A new name for a classic Cambrian Swedish brachiopod,
Tallatella undosa (Moberg)

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Abstract: The brachiopod originally described as *Kuturgina undosa* Moberg, 1892 from the early Cambrian (Cambrian Series 2, Stage 4) När Shale of Kalmar, Sweden has experienced a long and turbulent history since the original description over 100 years ago. Uncertainties regarding key morphological characters has resulted in the species taxonomically hopping between genera until it was recently assigned to the poorly known genus *Cryptotreta* Pelman, 1977 and subsequently transferred to the problematic paterinate family Cryptotretidae. Despite members of this group representing the oldest brachiopods in the fossil record, they remain enigmatic, both taxonomically and phylogenetically. The identification of the brachiopod species from the När Shale as a cryptotretid means that this brachiopod was the first member of the family to be discovered, yet its systematic position is far from certain. Examination of type material in addition to supplementary material acquired from the Skäggenäs peninsula, Sweden has elucidated many of the previous ambiguous morphological characteristics of the species. The new morphological information acquired here has resulted in the erection of a

new paterinate genus, *Tallatella* gen. nov., to accommodate the Swedish material previously described as *Cryptotreta undosa*.

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Introduction:

Paterinate brachiopods represent the oldest lineage of the Brachiopoda, with members of the Cryptotretidae (*Aldanotreta* Pelman, 1977, *Cryptotreta* Pelman, 1977 and *Tumulduria* Missarzhevsky in Rozanov et al., 1969) first appearing in the early Tommotian (Terreneuvian, Stage 2; Pelman 1979; Kouchinsky et al. 2012) of Siberia. Paterinates possess an organophosphatic shell and a strophic hinge (Laurie 2000), a curious combination of morphological characteristics that links the group to two major brachiopod clades, the Linguliformea and Rhynchoneliiformea (Williams et al. 1998). The Paterinate amalgamation of morphological features, combined with the lack of internal morphological detail, has led to some confusion regarding their evolutionary history within the Brachiopoda (see Williams et al. 1998; Laurie 2000). This is especially the case for the oldest members of the group, the cryptotretids, with uncertainties hovering over the systematic and phylogenetic position of many genera in the family. One member of the cryptotretids,

Askepasma Laurie, 1986 has gained considerable attention in the last few years with morphological, ontogenetic and microstructural details showing a close evolutionary relationship to tommotiids, interpreted members of the brachiopod stem group with a tubular scleritome composed of multiple phosphatic sclerites (Skovsted et al. 2008, 2009, 2011; Balthasar et al. 2009; Holmer et al. 2011; Topper et al. 2013; Larsson et al. in press). Despite the groups' significance, *Askepasma* is the only member of the Cryptotretidae that has been adequately documented (Laurie 1986; Holmer et al. 2006; Topper et al. 2013), with the remaining genera based on only limited material, the majority of which have been poorly illustrated and neglected since the original generic description.

Fossils from the När Shale Member of the Fågelås Formation in the Kalmar area (formerly Kalmar sandstone), were first described by Moberg (1892) from erratic boulders found along the west coast of the Swedish island of Öland. The distinctive glauconitic sandstone that sparsely crops out on the southeastern coast of mainland Sweden is probably best known for its well-preserved specimens of the early Cambrian problematic disc-shaped fossil *Mobergella* Hedström, 1923 (e.g. Moberg 1892; Hedström 1923, 1930; Åhman & Martinsson 1965; Bengtson 1968, 1970). Occurring in near equal individual abundance with *Mobergella*, is a poorly understood brachiopod originally described as *Kutorgina undosa* Moberg, 1892. This species has had a long and convoluted history since the original description by Moberg (1892) over 100 years ago. Originally considered a Kutorginid, the species was quickly recognized by Walcott (1912), based on Moberg's (1892) original description and illustrations as a member of the Paterinid family and

transferred to the genus *Micromitra* Meek, 1873. This did little to resolve the taxonomic uncertainties associated with the Swedish specimens as *Micromitra* at the turn of the 20th century incorporated a wide range of brachiopod forms, including 26 species (Walcott 1912, p. 334), clustered together predominantly on the basis of surface ornament and the possession of a pseudodeltidium (Walcott 1912; homeodeltidium according to Laurie 2000). The Öland specimens were considered by Walcott (1912) to belong to the *Paterina* Beecher, 1891 subgenus of *Micromitra*, on the basis of possessing a surface ornament consisting of simple concentric striae and lines of growth.

Åhman & Martinsson (1965) documented specimens referred to *Micromitra undosa* (subgeneric assignment had since been dropped) from the När Shale Member at Äspelund on Skäggenäs peninsula, Sweden. Thousands of specimens were recovered, however the assemblage was extremely fragmentary and poorly preserved and only a single specimen was illustrated (Åhman & Martinsson 1965, fig. 2). The Swedish specimens remained under the taxonomic umbrella of *Micromitra*, until an overhaul of the Paterinida by Williams et al. (1998) saw the species transferred to the Cryptotretidae and the poorly known and previously monospecific Siberian genus *Cryptotreta* Pelman, 1977. No detailed description or reasons behind the generic reassignment were discussed, however all Cryptotretid genera were interpreted to possess a shell consisting of stratiform laminae imprinted with rhombic or hexagonal depressions (Williams et al. 1998). Holmer et al. (2008a) focusing on shell fabrics, documented supposed setal structures in the ventral valves referred to *Cryptotreta? undosa* from the När Shale Member (material collected by Åhman & Martinsson, 1965). Holmer et al. (2008a) only

questionably assigned the species to *Cryptotreta* but the reasons for the taxonomic uncertainty were not discussed.

Undoubtedly the early paterinates are pivotal for our understanding of the origin and evolution of the Brachiopoda, yet many representatives of the group are poorly known and have long been neglected. The identification of the brachiopod species from the När Shale Member in the Kalmarsund area as a cryptotretid means that this brachiopod was the first member of the family to be discovered, yet its systematic position is far from certain and indeed the entire Cryptotretidae family is currently taxonomically besieged by doubts following the transferal of *Salanygolina* to a new Paterinate family, the Salanygolinidae (Holmer et al. 2009), the suggestion that *Dzunarzina* Ushatinskaya, 1993 be synonymized with *Askepasma* (Williams et al., 1998) and the possible reassignment of the type genus *Cryptotreta* based on the possible presence of a ventral perforation (Holmer et al. 2009). In order to help resolve some of the pervasive taxonomic problems surrounding early Cambrian paterinates, type material of *Kutorgina undosa* has been examined (Fig. 2A) in addition to supplementary new material from the När Shale Member of mainland Sweden (Figs 2B-O, 3). These specimens have elucidated many of the previously ambiguous morphological characteristics of the species, including key information not observed in the original description. The new morphological information obtained here has resulted in the erection of a new paterinate genus, *Tallatella* gen. nov., to accommodate the material originally described as *Kutorgina undosa*. Family assignment of the new genus though is left open, awaiting a thorough revision of the Cryptotretidae and related early Cambrian paterinid taxa.

Materials and locality

The Lower Cambrian glauconite-rich, intercalated siltstones and sandstones cropping out on the southeastern coast of the Swedish mainland have, until recently, been referred to the Kalmarsund sandstone (e.g. Moberg 1892; Holst 1893; Åhman & Martinsson 1965; Bengtson 1968). The validity of the Kalmarsund sandstone as a member of the File Haidar Formation was questioned by Nielsen and Schovsbo (2007) on the suspicion that the lithological characteristics of the sandstone merely reflected diagenesis and consequently should not be ranked as a separate member. It was suggested that the Kalmarsund sandstone represents the Viklau, När Shale and När Sandstone members of the File Haidar Formation (Nielsen & Schovsbo 2007). More specifically, the well-known fossiliferous glauconitic horizon yielding *Mobergella* and *Tallatella* gen. nov. represents the När Shale Member (Nielsen & Schovsbo 2007). This was formalized in a comprehensive review of the Lower Cambrian sequence stratigraphy of Scandinavia (Nielsen & Schovsbo 2011) with the När Shale Member roughly equating to the *Heliosphaeridium dissimulare* – *Skiagia ciliosa* Acrirach zone and the *Holmia kjerulfi* and ‘*Ornamentaspis*’ *linnarssoni* Trilobite zones, corresponding to Cambrian Series 2, Stage 4 (Nielsen & Schovsbo 2011).

The original description of *Kutorgina undosa* was based on specimens from erratic boulders of the När Shale Member recovered from a number of localities on the coast of the Swedish island of Öland (Moberg 1892). Outcrop of the När Shale Member on Öland and on mainland Sweden is sparse, only cropping out in a few places in the Småland province on the Swedish

mainland, namely on the Skäggenäs Peninsula (Fig. 1). Outcrop of the fossiliferous layer containing *T. undosa* and *M. holsti* is even rarer, Åhman & Martinsson (1965) documented an assemblage of *T. undosa* and *M. holsti* from a locality between Äspelund and Lindö on the Skäggenäs peninsula (Fig. 1B), the outcrop though was subsurface and only obtainable as a result of the construction of a water-well in the floor of a garage. Bengtson (1968) documented *Mobergella* from the shore of Venenäs in the northern region of the Skäggenäs Peninsula (Fig. 1B) and although the samples were from isolated boulders, the presence of similar quartzite fragments *in situ* in nearby outcrops suggest minimal transportation. Despite the lack of outcrop, lithographic information from drill cores has confidently established an accurate stratigraphic age for the När Shale Member (see Nielsen and Schovsbo, 2007, 2011). All of the specimens examined herein (Figs 2B-O, 3), with the exception of the Öland lectotype (Fig. 2A) was part of the original, extensive collections from Äspelund made by Åhman & Martinsson (1965).

Systematic Palaeontology

All figured specimens are housed at the Swedish Museum of Natural History in Stockholm (depository acronym NRM), the Museum of Evolution, Uppsala (depository acronym PMU), Sweden and the Geological Survey of Sweden, Uppsala (depository acronym SGU), Sweden.

PHYLUM BRACHIOPODA DUMÉRIL, 1806

SUBPHYLUM LINGULIFORMEA WILLIAMS, CARLSON, BRUTON, HOLMER AND POPOV, 1996

CLASS PATERINATA WILLIAMS, CARLSON, BRUTON, HOLMER AND POPOV,
1996

ORDER PATERINIDA ROWELL, 1965

SUPERFAMILY PATERINOIDEA SCHUCHERT, 1893

FAMILY UNCERTAIN

Remarks. – The Cryptotretidae is currently in a state of disarray, largely due to the morphological uncertainties surrounding the poorly known type genus, *Cryptotreta*. Based on limited material, many morphological features of *Cryptotreta* are undefined and the potential presence of a ventral perforation (see Holmer et al. 2009) could see the genus (together with the probably related *Tumulduria*; see Skovsted et al. in press) reassigned to another family. *Aldanotreta*, described in the same publication as *Cryptotreta*, was comparably established on few specimens, with limited illustrations and no details regarding internal morphology (Pelman, 1977). Of the remaining cryptotretid genera, the Mongolian genus, *Dzunarzina* Ushatinskaya, 1993 has been suggested to be a junior synonym of *Askepassa* (see Williams et al. 1998) and *Salanygolina* has already been transferred to another family due to the possession of an anterior shell opening and colleplax in the ventral valve (Holmer et al. 2009). Undoubtedly members of the family require revision and although, *Tallatella* gen. nov. displays paterinate characteristics and even some morphological similarities to particular cryptotretid genera (in particular to *Askepassa*), the family-level assignment is herein left open awaiting clarification of the type genus.

Tallatella gen. nov.

Type species. *Tallatella undosa* (Moberg) from the Cambrian Series 2, Stage 4, När Shale Member of Sweden.

Etymology. Derived from the Latin prefix *talla*, meaning the layer of an onion. Referring to the layered shell structure of the brachiopod and the Shrek quote from the namesake movie that onions have layers.

Diagnosis. Shell strophic, sub-quadrate to semi-circular in outline and ventribiconvex; ventral valve with well-defined, catacline to slightly procline interarea with a well-developed triangular homeodeltidium. Dorsal valve gently convex with low, hypercline interarea with homeochilidium. Shell ornament consisting of fine concentric growth lines, disrupted by nickpoints bearing a polygonal micro-ornamentation.

Remarks. The understanding of the Kalmarsund brachiopod species has been hindered for over a century, largely due to the apparent lack of well-preserved material, despite the large number of individual specimens that have been collected from Öland (Moberg 1892) and the Skäggenäs peninsula (Åhman & Martinsson 1965). Many specimens in the collections are fragmentary and poorly preserved, yet the numerous blocks of När Shale inspected from the original collections of Åhman & Martinsson (1965) yielded approximately 30 well-preserved specimens of *T. undosa*. In terms of discernible material, ventral valves dominated (Fig. 2) with only a few dorsal valves present in the

collections (Fig. 3A-D). The interiors of both valves are also rare, present only in low numbers (eg. Fig. 3F). That said, the well-preserved specimens in the assemblage, has elucidated many morphological characteristics that were not observed in previous descriptions and has allowed for a much greater understanding of this taxonomically problematic species.

Since the late 1990s the Swedish brachiopod species has been affiliated with the little known Siberian paterinate species *Cryptotreta*. The genus *Cryptotreta* is currently defined as transversely ovate with a well-defined, orthocline, ventral pseudointerarea with a narrow median ridge and possessing a moderately convex dorsal valve, with a low pseudointerarea (Laurie 2000, p. 153, fig. 85). The majority of morphological differences pertain to the ventral valve, differing in general outline and details regarding the interarea (pseudointerarea *sensu* Laurie 2000). The orthocline ventral interarea with a narrow median ridge of *Cryptotreta* distinctly contrasts with the catacline interarea and triangular homeodeltidium of *Tallatella* (compare Fig. 2F-G, N with Laurie 2000, fig. 85a). *Cryptotreta* also appears to share a unique valve morphology with the genera *Salanygolina* and *Tumulduria* possessing an almost flat dorsal valve with vestigial interarea and a strongly convex ventral valve with orthocline interarea with a narrow central ridge and a secondary shell opening associated with a colleplax anterior of the ventral umbo (Holmer et al. 2009; Skovsted et al. in press).

The dorsal valves of *Cryptotreta* and *Tallatella* gen. nov. on the other hand, are similar in many aspects, the valve outline and the possession of a low, dorsal interarea (compare Fig. 3A-C with Laurie 2000, fig. 85d) make the two dorsal valves relatively congruent. The presence of a homeochilidium

easily observed in *Tallatella* (Fig. 3D), cannot be verified in the available *Cryptotreta* illustrations and is not mentioned in the previous morphological descriptions. However, the differences in ventral valve outline, interarea and the presence of a homeodeltidium together with the recent suggestion that *Cryptotreta* possesses a *Salanygolina*-like ventral umbonal foramen (Holmer et al. 2009; Topper et al. 2013; Skovsted et al. in press) firmly places the Swedish species outside the concept of *Cryptotreta*.

Tallatella gen. nov. is most closely comparable with *Dzunarzina* and the Australian specimens of the genus *Askepasma*, in particular the type species, *A. toddense* Laurie, 1986. Whether *Dzunarzina* is a representative of *Askepasma* remains unclear until type material of the Mongolian genus is examined. *Askepasma* and *Tallatella* share some striking similarities predominantly in shell outline and the height and inclination of the dorsal and ventral interareas (see Topper et al. 2013, figs 2-3). Both genera are invariably plicate and the dorsal valves of both genera possess a homeochilidium. The significant morphological difference between the two genera is the presence of a homeodeltidium in *Tallatella* (Fig. 2F-G) a morphological feature absent in *Askepasma*, which displays an open delthyrium (Topper et al. 2013, fig. 2). The distinct ornamentation of closely packed hexagonal pits seen in *Askepasma* (Topper et al. 2013, fig. 2C₂) is absent in *Tallatella*, the Swedish genus instead displaying an ornamentation of weakly impressed polygonal structures (Figs 2O, 3G). The only other comparable cryptotretid with a ventral homeodeltidium is *Aldanotreta* from Cambrian Stage 2 of Siberia that has a concave, procline interarea with a wide homeodeltidium (Pelman 1977; Laurie 2000; CBS pers. obs.) and more strongly convex shells compared to *Tallatella*.

The combination of morphological features such as the sub-quadrate shell outline, the presence of a homeodeltidium and homeochilidium and inclination of both ventral and dorsal interareas make the specimens from the När Shale Member of Sweden unique, distinguishing it from other genera within the paterinates. Consequently a new genus, *Tallatella* gen. nov. is erected herein to accommodate the perplexing Swedish material that has previously been assigned to *Cryptotreta undosa*.

Tallatella undosa (Moberg, 1892)

Figs 2–3

1892 *Kutorgina undosa* Moberg, p. 112, pl. 3, figs 10–12.

1892 *Kutorgina* sp. Moberg, p. 114.

1892 *Acrothele* sp. Moberg, p. 114, pl. 3, fig. 9.

1892 *Obolella* sp.? Moberg, p. 115, pl. 3, figs 1, 2.

1912 *Micromitra (Paterina) undosa* Walcott, p. 356, fig. 28.

1965 *Micromitra undosa* Åhman & Martinsson, p. 142, fig. 2.

1977 *Micromitra undosa* Bengtson, fig. 1G.

1998 *Cryptotreta undosa* Williams, Popov, Holmer & Cusack, pl. 1, fig. 5; pl.

4, figs 4-7; pl. 5, figs 1-5.

2008 *Cryptotreta? undosa* Holmer, Popov & Streng, p. 6, fig. 2

Lectotype. Ventral valve SGU5240 as designated by Walcott (1912, p. 356) from an erratic boulder of the När Shale Member on the western coast of Öland (Fig. 2A).

Other material examined. Approximately 30 specimens were examined under the SEM of which 9 specimens have been illustrated herein. Specimens are from a single locality on the Skäggenäs Peninsula all collected by Åhman & Martinsson (1965). Approximately an additional fifty other fragmentary specimens exhibiting variable degrees of preservation are present in the assemblage studied herein.

Diagnosis. As for genus by monotypy.

Description. Ventribiconvex shell with straight posterior margin outline (maximum width 7.4 mm, maximum length 6.3 mm). Ventral valve sub-quadrate to semi-circular and moderately convex with weakly expressed anterior sulcus (Fig. 2C, I). Ventral umbo located close to posterior margin. Ventral interarea low, catacline to slightly procline with wide, triangular delthyrium covered by a gently convex homeodeltidium projecting slightly beyond the posterior margin (Fig. 2F). Central portion of homeodeltidium with shallow, triangular emargination. Internal surface of ventral valve with weakly expressed pinnate mantle canals (Fig. 3E-F). Dorsal valve gently convex, hypercline with narrow interarea with wide, triangular notothyrium covered by a homeochilidium (Fig. 3A-C). Larval shells of both valves bulbous, transversely ovate, approximately 500 µm wide with central, V-shaped mound and multiple radial furrows along the lateral and anterior margins (Fig. 2F, J). Post-larval shell with fine concentric fila and multiple nickpoints (Fig. 3H). Partially exfoliated surfaces exhibit a reticulate micro-ornament with individual polygons about 5-10 µm across (Figs 2O, 3G). Cross sections

through shell laminae sometimes reveal that these are composed of poorly defined orthogonal columns (Fig. 3I-J).

Remarks. The original faunal assemblage documented by Moberg (1892) from the När Shale contained five (some questionably assigned) different brachiopod species, across four different genera. The material illustrated was poorly preserved (Moberg 1892, pl. 3, figs 1, 2, 9-14) and the corresponding descriptions were tenuous. *Kutorgina? alata* Moberg, 1892 has since been recognized as an arthropod (*Eolimulus* see Bergström, 1968) and after looking through the collections of När Shale material the remaining brachiopod specimens are here recognized as representatives of *Tallatella undosa*. No other brachiopod species were found in the blocks of När Shale and the original discrimination of taxa was most probably due to variable preservation combined with the orientation of individual brachiopod valves in relation to the face of the rock sample. Moberg (1892) did not designate a holotype for *Kutorgina undosa* and a lectotype was designated by Walcott (1912, p. 356) based on Moberg's (1892, pl. 3, fig. 12) original illustrations. Examination of the lectotype (reproduced here Fig. 2A) has revealed that the specimen is predominantly a mould, basically devoid of actual shell material. The designation of a lectotype cannot be officially altered, however we suggest that the ventral valve specimen (PMUxx, Fig. 2B-F) be utilized when directly comparing the species in future scientific studies.

The reticulate ornament of exfoliated shell surfaces and the corresponding orthogonal columns (Fig. 3I-J) is closely comparable to the prismatic shell structure of *Salanygolina* (Holmer et al. 2009) although the

shell of *Tallatella* appears to be more strongly mineralized. The structure is also comparable to the reticulate and columnar shell structures of other paterinids as well as some tommotiids (Williams et al. 1998; Balthasar et al. 2009).

Holmer et al. 2008a (p. 6, fig. 2) described circular structures (diameter approximately 10 μ m) from a ventral valve of *Tallatella* from Kalmarsund originally figured by Åhman & Martinsson (1965). These structures were interpreted by Holmer et al (2008a) as penetrative setal tubes and were considered to be akin to similar structures in *Askepasma*. The circular pitted secondary shell structure was considered to show similarities to the columnar fabric in the tannuolid *Micrina* (Tate) and the stem group brachiopod *Mickwitzia* (Schmidt, 1888; see Holmer et al. 2008b). Despite investigating multiple specimens from the same locality, we failed to find any evidence of shell penetrative setal tubes in *Tallatella* and the structures illustrated by Holmer et al (2008a) could either represent examples of follicular setae fortuitously incorporated into the shell of a single individual or alternatively, represent unusual preservation of the reticulate ornament commonly found on exfoliated surfaces of *Tallatella*.

Occurrence. Traditional early Cambrian (Cambrian Series 2, Stage 4; *Holmia kjerulfi* and ‘*Ornamentaspis linnarssoni* Trilobite zones) of the När Shale Member on the Skäggenäs Peninsula and island of Öland, Sweden.

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Fig. 1. A. Map showing location of Skäggenäs peninsula and Öland in southeastern Sweden. *B.* Map showing locations of areas discussed in text, including Äspelund and Venenäs, where samples were collected by Åhman & Martinsson (1965) and Bengtson (1968, 1977) and the localities on Öland where the type material was collected. Figure modified from Bengtson (1968, fig. 1).

Fig. 2. Tallatella undosa (Moberg) from the När Shale of Sweden, Cambrian Series 2, Stage 4. All specimens (with the exception of 2A) are from Äspelund on the Skäggenäs peninsula (locality of Åhman & Martinsson 1965). **A**, lectotype, ventral valve plan view, SGU5240, collected from Stora Rör, western coast of Öland, Sweden, scale bar 2 mm. **B-F**, ventral valve, PMUxx; **B**, plan view; **C**, lateral view; **D**, lateral view; **E**, posterior view; **F**, close up of larval shell, scale bar 200 µm. **G-K**, ventral valve, PMUxx; **G**, posterior view, scale bar 1 mm; **H**, plan view, scale bar 1 mm; **I**, lateral view, scale bar 1 mm; **M**, ventral valve, PMUxx; **N**, ventral valve, PMUxx; **O**, ventral valve, PMUxx.

J, close up of larval shell, scale bar 250 μ m; K, anterior view, scale bar 1 mm. **L-O**, ventral valve, NRM141302; L, plan view; M, posterior view; N, lateral view; O, close up of polygonal ornament, scale bar 25 μ m. All scale bars 2.5 mm unless otherwise stated.

Fig. 3. Tallatella undosa (Moberg) from the När Shale of Sweden, Cambrian Series 2, Stage 4. All specimens are from Äspelund on the Skäggenäs peninsula (locality of Åhman & Martinsson 1965). **A-B**, dorsal valve, NRM141303; A, oblique plan view, scale bar 2.5 mm; B, lateral view, scale bar 2.5 mm. **C-D**, dorsal valve, PMUxx; C, oblique plan view, scale bar 1 mm; D, close up of larval shell and homeochilidium, scale bar 500 μ m. **E**, plan view of ventral valve showing impressions of pinnate mantle canals, scale bar 1 mm, PMUxx. **F-G**, ventral valve, PMUxx; F, plan view of ventral valve interior,

scale bar 2.5 mm; G, close up of polygonal ornament, scale bar 100 μm . **H**, close up of external ornament showing nickpoints, scale bar 250 μm , PMUxx. **I-J**, ventral valve, NRM141304; I, poorly defined orthogonal columns, scale bar 100 μm ; J, close up of poorly defined orthogonal columns, scale bar 50 μm .