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Setatella significans, a new name for mickwitziid stem group brachiopods from the lower Cambrian of Greenland and Labrador.

¹Skovsted, C.B., ¹Streng, M., ²Knight, I. & ¹Holmer, L.E.

¹*Department of Earth Sciences, Palaeobiology, Uppsala University, SE-752 36 Uppsala, Sweden* [Christian.Skovsted@geo.uu.se, Lars.Holmer@pal.uu.se, Michael.Streng@geo.uu.se]

²*Government of Newfoundland and Labrador, Mines and Energy, Geological Survey Division, P.O. Box 8700, St. John's, Newfoundland, Canada A1B 4J6* [ianknight@gov.nl.ca]

Setatella significans gen. et sp. nov. from the Lower Cambrian of North-East Greenland, originally described under the name '*Mickwitzia* cf. *occidens*', is introduced as a probable stem group brachiopod. Newly collected specimens of *Setatella significans* from the Forteau Formation of southern Labrador exhibit new morphological details and provide a better understanding of its ontogeny. *Setatella significans* differs from species of *Mickwitzia* in

having a ventral pseudointerarea and hemiperipheral growth in both valves. *Setatella significans* probably belongs to the derived stem group of the Linguliformea that can be differentiated from the more primitive *Mickwitzia*. The geographic range of *Setatella* is extended to southern Labrador.

Key words: Brachiopoda, *Mickwitzia*, shell penetrating setae, lower Cambrian, Greenland, Labrador

Introduction

The discovery of fragmentary brachiopod-like valves with tubular perforations originally housing shell penetrating setae (setigerous tubes) in the Lower Cambrian of North-East Greenland (Holmer et al. 2002) prompted comparison to similar structures in problematic tannuolinid tomotiids (Williams & Holmer 2002) and instigated a new phase in the search for the origin of the phylum Brachiopoda. Subsequently, evidence for shell penetrating setae has been found in a wide range of brachiopods from Cambrian and Ordovician strata (Balthasar 2004; Holmer & Caron 2006; Holmer et al. 2008a; Jin et al. 2008; Popov et al. 2009) and the structure of recently discovered articulated tomotioid scleritomes has further strengthened the tomotioid-brachiopod link (Skovsted et al. 2008, 2009a; Holmer et al. 2008b; Balthasar et al. 2009). The original specimens from North-East Greenland were referred to the genus *Mickwitzia* Schmidt, 1888 by Holmer et al. (2002) and were considered close to *Mickwitzia occidentis* Walcott, 1908 from the Lower Cambrian of Nevada by Skovsted & Holmer (2003). However, investigation of *Mickwitzia muralensis* from western Canada

(Balthasar 2004), *Mickwitzia* sp. from South Australia (Skovsted et al. 2009b), additional material of *M. occidentis* from Nevada (M. Streng pers. obs.), and the type species of *Mickwitzia*, *M. monilifera*, from Sweden (L.E. Holmer pers. obs.) demonstrate that the morphology of the Greenland specimens differs significantly from the genus *Mickwitzia*. For this reason, and partly based on newly discovered shells from the Forteau Formation of southern Labrador, a brief redescription of the Greenland material and the introduction of the new name *Setatella significans* is warranted.

Material, methods and geological setting

In North-East Greenland *Setatella* occurs in the Bastion and Ella Island Formations which crops out between Ella Island and CH Ostenfeld Nunatak in the fjord region (Fig. 1A, B). These occurrences were discussed by Skovsted & Holmer (2003, 2005) and described in detail by Skovsted (2004, 2006). No new material from these localities is available for study at the present time and no new information concerning the geological setting or geographical location of the material is at hand. All illustrated specimens from Greenland are housed in the collections of the Geological Museum of Copenhagen (MGUH).

New collections of *Setatella* were recovered from the lower Cambrian Forteau Formation of southern Labrador (Fig. 1C). The new specimens were recovered in 2007 from a small quarry through archaeocyathid-rich limestones of the lower Forteau Formation east of L'anse aux Loup, close to Route 510 (Fig. 1D, E). All illustrated specimens from the Forteau Formation are housed in the collections of the Provincial Museum of Newfoundland and Labrador, St. John's (NFM).

All specimens from Greenland and Labrador investigated here were recovered from acid resistant residues of limestone samples digested in 10% acetic acid. The specimens were wet

sieved and separated from the residues by heavy mineral separation (sodium polytungstate). Selected specimens were gold-coated and investigated at the SEM facility of the Department of Biological Structural Analysis at Uppsala University.

Systematic Palaeontology

Incertae sedis

Organophosphatic, bivalved stem-group brachiopods

Setatella gen. nov.

Type and only species: *Setatella significans* gen. et sp. nov. from the lower Cambrian (Middle Dyeran, Cambrian series 4) of North-East Greenland (Bastion and Ella Island Formations) and southern Labrador (lower Forteau Formation).

Diagnosis: Organophosphatic brachiopod with biconvex shell. Valve exterior with fine concentric fila with nickpoints and regularly distributed pustules. Stratiform shell structure with two types of columnar elements perpendicular to lamination; narrow, acrotretid-like columns and larger tubular structures penetrating the entire shell. Ventral and dorsal pseudointerarea with open striated tubes inserted horizontally within and between shell laminae; triangular ventral pseudointerarea orthocline to anacline with shallow pedicle notch and propareas. Triangular dorsal pseudointerarea orthocline and undifferentiated.

Differs from *Mickwitzia* Schmidt, 1888 by the presence of a ventral pseudointerarea with a

pedicle groove, hemiperipheral growth in both valves and in the lack of projections of the setigerous tubes into the shell cavity. Differs from all linguliform brachiopods by the combination of a columnar shell structure with striated shell penetrating tubes on the pseudointerarea.

Etymology: In reference to the prominent setigerous tubes of the type species.

Discussion: *Setatella* differs from *Mickwitzia* in a number of morphological and ultrastructural characters. The most notable difference is the presence of a lingulid-like pseudointerarea in the ventral valve of *Setatella* and the consequent hemiperipheral growth. The ventral valve of *Mickwitzia* exhibits a sub-central apex and holoperipheral growth (Walcott 1912; Rowell 1977; Balthasar 2004; M. Streng and L.E. Holmer pers. obs.) and lacks a pseudointerarea. Other differences include the small, sub-circular juvenile shells in *Setatella* ornament by fila and fine radiating ridges and the presence of a ventral pedicle notch, both features apparently missing in *Mickwitzia*. Also, the cone-shaped internal extensions of the setal tubes in *Mickwitzia* lack counterparts in *Setatella*. Nevertheless, *Setatella* and *Mickwitzia* share the presence of setigerous tubes and both probably belong within a loosely defined ‘mickwitziid’ stem group of the Linguliformea.

Setatella significans sp. nov.

Figures 2, 3

- ?1957 *Mickwitzia* sp., Cowie and Adams, p. 26.
- ?1996 ‘Perforate plate’ Landing and Bartowski, p. 759, figs 9.16–9.17.
- 2002 *Mickwitzia* cf. *occidens* Walcott; Holmer, Skovsted and Williams, text-figs 2–3.
- 2003 *Mickwitzia* cf. *occidens* Walcott; Skovsted and Holmer, p. 2, figs 3–5, 7–12, *non* fig. 8C.
- 2005 *Mickwitzia* cf. *occidens*. Skovsted & Holmer, p. 327, pl. 1, figs 9-13.

Holotype: MGUH 26309; fragmentary dorsal valve with well developed pseudointerarea with preserved, horizontally inserted setigerous tubes (Fig. 2A-D) from sample 314814, collected 37 m above the base of the Ella Island Formation, Albert Heim Bjerre (see detailed geographical information in Cowie & Adams 1957 and Skovsted 2006).

Diagnosis: As for genus.

Etymology: In reference of the species significance for our understanding of the early evolution of the brachiopod stem group.

Material: 433 specimens preserving the umbo from the Bastion and Ella Island formations of North-East Greenland, the majority of which are too poorly preserved for valve type to be determined, as well as numerous shell fragments. Four specimens preserving the umbo, and

24 additional shell fragments from the Forteau Formation of southern Labrador (samples LLQ3-7 through LLQ3-10).

Discussion: The Greenland material of *Setatella significans* was described in detail by Skovsted & Holmer (2003). The new material of the species from the Forteau Formation of southern Labrador supplements the original description in a number of ways. The most important new observation is the presence of a pedicle notch in adult ventral valves, contrasting with the interpretation by Skovsted & Holmer (2003) that the pedicle notch is only present in juvenile specimens. The presence of a pedicle notch in adult ventral valves facilitates proper recognition of valve types and in particular a better characterization of the dorsal valve morphology. Skovsted & Holmer (2003) noted that the dorsal valves are rare in the Greenland collections. However, this is partly based on the erroneous inclusion of a specimen exhibiting holoperipheral growth (Skovsted & Holmer 2003, fig. 8c). In addition to the different growth direction, this specimen differ from all other specimens of *Setatella* from Greenland and Labrador in the presence of a distinct concentric and radial ornament, and is not included in *Setatella significans* herein. In all other specimens the dorsal pseudointerarea is orthocline and valve growth is hemiperipheral. The triangular dorsal pseudointerarea lack a pedicle notch while the ventral pseudointerarea is orthocline to anacline, weakly triangular with a relatively well defined pedicle notch and propareas. In all other respects we refer to the description presented by Skovsted & Holmer (2003).

The new material from the Forteau Formation of Labrador is fragmentary and difficult to characterize on purely morphological terms. The same applies to the larger collections from Greenland, and as discussed by Skovsted & Holmer (2003) probably reflects the poor mineralization of the original shell. The new collections exhibit a shell structure identical to

that of the type material of *Setatella* from Greenland, and combined with the similarities in the morphology of the pseudointerarea (i.e. horizontally inserted setigerous tubes) justifies the inclusion of both collections in a single species.

Cowie and Adams (1957, p. 26) reported, but never described or illustrated possible specimens of *Mickwitzia* from the Bastion Formation of Ella Island and Albert Heim Bjerge. Although it has not been possible to locate any non-trilobite specimens from the collections of Cowie and Adams (M.G. Bassett pers com. 2003), these reported specimens may represent *Setatella significans*.

As discussed by Skovsted & Holmer (2005), specimens referred to as ‘perforated plate’ from the Taconic Allochthon of New York State (Landing & Bartowski 1996, figs 9.16–9.17) possible represent poorly preserved specimens of *Setatella significans*. Morphologically similar specimens are common in the collections of fragmentary valves from the Bastion Formation of North-East Greenland (Skovsted & Holmer 2003, fig. 4; Skovsted & Holmer 2005, pl. 1, fig. 13).

Occurrence: Upper lower Cambrian, middle Dyeran Stage (International Stage 2, Series 4), of North-East Greenland, southern Labrador and possibly the Taconic Allochthon of New York State.

The significance of *Setatella*

Ever since the discovery of setigerous tubes in mickwitzids (Holmer et al. 2002; Skovsted & Holmer 2003) these brachiopods have figured prominently in discussions on the origin and early evolution of the Brachiopoda. The main reason for this is the presence of similar shell

penetrating setae in tannuolinid tommotiids which also show some morphological similarities to brachiopods (Williams & Holmer 2002; Holmer et al. 2008b). The discovery that shell penetrating setae are more widespread among Cambro-Ordovician brachiopods than previously thought illustrates the importance of this feature in the early evolution of the phylum (Jin et al. 2008; Holmer et al. 2008a) and the differences between *Mickwitzia* and *Setatella* described herein should be interpreted in the light of these findings.

Setatella exhibits a number of derived linguliform characteristics, including a pseudointerarea and hemiperipheral growth in both valves, a ventral pedicle notch, a small sub-circular juvenile shell with fila and nickpoints and a stratiform columnar shell structure, all of which are absent in *Mickwitzia* from western Canada, South Australia, Nevada and Sweden (Balthasar 2004; Skovsted et al. 2009b; M. Streng and L.E. Holmer pers. obs.). This implies that *Setatella*, compared to *Mickwitzia*, occupies a more derived position in the linguliform stem group, possibly close to the base of the linguliform crown group.

This hypothesis combined with the recent reinterpretation of the tannuolinid tommotiid *Micrina* as a brachiopod-like bivalved shell (Holmer et al. 2008b) suggests that the linguliform stem group should include a range of ‘mickwitziid’ taxa exhibiting shell penetrating setae. Although we can identify basal (i.e. *Micrina*), intermediate (*Mickwitzia*) and advanced (*Setatella*) members of this stem group, the possibility that other known problematic fossils, such as *Microschedia* Geyer, 1994, *Cowiella* Hinz, 1987 and *Stratosia* Vassilieva, 1998, also belong within this stem group remains to be explored.

The discovery of the scleritome of *Paterimitra* (Skovsted et al. 2009a) indicate that a second lineage of tommotiids exhibiting brachiopod-like sclerites but lacking setigerous tubes, evolved simultaneously with the tannuolinid-linguliform lineage. The morphology, micro ornament and shell structure of *Paterimitra* is very similar to that of *Askepasma*, a

paterinid brachiopod from the Lower Cambrian of South Australia (Balthasar et al. 2009). *Askepasma* and other paterinids combine an organophosphatic shell mineralogy with shell morphologies closely comparable to kutorginids, chileids and other early calcareous brachiopods. Thus, an independent origin of the bivalved shell of linguliform and calcareous brachiopods from different tommotiid ancestors is a distinct possibility (Skovsted et al. 2009a)

The preservation of *Setatella* in Greenland is unusual, and radically different from the preservation of the co-occurring lingulid brachiopods *Eoobolus* and *Botsfordia* (Skovsted & Holmer 2003, 2005). In Labrador the situation is similar, with poorly preserved shells of *Setatella* occurring together with much better preserved specimens of *Paterina* and *Micromitra* (CBS pers. obs.). The Greenland specimens are invariably fragmentary, and usually exhibit regions where the shell was differentially composed of carbonate and phosphate (Skovsted & Holmer 2003) and this has resulted in very unusual fossils where the shell has been partly dissolved during acid preparation (Skovsted & Holmer 2005, pl. 1, figs 12, 13). The most likely explanation for this phenomenon is that the originally very weakly mineralized shell was differentially recrystallised. The fact that almost all well preserved specimens appear to preserve the umbonal region suggest that this was the only portion of the shell with significant levels of shell mineralization. The anterior parts of the shell in *Setatella* were thus more or less unmineralised, a situation mirroring the condition in some problematic Cambrian brachiopods, including *Acantotretella* from the British Columbia and South China (Holmer & Caron 2006; Hu et al. in press) and *Lingulosacculus* from British Columbia (Balthasar & Butterfield 2009).

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Figure captions

Fig. 1. Geographical locations and simplified stratigraphy of localities yielding *Setatella*. **A**, Map of North America with field areas indicated. **B**, Simplified Cambrian stratigraphy of North-East Greenland with approximate range of *Setatella significans* gen et sp. nov indicated. **C**, Simplified Cambrian stratigraphy of southern Labrador and western Newfoundland. **D**, Geological map of southern Labrador with field locality indicated. **E**, Stratigraphic section of L'anse aux Loup quarry section 3 with the stratigraphic range of samples yielding *Setatella significans* gen. et sp. nov. indicated.

Fig. 2. *Setatella significans* gen. et sp. nov. from the lower Cambrian of Albert Heim Bjerge, North-East Greenland. **A-D**, dorsal valve, MGUH 26309, Holotype; from sample GGU 314814, Ella Island Formation; **A**, internal view of specimen with pseudointerarea, scale bar equals 200 µm. **B**, detail of pseudointerarea with multiple setigerous tubes, scale bar equals 200 µm. **C**, detail of setigerous tubes, scale bar equals 10 µm. **D**, detail of striated surface of setigerous tube, scale bar equals 2 µm. **E, F**, ventral valve, MGUH 26300, from sample 314835, Bastion Formation; **E**, Oblique external view of apical part of valve, scale bar equals 200 µm. **F**, close up of juvenile shell with nickpoints and fila and potential pedicle notch, scale bar equals 100 µm. **G**, valve fragment, MGUH 26370, from sample 314816, Ella Island Formation; scale bar equals 200 µm. **H**, valve fragment, MGUH 26315, from sample 314816, Ella Island Formation; detail of columnar shell structure; scale bar equals 20 µm.

Fig. 3. *Setatella significans* gen. et sp. nov. from the lower Cambrian Forteau Formation, L'anse au Loupe, southern Labrador. **A**, ventral valve, NFM-zz1, sample LLQ3-7; external view. **B, C**, ventral valve, NFM-zz2, sample LLQ3-9; **B**. internal view showing pedicle notch. **C**. oblique internal view. **D**, ventral valve, NFM-zz3, sample LLQ3-9; internal view showing pedicle notch. **E-G**, dorsal valve, NFM-zz4, sample LLQ3-7; **E**. internal view. **F**. oblique posterior view. **G**. detail of pseudointerarea with open setigerous tubes. **H, I**, valve fragment, NFM-zz5, sample LLQ3-9; **H**. overview. **I**. detail of columnar shell structure with open setigerous tubes. All scale bars equal 100 μm .