The Problematic Early Cambrian Fossil Tumulduria incomperta Represents the Detached Ventral Interarea of a Paterinid Brachiopod

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The problematic early Cambrian fossil *Tumulduria incomperta* represents the detached ventral interarea of a paterinid brachiopod

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The organophosphatic early Cambrian (Terreneuvian, Cambrian Stage 2) fossil *Tumulduria incomperta* has been problematic ever since its original description in 1969. Comparison of abundant specimens from the Lower Cambrian of Siberia with co-occurring brachiopod valves show that *T. incomperta* represents the central portion of the ventral interarea of a paterinid brachiopod similar to *Cryptotreta neguertchenensis*, and that the domed central portion of typical *Tumulduria* specimens represents the ridge-like pseudodeltidium of the interarea.

Key words: Brachiopoda, problematica, Tommotian Stage, Terreneuvian, Cambrian, Siberia.

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Introduction

Lower Cambrian successions from around the world have yielded a wealth of small plate-, cone-, and spine-shaped fossils, often collectively referred to as "Small Shelly Fossils" (often abbreviated SSF; Rozanov et al. 1969; Matthews and Missarzhevsky 1975; Missarzhevsky 1989; Qian and Bengtson 1989; Bengtson et al. 1990; Bengtson 2004). These fossils represent a significant portion of the known record of body fossils from the first half of the Cambrian Period and have long been considered problematic in terms of biological function and affinity (Bengtson et al. 1990), but during the last two decades many SSF taxa have been shown to belong to the stem, or even crown groups of modern phyla (Conway Morris and Peel 1995; Vinther and Nielsen 2005; Skovsted et al. 2008). However, some characteristic SSF taxa remain biologically problematic (Kouchinsky et al. 2012), and *Tumulduria incomperta* Missarzhevsky, in Rozanov et al. 1969 from the lower Cambrian of Siberia is one such problematic taxon.

As originally defined, *Tumulduria incomperta* consists of small, bilaterally symmetrical plates with a central ridge and very variable lateral fields, all ornamented by transverse folds or ridges. In the original description, Missarzhevsky (in Rozanov et al., 1969: 175) compared the bilaterally symmetrical plates of *Tumulduria* to chiton plates, but similar fossils were later interpreted as trilobite remains by Fedorov et al. (1979), causing considerable interest in the palaeontological community as the oldest known trilobites (Repina 1981; Glaessner 1984; Khomentovsky 1986). However, based on detailed study of new material from Siberia, Bengtson et al. (1987) were able to demonstrate unequivocally that *Tumulduria* is highly variable morphologically and that the plates grew by accretion. Consequently, any similarity of individual specimens to different parts of the trilobite carapace is superficial and *Tumulduria* has since been regarded as a problematic fossil (Rozanov et al. 2010; Maloof et al. 2010; Kouchinsky et al. 2012). Bengtson et al. (1987) compared the preservation of *Tumulduria* and co-occurring organophos-

phatic brachiopods, but herein we show that *Tumulduria incomperta* more specifically represents the detached central portion of the ventral interarea of a paterinid brachiopod.

The Order Paterinida is a problematic group of Cambrian to Ordovician phosphatic-shelled brachiopods that includes some of the oldest known members of the phylum (Laurie 2000). The oldest paterinids have been placed in the problematic Family Cryptotretidae, which include several poorly known genera that may not all be closely related (Topper et al. 2013). The generic name *Cryptotreta* was proposed by Pelman (1977) for brachiopods from the Tommotian Stage of the Siberian Platform exhibiting a strophic hinge and an orthocline ventral interarea with a narrow, convex, ridge-like pseudodeltidium but without clear evidence of an open delthyrium. *Cryptotreta* is very similar to the somewhat younger *Salanygolina* Ushatinskaya, 1987, from Mongolia. The better-known *Salanygolina* has been shown to possess both a narrow ridge-like pseudodeltidium as well as a large foramen anterior to the ventral umbo (Ushatinskaya 1987), partly closed by a colleplax (Holmer et al. 2009), and identical structures can be found in the enigmatic chileids (Popov and Tikhonov, 1990; Popov and Holmer 2000). A similar ventral umbonal foramen appears to be present also in *Cryptotreta* (Laurie 2000; Galina T. Ushatinskaya, personal communication 2012). However, all other genera commonly referred to the Cryptotretidae, including the well-studied *Askepasma* Laurie, 1986 from Australia (Laurie 1986; Topper et al. 2013) and the Siberian *Aldanotreta* Pelman, 1977, differ from *Salanygolina* and *Cryptotreta* by the absence of an orthocline ventral interarea and a foramen anterior to the ventral umbo.

Institutional abbreviations.—GIN, Geological Institute of the Russian Academy of Sciences, Moscow, Russia; NRM, Swedish Museum of Natural History, Stockholm, Sweden.

Material and methods

The bulk of the available material is derived from samples collected by Anatoly K. Val'kov from the lowermost part of the Pestrotsvet Formation, *Nochoroicyathus sunnaginicus* Zone, Tommotian Stage, southeastern Siberian Platform. The geological setting and stratigraphical context of the sampled area were recently summarized by Khomentovsky and Karlova (2005), Varlamov et al. (2008), and Rozanov et al. (2010). Sample 449 was collected from the left bank of the Aldan River, 1–2 km upstream of the mouth of the Ennyues River (= section M403 in Rozanov et al. 1969). Sample 525 was collected from the left bank of the Aldan River, 7 km upstream the Ulakhan-Sulugur Brook. Sample 1793 was collected from the left bank of the Aldan River, at the Byukteleekh Brook, 25 km downstream of the "Dvortsy" section (= section M407 in Rozanov et al. 1969). Samples 1825 and 1832 were collected from the Mount Konus section on the right bank of the Uchur River, upper reaches of the Kholobolokh (1825) and Malyj Chajdakh (1832) rivulets (see Khomentovsky et al. 1990). In addition, several hundred small specimens, including *Tumulduria* plates, incomplete dorsal valves and indeterminable shell fragments were derived from samples collected in 1990 by John S. Peel (JSP 1990 27/1) from about 30 cm above the base of the Pestrotsvet Formation (bed 15; *Nochoroicyathus sunnaginicus* Zone, early Tommotian Stage) at the reference section at "Dvortsy" on the Aldan River, Siberia.

All samples were prepared by dissolution in buffered acetic acid (7–10%) and the resulting residues sieved and scanned for microfossils using a stereomicroscope. Selected fossils were mounted and coated by gold prior to SEM study at the Swedish Museum of Natural History in Stockholm.

Tumulduria as a brachiopod

The lateral fields of the broadly triangular plates of *Tumulduria incomperta* are highly variable in shape and size relative to specimen length, and lateral margins are usually uneven (Fig. 1). The median ridge is very similar in morphology to the ridge-like pseudodeltidium of the ventral interarea of *Cryptotreta* and the lateral flanks are reminiscent of the flat, orthocline ventral interarea itself (Pelman 1977; Laurie 2000). In width, the convex pseudodeltidium of *T. incomperta* typically varies from 200 to 500 μm, which is comparable to the pseudodeltidium found on complete ventral valves of *Cryptotreta neguertchenensis* (see Laurie 2000). The variable transverse lineation of the plates often shows a distinct deflection towards the oldest part of the plate (as indicated by the overlapping shell layers) across the ridge, which is also the case in the pseudodeltidium of *C. neguertchenensis* and presumably reflects the small embayment of this part of the ventral interarea (Laurie 2000: fig. 85A). Comparison could also be made with the ventral interarea of *Salanygolina obliqua* Ushatinskaya, 1987 from the lower Cambrian of Mongolia, where a narrow and convex pseudodeltidium of similar morphology divides the flat, triangular interarea (Holmer et al. 2009: text-fig. 4A).

Complete specimens of ventral valves are lacking in our collections, mirroring the absence of complete ventral valves in most collections of *Cryptotreta* and *Salanygolina*. In the case of *Cryptotreta* and *Salanygolina*, the lack of complete ventral valves is presumably a consequence of fragmentation due to structural weakness caused by the large umbonal foramen (see also Pelman 1977 and Holmer et al. 2009) and a similar umbonal foramen was probably present also in *Tumulduria*. However, one specimen exhibits the central ridge and one complete lateral half of the triangular interarea (Fig. 2A), effectively bridging the morphological gap between typical specimens of *T. incomperta* and complete ventral valves of other cryptotretid brachiopods. Although incomplete, this specimen shows that the interarea originally was a flat, obtusely triangular plate (the specimen is broken parallel to the pseudodeltidium and thus represents only the left lateral half of the interarea; Fig. $2A_1$, A_2) with a well marked pseudodeltidium (Fig. $2A_3$). The plate exhibits uneven transverse growth-

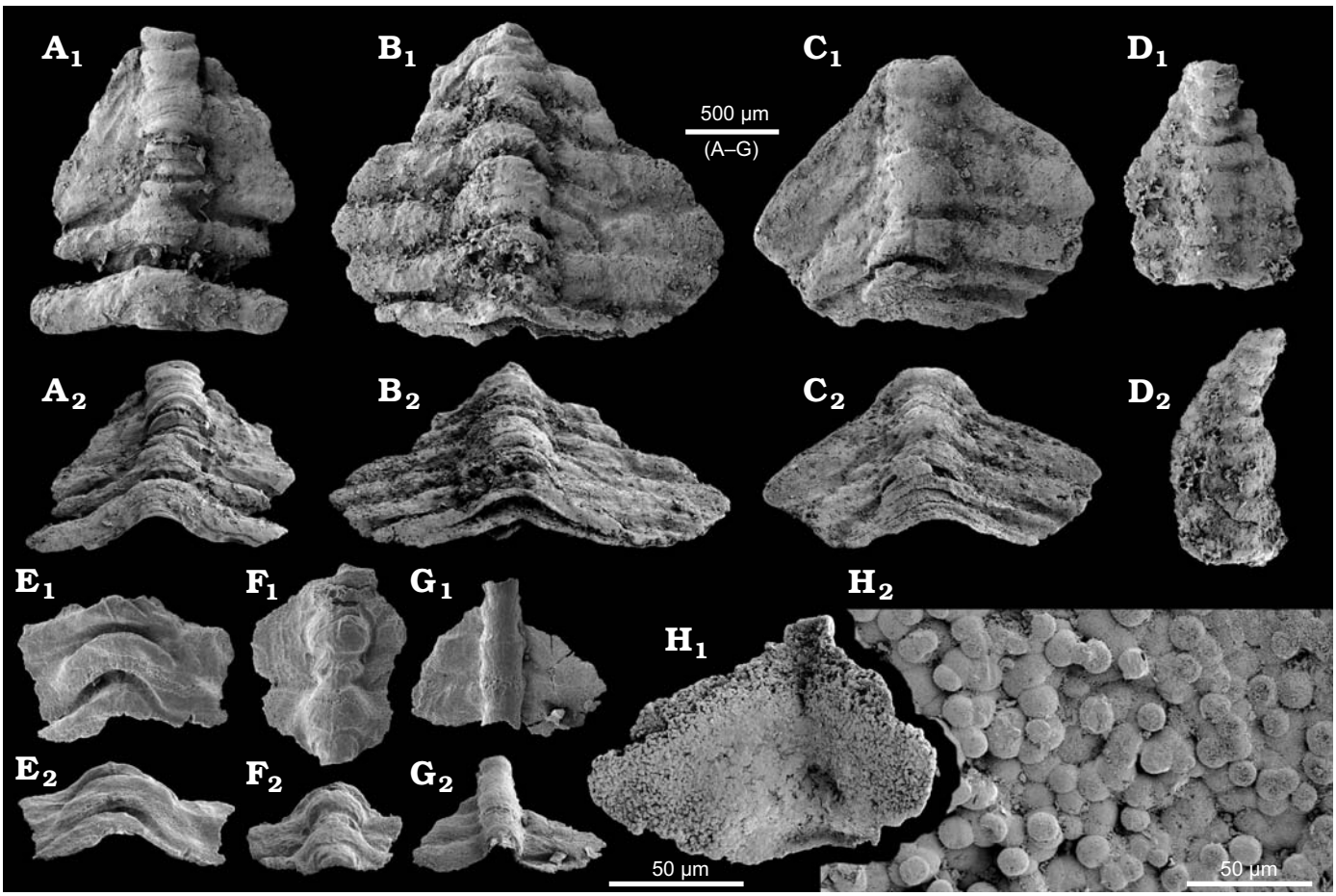

Fig. 1. Paterinid brachiopod *Tumulduria incomperta* Missarzhevsky in Rozanov et al, 1969. Typical *Tumulduria* plates with pseudodeltidium and partially preserved lateral flanks representing ventral interarea. Aldan and Uchur River area, *Nochoroicyathus sunnaginicus* Zone, Siberia. **A**. NRM Br141128, sample 1825; A_1, view from above; A_2, oblique posterior view. **B**. NRM Br141129, sample 1825; B_1, view from above; B_2, oblique posterior view. **C**. NRM Br141130, sample 1825; C_1, view from above; C_2, oblique posterior view. **D**. NRM Br141131, sample 1825; D_1, view from above; D_2, oblique lateral view. **E**. NRM Br141132, sample JSP 1990 27/1; E_1, view from above; E_2, oblique posterior view. **F**. NRM Br141133, sample JSP 1990 27/1; F_1, view from above; F_2, oblique posterior view. **G**. NRM Br141134, sample JSP 1990 27/1; G_1, view from above; G_2, oblique posterior view. **H**. NRM Br141135, sample 1825; H_1, internal view; H_2, detail of internal surface with botryoidal structures.

lines and an oblique, centrally placed flexure-line. The flexure line presumably represents a zone of weakness, and its inclination (about 30˚) corresponds roughly to the slope of the lateral margins in typical *Tumulduria* plates (around 25–40˚ in larger specimens in our collections; Fig. 1A–D). A similar specimen was illustrated together with other specimens of *Tumulduria* as "Skeletal Problematicum 1" by Meshkova (1974: pl. 26: 3). The specimen illustrated by Meshkova (1974) appears to be more complete and preserves part of both lateral fields of the interarea, complete with flexure lines, pseudodeltidium and the posterior margin with a central embayment. Other fragmentary specimens in our collections preserve an acute linear fold which probably represents the lateral junction of the interarea and general shell surface and support the interpretation of the interarea as a flat, triangular plate separated from the rest of the shell by a sharp fold (Fig. 2B).

In most samples investigated by us, we find an association of the problematic fossil *Tumulduria incomperta* with indeterminable brachiopod shell fragments and flat to gently convex and weakly sulcate brachiopod valves (Fig. 3). The associated shells are strongly reminiscent of the dorsal valves of cryptotretid brachiopods, including the genera *Cryptotreta* and *Aldanotreta* which are known to occur in the Tommotian of the Siberian Platform (Pelman 1977, 1979). Although isolated dorsal valves of cryptotretids may be difficult to separate morphologically, the valves occurring with *Tumulduria* in the Pestrotsvet Formation differ from the dorsal valves of all described cryptotretids in having an extremely small interarea divided by an open triangular notothyrium.

In addition to the co-occurrence and morphological similarities of *Tumulduria* plates and associated cryptotretid dorsal valves, the apparent botryoidal shell structure is very similar between typical specimens of *T. incomperta* and co-occurring flat brachiopod valves (compare Figs. $1H_2$ and $3D_2$). The botryoidal structure is observable on the internal surface of all available specimens, but is not apparent on external surfaces. This similarity in preservation of the shell structure was also noted by Bengtson et al. (1987: 368) although the illustrated

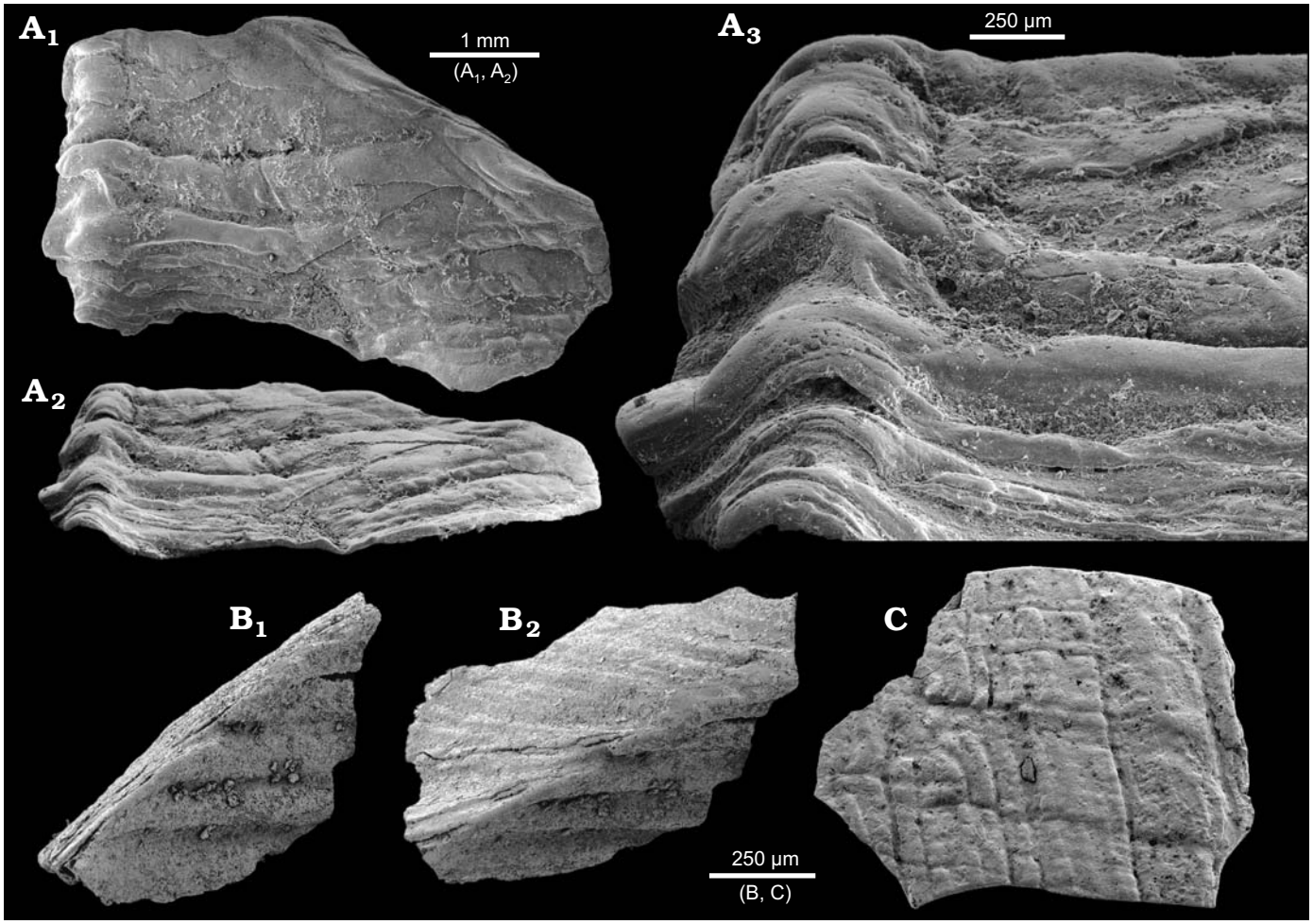

Fig. 2. Paterinid brachiopod *Tumulduria incomperta* Missarzhevsky in Rozanov et al, 1969. Fragmentary valves. Aldan and Uchur River area, *Nochoroicyathus sunnaginicus* Zone, Siberia. **A**. NRM Br141136, sample 449, left lateral half of ventral interarea; A_1, view from above; A_2, oblique posterior view; A_3, detail of pseudodeltidium in oblique view. **B**. NRM Br141137, sample 1832, fragment preserving junction of ventral interarea and ventral shell surface; B_1, view from posterior; B_2, oblique posterolateral view. **C**. NRM Br141138, sample 525, fragment of shell surface with fila and nick points.

brachiopod valves were identified as belonging to *Aldanotreta sunnaginensis* (Bengtson et al. 1987: fig. 7). Although the botryoidal structure is most likely of diagenetic origin, the close similarity in preservation provide a strong indication that the original composition and shell structure of typical *Tumulduria* plates and co-occurring cryptotretid brachiopod valves were identical or, at least, very similar.

Based on the observed occurrence patterns as well as morphological and ultrastructural similarities we conclude that *Tumulduria incomperta* is likely to represent the detached central portion of the ventral interarea of a cryptotretid brachiopod and that the associated brachiopod valves represent the dorsal valve of the same taxon.

Systematic palaeontology

Phylum Brachiopoda Duméril, 1806

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

Order Paterinida Rowell, 1965

Superfamily Paterinoidea Schuchert, 1893

Family Cryptotretidae Pelman, 1979

Genus *Tumulduria* Missarzhevsky in Rozanov et al., 1969

Type species: *Tumulduria incomperta* Missarzhevsky in Rozanov et al., 1969 from the *Nochoroicyathus sunnaginicus* Zone, Tommotian Stage, Cambrian Series 2, of the Aldan River area, southeastern Siberian Platform.

Emeded diagnosis.—Ventral valve with orthocline, flat, triangular interarea with a narrow pseudodeltidium. Interarea with low, transverse ribs and furrows and oblique, poorly developed flexure lines. Dorsal valve flat or slightly convex and gently sulcate. Catacline dorsal interarea reduced and developed as a low elongate ridge along the posterior margin; dorsal triangular notothyrium open.

Tumulduria differs from *Aldanotreta* Pelman, 1977, *Dzunarzina* Ushatinskaya, 1993, and *Askepasma* Laurie, 1986 in having an orthocline, triangular ventral interarea with a

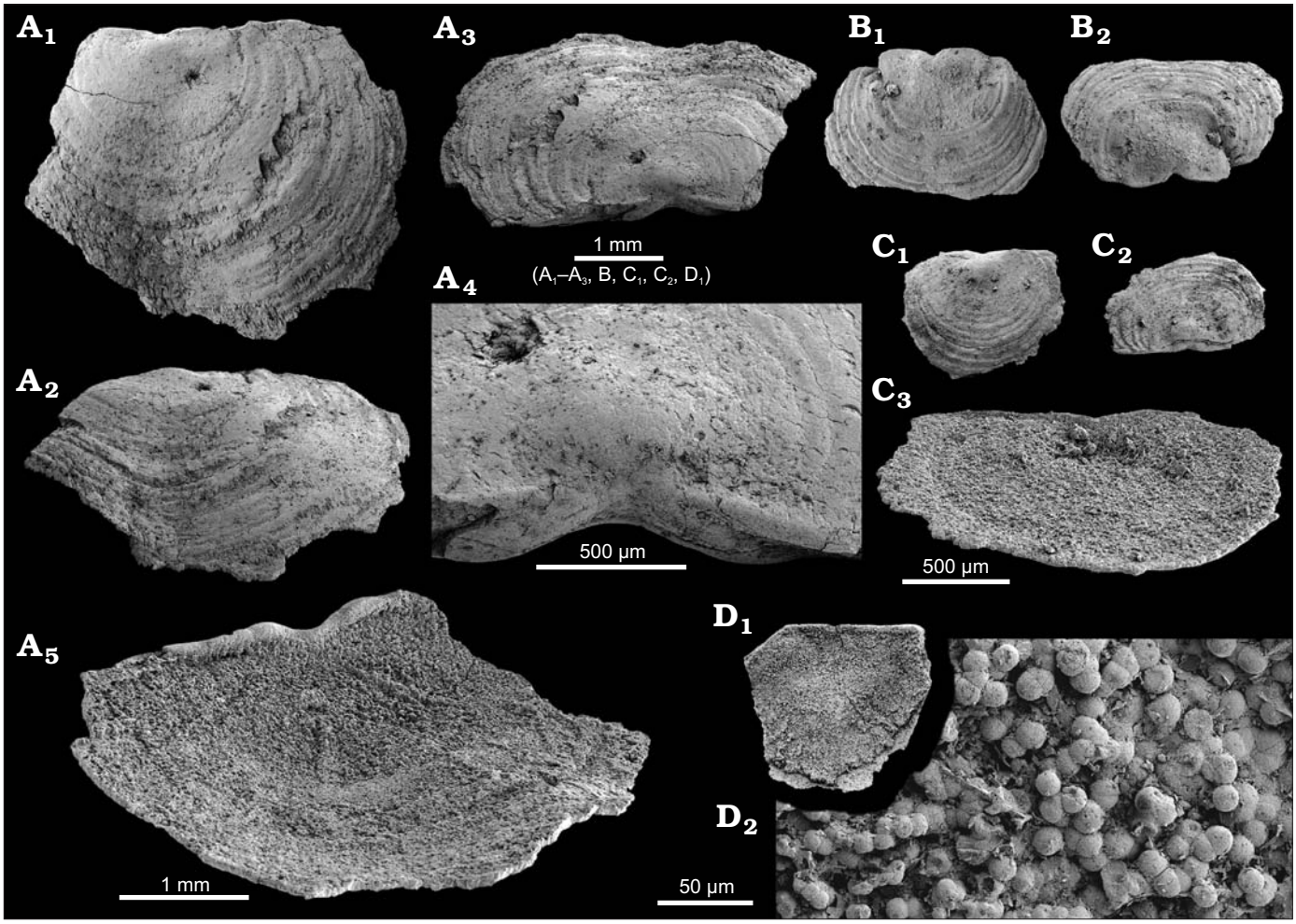

Fig. 3. Paterinid brachiopod *Tumulduria incomperta* Missarzhevsky in Rozanov et al, 1969. Dorsal valves. Aldan and Uchur River area, *Nochoroicyathus sunnaginicus* Zone, Siberia. **A**. NRM Br141139, sample 1793; A_1, dorsal view; A_2, oblique anterior view; A_3, oblique posterior view; A_4, detail of cardinal area in oblique posterior view; A_5, oblique anterolateral view of internal surface. **B**. NRM Br141140, sample 1825; B_1, dorsal view; B_2, oblique posterior view. **C**. NRM Br141141, sample 1832; C_1, dorsal view; C_2, oblique posterior view; C_3, oblique anterior view of internal surface. **D**. NRM Br141142, sample 1832; D_1, internal view; D_2, detail of internal surface with botryoidal structures.

narrow pseudodeltidium and a low ridge-like dorsal interarea. It differs from *Cryptotreta* Pelman, 1977 in having more irregular transverse ornament on the ventral interarea and an open triangular notothyrium lacking a chilidium. It differs from *Salanygolina* Ushatinskaya, 1987 in its more strongly sulcate dorsal shell, small dorsal interarea with open notothyrium and in lacking the pustulose adult microornament.

Discussion.—The rationale behind the reinterpretation of *Tumulduria incomperta* as a paterinid brachiopod is outlined above. Based on the shared presence of an orthocline ventral interarea with a pseudodeltidium and an inferred foramen anterior to the umbo, *Tumulduria* is likely to be closely related to *Cryptotreta* from the Siberian Platform and *Salanygolina* from the lower Cambrian of Mongolia. The relationship of *Tumulduria* to other genera included in the Cryptotretidae is less clear.

Geographic and stratigraphic range.—*Tumulduria* is known from the *Nochoroicyathus sunnaginicus* Zone, Tommotian Stage (Terreneuvian Series, Cambrian Stage 2), southeastern Siberian Platform, from sections along the Aldan River and from the Uchur-Maya region representing the transitional facies belt (Rozanov et al. 1969; Khomentovsky et al. 1990; Rozanov and Zhuravlev 1992; Khomentovsky and Karlova 2005).

Tumulduria incomperta Missarzhevsky in Rozanov et al., 1969

Figs. 1–3.

1969 *Tumulduria incomperta* sp. nov. Missarzhevsky; Rozanov et al. 1969: 175, pl. 6: 5, 6.
1974 Skeletal Problematica 1; Meshkova 1974: 193, pl. 26: 1–3, 6–7.
1987 *Tumulduria incomperta* Missarzhevsky; Bengtson et al. 1987: 364, figs 1–6. (cum. syn.).
1987 *Aldanotreta sunnaginensis* Pelman; Bengtson et al. 1987: fig. 7.
1989 *Tumulduria incomperta* Missarzhevsky; Missarzhevsky 1989: 215, pl. 28: 6, 9.
1992 *Tumulduria incomperta* Missarzhevsky; Rozanov and Zhuravlev in Lipps and Signor 1992: 257, fig. 9, panel 78.

1998 *Tumulduria incomperta* Missarzhaevsky; Vasil'eva 1998: 115, pl. 44: 3, 7.

2008 *Tumulduria incomperta* Missarzhevsky; Varlamov et al. 2008; pl. 13: 12, 13.

2010 *Tumulduria incomperta* Missarzhevsky; Rozanov et al. 2010: 86, pl. 59: 5, 6.

Holotype: GIN 3593/138. Partial ventral interarea with narrow central pseudodeltidium and broken lateral margins. From *Aldanocyathus sunnaginicus–Tiksitheca licis* Zone, Aldan River.

Type locality: Aldan River, left bank, 7 km west of settlement Ugino (section M402 in Rozanov et al. 1969).

Type horizon: Tommotian Stage, *Nochoroicyathus sunnaginicus* Zone, Cambrian.

Diagnosis.—As for genus.

Material.—The available material consists of 34 partially complete ventral interareas, 15 dorsal valves and possible shell fragments collected from the Aldan and Uchur River regions (Pestrotsvet Formation, *Nochoroicyathus sunnaginicus* Zone, Tommotian Stage, southeastern Siberian Platform).

Description.—The morphology of both isolated *Tumulduria* interareas and associated ventral valve fragments (Figs. 1, 2) is described above. The dorsal valves are flat or very gently convex with a straight posterior margin and a weakly developed anterior sulcus (Fig. 3). Growth is hemiperipheral. Dorsal interarea is absent or vestigial in smaller specimens (Fig. 3B, C), but larger specimens exhibit a low, catacline interarea (Fig. 3A). Under the slightly elevated umbo the dorsal interarea is divided by a small, triangular notothyrium lined on both sides by weakly defined ribs (Fig. $3A_4$). The internal morphology is poorly preserved, but one large specimen shows a weakly defined pair of ridges radiating from the umbonal region (Fig. $3A_5$).

The surface sculpture of the shell consists of fine concentric fila and variable, often slightly uneven, low ribs and furrows (transverse furrows on ventral interarea; Fig. $2A_3$). On some shell fragments from larger shells, the concentric ornament is complemented by fine transverse furrows and nick points (Fig. 2C).

Discussion.—As discussed above, no complete ventral valves of *Tumulduria* are known, but based on comparison with *Cryptotreta* and *Salanygolina* the ventral valve is assumed to have been strongly convex with an orthocline triangular interarea with a narrow pseudodeltidium. Anterior to the umbo the shells are assumed to have had a large foramen, possibly with a colleplax, and as in *Cryptotreta* and *Salanygolina* (where complete ventral valves are very rarely preserved) the structural weakness introduced by the umbonal foramen could account for the lack of preserved ventral valves.

The ornament, particularly on the ventral interarea, is generally more chaotic than in other cryptotretid brachiopods, including the other Siberian taxa *Aldanotreta* and *Cryptotreta*, and there is no trace of a pustulose micro-ornament such as in *Salanygolina*.

Stratigraphic and geographic range.—Same as for genus by monotypy.

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