that uniquely combines an organophosphatic shell with a strophic hinge (Laurie 2000). The early appearance and unusual character combination of paterinids, as well as the distinct similarities in morphology and shell structure to stem group brachiopods (i.e. the tommotiids *Eccentrotheca* Landing et al. 1980 and

Paterimitra Laurie, 1986), suggest that paterinids may be pivotal to our understanding of early brachiopod evolution (Williams et al. 1998; Skovsted et al. 2008, 2009, 2011; Balthasar et al. 2009; Holmer et al. 2009; Topper et al. 2013; Topper & Skovsted in press; Larsson et al. in press). This is particularly true for the earliest paterinids, often referred to the Family Cryptotretidae, which has been shown to include members with unusual and poorly understood morphologies such as large anterior openings in the ventral valve (Pelman 1977; Ushatinskaya 1987; Holmer et al. 2009).

The early Cambrian succession of the Siberian Platform has yielded the oldest known paterinids and a better understanding of these early taxa will be very important for our understanding of the origin of the phylum Brachiopoda (Pelman 1977; Ushatinskaya 2008; Skovsted et al. in press). One of the oldest known organophosphatic brachiopod taxa from Siberia was originally described under the name *Cryptotreta nequertchensis* Pelman, 1977. However, the generic name *Cryptotreta* Pelman, 1977 is a junior homonym of *Cryptotreta* Blanc & Foote, 1961 – a recent fruit fly genus from California (Blanc & Foote 1961; Foote & Blanc 1963). For this reason we propose the name *Pelmanotreta* gen. nov. to replace *Cryptotreta* Pelman, 1977.

Material and methods:

The investigated material was mainly derived from sections through the lower Cambrian Pestrotsvet Formation, at Zhurinsky Mys (Tommotian stage, *Dokidocyathus lenaicus* zone, bed 3 – see Varlamov et al., 2008, p. 72, figs 27, 29) and Oy-Muran (Atdabanian stage, *Leptosocyathus polyseptus* zone, beds 2, 3 (Varlamov et al., 2008, p.95, fig. 38), in the middle reaches of the Lena River, southeastern part of the Siberian Platform. Additional material is available from the Malaya Kuonamka and Bol'shaya Kuonamka River, eastern flanks of the Anabar Uplift, northern part of the Siberian Platform.

Systematic Palaeontology:

Repository. – All illustrated specimens are housed in the palaeontological collections of the Paleontological Institute, Moscow, Russia (PIN) and the Swedish Museum of Natural History (NRM).

Phylum BRACHIOPODA Duméril, 1806

Class PATERINATA Williams, Carlson, Brunton, Holmer and Popov, 1996

Order PATERINIDA Rowell, 1965

Superfamily PATERINOIDEA Schuchert, 1893

?Family Salanygolinidae Holmer, Pettersson Stolk, Skovsted, Balthasar and Popov, 2009

Genus *Pelmanotreta* gen. nov.

- Non 1961 *Cryptotreta* Blanc & Foote; p. 82.
Non 1963 *Cryptotreta* Blanc & Foote; Foote & Blanc, p. 14.
1977 *Cryptotreta* Pelman; p. 53.

Type species. – *Cryptotreta neguertchensis* Pelman, 1977 from the lower Cambrian Tommotian and Atdabanian Stages of Siberia. Monotypic.

Diagnosis. – Transversely ovate, biconvex organophosphatic shell with strophic hinge. Ventral valve with high, orthocline almost planar interarea divided by narrow delthyrium mainly covered by convex, ridge-like homeodeltidium. Dorsal valve with shallow sulcus; dorsal interarea very low, anacline with narrow, convex chilidium closing the notothyrium. Ornament of fine, concentric growth-lines. Shell ultrastructure composed of laminae with hexagonal prisms. Ventral interior with septate umbonal region. Dorsal interior with transverse platforms anterior to interarea and pinnate mantle canals.

Differ from *Tumulduria* Missarzhevsky in Rozanov et al., 1969 in having ornament of regular transverse fila on the ventral interarea and in the presence of a small chilidium restricting the notothyrium. Differ from *Salanygolina* Ushatinskaya, 1987 by the smaller and narrower homeodeltidium and in having apical septa in the ventral umbonal area, a narrow chilidium and shallow dorsal sulcus. Differ from *Aldanotreta* Pelman, 1977, *Askepasma* Laurie, 1986, *Dzunarzina* Ushatinskaya, 1993 and *Tallatella* Topper & Skovsted (in press) by the orthocline ventral interarea with delthyrium restricted by a homeodeltidium and the reduced, anacline dorsal interarea.

Etymology. – In reference to the important contributions to Cambrian brachiopod studies, including the finding and identification of cryptotretid brachiopods, by the late Yu.L. Pelman.

Discussion. – Dorsal valves of *Pelmanotreta* are relatively common in the Pestrotsvet Formation (Tommotian and Atdabanian stages) of the Siberian Platform, but because of the rarity of well preserved ventral valves the genus remains poorly understood. The same situation applies to several other morphologically similar cryptotretid brachiopods; *Tumulduria* Missarzhevsky in Rozanov et al., 1969 from slightly older strata in Siberia (Skovsted et al. in press) and *Salanygolina* Ushatinskaya, 1987 from the lower Cambrian (Botoman equivalent, Cambrian Stage 4) of Mongolia. However, in the few complete ventral valves presently known for *Salanygolina*, a large shell perforation is present anterior to the ventral umbo, which is partially closed by a colleplax (Ushatinskaya, 1987; Holmer et al. 2009). This morphology likely reduced the structural strength of the shell and presumably explains the paucity of ventral valves in *Salanygolina* (Holmer et al. 2009). The same phenomenon could also

explain the absence of ventral valves in *Tumulduria* (see discussion in Skovsted et al. in press) and *Pelmanotreta*, if a ventral umbonal opening was present in these taxa. Although some small or poorly preserved ventral valves of *Pelmanotreta* appear to show an anterior shell opening (see Pelman 1977, pl. 21, fig. 4 and Laurie 2000, fig. 85b), no conclusive evidence in favor of this hypothesis is available at the present time and the presence of apical septa connecting the margin of the interarea with the ventral valve floor in *Pelmanotreta* appear to preclude a functional apical opening in this genus, at least in adult specimens. However, the dorsal valve morphology and the shape of the orthocline ventral interarea of *Pelmanotreta* are closely comparable to their counterparts in *Salanygolina* and *Tumulduria*, suggesting a close phylogenetic link between these taxa.

Cryptotreta Pelman, 1977 was used as the type genus for the Family Cryptotretidae Pelman, 1979. However, as the name of the type genus is preoccupied, the Family name Cryptotretidae Pelman, 1979 should be abandoned (the valid genus *Cryptotreta* Blanc & Foote 1961 is not included in this family). Holmer et al (2009) proposed the Family Salanygolinidae Holmer et al., 2009 for the genus *Salanygolina* Ushatinskaya, 1987 and differentiated this family from Cryptotretidae Pelman, 1979 based on the poor understanding of the morphology of *Cryptotreta* Pelman, 1977, in particular the uncertain presence of an anterior ventral shell opening and colleplax. As documented herein, the ventral valve morphology in *Pelmanotreta* gen. nov. remains poorly understood as most known specimens appear to lack the apical region. Both *Pelmanotreta* and *Salanygolina* have an almost planar ventral interarea with very narrow delthyrium almost completely covered by the convex, ridge-like homeodeltidium, a unique morphology within the Paterinata which probably represents a plesiomorphic character.

The shell ultra-structure of *Pelmanotreta* is also very similar to that of *Salanygolina*. Consequently, we conclude that *Pelmanotreta* like the similar, and likewise poorly known *Tumulduria* (see discussion in Skovsted et al. in press), may belong to the same family as *Salanygolina*. The characteristic orthocline interarea with a narrow, ridge-like homeodeltidium is not present in other genera previously referred to Cryptotretidae, such as *Aldanotreta* Pelman, 1977, *Dzunarzina* Ushatinskaya 1993, *Askepasma* Laurie, 1986 or the recently described *Tallatella* Topper & Skovsted in press, but the exact relationships of these taxa to the Salanygolinidae are presently uncertain. However, the Family level taxonomy of cryptotretid paterinids is in need of revision, and we choose to leave the Family level assignment of *Pelmanotreta* as uncertain until a full revision of the cryptotretids is available.

Pelmanotreta neguertchensis (Pelman, 1977)

Figures 1-3

1977 *Cryptotreta neguertchensis* Pelman, p. 54, pl. 21, figs 2-6, pl. 22, figs 1-2.

2000 *Cryptotreta neguertchensis* Pelman; Laurie, fig 85.

2010 *Cryptotreta neguertchensis* Pelman; Rozanov et al., p. 81, pl. 47, figs 1-9.

We have tried to access the type material of *Cryptotreta* Pelman, 1977 but the specimens illustrated by Pelman (1977, 1979) appear to be lost (I.V. Korovnikov pers. com. 2013).

Diagnosis. – As for genus.

Material. – Numerous dorsal valves from multiple samples of lower Cambrian limestone from Zhurinsky Mys and Oy Muran (middle reaches of the Lena River), Malaya Kuonamka and Bol'shaya Kuonamka rivers (eastern flanks of the Anabar Uplift; see Online Appendix 2 in Kouchinsky et al. in press for occurrences therein). Multiple fragments of ventral valves and one almost complete ventral valve as well as a single poorly preserved articulated specimen from Zhurinsky Mys.

Description. – Shell ventribiconvex. Ventral valve ovate, moderately convex, up to 9 mm wide, representing 90-110% of valve length (Fig. 1A-D). Ventral interarea planar, orthocline, with a narrow, ridge-like homeodeltidium almost completely closing the delthyrium (Fig. 1B, E). The umbonal region is damaged in available specimens, but a single ventral valve reveals a series of three, possibly four concave internal walls or septa connecting the interarea with the anterior valve floor, effectively sealing off the apical region of the valve (Fig. 1F-I). The last formed septum appears to attach to the margin of the interarea and connects to the opposing shell wall anterior of the interarea (Fig. 1G).

Dorsal valve with hemiperipheral growth, weakly convex, slightly transverse, up to 9 mm wide, representing about 130-140 % of length (Fig. 2A-C, F, I, J) with broad, shallow sulcus. Anacline dorsal interarea developed as a complete, narrow, transverse ridge along and below the entire posterior margin (Fig. 2K, L). Narrow notothyrium completely closed by a gently convex homeochilidium (Fig. 2M). Dorsal interior with transversely elongate, thickened platforms developed parallel to the interarea (Fig. 2K) and shallow imprints of pinnate mantle canals along the anterior border (Fig. 2L). Visceral area and muscle scars indiscernible. Dorsal larval shell semicircular, about 275 µm wide, slightly raised over the shell and divided by four to six narrow radial furrows and ridges (Fig. 2D, E, G, H).

Both valves are ornamented by fine concentric fila, regularly interrupted by nick-points, sometimes giving the appearance of fine radial grooves (Fig. 2C-E). The shell consists of phosphatic laminae, about 10-20 µm thick (Fig. 3F) and is composed of hollow, polygonal prisms oriented with the long axis normal to the shell surface (Fig. 3A-C). Walls of individual polygons are not well preserved, but polygons appear to be 5-7 µm wide on average (Fig. 3B). In some specimens the polygonal structure is preserved as a negative with small pustules surrounded by voids forming a polygonal pattern (Fig. 3D, E).

Remarks. – Although shells attributable to *Pelmanotreta* n. gen. are geographically widespread on the Siberian Platform and ranges through most of both the Tommotian and Atdabanian Stages, only a single species have hitherto been identified; *Pelmanotreta neguertchensis* (Pelman, 1977). Material

in our collections differs slightly in details of morphology and ornament, but the collections are, in most cases, limited to dorsal valves. We note that as the dorsal valves of *Pelmanotreta*, *Salanygolina* and *Tumulduria* are similar in shape and dimensions and mainly differ by small modifications of the dorsal interarea, species identification within each genus will likely require detailed knowledge of ventral valve morphology and an analysis of differences in surface sculpture.

Occurrence. – Middle Tommotian to middle Atdabanian *Dokidocyathus regularis* to *Nochoroicyathus kokoulini* zones of the Siberian Platform, Russian Federation (Cambrian International Stage 2-3).

Discussion

The septate ventral valve

The ventral valve of *Pelmanotreta* with its repeated transverse septa connecting the ventral interarea with the valve floor is unique among brachiopods and appears to suggest that the valves had a radically different function from the ventral valve of the otherwise extremely similar *Salanygolina*.

The function of the characteristic anterior opening in *Salanygolina* is most likely related to attachment, like in some morphologically similar (and likewise poorly known) early rhynchonelliforms, the chileides (Popov & Holmer 2000; Holmer et al. 2009; Zhang et al 2011). However, the umbonal perforation of the ventral valve in *Salanygolina* can also be compared to the anterior sinus in the S1 sclerite of the stem group brachiopod (tommotiid) *Paterimitra* (Larsson et al. in press). This would suggest that the umbonal opening is a relict tommotiid character in the bivalved shell of *Salanygolina*, perhaps connecting the earliest paterinids with both the brachiopod stem group and with the earliest rhynchonelliform brachiopods.

The apparent discrepancy between the ventral umbonal perforation in *Salanygolina* and the septate ventral valve in *Pelmanotreta* may relate to ontogenetic changes. The best evidence for an umbonal opening in *Pelmanotreta* come from small, articulated specimens illustrated by Pelman (1977, pl. 21, fig. 4). These specimens exhibit what appears to be a large anterior ventral opening but as the entire apex of the ventral valve are missing in these specimens, it is possible that the opening is a result of mechanical damage. However, it is also possible that juveniles or small adults of *Pelmanotreta* had a functional ventral umbonal shell opening like *Salanygolina*, but that this opening was closed in later growth stages by the formation of internal septa, sealing off the entire apical region. According to this hypothesis, the septate ventral valve of *Pelmanotreta* can be interpreted as a first step towards evolutionary loss of the ventral shell opening in paterinid brachiopods. Internal septa are relatively common in sclerites of tommotiid members of the brachiopod stem group (Bengtson et al. 1990) and in particular the mitral sclerites of *Micrina* sometimes exhibit apical septation resembling that of *Pelmanotreta* (Balthasar et al. 2009, supplementary figure DR1). However, apical septa in *Micrina* are more numerous than in *Pelmanotreta* and may represent phosphatized second order laminae in an otherwise poorly mineralized shell structure (Balthasar et al. 2009).

Early ontogeny

Pelmanotreta neguertchensis preserve the earliest record of a larval shell in brachiopods yet documented. Unfortunately only dorsal valves were available for study. The metamorphic shell of *Pelmanotreta* does not exceed 275 μm width. It is outlined by a distinct halo. Fine concentric ornament interrupted by nick-points suggest that adult marginal setae were present and that a differentiated, mineralized shell had been developed by that time. The posteromedial part of the metamorphic shell is occupied by a hemispherical median mound about 60 μm in diameter, which is interpreted as the metamorphic protegulum (see also Popov et al. 2008, Holmer et al. 2009). The lateral flanks of the median mound, within the area about 135 μm wide, are occupied by the three pairs of swollen, drop-shaped lobes. These lobes are connected by radial ridges with the outer margin of the metamorphic shell and a few finer ridges are present in the interspaces between them. In addition a faint median ridge or furrow is developed anterior to the median mound.

The dorsal metamorphic shell of *Pelmanotreta* shows remarkable similarity to that of *Salanygolina* as documented by Holmer et al. (2009). In both taxa three growth zones can be recognized: (1) the median mound corresponding to the protegulum; (2) the intermediate zone occupied by inflated lobes indicating position of larval setal sacs; and (3) the outer zone, which probably corresponds to the growth stage when the larval setae were lost and replaced by the adult marginal setae, but before secretion of the adult, mineralized shell was commenced. As was pointed by Holmer et al. (2009) the radial ridges were formed along the stress points on the growing shell caused by the muscle sets controlling the movement of setae (see also Williams and Holmer 1992). There are also some differences, including the absence of the dorsal posterior fringe and the presence of the third pair of lobes on the larval shell in *Pelmanotreta*. The metamorphic shell of *Pelmanotreta* is also significantly smaller with the protegulum only half the width of that in *Salanygolina*.

The differentiation of the dorsal larval shell into two zones, the median mound (protegulum) and the outer zone, occupied by the impression of paired larval mantle sacs, is typical for the early Palaeozoic brachiopods with an inferred planktotrophic larva. This morphology is characteristic for derived paterinides (Williams et al. 1998) and siphonotretides (Popov et al. 2009) among linguliforms, billingsellides (Popov et al. 2007) and strophomenides (Bassett et al. 2008) among strophomenates, orthides (Madison 2004) and gonambonitids (Popov et al. 2007) among rhynchonellates. The presence of a similar larval shell morphology in distantly related groups of brachiopods may suggest that it is a plesiomorphic character for the phylum. In *Pelmanotreta* and *Salanygolina* the morphology of the dorsal larval shell is further complicated by the presence of the intermediate, outer zone. At that stage the animal acquired adult marginal setae before secretion of the fully differentiated, mineralized shell commenced. In *Salanygolina* this feature may have been related to the delayed secretion of the ventral valve (Holmer et al. 2009), which can be used as an indirect evidence of similar character of the attachment in *Pelmanotreta* during the settlement of the larva and subsequent metamorphosis. The inferred presence of three pairs of larval setal sacs in *Pelmanotreta* has no analogy in any studied extinct brachiopods and it has only been documented in the Recent *Novocrania* (Nielsen 1991). In the lecithotrophic larva of *Novocrania* the posterior pair of larval setal sacs are present at the free-swimming stage, but disappear shortly after settlement and only two posterior pairs covered by the growing dorsal valve remain during metamorphosis. In *Pelmanotreta* all three pairs of larval sacs leave impressions on the metamorphic shell, which may suggest shell growth during the free-swimming stage and therefore planktotrophic character of the larva. It is probable that the outer zone of the larval shell in *Pelmanotreta* formed after settlement.

The presence of three pairs of larval sacs in the earliest known brachiopod suggests that presence of two pairs of larval setal sacs in the Family Paterinidae and rhynchonelliforms can be considered as derived character.

Ultrastructure

Popov & Ushatinskaya (1987) and Ushatinskaya et al. (1988) described a prismatic hexagonal shell structure in *Pelmanotreta* and a similar shell structure was described for *Salanygolina* by Ushatinskaya (1987). However, Williams et al. (1992, 1998) reported a spheroidal shell structure for these and other paterinids, a view which was largely accepted by other authors (Laurie 2000; Williams & Cusack 2007). More recently Holmer et al (2009) confirmed the presence of hexagonal prisms in the shell of *Salanygolina*, and a similar shell structure is also obvious in *Pelmanotreta*. This type of shell structure is also found in *Askepasma* (Topper et al. 2013) and *Tallatella* (Topper & Skovsted in press), suggesting that it was common to all 'cryptotretid' brachiopods of the early Cambrian. The hexagonal structure is also found in the stem group to the brachiopod phylum, at least in the tommotiids *Eccentrotheca* and *Paterimitra* where the densely laminate shell shows a pervasive superstructure of hexagonal prisms composed of organic walls (Balthasar et al. 2009; Larsson et al. in press). However, no hexagonal prisms are known from the shell of the oldest 'cryptotretid' brachiopods from the Siberian Platform, *Aldanotreta* and *Tumulduria* (from the earliest Tommotian *Nochoroicyathus sunnaginicus* Zone). The shell of these taxa exhibit a spherulitic, presumably recrystallized structure (Skovsted et al. in press).

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Figure 1. *Pelmanotreta neguertchensis* (Pelman, 1977) from the lower Cambrian Tommotian stage, zone *Dokidocyathus lenaicus*, bed 3 of Zhurinsky mys section, Right bank of Lena River, Siberian Platform. A, PIN 4194/22; ventral valve exterior, scale bar equal 2 mm. B, PIN 4194/23; ventral valve with broken apex revealing mould of orthogonal interarea, scale bar equals 2 mm. C-E, PIN 4194/10; articulated specimen, scale bars equal 1 mm; C, dorsal view showing outline of dorsal valve and orthogonal ventral interarea; D, apical view showing ventribiconvex shell shape; E, detail of C showing morphology of ventral interarea with narrow deltidium. F-I, PIN 4194/25; ventral valve, scale bars equals 300 μ m; F, ventral valve interior showing remains of broken ventral interarea on left

lateral side; G, oblique view of ventral interior showing apex closed by gently curved apical septum; H, oblique apical view showing broken interarea; I, detail of H showing hollow ventral apex with remains of two transverse septa (indicated by arrows).

Figure 2. *Pelmanotreta nequertchensis* (Pelman, 1977) from the lower Cambrian of the Siberian Platform. A, PIN 4194/11, from Tommotian stage, *Dokidocyathus lenaicus* zone, bed 3 of Zhurinsky mys section , Right bank of Lena River, Siberian Platform; dorsal valve exterior, scale bar equals mm. B, PIN 4194/2C, from Tommotian stage, zone *Dokidocyathus lenaicus*, bed 3 of Zhurinsky mys section , Right bank of Lena River, Siberian Platform; dorsal valve exterior, scale-bar equals mm. C, NRM Br141310, from Malaya Kuonamka River, eastern flanks of the Anabar Uplift, dorsal valve exterior. D, E, NRM Br141311, from Malaya Kuonamka River, eastern flanks of the Anabar Uplift, dorsal valve; D, exterior view; E, detail of D showing juvenile shell, scale-bar equals 200 μ m. F, dorsal valve exterior. G, H, PIN 4194/14, from Tommotian stage, zone *Dokidocyathus lenaicus*, bed 3 of Zhurinsky mys

section , Right bank of Lena River, Siberian Platform, dorsal valve; G, exterior view; H, detail of G showing larval shell morphology, scale-bar equals 50 μm . I, J, dorsal valve; I, dorsal valve exterior; J, oblique posterolateral view showing dorsal convexity. K-M, , dorsal valve; K, interior view showing faint radiating pinnate mantle canals; L, oblique lateral view showing straight, anacline interarea; M, detail of interarea in posterior view showing narrow, gently convex chilidium. Unless otherwise stated all scale bars equal 500 μm .

Figure 3. *Pelmanotreta neguertchensis* (Pelman, 1977) from the lower Cambrian Atdabanian stage, zone *Leptosocyathus polyseptus* zone, beds 2,3 of Oy-Muran section, Right bank of Lena River, Siberian Platform. A-C, PIN ZZZZ3, dorsal valve; A, interior shell surface; B, detail of A showing hollow hexagonal prisms in orthogonal view; C, detail of hexagonal prisms along broken shell edge in oblique view. D, E, PIN 4194/26, dorsal valve; D, interior shell surface; E, detail of D showing phosphatized hexagonal prisms in orthogonal view. F, PIN ZZZZ4, oblique view of broken shell edge showing multiple shell laminae. Scale bars equal 30 μm in A, D, F and 10 μm in B, C, E.