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Permian spiriferellid brachiopods from northern Pangaea: taxonomy, biostratigraphy, macroevolution and implications for palaeoenvironmental and palaeobiogeographical reconstructions

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This study reports diverse spiriferellid brachiopods from the Permian rocks of Svalbard and adjacent areas (Arctic Canada and Subpolar Urals of Russia) located at the northern margin of Pangaea. In total, 11 brachiopod species in four genera are recognized and described in detail, including two new species (*Spiriferella protodraschei* and *Arcullina*? *enokiani*). According to our taxonomic investigation, morphological characteristics of the ventral sulcus and dorsal fold are relatively stable within each species, in spite of considerable intraspecific variations in shell outline and macro-ornamentation. In addition, both the arrangement of pustules, as a shell surface micro-ornamentation, and the development of delthyrial coverings are shown to be significant features for inferring phylogenetic relationships and for defining species. The best-known but still questionable taxon, *Spiriferella keilhavii*, is here identified as an endemic species restricted to Bjørnøya and, possibly, to central East Greenland; it is phylogenetically closest to *S. loveni*. Following the taxonomic revision, the stratigraphical ranges of the spiriferellids within the Kapp Starostin Formation in Spitsbergen are fully refined: three species, *S. protodraschei*, *A. polaris* and *Timaniella wilczeki*, are confined to the lowermost Vøringen Member (late Artinskian–early Kungurian), whereas *S. loveni* dominates the overlying members with a much longer stratigraphical range (late Kungurian–Lopingian?). This abrupt compositional change, along with comparable changes in other taxonomic groups, can be explained by a palaeoclimatic shift from cool to cold conditions between the Vøringen Member and the overlying Svenskeegga member. A similar biotic transition is identified between the Hambergfjellet and Miseryfjellet formations in Bjørnøya. On the other hand, *S. loveni* is abundant in the Late Permian strata of central East Greenland, but there it appears to be more costate in plication compared to its counterpart from Spitsbergen. It is suggested that this alteration in shell ornamentation may represent a possible response (adaptation) to warming arising from the southward migration of the species.

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Keywords: *Spiriferella*; *Arcullina*; *Edrimatus*; *Timaniella*; Kapp Starostin Formation; Spitsbergen

Introduction

Spiriferellidae was one of the most representative brachiopod clades in the Boreal Realm during the late Palaeozoic (Waterhouse *et al.* 1978; Waterhouse & Waddington 1982). To date, more than 30 spiriferellid species have been reported from the northern marginal shelf areas of Pangaea (e.g. de Verneuil 1845; von Buch 1847; Toula 1873, 1875; Tschernyschew 1902; Wiman 1914; Tschernyschew & Stepanov 1916; Frebold 1931, 1937; Stepanov 1937; Dunbar 1955, 1962; Gobbett 1964; Nelson & Johnson 1968; Waterhouse *et al.* 1978; Waterhouse & Waddington 1982; Kalashnikov 1998; Angiolini & Long 2008). However, many of these species have remained poorly defined and understood owing to a number of factors, including the great range of morphological variation in each species, limited material (both taxonomic and stratigraphical) available for many previous studies, and/or insufficient description and illustration of crucial morphological features. Consequently, the utility of this group for establishing an improved biostratigraphy as well as for

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*Corresponding authors. Emails: sangminlee76@gmail.com; guang@uow.edu.au palaeoenvironmental and macroevolutionary interpretations has been significantly compromised, or led to incorrect conclusions in some cases.

In recent years, a considerable number of detailed stratigraphical studies have been conducted on the Kapp Starostin Formation in Svalbard, Arctic Norway, in attempts to decipher its depositional and palaeoenvironmental conditions before the advent of the Mesozoic Era (e.g. Blomeier *et al.* 2013; Dustira *et al.* 2013; Bond *et al.* 2015, 2018; Grasby *et al.* 2016; Uchman *et al.* 2016; Jafarian *et al.* 2017). Notably, Bond *et al.* (2015) provided biostratigraphical and chemostratigraphical data based mainly on brachiopod material, which led these authors to propose that a conspicuous end-Guadalupian (Capitanian) mass extinction occurred in the Boreal Realm, prior to the end-Permian catastrophic event. Despite the high resolution of the stratigraphical data in their paper, however, the brachiopod biostratigraphy deployed could be improved with a more robust taxonomy of the spiriferellids, which would lead to better faunal correlation between Spitsbergen and central East Greenland.

In this context, it is evident that the taxonomy and systematic palaeontology of Permian brachiopods from the Kapp Starostin Formation and time-equivalent units in the Arctic region need to be modernized before their stratigraphical extinction patterns can be deciphered. Additionally, as Permian spiriferellid brachiopods were widely distributed in the northern marginal regions of Pangaea, they are important for interpreting the late Palaeozoic palaeoenvironmental and palaeoclimatic dynamics of northern Pangaea. Until now, these palaeoecological aspects have not been investigated, especially in terms of the morphological adaptations of spiriferellids to varied local depositional and palaeoclimatic conditions.

In an attempt to address these issues and to narrow the knowledge gap with respect to the spiriferellid clade, we have gathered several collections (>500 specimens in total) of Permian spiriferellid specimens from three separate basins (Svalbard, Sverdrup Basin in Arctic Canada and Timan-Pechora Basin in north-western Russia) in the northern margin of Pangaea (Fig. 1), mostly with detailed stratigraphical and geographical information. Based on all of these collections, this paper

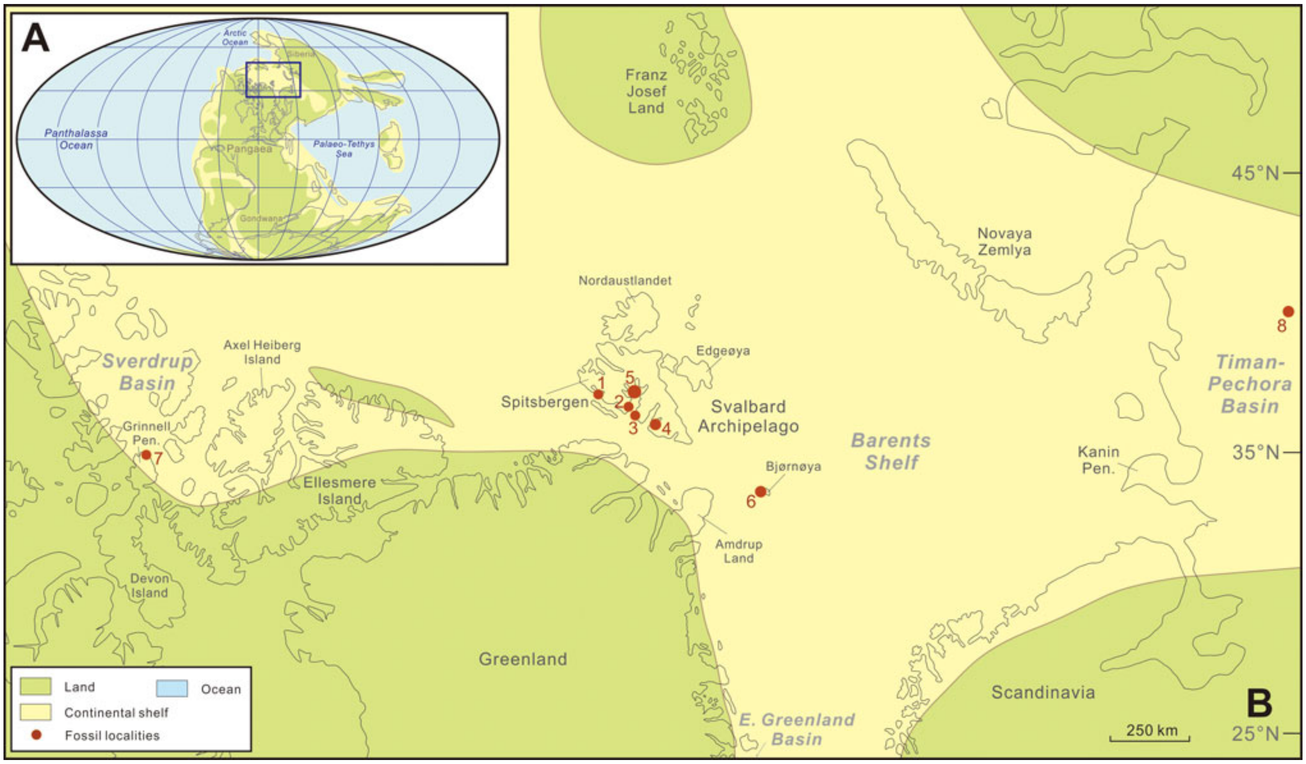

Figure 1. Fossil localities on Permian reconstruction map. Note that the base map represents palaeogeography during the late Cisuralian (Artinskian–Kungurian). **A,** global palaeogeographical map. Base map modified from A. M. Ziegler *et al.* (1997), Reid *et al.* (2007) and Angiolini *et al.* (2013). **B,** reconstruction of the northern margin of Pangaea including Sverdrup Basin, Greenland, Svalbard, Barents Shelf and Timan-Pechora Basin. Locality sections: **1**, Scheteligfjellet; **2**, Trygghamna; **3**, Festningen; **4**, Ahlstrandodden and Reinodden; **5**, Idodalen and Skansbukta, all in Spitsbergen; **6**, Miseryfjellet in Bjørnøya; **7**, Lyall River in Grinnell Peninsula of Devon Island; **8**, Kozhim River in Subpolar Urals. Base map modified from Stemmerik & Worsley (2005). More detailed locality sections in Spitsbergen (1–5) are explained in Supplementary material 1.

focuses on a detailed systematic study of Permian spiriferellid brachiopods. The specific aims of this paper are: (1) to systematically document the spiriferellid species with their taxonomic revision; (2) to recognize the intraspecific variation in each species as well as morphological differences between similar species; (3) to discuss the biostratigraphical value of spiriferellids with a view to refining their significance for more detailed stratigraphical correlation across the Arctic region; (4) to explore the phylogeny of spiriferellid brachiopods based on their detailed morphological characteristics; and (5) to discuss how spiriferellid morphology responded to palaeoenvironmental variability during the Permian.

Material and methods

The majority of the specimens described herein were collected from eight localities in Spitsbergen during three intensive geological expeditions over several decades, firstly conducted by a Japanese party (led by Prof. K. Nakazawa) in 1986 (see Nakazawa *et al.* 1990), followed by the Japanese-Norwegian Research Group in 1989–1991 (see Nakamura 1992), and most recently performed by the Korea Polar Research Institute in 2012–2016. In addition, three other (but smaller) collections have been included here for taxonomic revision and comparison. These include: a few specimens from the Natural History Museum in Oslo, originally collected from Svalbard (Bjørnøya as well as Spitsbergen); several spiriferellid specimens originally collected from the Grinnell Peninsula of Devon Island (Sverdrup Basin) by officers from the Geological Survey of Canada, currently housed at Deakin University (Melbourne, Australia); and a small collection from the Kozhim River Section (Subpolar Urals, Russia) collected by one of the authors (GRS) in 1995. Lastly, some type specimens, stored at the Museum für Naturkunde in Berlin and at the Naturhistorisches Museum Wien, are also referred to and illustrated in this paper.

All of the figured specimens (except the type specimen of *Spiriferella keilhavii*) were coated with ammonium chloride and then photographed. Several specimens were transversely (parallel to the shell maximum width line) serially sectioned mechanically, in order to inspect their detailed internal structures. Each thin-section was mounted on a glass slide and photographed at the Andong National University (Andong, Republic of Korea). In addition, the internal structure of *Timaniella harkeri* was reconstructed using X-ray microtomographic analysis with a SkyScan 1172 system at the dental Research Institute of Seoul National University (Seoul, Republic of Korea).

Institutional abbreviations

GSC, Geological Survey of Canada, Ontario, Canada; **KOPRI**, Korea Polar Research Institute, Incheon, Korea; **MB.B**, Museum für Naturkunde, Berlin, Germany; **NHMW**, Naturhistorisches Museum Wien, Vienna, Austria; **NMV P**, Department of Invertebrate Palaeontology, Museum Victoria, Melbourne, Australia; **PMO**, Natural History Museum, Oslo, Norway.

Geological settings and fossil localities

Northern margin of Pangaea during the late Palaeozoic

During the late Palaeozoic, the northern marginal shelf of Pangaea was composed of the current Arctic regions including, from west to east, the Canadian Arctic Islands (Sverdrup Basin), North Greenland, Svalbard, Barents Shelf, Novaya Zemlya, the Kanin Peninsula (NW Russia) and the Timan-Pechora Basin (Fig. 1; P. A. Ziegler 1988; Golonka & Ford 2000; Stemmerik & Worsley 2005; Angiolini *et al.* 2013). The west-east oriented shelf was positioned at around 20°N palaeolatitude in the Mississippian and reached to 45°N palaeolatitude in the Lopingian as a result of its northward drift (Golonka & Ford 2000; Stemmerik & Worsley 2005). The Ural seaway connecting the northern marginal shelf of Pangaea to the Palaeo-Tethys was closed off by the collision between Baltica and Kazakstan in the Cisuralian (Fig. 1A; P.A. Ziegler 1988; Shi *et al.* 1995; Puchkov 1997; Fokin *et al.* 2001). With the closure of the Ural seaway, the proto-Atlantic seaway connecting Svalbard and the Barents Shelf with East Greenland and north-west Europe started to develop. As a result, the Zechstein Basin was formed with the development of a large epeiric sea extending southward into northern and central Europe, covering parts of Britain, Germany and Poland in the Middle–Late Permian (Heeremans *et al.* 2004).

The overall stratigraphy, broad correlation and age assignments for the Upper Palaeozoic successions of the northern margin of Pangaea have been discussed in several papers, but the specific ages for many of the stratigraphical units remain unclear. Among these successions, the stratigraphical correlation among the Permian strata in the Sverdrup Basin, Greenland and Svalbard has been relatively well established (Fig. 2; Stemmerik & Worsley 1989, 1995, 2005; Samuelsberg & Pickard 1999; Stemmerik 2000). These successions commonly present a consistent and continuous climatic transition from warm conditions to cold regimes throughout the Permian (Beauchamp 1994; Beauchamp

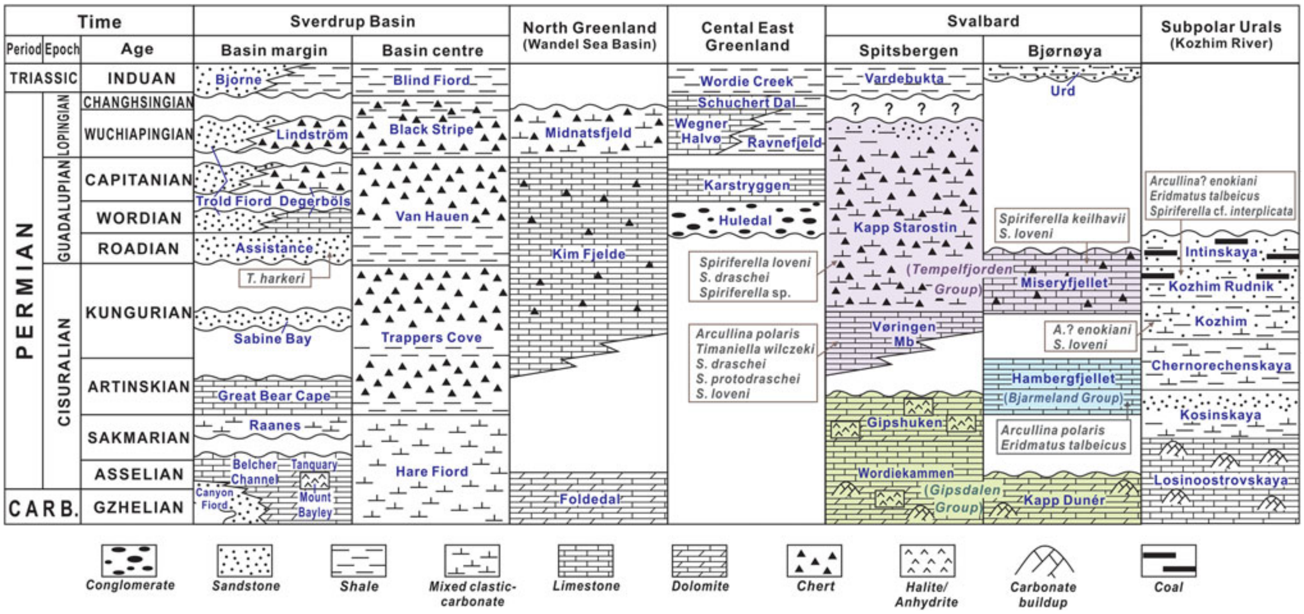

Figure 2. Permian lithostratigraphical correlation among northern Pangaean regions under the international chronostratigraphical scheme, together with spiriferellid species recognized in this study. Source data for the Sverdrup Basin from Beauchamp *et al.* (2009); Greenland from Stemmerik & Worsley (2005) and Sørensen *et al.* (2007); Svalbard from Dallmann (1999); and the Subpolar Urals from Chuvashov *et al.* (1993) and Enokian *et al.* (1993). The chronostratigraphical positions of lithostratigraphical units from the Subpolar Urals were adjusted according to Lozovsky *et al.* (2009). More detailed lithostratigraphical units in Svalbard are demonstrated in Supplementary material 1, Fig. S2.

& Desrochers 1997; Stemmerik 2000; Beauchamp & Baud 2002; Stemmerik & Worsley 2005; Reid *et al*. 2007; Blomeier *et al*. 2009, 2011). This sequence of climatic change has been linked to the gradual northward shift of Pangaea and closure of the Ural seaway (Beauchamp & Baud 2002; Stemmerik & Worsley 2005; Reid *et al*. 2007; Worsley 2008).

Stratigraphy and fossil localities in Svalbard (Spitsbergen and Bjørnøya)

Upper Palaeozoic successions are widely distributed on the major islands of Svalbard including Spitsbergen, Nordaustlandet and Bjørnøya (Dallmann 1999). The deposition of these successions was controlled mainly by major structural elements (Steel & Worsley 1984). Throughout the Carboniferous, narrow troughs and adjacent highs were mostly developed along currently NNE-SSW oriented fault lines by extensional tectonism, which led to differential sedimentation between the troughs. However, following the cessation of tectonic movement in the Late Carboniferous, stable marine shelf conditions developed (except for southern Spitsbergen), and continued until the Late Permian with continuous subsidence (Dallmann 1999; Stemmerik & Worsley 2005).

The Permian strata in Svalbard are composed of four groups: the Gipsdalen, Bjarmeland, Tempelfjorden and Sassendalen groups in ascending order (Fig. 2; Supplementary material 1, Fig. S2; Dallmann 1999). The Gipsdalen Group, lasting from the Serpukhovian (Late Carboniferous) to the early Artinskian, consists of diverse lithostratigraphical units, which together represent a gradual transition from terrestrial clastic deposition to marine carbonate deposition through progressive transgression and basin deepening (Johannessen & Steel 1992; Hüneke *et al.* 2001). Thus, the upper part of the group is characterized by widely distributed carbonates and evaporites developed under warm and arid conditions, represented by the Wordiekammen and Gipshuken formations in Spitsbergen and the Kapp Dunér Formation in Bjørnøya (Fig. 2; Supplementary material 1, Fig. S2).

The Bjarmeland Group (Artinskian) is composed of a single lithological unit, the Hambergfjellet Formation, recognized only in Bjørnøya (Fig. 2; Supplementary material 1, Fig. S2). This formation consists mainly of bioclastic sandy limestone, unconformably overlying the Kapp Dunér Formation of the Gipsdalen Group. The marine fauna in the Bjarmeland Group seems to be transitional, correlating to the uppermost part of the Gipshuken Formation in the Gipsdalen Group as well as to the lowest Vøringen Member in the Tempelfjorden Group in Spitsbergen (Nakrem 1991; Dallmann 1999). According to Worsley *et al.* (2001), the Hambergfjellet Formation is well matched with the contemporaneous lithological units of other regions in the northern margin of Pangaea, such as the Great Bear Cape Formation in the Sverdrup Basin and the lowermost Kim Fjelde Formation in the Wandel Sea Basin (Fig. 2).

The Bjarmeland Group is disconformably overlain by the Tempelfjorden Group, the latter a mixed carbonate and siliciclastic succession deposited in relatively stable marine shelf environments. In Bjørnøya the Miseryfjellet Formation (late Kungurian?) (Nakrem 1991) represents the Tempelfjorden Group, whereas the group is characterized by the Kapp Starostin Formation (late Artinskian to Lopingian?) in most areas of Spitsbergen (Fig. 2; Supplementary material 1, Fig. S2). Both formations are composed of mixed siliciclastics and carbonates, suggesting that the deposition occurred under open-marine, cooler and deeper conditions (Dallmann 1999; Stemmerik & Worsley 2005; Blomeier *et al*. 2013). However, the development of spiculitic shales was limited to the Kapp Starostin Formation, probably indicating that the Kapp Starostin Formation was formed in more basinal conditions than the Miseryfjellet Formation (Worsley *et al.* 2001).

The Vøringen Member (late Artinskian to early Kungurian), defined as the basal part of the Kapp Starostin Formation (Fig. 2), is composed mainly of bioclastic limestones with abundant brachiopods, bryozoans, crinoids and other marine fossils. This bioclastic limestone unit is interpreted to have been deposited in nearshore environments (Nakrem 1994; Blomeier *et al.* 2011). The lithological contrast with the underlying upper part of the Gipshuken Formation (which is dominated by dolomites) indicates a widespread marine transgression during the Artinskian (Steel & Worsley 1984; Ezaki *et al.* 1994; Blomeier *et al*. 2011). Upward, the overlying Svenskeegga member (Supplementary material 1, Fig. S2) consists of cherts and siliceous shales with intercalated bioclastic limestones; these sediments have been interpreted as relatively deep marine deposits (Ezaki *et al.* 1994; Dallmann 1999; Blomeier *et al.* 2013). The upper part of the Kapp Starostin Formation consists of silicified shales, glauconitic sandstones and sandy limestones; together, they suggest sedimentation in shoreface to deeper shelf environments (Ezaki *et al.* 1994; Ehrenberg *et al.* 2001; Hüneke *et al.* 2001; Blomeier *et al*. 2013). Several local units, including the Hovtinden and Stensiöfjellet members, have been included in the upper part of this formation (Supplementary material 1, Fig. S2). However, their age and stratigraphical correlation have not been fully resolved (Dallmann 1999).

The Tempelfjorden Group is overlain by the Sassendalen Group (latest Permian to Middle Triassic). The Vardebukta Formation, representing the basal part of the Sassendalen Group in Spitsbergen (Fig. 2; Supplementary material 1, Fig. S2), is composed mainly of non-siliceous dark shales and siltstones, suggesting the demise of biogenic silica production during latest Permian to Early Triassic times (Ehrenberg *et al*. 2001; Worsley 2008). Contrary to the distinct lithological change, the possible existence of a hiatus between the Tempelfjorden and Sassendalen groups, as well as across the Permian–Triassic boundary in Spitsbergen, is still a matter of debate (Mørk *et al.* 1989; Stemmerik & Worsley 2005; Nakrem *et al.* 2008; Blomeier *et al.* 2011).

The majority of the brachiopod specimens collected in Spitsbergen came from eight fossil localities representing the Kapp Starostin Formation. These localities are widely distributed in western and central Spitsbergen, including Oscar II Land (Scheteligfjellet and Trygghamna sections), outer Isfjorden (Festningen section), Wedel Jarlsberg Land (Reinodden and Ahlstrandodden sections) and Dickson Land (Idodalen and Skansbukta A/B sections) (Fig. 1; Supplementary material 1, Fig. S1). The basal Vøringen Member, consistently composed of fossiliferous bioclastic limestones, is distinctly recognized in all the sections despite its regional variation in thickness. In comparison, the overlying strata demonstrate significant variations in both lithology and thickness among the studied sections, represented by biogenic chert, siliceous or calcareous shale, black shale, bioclastic limestone and glauconitic sandstone (Fig. 3). Detailed explanations of these sections are provided in Supplementary material 1.

In addition to the specimens that we collected from these eight localities, we have also examined some material housed at PMO. These specimens were collected from the Kapp Starostin Formation from several localities on Spitsbergen (e.g. Skansbukta, Kapp Wijk and Tolmodryggen) by various expeditions during the last century. As no details were provided regarding where precisely they were derived from within the formation, these materials were used only for the purpose of taxonomic comparison. Likewise, several spiriferellid specimens from the Hambergfjellet and Miseryfjellet formations in Bjørnøya, also housed and examined at PMO, are referred to in this study for taxonomic comparison due to their relatively good preservation, but their detailed stratigraphical positions within each of the formations are unknown.

Stratigraphy and fossil locality in Grinnell Peninsula of Devon Island

In addition to the fossils from Spitsbergen, several specimens of *Timaniella harkeri* were also examined. These were collected from GSC locality 26406, from the Lyall River section located on the Grinnell

Figure 3. Simplified stratigraphical columns of the Kapp Starostin Formation in Spitsbergen with occurrences of spiriferellid species. The correlation among the columnar sections is based on the lithology as well as on the whole brachiopod assemblages. The stratigraphical interval represented by the *Timaniella wilczeki–Arcullina polaris* assemblage corresponds to the Vøringen Member, the basal bioclastic limestone unit of the formation. The overlying beds of the formation are characterized by the dominance of *Spiriferella loveni*, which extends to the near top of the formation. These two spiriferellid assemblages are interpreted to denote cool- and cold-water conditions, respectively. **Abbreviations: M**, lime mudstone; **W**, wackestone; **P**, packstone; **G**, grainstone; **m**, mudstone; **ss**, siltstone; **fs**, fine sandstone; **ms**, medium sandstone; **cs**, coarse sandstone.

Peninsula of Devon Island, Arctic Canada, within the Sverdrup Basin (Fig. 1; Harker & Thorsteinsson 1960).

During the late Palaeozoic, the Sverdrup Basin was bound with North Greenland, Svalbard and the Barents Shelf to the east; together they formed the central part of the northern margin of Pangaea (Fig. 1). The Lyall River section represents a Carboniferous–Permian succession for the most proximal part in the southern margin of the basin (Figs 1, 2; Beauchamp & Thériault 1994; Beauchamp *et al.* 1998). According to Beauchamp & Thériault (1994), the section is composed of seven formations and GSC locality 26406 represents the Assistance Formation (Roadian) (Fig. 2). This formation in the section is dominated by unconsolidated sands, providing well-preserved marine fossils (Harker & Thorsteinsson 1960; Beauchamp & Thériault 1994). It is unconformably underlain by the bioclastic limestone of the Great Bear Cape Formation (Artinskian), whereas the glauconitic sandstone-dominated Trold Fiord Formation (Wordian to Lopingian?) conformably overlies. More details about the Lyall River section and GSC locality 26406 are available in Harker & Thorsteinsson (1960), Beauchamp & Thériault (1994) and Beauchamp *et al.* (1998).

Stratigraphy and fossil locality in the Kozhim River section, Subpolar Urals, Russia

A small spiriferellid brachiopod collection obtained from Permian strata in the Kozhim River section, Subpolar Urals, is also included herein (Figs 1, 2). The Kozhim River section presents extensive Palaeozoic (Ordovician–Permian) strata exposed along the Kozhim River through the Ural Mountains in north-west Russia (Iosifidi & Khramov 2013). The Permian deposits are well exposed downstream from Losinyi Island (Enokian *et al.* 1993; Chuvashov *et al.* 1993), ranging from the Asselian to, possibly, the Guadalupian (Fig. 2).

The lowermost Losinoostrovskaya Formation in the section extends stratigraphically from the Gzelian to the Sakmarian (Fig. 2) and is dominated by carbonate reef deposits (Enokian *et al.* 1993). According to Wahlman & Konovalova (2003), the lower part of the formation consists of fenestrate bryozoan-*Tubiphytes* cementstone bioherms whereas the upper part is predominated by *Palaeoaplysina*-phylloid algal bioherms. The Kosinskaya Formation (Sakmarian–Artinskian), composed of a siltstone-dominated lower unit and a sandstone-dominated upper unit, conformably overlies the Losinoostrovskaya Formation (Chuvashov *et al.* 1993). The subsequent Chernorechenskaya Formation (Artinskian–early Kungurian) comprises siltstones intercalated with sandstones, marls and limestones. The Kozhim Formation consists of alternating siltstones and sandstones, whereas the overlying Kozhim Rudnik Formation is dominated by sandstones (Chuvashov *et al.* 1993). Both the Kozhim and Kozhim Rudnik formations are fossiliferous, particularly in terms of brachiopods, bivalves and bryozoans. The boundary between these two stratigraphical units was proposed as an alternative global stratotype point dividing the Kungurian and Ufimian stages (lower boundary of the 'Upper Permian' in the Russian scheme) by Grunt *et al.* (1998). However, as the Ufimian Stage was correlated with the upper part of the Kungurian Stage under the International Stratigraphic Scale in Gradstein *et al.* (2004) (see Lozovsky *et al.* 2009), both of these formations are considered to be of Kungurian age (Fig. 2). The uppermost Intinskaya Formation (Roadian?) is also composed mainly of siltstones and sandstones, with some conglomerate layers (Chuvashov *et al.* 1993). Coal seams are intercalated in the upper part of the Kozhim Rudnik Formation and throughout the Intinskaya Formation. More details about the Kozhim River section are given in Enokian *et al.* (1993), Chuvashov *et al.* (1993), Grunt *et al.* (1998) and Shishlov & Zhuravlev (2001). In particular, Grunt *et al.* (1998, figs 25, 26) provided detailed whole columnar sections for both the Kozhim and Kozhim Rudnik formations.

Our spiriferellid specimens from this section were collected from Kungurian strata (Kozhim and Kozhim Rudnik formations) (Fig. 2). According to earlier brachiopod studies on the section (e.g. Grunt *et al.* 1998; Kalashnikov 1998), seven spiriferellid species have been recognized from these two formations: *Spiriferella saranae*, *S. gigantean*, *S. draschei*, *S. vojnovskii*, *S. wimani*, *Eridmatus talbeicus* and *Arcullina mica*. To this list, we now add at least two additional spiriferellid species (*Spiriferella* cf. *S. interplicata* and *S. loveni*; see also Fig. 2), based on our study of specimens collected from this section.

Biostratigraphy and age of spiriferellids from the Kapp Starostin Formation, Spitsbergen

The stratigraphy and age range of the Kapp Starostin Formation in Spitsbergen have been debated for several decades, due mainly to the scarcity of biostratigraphically important microfossils (e.g. conodonts, foraminiferans and palynomorphs). A few studies (Szaniawski & Małkowski 1979; Nakrem *et al.* 1992; Igo 1995; Buggish *et al.* 2001) have reported rare conodonts of Artinskian–Kungurian age from the Vøringen Member. The rather restricted faunule contains the stratigraphically important species *Neostreptognathodus pequopensis*, which has a late Artinskian distribution (Henderson *et al.* 2012; Henderson 2018). Based on the conodont occurrences, the deposition of the Vøringen Member can be reasonably considered to have commenced, at least, in the late Artinskian. By comparison, the biostratigraphy and age determinations for the upper units of the Kapp Starostin Formation are far less certain and remain a matter of continuous debate (see Shen *et al.* 2005, fig. 3), primarily due to the extreme scarcity and poor preservation of conodonts throughout the succession.

Several different views have been expressed with respect to the ages of the brachiopod assemblages in the Kapp Starostin Formation. According to Stepanov (1957; see also Gobbett 1964), all of the brachiopod assemblages from this formation could be considered a single fauna characterizing a crucial stage of the Permian timescale in the Arctic (Svalbardian Stage). On the other hand, following detailed field collecting and stratigraphical analysis, Nakamura *et al.* (1987, 1992) proposed a succession of five brachiopod biozones spanning the Kapp Starostin Formation, consisting of *Horridonia timanica* (Kungurian), *Paeckelmanella* sp. (*Waagenoconcha* sp. A in the old scheme) (Kungurian–Roadian), *Megousia weyprechti* (Roadian–Capitanian), *Pterospirifer alatus* (Capitanian) and *Haydenella wilczeki* (Capitanian) zones in ascending order. However, this biostratigraphical scheme was criticized by Stemmerik (1988), who concluded that the four upper brachiopod biozones actually represent local ecological communities with strong local environmental control rather than a succession of broad, basin-wide biostratigraphical horizons. At this point, it should be noted that Bond *et al.* (2015) recently recognized an extinction event corresponding to the boundary between the two uppermost brachiopod biozones in Nakamura *et al.* (1987, 1992), considered by these authors to represent the mid-Capitanian mass extinction. In their study, although Bond *et al.* (2015) regarded the brachiopods and bivalves from the uppermost *H. wilczeki* Zone of Nakamura *et al.* (1987, 1992) as a post-extinction recovery fauna, no details were offered about the pre-extinction faunas, presumably because the Vøringen Member was excluded from their study.

Nakrem *et al.* (1992) provided a comprehensive review of the Permian biostratigraphy of Svalbard based on all available fossil data (including brachiopods, bryozoans, conodonts, foraminifera and palynomorphs), suggesting that the Vøringen Member represents the late Artinskian–Kungurian whilst the upper members of the Kapp Starostin Formation would be of Kungurian–Wordian age. However, it is also noteworthy that both Nakamura *et al.* (1992) and Nakrem *et al.* (1992) pointed out the possibility that the uppermost part of the formation, a short stratigraphical interval characterized by condensed sedimentation and lacking well-preserved fossils, might represent the Lopingian.

In addition to biostratigraphy, chemostratigraphical approaches have been applied to the Kapp Starostin Formation, all in favour of a continuous succession between the Kapp Starostin Formation and the overlying Vardebukta Formation. Under this scenario, it would mean that at least the uppermost part of the Kapp Starostin Formation represents the late Changhsingian, and that the Permian–Triassic boundary could be located in the basal interval of the Vardebukta Formation (Gruszczyński *et al.* 1989; Wignall *et al.* 1998; Nakrem *et al.* 2008; Nabbefeld *et al.* 2010; Dustira *et al.* 2013; Bond *et al.* 2015; Grasby *et al.* 2016).

With the taxonomic revision carried out in this paper, the biostratigraphy of spiriferellids from the Kapp Starostin Formation appears to be straightforward, showing two distinct assemblages divided by the boundary between the basal Vøringen Member and the overlying unit (Fig. 3). The lower assemblage, confined to the Vøringen Member, is characterized by the occurrence of *Timaniella wilczeki*, in association with *Arcullina polaris* and, less commonly, *Spiriferella protodraschei*. In contrast, the younger assemblage is dominated by *S. loveni*, in terms of both stratigraphical occurrences and abundance. Although *S. loveni* is also present in the Vøringen Member of the Scheteligfjellet and Trygghamna sections in Oscar II Land (western part of Spitsbergen), there it was invariably found in the upper part of this member with very low abundance (relative to their abundance in overlying units). *Spiriferella draschei* is mostly common in the Vøringen Member, but also occurs in the upper layer of the Skansbukta B section (central Spitsbergen). Overall, our two-fold spiriferellid-based biostratigraphical subdivision of the Kapp Starostin Formation does not match with the general brachiopod biozonation scheme of Nakamura *et al.* (1987, 1992), although the lower assemblage characterized by *T. wilczeki* may be considered equivalent to the *H. timanica* Zone of Nakamura *et al.* (1987, 1992) as both are restricted to the Vøringen Member. It is also evident that our two assemblages are incongruent with the biostratigraphy of spiriferellid species presented by Bond *et al.* (2015).

The lower spiriferellid assemblage, from the Vøringen Member, seems to be well matched with the late Artinskian–Kungurian age generally suggested for the member. The two key species in this assemblage, *T. wilczeki* and *A. polaris*, exhibit nearly identical morphology to the same or closely related species from the Kungurian strata of northern Timan, Russia (see

Barchatova 1968, 1970; Kalashnikov 1998). Grunt *et al.* (1998, table 12) erected a more specific biozone with these two species representing the Solikamsk Horizon of the Ufimian Stage (here placed within the late Kungurian under the modern International Stratigraphic Scale) in the East European Platform, broadly supporting the Kungurian age of the assemblage. Specimens assignable to *A. polaris* have also been reported from the Artinskian–Kungurian strata in Yukon (Nelson & Johnson 1968). (Strictly speaking, the emergence of these species seemed to have been delayed in the more easterly located East European Platform compared to their occurrence in Svalbard and Yukon [Fig. 1], possibly due to the gradual eastward cooling progress across the northern margin of Pangaea during the Permian. See 'Morphological and ecological responses to climate changes', below, for further discussion.)

By comparison, the age of the *S. loveni*-dominated upper assemblage is less straightforward. This is, in part, because there are few other spiriferellid species co-occurring with *S. loveni*, and because this assemblage straddles a much thicker stratigraphical interval than does the lower assemblage (Fig. 3). According to our taxonomic revision and palaeobiogeographical data, *S. loveni* appears to be very common in numerous post-Artinskian deposits along the northern margin of Pangaea, in central East and North Greenland (Dunbar 1955, 1962), Arctic Canada and Yukon (Tschernyschew & Stepanov 1916; Harker & Thorsteinsson 1960; Waterhouse & Waddington 1982) and the Subpolar Urals (this study). Of these records, it needs to be pointed out that a large number of specimens previously assigned to '*S. keilhavii*' by Dunbar (1955), but here reassigned mainly to *S. loveni*, are known from the Lopingian strata of central East Greenland (both the Wegener Halvø and Schuchert Dal formations; see Fig. 2). These Greenland specimens might suggest that the youngest age for the *S. loveni*-dominated assemblage, and thus the near top of the Kapp Starostin Formation (Fig. 3), could be extended to the Lopingian (most likely, Wuchiapingian).

Revision of spiriferellid species from Svalbard and their macroevolution

Spiriferella keilhavii (von Buch, 1847), originally reported from the Miseryfjellet Formation, in Miseryfjellet of Bjørnøya (Figs 1, 2), has been poorly understood, due to the discrepancy between von Buch's original drawing (Fig. 4A, B) and his description of the species. Wiman (1914) commented that von Buch's drawing was constructed from multiple specimens and that the features illustrated in the drawing were not entirely consistent with the descriptions given by von Buch to the species. Consequently, this species has since been interpreted and defined variably by different researchers. In particular, it has been continually compared with other spiriferellid species reported from the Permian of Svalbard, including *Spirifer wilczeki* Toula, 1873, *Spirifer draschei* Toula, 1875, and *Spirifer parryana* (not Hall) Toula, 1875 (= *S. loveni* Diener, 1903) (Fig. 4; see Systematic palaeontology). Many previous works either considered these species to be varieties of *S. keilhavii* or partly synonymized them with it. As a result, these taxonomic treatments in most cases have considerably modified and confused the definition and identity of *S. keilhavii* as well as those of other related species.

Von Buch's original specimens were redrawn by Frech (1901) (reproduced here in Fig. 4C, D) and the figures demonstrate, similar to the lectotype designated herein, that *S. keilhavii* is characterized by the following morphological features: slightly transverse to isometric outline, narrow sulcus with costae, broadly plicate lateral slopes, low interarea, and low, anteriorly broadening fold with median groove. The probable topotype specimens (stored at PMO) are also consistent in these features and, furthermore, confirm additional characteristics of this species including seven or more plicae on each side of the ventral valve, strongly thickened ventral apical callus, and the absence of pseudodeltidium. The combination of all of these morphological features sufficiently supports the separation between *S. keilhavii* and other spiriferellid species. *Spirifer wilczeki* (Fig. 4K, L), which is here reassigned to *Timaniella* Barchatova, 1968, differs in its more transverse outline, more angular plication, and more distinct and posteriorly extending costation on the whole shell. *Spiriferella draschei* (Fig. 4I, J) is distinguished by its more elongate outline, a more strongly incurved ventral beak, high interarea, and a broad sulcus. *Spiriferella protodraschei*, a new species from the Vøringen Member erected in this study, is also separated from *S. keilhavii* in having the fold with an acute crest and more distinct costation on the lateral slopes.

Spiriferella loveni (Fig. 4E–H) seems to be the most closely related species to *S. keilhavii*. These two species share considerable morphological features, such as the narrow sulcus with two parallel median costae, broad plication on lateral slopes, lack of distinct costation on plicae, flattened fold, and no pseudodeltidium. Thus, they were considered conspecific in some previous studies (e.g. Wiman 1914; Dunbar 1955; Gobbett 1964). Nevertheless, our large collection of *S. loveni* (>200 specimens) shows their clear distinction in that the

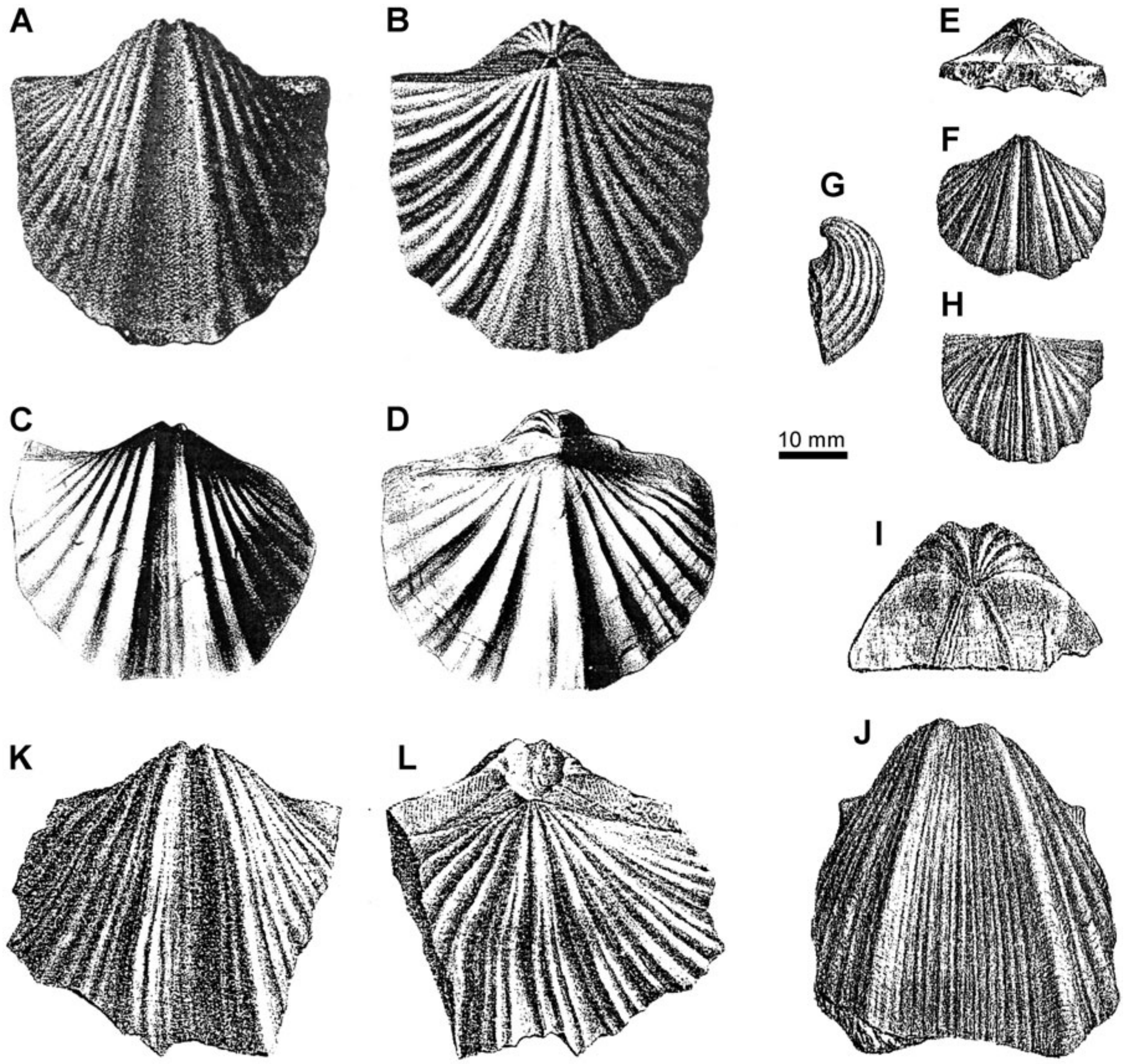

Figure 4. Original images of spiriferellid species from Svalbard. **A, B,** *Spirifer keilhavii* von Buch, 1847 (fig. 2b, 2a). **C, D,** *Spirifer keilhavii* re-drawn by Frech (1901, pl. 57c, fig. 1c, 1b). **E–H,** *Spirifer parryanus* (not Hall) Toula, 1875 (pl. 7, fig. 8b, 8a, 8c, 8d). **I–J,** *Spirifer draschei* Toula, 1875 (pl. 7, fig. 4a, 4c). **K–L,** *Spirifer wilczeki* Toula, 1873 (pl. 1, fig. 3a, 3b).

number of plicae in *S. loveni* (generally four to five, maximum six plicae on each side of ventral valve) is consistently less than that of *S. keilhavii* (seven or more, up to 10 on each side). Also, considering that, compared to the relatively wide distribution of *S. loveni* in the northern margin of Pangaea, genuine *S. keilhavii* seems restricted mostly to the Miseryfjellet Formation of Bjørnøya, it is plausible that *S. keilhavii* was evolved from *S. loveni* and was endemic to Bjørnøya. The only exception to this highly endemic distribution is the occurrence of a few specimens discovered in the Lopingian strata of central East Greenland. According to the description of Dunbar (1955, p. 141, pls 25–27), the majority of his '*S. keilhavii*' specimens have five or six plicae on each side (and, therefore, are assignable to *S. loveni*), whereas a small number of other shells possess seven or more plicae (possibly genuine *S. keilhavii*). It is therefore plausible that both *S. loveni* and *S. keilhavii* migrated southward through the Zechstein seaway to central East Greenland where they diversified and attained large populations during the Lopingian.

Phylogenetically meaningful characters of spiriferellid species have been identified through our detailed morphological examination and taxonomic revision. Of them, we here emphasize two characters that are significant in deciphering the phylogeny of spiriferellids as well as in aiding their taxonomic identification: (1) the development of pustules and (2) the development of delthyrial coverings. The presence of pustules, as a shell surface micro-ornamentation, has been known as one of

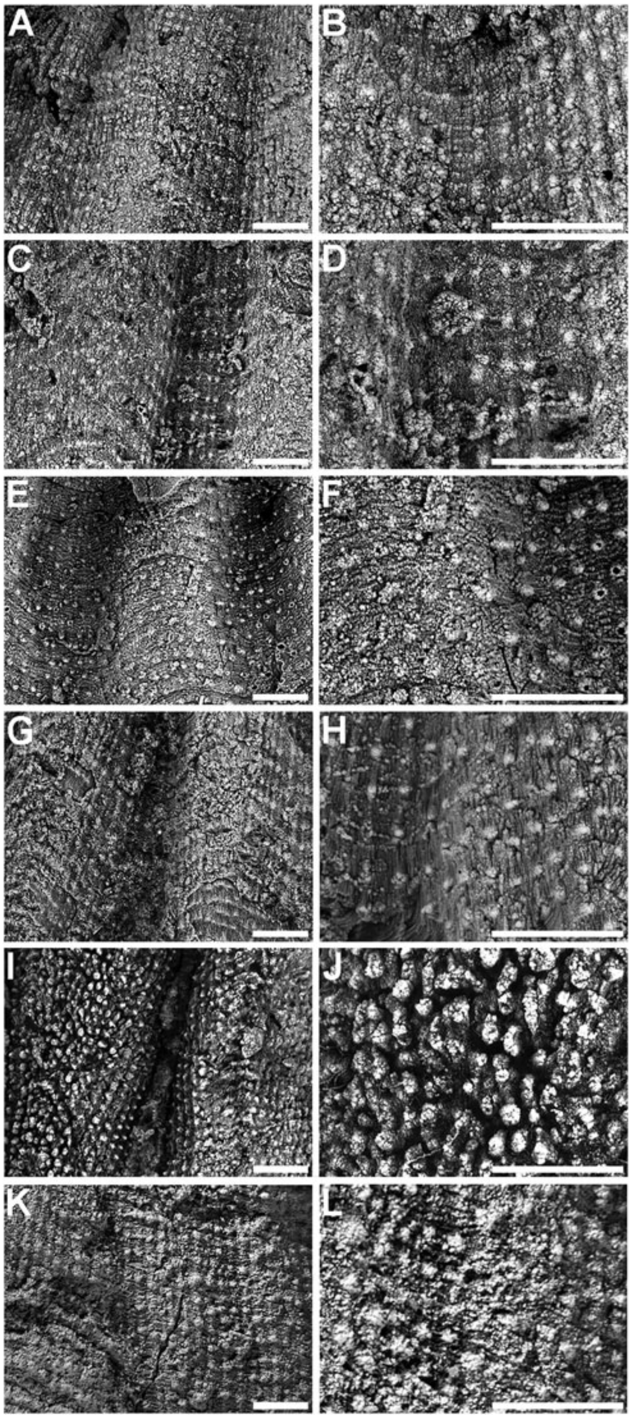

Figure 5. Shell micro-ornamentation of some Permian spiriferellid species from Spitsbergen and the Subpolar Urals. **A, B,** *Spiriferella protokeilhavii* sp. nov. Lee & Shi. **C, D,** *Spiriferella draschei* (Toula, 1875). **E, F,** *Spiriferella loveni* (Diener, 1903). **G, H,** *Timaniella wilczeki* (Toula, 1873). **I, J,** *Arcullina polaris* (Wiman, 1914). **K, L,** *Arcullina*? *enokiani* sp. nov. Lee & Shi. Scale bars: 1 mm.

the most representative characteristics in this group (Carter *et al*. 2006, p. 1805), but its intra- and inter-specific variations have been unclear. Based on careful observation of a large number of specimens with well-preserved original shell external surfaces, three different pustule arrangements are recognized. Each spiriferellid species generally bears only a single pustule pattern among the three, and the same or very similar development of pustules seems to be maintained among close relatives despite some modifications in shell macro-ornamentation. The pustules of two *Spiriferella* species, *S. protodraschei* (Fig. 5A, B) and *S. draschei* (Fig. 5C, D), are arranged along both capillae and growth lamellae, forming a reticulated structure that remarkably resembles the pustule arrangement of *T. wilczeki* (Fig. 5G, H). The shell surface of *S. loveni* is fully covered by same-sized pustules, but they are distributed dominantly along wavy growth lamellae (Fig. 5E, F). A comparable arrangement of pustules with that of *S. loveni* was noted in '*S. keilhavii*' from central East Greenland by Dunbar (1955, pl. 26, figs 9–11; see also Fig. 6), supporting their conspecific or very close relationship. On the other hand, the species of *Arcullina* Waterhouse, 1968 exhibit large granular pustules, densely distributed on the whole shell surface (Fig. 5I–L), which could imply a more distant relationship from the other spiriferellid species in Svalbard.

The delthyrium, as the gateway of the pedicle in a brachiopod shell, is open or variably closed in the spiriferellids. The common presence of delthyrial coverings in *Spiriferella* and allies has been recognized since early studies (e.g. Tschernyschew 1902), but their ontogenetic development, functional aspects and significance for phylogeny and taxonomy have only received rare attention (Cooper & Grant 1976, p. 2223; Waterhouse *et al.* 1978, p. 417), mainly due to their low preservation potential (see Shen *et al.* 2001). Notwithstanding the possible impact of preservation, two distinct types of delthyrial coverings with potential phylogenetic significance are identified and discussed here. The first type is characterized by the development of a pseudodeltidium, defined as a single convex plate developed from the apex of the delthyrium and extending anteriorly, covering the delthyrium either partially or completely (Williams & Brunton 1997). Waterhouse (2016, p. 13) claimed that this type of covering plate in the spiriferellids (as well as in all other groups of Spiriferida) is different in nature from the genuine pseudodeltidium structure of other brachiopod groups (Strophomenida, Productida and Orthotetida), thus proposing a replacement term, 'delthyrial cover plate'. However, the plate preserved in our specimens is, in general, very firmly attached to the interarea as an integral part and,

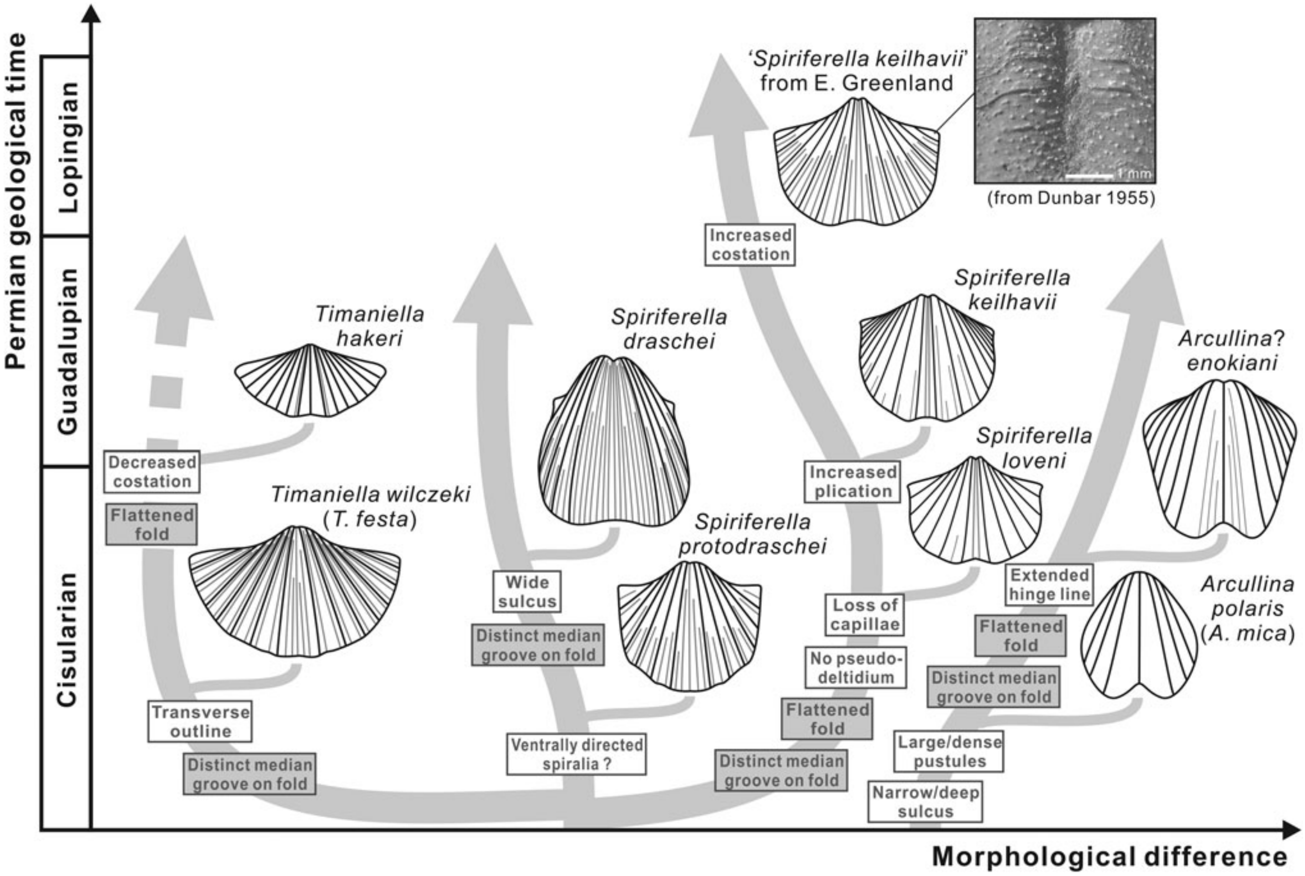

Figure 6. Hypothetical evolutionary pattern of some spiriferellid species in northern Pangaea during the Permian. Thick grey arrows indicate the phylogenetic stocks, each composed of closely related taxa. Text boxes explain the character transitions at the nodes of the phylogenetic tree (white box, homology; shaded box, homoplasy).

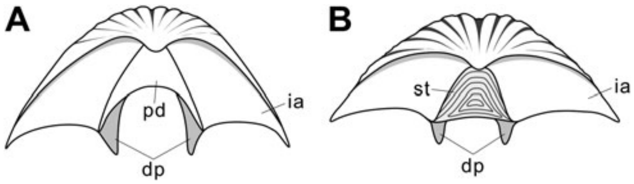

Figure 7. Two different types of delthyrial coverings recognized in Permian spiriferellid species in northern Pangaea. **A,** typical pseudodeltidium of *Arcullina polaris*. **B,** stegidia developed in *Spiriferella loveni* (the stegidia are reconstructed from serial sections of a well-preserved specimen). **Abbreviations: dp**, dental plates; **ia**, interarea; **pd**, pseudodeltidium; **st**, stegidia.

therefore, is here referred to as the pseudodeltidium (Fig. 7A). The pseudodeltidium is very common, particularly in species from the older strata in Svalbard, such as *S. protodraschei*, *S. draschei*, *T. wilczeki* and *A. polaris*. A rudimentary structure of the pseudodeltidium (confined to the apex of the delthyrium) has been detected rarely on the delthyrium of *S. loveni*.

The second type of delthyrial covering is considerably different from the pseudodeltidium of the first type. This structure is generally placed under the delthyrium, developed from each lateral margin of the delthyrium and connected medially. As the structure seems to be formed by a combination of several small platelets (Fig. 7B), it is here provisionally regarded as stegidia, although it is not exactly the same as the typical stegidia shown by Williams & Brunton (1997, fig. 320). The development of the stegidia can be seen exclusively in several specimens of *S. loveni* from the Kapp Starostin Formation of Spitsbergen. The majority of *S. loveni* specimens do not present any covering structure, similar to *S. keilhavii* from the Miseryfjellet Formation in Bjørnøya. However, as the intact preservation of delicate stegidia is known to be extremely rare (Waterhouse 2016, pp. 14–15), it is reasonable to assume that *S. loveni* would originally have possessed stegidia during at least part of their lifetime. Under this scenario, the distinct contrast in the development of the delthyrial covering among spiriferellid species could imply that the pseudodeltidium represents an ancestral trait to all the spiriferellid species in Svalbard, whereas the loss of the pseudodeltidium and development of the stegidia denotes a derived trait to the spiriferellid species that lasted until the Lopingian (*S. loveni* and, possibly, *S. keilhavii*). Features of the delthyrial coverings in each species are described and illustrated in more detail in the 'Systematic palaeontology' section.

After compiling and analysing a detailed data set of the morphological characteristics of spiriferellid species, we also made a preliminary phylogenetic reconstruction for Permian spiriferellid species from Svalbard and adjacent areas in northern Pangaea (Fig. 6). Several interesting features can be noted from this reconstruction. First, in spite of certain morphological distinctions between the typical *S. draschei* and the new species *S. protodraschei*, several transitional forms between them also existed, suggesting that these two species might have evolved from the same stock. Secondly, *Spiriferella loveni* and *S. keilhavii* together appear to form another distinct stock, separable from the *S. protodraschei–S. draschei* lineage in macro-morphological characters (e.g. the pattern of costation and development of delthyrial coverings) as well as in shell micro-ornamentation (arrangement of pustules). '*Spiriferella keilhavii*' reported from Lopingian strata in central East Greenland by Dunbar (1955) is here considered to be mostly derived from *S. loveni* through the increase of costation, probably representing the last survivors of the clade (Fig. 6). Thirdly, the morphological similarity between *Timaniella* and *Spiriferella* suggests their close ancestry. In particular, *T. wilczeki* seems to have branched out from the early ancestor of the *S. protodraschei–S. draschei* lineage by attaining a more transverse outline. *Timaniella harkeri* from Devon Island (Sverdrup Basin) may have evolved from the same stock by developing a more transverse and less costate shell (Fig. 6). However, this interpretation needs to be tested further, especially in regard to the micro-ornamentation on the shell surface. Finally, the stock represented by *Arcullina* has many unique morphological features not shared with the other spiriferellid lineages (e.g. narrow and deep sulcus, swollen pustules and extended ventral adminicula), likely suggesting that it separated from their common ancestor much earlier than the other stocks (Fig. 6).

With the phylogenetic reconstruction, we have also detected two phylogenetically less important characteristics (probable homoplasy) in spiriferellids; one feature is the development of a distinct median groove on the fold, and the other the formation of a flattened fold. Although these features may prove to be valuable for species-level taxonomy, it seems that they evolved independently in each stock (Fig. 6), possibly as a response to local environmental/ecological determinants. If so, this could indicate that ecological/environmental forces would have driven the evolution and innovation of the fold morphology of spiriferellids in at least the northern marginal shelf of Pangaea during the Permian. This inference is conjectural at this stage and will require comparative examination and verification through parsimony and/or Bayesian analyses in future.

Morphological and ecological responses to climate changes

It is known that, since the termination of the Late Palaeozoic Ice Age (LPIA), there were several climatic fluctuations through the Permian, and also that some biotas from mid- to high-latitudinal regions were influenced by these climatic changes (e.g. Shi & Waterhouse 2010; Waterhouse & Shi 2010). However, the northern marginal shelf of Pangaea appears to have experienced a progressive and sustained climatic shift (cooling) through the Permian (Beauchamp 1994; Beauchamp & Desrochers 1997; Stemmerik 1997, 2000; Blomeier *et al.* 2011). This progressive climatic transition has generally been explained by a combination of the continuous northward movement of Pangaea and the closure of the Ural seaway (Fig. 8; Beauchamp & Baud 2002; Stemmerik & Worsley 2005; Worsley 2008). A strong link between this climatic change and biotic responses has been drawn and demonstrated by the pronounced change from photozoan-dominated to heterozoan-dominated benthic faunas around the Artinskian across the northern marginal shelf of Pangaea (Stemmerik 1997; Ehrenberg *et al.* 2001; Hüneke *et al.* 2001; Beauchamp & Baud 2002; Reid *et al.* 2007; Blomeier *et al.* 2011). In contrast to the photozoan association containing warm-water components, such as colonial corals and fusulinids, the heterozoan-dominated fauna (composed mainly of brachiopods, bryozoans and siliceous sponges) is characterized by cool- to cold-water elements of the Boreal Realm. As a part of the climate-forced faunal transition, spiriferellid brachiopods also became explosively abundant and diverse in the northern margin of Pangaea from the late Cisuralian (Fig. 8B) and, subsequently, occupied a significant ecological niche under the cool to cold climatic regime, probably until the end Permian (Waterhouse & Waddington 1982; Shi *et al.* 1995; Shi & Grunt 2000; Reid *et al.* 2007).

In order to identify the detailed biotic responses of spiriferellids to the climatic cooling through the Permian, we examined the palaeogeographical distributions and shell ornamentation of a number of widely distributed spirfierellid species across the northern marginal shelf of Pangaea (Fig. 8). The results show that

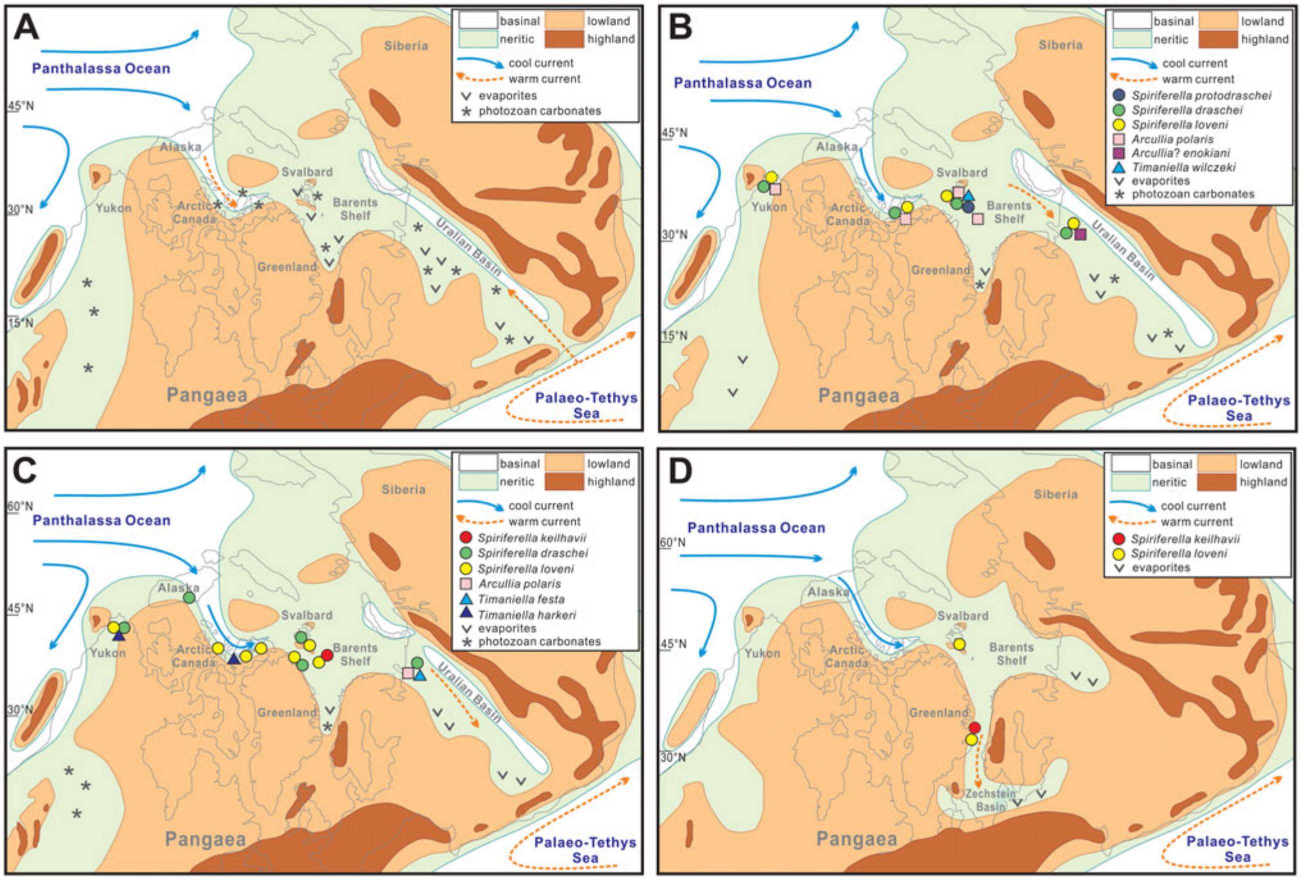

Figure 8. Palaeobiogeographical distributions of selected spiriferellid species in northern Pangaea throughout the Permian. **A,** Asselian–Sakmarian; **B,** Artinskian–early Kungurian; **C,** late Kungurian–Capitanian; **D,** Lopingian. Base map with evaporate and photozoan carbonate occurrences modified from Reid *et al.* (2007). Brachiopod occurrence data for Yukon from Nelson & Johnson (1968) and Waterhouse & Waddington (1982); for Alaska from Brabb & Grunt (1971); for Arctic Canada from Tschernyschew & Stepanov (1916), Harker & Thorsteinsson (1960), Waterhouse & Waddington (1982), Reid *et al.* (2007) and this study; for Greenland from Dunbar (1955, 1962); Svalbard from Wiman (1914) and this study; and for Urals from Tschernyschew (1902), Barchatova (1968), Kalashnikov (1998) and this study.

both the variation in costation pattern of spiriferellids and their species association closely tracked the change of habitat temperature. In general, the frequency of costation on spiriferellid shell surfaces tends to decrease with the advent of cold-water conditions. Spiriferellid species with numerous fine costae (e.g. *T. wilczeki* and *S. protodraschei*) are stratigraphically restricted to the Vøringen Member (late Artinskian–early Kungurian), representing a rather cool-water environment in Spitsbergen (Figs 3, 6, 8B), whereas the overlying members of the Kapp Starostin Formation (late Kungurian–Lopingian?) deposited in cold-water settings are dominated by *S. loveni*, having broad plicae with only a few costae (Figs 3, 6, 8C, D). To this end, we also note the reduction of costation in *T. harkeri* from the Assistance Formation (Roadian), which contrasts strongly with *T. wilczeki*. This difference might be explained by differential temperature regimes experienced by the two species of *Timaniella* at different times and different locations. Likewise, it is interesting to note that *S. loveni* from both the Wegener Halvø (Wuchiapingian) and Schuchert Dal (Changhsingian) formations of central East Greenland, located in lower palaeolatitudes, also tends to show more frequent costae than do conspecific specimens from the more northerly (colder) Spitsbergen localities (Figs 6 and 8D; see also Dunbar 1955). The reason why spiriferellid brachiopods tend to possess fewer plicae and costae in colder conditions or higher latitudes is not yet fully understood, but it may bear on the level of predation pressure in the environment. According to several previous studies (e.g. Leighton 1999; Dietl & Kelley 2001), the ribbing ornamentation (plicae and costae) of brachiopod shell surfaces may function as an anti-predatory defence device and would therefore vary in accordance with predation pressure. Using this scenario, the tendency of spiriferellids to become less fasciculate in colder conditions could be explained as representing a morphological adaptation to reduced predation pressure as the climate became colder. In this context, the ornamentation of *A. polaris* is notable because it lacks costae but has been found only in relatively warm environments. Without costae, this species would have been vulnerable to predation, especially in warmer conditions. On the other hand, this species possesses strongly swollen pustules on its shell surface (Fig. 5I, J), which may have functioned to hinder predators, in place of costae. In addition, the palaeogeographical distributions of spiriferellid species suggest that the Permian cooling, in general, gradually progressed eastward along the northern marginal shelf of Pangaea (from the Sverdrup Basin through Svalbard to the Urals). The representatives of cool climatic conditions (e.g. *A. polaris* and *T. wilczeki*) first occurred in Artinskian or even earlier times in western regions (including Svalbard) (Fig. 8B), whereas the corresponding species did not appear in the Urals until the late Kungurian (Fig. 8C). The absence of the *S. loveni*-dominated association in the deposits of the Urals might also indicate that the climatic condition in this region was relatively warm (compared to Svalbard and Greenland). A further line of evidence in support of the inferred north-westerly cooling trend in the northern margin of Pangaea comes from the sporadic appearance of spiriferellid-rich brachiopod associations in the Sakmarian strata of the Sverdrup Basin (Harker & Thorsteinsson 1960; Reid *et al.* 2007); these data possibly represent the earliest Permian cooling signal in north-western Pangaea, which evidently precedes the invasion of a similar fauna in Svalbard (no earlier than Artinskian).

On the other hand, Blomeier *et al.* (2011) explained that Permian cooling in the northern margin of Pangaea gradually extended from deep- to shallow-water environments. This implies that the discordance in the timing of spiriferellid associations among the different basins might be affected by bathymetric differences in depositional environments.

Concerning the global climatic pattern, several studies based on sections from the low-latitude Tethys regions have documented a significant warming trend from the Late Permian to the Early Triassic (e.g. Kearsey *et al.* 2009; Joachimski *et al.* 2012; Schobben *et al.* 2014), pointing to possible lethal warming as the main cause of the end-Permian mass extinction (Sun *et al.* 2012). However, the spiriferellid assemblages from the Kapp Starostin Formation do not show any signal of such a rapid warming trend, even in the specimens from the uppermost fossil-bearing horizon in Festningen (~10 m below the top of the formation). This discrepancy (from low-latitude Tethyan sections) may be explained either by (1) that the warming in the northern marginal shelf regions of Pangaea was not as pronounced as that in the Tethys regions, at least, during the Lopingian; or by (2) that the age for the uppermost part of the Kapp Starostin Formation is older than the Lopingian (which would imply that if high-latitude warming did occur during the Permian–Triassic transition, it would have occurred in the latest Lopingian or the earliest Triassic, slightly later than in the Tethys regions).

Systematic palaeontology

The classification of the Spiriferellidae adopted here generally follows Carter *et al.* (2006) and Gourvennec & Carter (2007). All morphological terms are in current use, as in Williams & Brunton (1997). Detailed information for each registered specimen (e.g. locality, horizon and size measurements) is provided in Supplementary material 2.

Order **Spiriferida** Waagen, 1883
Suborder **Spiriferidina** Waagen, 1883
Superfamily **Spiriferoidea** King, 1846
Family **Spiriferellidae** Waterhouse, 1968

Diagnosis. Shell outline considerably variable from elongate to transverse; ventral valve more convex and thicker than dorsal valve; lateral slopes commonly plicate, regularly or irregularly costate; sulcus and fold often distinctly defined; median furrow on fold variably developed; delthyrium open or occluded by variable delthyrial coverings, such as pseudodeltidium, deltidial plates, delthyrial plates and stegidia; pustules typical as micro-ornament, but absent in some taxa; dental plates strongly developed, with short to long adminicula; ventral umbonal region often greatly thickened.

Remarks. Spiriferellids have long been recognized owing to their distinctive morphology, wide distribution and abundance, particularly during the Permian. However, their intra-familial phylogeny and phylogenetic relationships with other spiriferide clades are still poorly defined, hampering a robust understanding of their phylogeny and classification. Waterhouse *et al.* (1978) summarized the overall evolutionary trends of spiriferellid species based on qualitative evidence, but since then many more taxa have been added to the family, underscoring a need for new analyses. Lee & Shi (2016) performed the first quantitative phylogenetic study of spiriferoid brachiopods using both cladistics and Bayesian analyses. Interestingly, their results showed that the phylogenetic position of spiriferellids is unstable, because they seem to either constitute the basal group of the spiriferoids as a whole or form a sister group to a large clade consisting of trigonotretids, spiriferines and imbrexiids.

Waterhouse (1968) first proposed the Subfamily Spiriferellinae with only two genera, *Spiriferella* Tschernyschew, 1902 and *Elivina* Frederiks, 1924, placing this subfamily in the Family Brachythyrididae. Later, Carter (1974) transferred Spiriferellinae into Spiriferidae, a view that has been followed by some later studies and also adopted in the revised Treatise for the classification of Spiriferoidea (Carter *et al*. 1994, 2006; Waterhouse 2004; Grunt 2006). Besides, some morphological similarities between the Spiriferellidae and Licharewiidae have been noted in some previous studies (Waterhouse 1968, 2004; Waterhouse & Waddington 1982; Shi & Waterhouse 1996), adding further uncertainty over the systematic position of *Spiriferella* and allies. However, the finding by Erlanger & Solomina (1989) that licharewiid shells are punctate supports a closer relationship of the licharewiids to punctate syringothyridoids than to impunctate spiriferoids.

Angiolini (2001) subdivided spiriferellids into two subfamilies, the Spiriferellinae and Hunzininae, based on the ratio of hinge width to shell maximum width, the lateral plications and the micro-ornamentation. Later, another subfamily, the Elivininae, was also proposed within the Spiriferellidae by Waterhouse (2004), grouping taxa with a narrow hinge line and without ventral umbonal thickening. All the spiriferellid species in the present study can be assigned to the Spiriferellinae. However, the phylogenetic significance of the characteristics defining the subfamilies has not been confirmed and, therefore, none of these subfamilies has been accepted in the revised Treatise (Carter *et al*. 2006; Gourvennec & Carter 2007).

On the other hand, Kalashnikov (1998) placed Trigonotretinae within Spiriferellidae, in contrast to Carter *et al*. (1994, 2006) who grouped the former together with the Neospiriferinae into Trigonotretidae. Kalashnikov's treatment might be supported by the study of Lee & Shi (2016, fig. 5) which showed a paraphyletic relationship between the spiriferellids and trigonotretines as one of the possible phylogenetic scenarios. However, the grouping of the Trigonotretinae with the Spiriferellidae also requires further testing, especially with respect to micro-ornamentaiton and detailed costation patterns.

Undoubtedly, the detailed characteristics of all spiriferellid taxa and their close allies (e.g. trigonotretines) still need to be described and more clearly defined, and only then could their phylogenetic relationships be properly tested and deciphered.

Genus ***Spiriferella*** Tschernyschew, 1902

Type species. *Spirifer saranae* de Verneuil, 1845, p. 169.

Remarks. As the name-bearing genus of the spiriferellid clade, *Spiriferella* is characterized by a number of highly distinctive morphological features, including: a commonly elongate outline, strongly plicate lateral slopes, a thick ventral apical callus formed by secondary shell thickening and small pustules on shell surface. These features together distinguish this genus from genera in other spiriferoid families.

In spite of the distinct morphology of this genus, the identity of its type species, *S. saranae*, is somewhat problematic (Waterhouse & Waddington 1982; Waterhouse 2004, 2016), particularly considering that the original types of the species as figured by de Verneuil (1845) are not consistent with the specimens assigned to the same species illustrated in Tschernyschew (1902). Unfortunately, this problem has been compounded by the fact that specimens figured not in de Verneuil (1845) but in Tschernyschew (1902) were considered the representatives of the type species in the revised Treatise (Carter *et al.* 2006, fig. 1198.1a–d).

We fully agree with Waterhouse (2004) that the dorsal fold with three distinct costae of the type specimen in de Verneuil (1845, pl. 6, fig. 15b) is considerably different from the simple dorsal fold with rounded crest figured by Tschernyschew (1902, pl. 40, fig. 7). The description of Tschernyschew (1902) seems to be based on the original material of de Verneuil (1845), mentioning the three costae on the dorsal fold of *S. saranae*. Therefore, it is assumed that Tschernyschew may have considered the different varieties of the dorsal fold a feature of intraspecific variation. However, after examining a large number of spiriferellid species and specimens, we consider the difference in fold (i.e. a dorsal fold with three distinct costae as in de Verneuil vs a smooth dorsal fold with rounded crest as in Tschernyschew) too great to be regarded as just intraspecific variation; instead, these differences strongly warrant the creation of separate species. Along these lines, Waterhouse & Waddington (1982, p. 19) proposed a new species, *S. barkhatovae* (or *S. barchatovae*), for two specimens illustrated in Tschernyschew (1902, pl. 12, fig. 4, pl. 40, fig. 7), and the species was later assigned to *Arcullina* by Waterhouse (2004, p. 200). Although Waterhouse (2004) regarded other specimens drawn in Tschernyschew (1902, text-figs 41–46) as *S. saranae*, their characteristics (e.g. solid pseudodeltidium and long ventral adminicula) resemble those of *Arcullina polaris* (see Wiman 1914, pl. 4, figs 13, 19, 20). Further, the median septum-like structure which was identified on the ventral floor of *S. saranae* by both Keyserling (1846) and Tschernyschew (1902) is observed in *A. polaris* (see below). All these features indicate that all the materials of Tschernyschew (1902) (and, possibly, those of Keyserling 1846) might represent the lineage of *Arcullina*, rather than that of *Spiriferella*. In order to clarify the diagnosis of the genus *Spiriferella*, the original material of de Verneuil (1845) has to be fully understood.

Several species of *Spiriferella* have been proposed and repeatedly reported from the Permian strata of Svalbard. However, for some of them their taxonomic identities remain unclear due to inconsistency in the descriptions and figures by different workers, compounded by inadequate preservation of the type material. We here attempt to revise all the known Permian spiriferellid species of Svalbard, based on large collections from Svalbard and adjacent regions, many of which are very well preserved, allowing us to document, clarify and illustrate some previously unknown or unclear morphological features. Of particular interest, as we have noted in the present study, the development of pustules as a shell surface micro-ornamentation seems to be a significant character with which to trace the phylogenetic relationships among spiriferellid species as well as to detect their taxonomic identities. In addition, the development of delthyrial coverings (e.g. pseudodeltidium and stegidia) is found to present an important phylogenetic signal in spiriferellids. As indicated by Waterhouse & Waddington (1982), morphological characteristics of the dorsal fold, such as its elevation and the development status of its median groove, are relatively stable within each species of *Spiriferella*, compared to the variation in outline and shell macro-ornamentation. However, it also needs to be noted that a similar transition of fold morphology has occurred independently in each of the spiriferellid clades (Fig. 6).

According to our revision here, *Spirifer keilhavii* von Buch, 1847, *Spirifer draschei* Toula, 1875, and *Spirifer loveni* Diener, 1903 (= *Spirifer parryanus* Toula, 1875) are retained within the genus *Spiriferella* although some modification of the species diagnoses is necessary, whilst *Spirifer wilczeki* Toula, 1873 is moved to *Timaniella* Barchatova, 1968. Meanwhile, *Spiriferina polaris* Wiman, 1914 had previously been proposed as the type species of another spiriferellid genus, *Arcullina*, by Waterhouse (1986).

Spiriferella keilhavii (von Buch, 1847)
(Figs 4A–D, 9A, 10)

1847 *Spirifer keilhavii* von Buch: 74, pl. 1, fig. 2a, b.

1901 *Spirifer keilhavii* von Buch; Frech: pl. 56c, fig. 1b, c.

1914 *Spiriferina keilhavii* (von Buch); Wiman: 36, pl. 2, figs 25–30; pl. 3, fig. 1.

1955 *Spiriferella keilhavii* (von Buch); Dunbar: 139, pl. 25, figs 4, 5, pl. 27, figs 6–9, 13, 14; *non* pl. 25, figs 1–3, 6–9, pl. 26, figs 1–11, pl. 27, figs 1–5, 10–11.

Diagnosis. Shell slightly transverse or isometric in outline, weakly to moderately convex. Lateral slopes gently steep, with seven or more plicae on each side of ventral valve. Ventral interarea low; delthyrium generally without pseudodeltidium. Sulcus generally narrow, distinctly defined near beak, with at least two costae divided by median groove. Fold low, broadening anteriorly; median groove on fold present, commencing at variable points. Lateral plication broad but marginal ones becoming much narrower, rarely branched. Ventral apical callus strongly thickened, burying adminicula.

Lectotype. According to Wiman (1914), the original figures of *S. keilhavii* von Buch, 1847 are composite drawings from several specimens (Fig. 4A, B). Two of the specimens of von Buch were re-drawn by Frech (1901), and Licharew & Einor (1939) selected the dorsal valve figured by Frech (1901, pl. 57c, fig. 1b; see also Fig. 4D) as the lectotype. However, the dorsal valve (MB.B.10546) is apparently missing (M. Aberhan, pers. comm. 2018) and, therefore, we here select the ventral valve (MB.B.10545) in Frech (1901, pl. 57c, fig. 1c; see also Figs 4C, 10A) as the lectotype.

Other material. Four ventral valves (PMO 226.005–226.008), all from the Miseryfjellet Formation in Miseryfjellet, Bjørnøya.

Description. Shell medium in size for genus, 45.5 mm wide and 43.5 mm long in lectotype (Fig. 9A). Outline slightly transverse or isometric with width/length ratio ranging from 1.038 to 1.268 (Supplementary material 2). Hinge line equal to maximum width; cardinal extremities obtuse.

Ventral valve weakly to moderately convex, with gently incurved beak. Ventral interarea low and slightly concave; denticles absent. Delthyrium triangular with delthyrial angle of around 40°; no pseudodeltidium. Sulcus generally narrow and shallow, originating from ventral beak, anteriorly forming 'V'-shaped commissure line, with at least two costae divided by distinct median groove. Ventral lateral slopes gently steep, having seven or more plicae on each side; plicae distinct, rounded to nearly flat, broad but marginal ones becoming very narrow, infrequently costate; costae on lateral slopes indistinct, mostly limited to anterior part if present. Micro-ornamentation absent or not preserved.

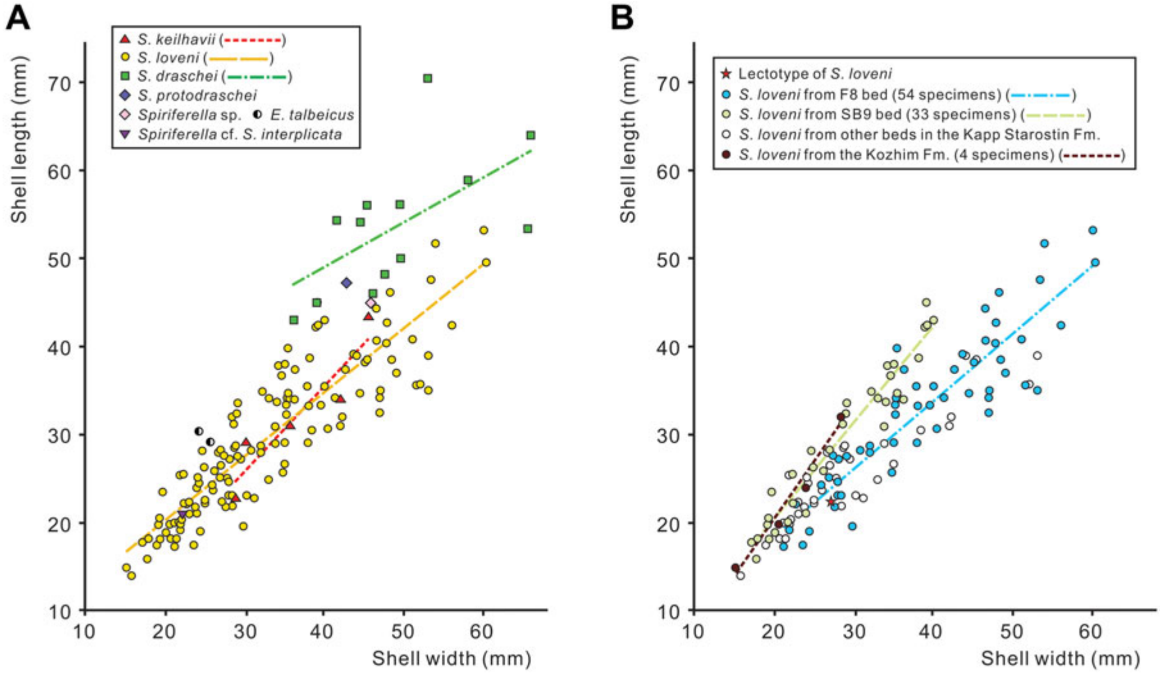

Figure 9. Shell measurements of *Spiriferella* and *Eridmatus* species (fragmentary shells and only dorsal valves were excluded; see also Supplementary material 2). **A,** variations in all of the *Spiriferella* and *Eridmatus* species included in this study. **B,** intraspecific variation in *S. loveni.*

Ventral interior with dental plates composed of thickened dental flanges and slightly diverging adminicula; ventral apical callus strongly developed, burying adminicula. Ventral muscle area longitudinally elliptical, medially bounded by thin low ridge.

Remarks. The identity of *S. keilhavii* has been poorly understood, since its type specimens were originally reported from the Miseryfjellet Formation in Bjørnøya by von Buch (1847). Although von Buch's original drawings (Fig. 4A, B) seemed to show the morphological details, they were inconsistent with his description of the species. Later it was also revealed that each of the drawings was constructed from multiple specimens (see Wiman 1914) that were possibly non-conspecific. Thus, without any precise revision of *S. keilhavii*, it has been vaguely compared with other spiriferellid species reported from the Permian of Svalbard, including *S. wilczeki* Toula, 1873, *S. draschei* Toula, 1875, and *S. parryana* (not Hall) Toula, 1875 (Fig. 4E–L). These species were either considered varieties of *S. keilhavii* (Licharew & Einor 1939; Stepanov 1937) or partly synonymized with it (Dunbar 1955; Gobbett 1964; Waterhouse & Waddington 1982). These taxonomic treatments, in most cases, have brought more confusion regarding the identity of *S. keilhavii* as well as other related species. In order to provide an improved understanding of these species, including their precise diagnoses and distinctions from one another, we have re-examined all the accessible type materials as well as their original figures and descriptions, in conjunction with our own spiriferellid collections from Svalbard.

Both the re-drawings of von Buch's original specimens by Frech (1901) (Fig. 4C, D) and the lectotype specimen (Fig. 10A) demonstrate that *S. keilhavii* is characterized by several distinct morphological features of its ventral valve, such as the isometric outline with abtuse cardinal extremities, relatively low ventral interarea, narrow sulcus with distinct costae, broad plication on lateral slopes, and rare costation on plicae. The additional materials inspected in this study (Fig. 10B–F) as well as the specimens illustrated by Wiman (1914, pl. 2, figs 25–29, pl. 3, fig. 1), all collected from the Miseryfjellet Formation, consistently present all of these characteristics. Further, these probable topotype materials confirm a couple of additional features: the general lack of pseudodeltidium on the delthyrium and seven or more plicae on each side of the ventral valve. Although one of Wiman's (1914, pl. 2, fig. 26) conspecific specimens seems to have a pseudodeltidium mostly covering the delthyrium, the majority of *S. keilhavii* specimens evidently lack the structure on the delthyrium (Fig. 10G; see also Wiman 1914, pl. 2, figs 28, 29). Shen *et al.* (2001) commented that the preservation of

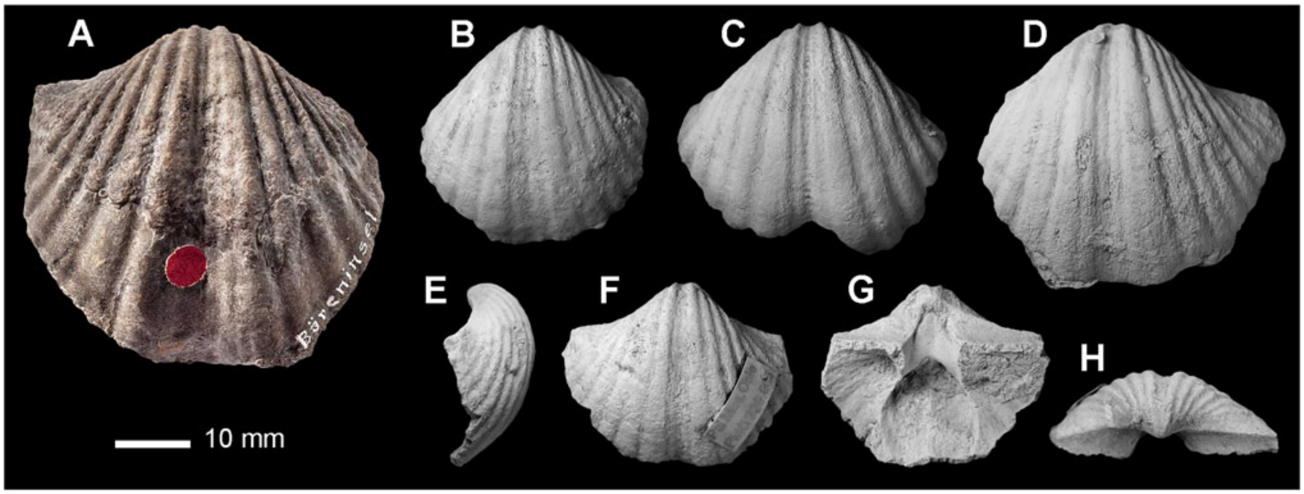

Figure 10. *Spiriferella keilhavii* (von Buch, 1847) from the Miseryfjellet Formation in Bjørnøya. **A,** lectotype (selected here), MB.B.10545, ventral view of a ventral valve (photographed by Martin Aberhan); **B,** PMO 226.006, ventral view of a ventral valve; **C,** PMO 226.008, ventral view of a ventral valve; **D,** PMO 226.007, ventral view of a ventral valve; **E**–**H,** PMO 226.005, lateral, ventral, dorsal and posterior views of a ventral valve.

pseudodeltidium in *Spiriferella* is variable. However, according to our observation, the pseudodeltidium of spiriferellid species from Svalbard, when present, seems to be very firmly attached to the ventral interarea, with a general consistency in each species. Therefore, it is unlikely that an absence of pseudodeltidium in *S. keilhavii* would be caused simply by post-mortem loss.

On the other hand, the features of the dorsal valve in Frech's (1901) re-drawings (Fig. 4D) seem to be somewhat problematic. The dorsal valve is characterized by plicae branching off in the anterior part of the valve as well as by possessing a weakly developed median groove on the fold. Unfortunately, apart from this redrawn dorsal valve, there were no other dorsal valves illustrated or referred to in Frech's study that showed this combination of characters. The dorsal valve of a well-preserved shell figured by Wiman (1914, pl. 2, fig. 26) differs from the type material in both its simple plicae and the distinct median groove on the fold, although the characteristics of the ventral valve are well matched with those of the type specimen. A few Greenland specimens figured by Dunbar (1955) also exhibit the branching pattern of plicae in the anterior part of the shell and all of them have a distinct median groove on the fold. On the basis of these observations, we here consider that the morphological disparity in the dorsal valve represents intraspecific variations within *S. keilhavii*. In spite of these variations, all the dorsal valves are semicircular in outline and share a low, anteriorly broadening fold, pointing to a strong conspecific relationship. Notably, intraspecific variation in the plication patterns is not limited to this species, as comparable variations have also been observed in some other spiriferellid species (e.g. *S. draschei* and *S. loveni*).

Based on the re-examination and subsequent taxonomic revision of *S. keilhavii*, we conclude that this species is sufficiently distinguished from all of the other spiriferellid species in Svalbard. *Timaniella wilczeki* differs in its more transverse outline, more angular plication, and more numerous and posteriorly extending costation on the whole shell. *Spiriferella draschei* is distinguished by its more elongate outline, more strongly incurved ventral beak, high ventral interarea, and much broader sulcus. *Spiriferella protodraschei*, a new species discovered from the Vøringen Member in this study, is similar to *S. keilhavii* in having the relatively narrow sulcus with a few costae, but it is distinguished by the narrower fold with a sharp crest as well as by the more frequent and distinct costation on lateral slopes. *Spiriferella keilhavii* seems to mostly resemble *S. loveni* in having a narrow sulcus, broad plication on lateral slopes and flattened dorsal fold, and in generally lacking a psuedodeltidium, which seem to suggest that they are phylogenetically close (see Fig. 6). However, these two species are clearly distinguished by the number of plicae on the ventral valve: *Spiriferella loveni* has four to six plicae on each side of the ventral valve, whereas *S. keilhavii* consistently bears seven or more (up to 10) plicae on each side.

Our newly refined definition of *S. keilhavii* restricts its palaeogeographical distribution and stratigraphical range, mostly to the late Kungurian Miseryfjellet Formation of Bjørnøya, although a considerable number of shells from the Cisuralian to Lopingian deposits from various places had been assigned to this species. The only occurrence of *S. keilhavvi* outside of Bjørnøya is a few specimens with seven or more plicae, figured by Dunbar (1955, pl. 25, figs 4, 5, pl. 27, figs 6–9, 13, 14) as *S. keilhavii*, from the Lopingian deposits of central East Greenland. At this point, it should be noted that the other specimens figured by Dunbar as *S. keilhavii* do not belong to this species and, instead, should be assigned to *S. loveni*, as discussed below. Obviously, these two species are very similar in morphology, and *S. loveni* is generally older than *S. keilhavii*. It is therefore possible that *S. keilhavii* evolved from an isolated population of *S. loveni* restricted to Bjørnøya at some stage in the late Cisuralian (Fig. 6).

Occurrence. Miseryfjellet Formation (late Kungurian) in Bjørnøya; Wegener Halvø (Wuchiapingian) and Schuchert Dal (Changhsingian) formations in central East Greenland.

Spiriferella loveni (Diener, 1903)
(Figs 4E–H, 5E, F, 7B, 9, 11–13)

1875 *Spirifer parryanus* Toula (*non* Hall, 1858): 256, pl. 7, fig 8a, b.

1903 *Spirifer loveni* Diener: 17.

1914 *Spirifer draschei* Toula; Wiman: 38, pl. 3, fig. 11; *non* pl. 2–10, figs 12–26.

1916 *Spiriferella parryana* (Toula); Tschernyschew & Stepanov: 82, pl. 11, fig. 4, pl. 12, figs 1–3.

1931 *Spiriferella parrayana* (Toula); Frebold: 18, pl. 5, figs 5, 6, 6a.

1937 *Spiriferella keilhavii* var. *parryana* (Toula); Stepanov: 147, pl. 8, figs 10, 11.

1937 *Spiriferella parryana* (Toula); Frebold: 45, pl. 11, fig. 6.

1937 *Spiriferella saranae* (de Verneuil); Frebold: 45, pl. 11, figs 7, 8.

1955 *Spiriferella keilhavii* (von Buch); Dunbar: 139, *non* pl. 25, figs 1–3, 6–9, pl. 26, figs 1–11, pl. 27, figs 1–5, 10, 11; *non* pl. 25, figs 4, 5, pl. 27, figs 6–9, 13, 14.

1960 *Spiriferella saranae* (de Verneuil) *sensu alto*; Harker & Thorsteinsson: 71, pl. 22, figs 4–8; *non* pl. 22, figs 1–3, pl. 23, figs 3, 4, 8.

1962 *Spiriferella* (?) *parryanus* (Toula); Dunbar: 9, pl. 1, figs 11–15.

1964 *Spiriferella* aff. *interplicata* (Rothpletz); Gobbett: 155, pl. 20, figs 4–6.

1968 *Spiriferella rajah* (Salter) subsp. A; Nelson & Johnson: 731, pl. 94, figs 7–9, 12; *non* pl. 94, figs 1–6, 10–11, 13–15, pl. 96, fig. 10.

1982 *Spiriferella*? *loveni* (Diener); Waterhouse & Waddington: 22, pl. 6, figs 1, 2; *non* pl. 5, figs 2–17.

1982 *Spiriferella leviplica* Waterhouse & Waddington: 26, pl. 7, figs 5–11.

1992 *Spiriferella saranae* (de Verneuil); Nakamura, Tazawa, & Kumon: pl. 4, figs 2, 5.

1992 *Spiriferella* sp. Nakamura, Tazawa, & Kumon: pl. 5, fig. 10.

Nomenclature. This species was originally named *Spirifer parryanus* by Toula (1875). However, as indicated by Diener (1903, p. 17), this name was already occupied by a brachiopod species that Hall (1858) proposed from the Devonian of Iowa. Diener thus renamed the species *Spirifer loveni*.

Diagnosis. Shell slightly transverse to elongate in outline, commonly with shortly alate cardinal extremities in adult stage. Delthyrium covered by stegidia but commonly not preserved, very rarely with rudimentary pseudodeltidium. Sulcus narrow, generally with a pair of median costae bounded by a median groove. Ventral lateral slopes with four to six plicae on each side. Fold low but well delimited, with generally wide and deep median groove commencing from dorsal beak. Plication broad and rounded, commonly simple but rarely unequally branched. Microornamentation with pustules arranged mainly along growth lamellae; capillae generally indistinct or absent. Dental plates composed of moderately thickened dental flanges and short adminicula.

Lectotype and paralectotypes. Toula (1875) proposed the present species, illustrating two specimens collected from Lovénberg in Spitsbergen, one ventral valve and one dorsal valve. After our inspection of the original material at NHMW, we can confirm that Toula's original figures were composite drawings from multiple specimens. We here select a ventral valve that is the most similar to the original illustration (Toula 1875, pl. 1, fig. 8a–c) as the lectotype (NHMW 1875/0041/0022; Fig. 12C– E) among the remaining syntype materials. Two other syntype specimens (NHMW 2017/0120/0001 [ventral valve] and NHMW 2017/0120/0002 [dorsal valve]; Fig. 12A–C, F, G) are here designated as paralectotypes.

Other material. One hundred and seventy-four specimens from the Kapp Starostin Formation in Spitsbergen (PMO A9883–9884, PMO 227.415, NMV P340298–340461, KOPRIF10003–10009), comprising five conjoined shells, 137 ventral valves and 32 dorsal valves; a conjoined shell from the Miseryfjellet Formation in Bjørnøya (PMO 226.013); five ventral valves from the Kozhim Formation in Subpolar Urals (NMV P340462–340466); additionally, more than 100 unregistered specimens were also examined.

Description. Shell variable in size, 27.3 mm wide and 23.1 mm long in lectotype, but reaching to 60 mm in width and 50 mm in length in largest material (Fig. 9). Outline generally pentagonal, with width/length ratio of 0.838–1.520; lateral profile ventribiconvex. Hinge line straight, mostly coincident with greatest width; cardinal extremities variable, but generally shortly alate in adult stage. Shell material strongly thickened in posterior of shell but thinning laterally and anteriorly.

Ventral valve variably convex, commonly with high convexity in large shell; umbonal region swollen, incurved, with maximum convexity. Ventral interarea low to moderately high (occupying around one-fifth to one-quarter of valve length), apsacline, horizontally and/or vertically striated; delthyrium triangular, mostly with delthyrial angle of 40–60°, frequently covered by stegidia or very rarely by rudimentary pseudodeltidium; stegidia placed below delthyrium, composed of several small platelets developing from each lateral margin of delthyrium and being connected medially (Figs 7B, 11B–E). Sulcus shallow to moderately deep, narrow between beak and mid-valve but anteriorly broadening, forming widely 'V'-shaped commissure line, mostly with a pair of median costae, occasionally bearing very weak additional lateral costae; median costae nearly parallel, slightly rounded, bounded by median groove starting near beak. Lateral ventral slopes with normally four to five plicae (never more than six) on each side; plicae, well rounded but flattening laterally, much broader than interspaces, originating from beak, generally simple but occasionally branched or costate on middle to anterior part of valve.

Dorsal valve mostly much less convex and thinner than ventral valve, with maximum convexity on umbonal region. Fold moderately wide, low, relatively angular, very distinctly divided by median groove, often having additional pair of lateral grooves on anterior part of valve, sometimes with weakly traced costae anteriorly; median groove deep, anteriorly broadening, originating from dorsal beak. Lateral plicae on dorsal valve more angular than those on ventral valve, with narrower interspaces, sometimes bearing only anteriorly developed weak costae.

Whole shell surface covered with fine growth lamellae and pustules; growth lamellae densely distributed, becoming more distinct anteriorly, wavy particularly on anterior of shell; pustules 0.06–0.20 mm in diameter, arranged mainly along growth lamellae, 10–15 pustules per 1 mm^2 on mid-valve (Fig. 5E, F); capillae generally less distinct, eventually disappearing in stratigraphically younger specimens.

Ventral interior with strongly thickened apical callus occupying considerable space under delthyrium; teeth strongly developed, supported by dental plates; dental plates composed of moderately thickened dental flanges and relatively short adminicula; ventral adminicula almost buried by shell thickening. Ventral muscle field relatively rounded and longitudinally oriented, occupying one-third to more than half of valve length, slightly elevated above valve floor, having very slender adductor scars medially and broad diductor scars laterally with vertical striation, posteriorly bounded by apical callus and adminicula; vascular markings radially developed, laterally and anteriorly surrounding muscle field, bearing numerous distinct pits.

Dorsal interior with sockets opened laterally; ctenophoridium small, transversely elliptical, without elevation, bearing more than 30 platelets (Fig. 11D); spiralia developed laterally, with around 14 whorls on each side (Fig. 11G–U).

Remarks. *Spiriferella loveni* is one of the most abundant brachiopod species in the Kapp Starostin Formation (Fig. 3). This species, represented by numerous shells (about 300 specimens in total), exhibits a considerable degree of both palaeogeographical (palaeoenvironmental) and stratigraphical (temporal) variation. Significantly, the width/length ratio of our specimens from the two most *S. loveni*-abundant horizons (F8 unit in the Festningen section and SB9 unit in the Skansbukta B section; see Fig. 3 and Supplementary material 2) demonstrates a plausible separation of two populations; the population from SB9 is more elongate in outline compared to specimens from F8 (Fig. 9B). This variation is likely to have been caused by environmental differences, especially in the type of substrate, as the F8 unit is composed of a limestone facies whereas the SB9 unit comprises a shale facies. In addition, the shell convexity and thickness of plicae are somewhat variable even in populations from the same horizon. Nevertheless, *S. loveni* still bears considerable morphological consistencies, which include two parallel median costae in the sulcus, generally simple plication on lateral slopes, and a low fold with a distinct median groove. These consistent characteristics sufficiently support the notion of a single species, also providing a strong distinction from the other spiriferellid species from Svalbard and adjacent regions.

In many previous works, *S. loveni* has been considered a junior synonym of *S. keilhavii* (e.g. Wiman 1914; Dunbar 1955; Harker & Thorsteinsson 1960; Gobbett 1964). Undoubtedly, these two species are morphologically very similar, suggesting their phylogenetic closeness (see Fig. 6), but differences are also very obvious, especially in terms of the number of plicae on lateral slopes. All of the specimens of *S. loveni* from Svalbard have four to six plicae on each side of the ventral valve, without exception. In contrast, the specimens of *S. keilhavii* reported from the type locality in Bjørnøya are

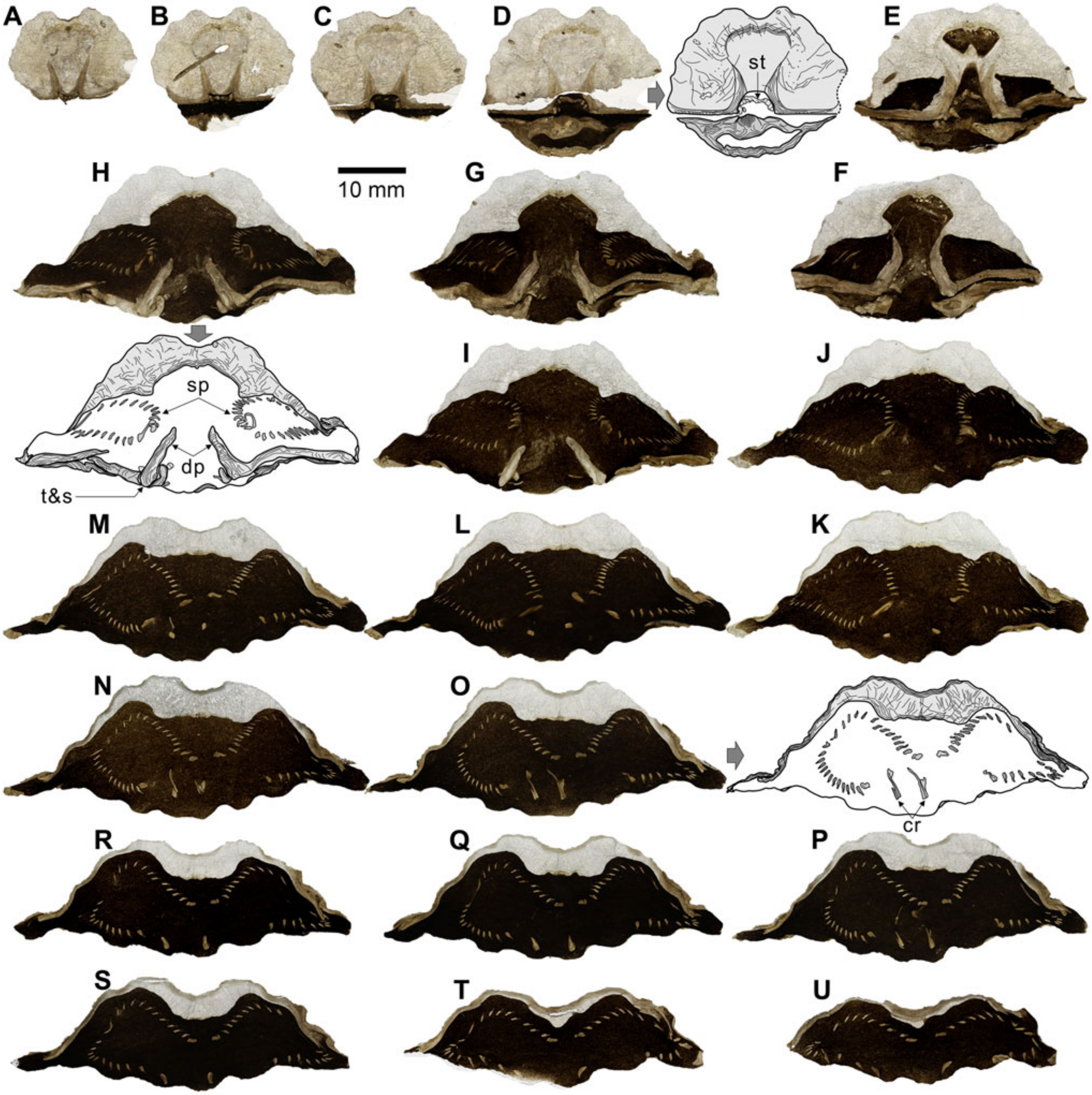

Figure 11. Serial sections of *Spiriferella loveni* (Diener, 1903), NMV P340298. The interval between adjacent sections is approximately 1 mm. **Abbreviations: cr**, crura; **dp**, dental plates; **sp**, spiralia; **st**, stegidia; **t&s**, tooth and socket.

consistently characterized by seven or more plicae, having very thin plication on the lateral margins. It is on this basis that we consider the specimens figured by Dunbar (1955, p. 141) from central East Greenland as *S. keilhavii* as belonging to two separate but related species: those with seven or more plicae (Dunbar 1955, pl. 25, figs 4, 5, pl. 27, figs 6–9, 13, 14) should be retained within this species, but the remaining specimens (Dunbar 1955, pl. 25, figs 1–3, 6–9, pl. 26, figs 1–11, pl. 27, figs 1–5, 10, 11) should be reassigned to *S. loveni* in consideration of their fewer (less than seven) and less fasciculate plicae.

The micro-ornamentation pattern of *S. loveni* is also distinguishable from those of most other spiriferellid species. In general, the pustules of spiriferellids are developed on the junctions of growth lamellae and capillae (Fig. 5A–D, G–L). However, in *S. loveni* the pustules are arranged solely along the growth lamellae (Fig. 5E, F),

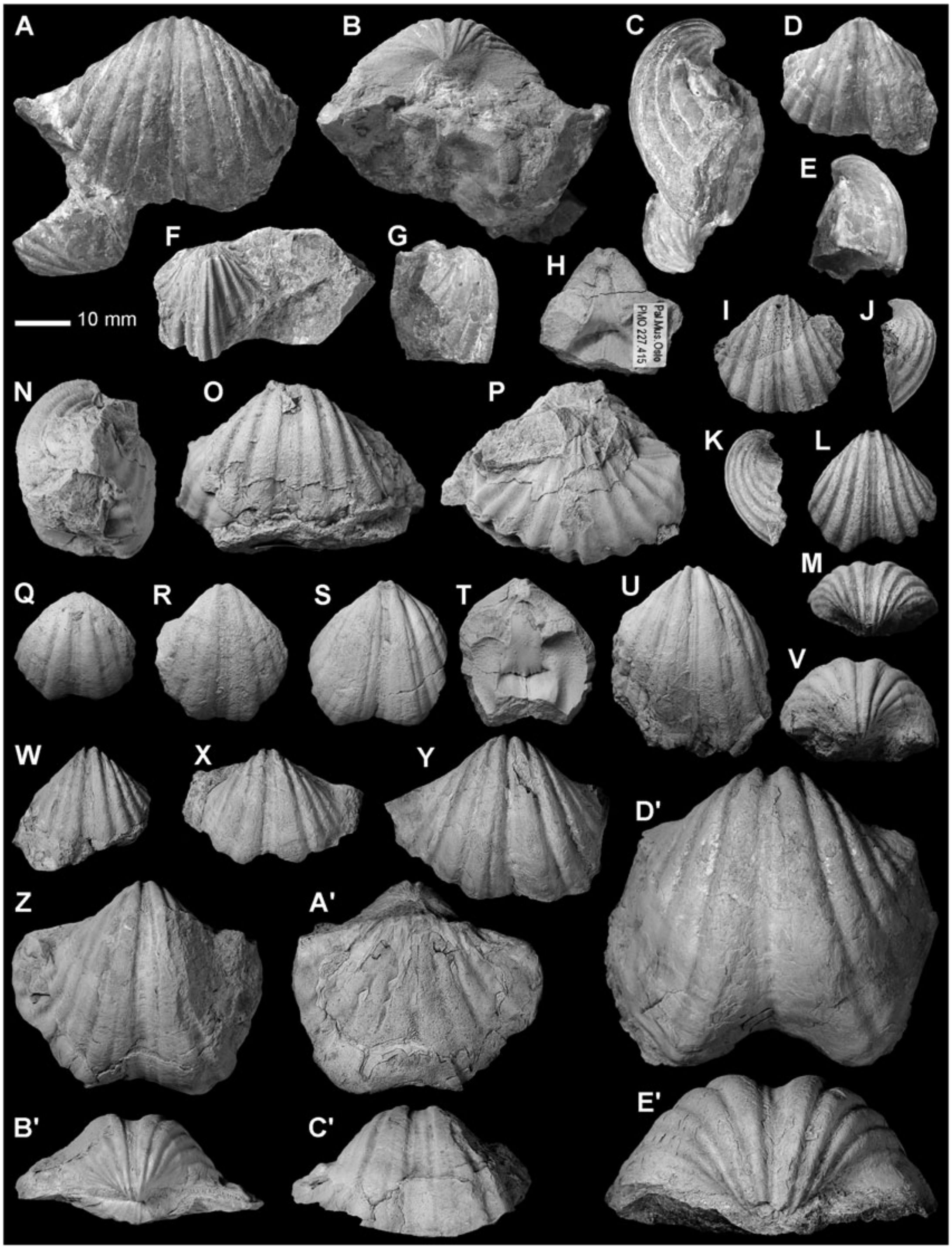

Figure 12. *Spiriferella loveni* (Diener, 1903) from the Kapp Starostin Formation in Spitsbergen (**A**–**M, W**–**E'**), the Miseryfjellet Formation in Bjørnøya (**N**–**P**) and the Kozhim Formation in the Subpolar Urals (**Q**–**V**). **A**–**C,** paralectotype, NHMW 2017/0120/0001, ventral, dorsal and lateral views of a ventral valve; **D, E,** lectotype (selected here), NHMW 1875/0041/0022, ventral and lateral views of a ventral valve; **F, G,** paralectotype, NHMW 2017/0120/0002, dorsal and lateral views of a dorsal valve; **H,** PMO 227.415, dorsal view of a ventral valve; **I, J,** PMO A9884, ventral and lateral views of a ventral valve; **K, M,** PMO A9883, lateral, ventral and posterior views of a ventral valve; **N, P,** PMO 226.013, lateral, ventral and dorsal views of a conjoined shell; **Q,** NMV P340464, ventral view of a ventral valve; **R,** NMV P340463, ventral view of a ventral valve; **S, T,** NMV P340462, ventral and dorsal views of a ventral valve; **U, V,** NMV P340466, ventral and posterior views of a ventral valve; **W,** NMV P340315, ventral view of a ventral valve; **X,** NMV P340316, ventral view of a ventral valve; **Y,** NMV P340320, ventral view of a ventral valve; **Z**–**C',** NMV P340298, ventral, dorsal, posterior and anterior views of a conjoined shell; **D', E',** NMV P340325, ventral and posterior views of a ventral valve. The lectotype and paralectotypes (**A**–**G**) were photographed by Andreas Kroh.

Figure 13. *Spiriferella loveni* (Diener, 1903) from the Kapp Starostin Formation in Spitsbergen. **A–C,** NMV P340399, ventral, lateral and posterior views of a ventral valve; **D, E,** NMV P340314, ventral and posterior views of a ventral valve; **F, G,** NMV P340409, ventral and anterior views of a ventral valve; **H, I,** NMV P340408, ventral and posterior views of a ventral valve; **J, K,** KOPRIF10007, ventral and posterior views of a ventral valve; **L,** NMV P340299, dorsal view of an internal mould of a conjoined shell; **M,** NMV P340308, latex cast of an internal mould of a ventral valve; **N–P,** NMV P340412, ventral, dorsal and posterior views of a ventral valve; **Q, R,** NMV P340419, ventral and posterior views of a ventral valve; **S, T,** NMV P340416, ventral and anterior views of a ventral valve; **U,** NMV P340379, ventral view of a posteriorly broken ventral valve; **V, W,** NMV P340429, posterior and ventral views of a ventral valve; **X–Z,** NMV P340300, ventral, dorsal and lateral views of an internal mould of a conjoined shell; **A', B',** NMV P340420, lateral and ventral views of a ventral valve; **C',** NMV P340459, dorsal view of a dorsal valve; **D',** NMV P340302, dorsal view of a conjoined shell; **E'–G',** NMV P340301, ventral, dorsal and anterior views of an internal mould of a conjoined shell; **H',** NMV P340435, dorsal view of a dorsal valve; **I',** NMV P340448, dorsal view of a dorsal valve; **J', K',** NMV P340436, dorsal and posterior views of a dorsal valve.

losing the capillae particularly in the specimens from stratigraphically upper horizons. As the shells from the lower horizons (including the Vøringen Member) have the pustules developed along both the growth lamellae and capillae, the modification of micro-ornamentation is seen as a morphological feature obtained within the species. The conspecific specimens from the younger (Lopingian) strata in central East Greenland also display pustules mostly arranged along growth lamellae (Dunbar 1955, pl. 26, figs 9–11; see also Fig. 6), further supporting the assignment of these specimens to *S. loveni*. Likewise, the specimens assigned to *S. loveni* from the older (Kungurian) strata in the Subpolar Urals also show relatively distinct capillae (Fig. 12Q–V).

In addition, *S. loveni* is characterized by the loss of pseudodeltidium and development of another type of delthyrial covering. The presence of a solid pseudodeltidium is common in the majority of spiriferellid species in Svalbard (e.g. *S. draschei*, *S. protodraschei*, *A. polaris* and *T. wilczeki*), possibly as an ancestral characteristic. In contrast, the pseudodeltidium is very rarely observed in *S. loveni*. Even when the structure is present, it appears rudimentary (developing as a tiny plate at the apex of the delthyrium), compared to the relatively large pseudodeltidium in other species. Instead, a stegidia-like structure that is located under the delthyrium and composed of several platelets has been observed from a few well-preserved specimens of *S. loveni*. This structure medially extends from each lateral margin of the delthyrium, forming a complete covering within the delthyrium (Figs 7B, 11B–E). The delthyrium of *S. keilhavii* is also represented by the general absence of pseudodeltidium, but similar stegidia have yet to be found.

Waterhouse & Waddington (1982, p. 22) reported *S. loveni* from the Permian deposits of Arctic Canada, including some specimens with variably costate shell surfaces within the species. The specimens bearing well-developed costae are here excluded from *S. loveni* (see the synonym list), because typical *S. loveni* is only weakly fasiculate. Further, Waterhouse & Waddington (1982, p. 28) proposed the new species *S. leviplica*, defining it mainly with a few simple lateral plicae and a low fold with a distinct median groove. However, these characteristics are well matched with those of typical *S. loveni* and, therefore, *S. leviplica* is here considered a junior synonym of *S. loveni*. Gobbett (1964) described *Spiriferella* aff. *interplicata* (Rothpletz, 1892) from the upper part of the Kapp Starostin Formation in Spitsbergen, but this species appears to be a juvenile representative of *S. loveni*, as also pointed out by Waterhouse & Waddington (1982, p. 25). Nakamura *et al*. (1992) reported *S. saranae* and *Spiriferella* sp. from the Kapp Starostin Formation, but all of them present the morphological characteristics of *S. loveni*. *Spiriferella borealica* Kalashnikov, 1998 from the Talata Formation (Kungurian) in Pai-Khoy Range (north Russia) resembles *S. loveni* in its relatively small shell, shortly alate cardinal extremities, and simple costae, but the former species has a narrower sulcus and weakly developed lateral plicae.

Occurrence. Kapp Starostin Formation (late Artinskian–Lopingian?) in Spitsbergen; Miseryfjellet Formation (late Kungurian) in Bjørnøya; Kim Fjelde Formation (Kungurian–Capitanian) in Amdrup Land, north-east Greenland; Wegener Halvø (Wuchiapingian) and Schuchert Dal (Changhsingian) formations in east Greenland; Great Bear Cape (Artinskian), Assistance (Roadian), Degerbö ls, Van Hauen (Guadalupian), and Trold Fiord (Wordian–Wuchiapingian) formations in Canadian Arctic Archipelago; Middle Recessive (Sakmarian?–Artinskian) and Tahkandit formations (Kungurian–Guadalupian) in Yukon; Kozhim Formation (Kungurian) in Subpolar Urals.

Spiriferella draschei (Toula, 1875)
(Figs 4I, J, 5C, D, 9A, 14–16)

?1855 *Spirifer keilhavii* von Buch; Salter: 386, pl. 36, figs 9, 10; *non* pl. 36, fig. 11.

1875 *Spirifer draschei* Toula: 239, pl. 7, fig. 4a–c.

1914 *Spirifer draschei* Toula; Wiman: 38, pl. 3, figs 3–10, 12–26; *non* pl. 3, figs 2, 11.

1916 *Spiriferella draschei* (Toula); Tschernyschew & Stepanov: 82, pl. 9, fig. 2a, b.

1939 *Spirifer* (*Spiriferella*) *rajah* Salter var. *saranaeformis* Frdericks; Licharew & Einor: 149, pl. 25, figs 1, 4.

1960 *Spiriferella keilhavii* (von Buch); Harker & Thrsteinsson: 72, pl. 22, figs 9, 10, pl. 23, figs 1, 2.

1962 *Spiriferella draschei* (Toula); Dunbar: 8, pl. 2, figs 11–14.

1964 *Spiriferella draschei* (Toula); Gobbett: 154, pl. 20, fig. 7.

1968 *Spiriferella saranae* (de Verneuil); Nelson & Johnson: 729, pl. 93, figs 1, 2; *non* pl. 93, figs 3–10, pl. 96, fig. 9.

1968 *Spiriferella rajah* (Salter) subsp. A; Nelson & Johnson: 731, pl. 94, figs 1–6, 10, 11, 13–15, pl. 96, fig. 10; *non* pl. 94, figs 7–9, 12.

1971 *Spiriferella draschei* (Toula); Brabb & Grant: 17, pl. 2, figs 26–28, 34, 35.

1972 *Spiriferella draschei* (Toula); Ifanova: 136, pl. 11, figs 4–7.

1982 *Spiriferella keilhavii* (von Buch); Waterhouse & Waddington: 28, pl. 6, figs 5–14; *non* pl. 4, fig. 15, pl. 6, figs 3, 4.

1990 *Spiriferella draschei* (Toula); Kalashinikov: pl. 5, fig. 3.

1998 *Spiriferella draschei* (Toula); Kalashinikov: 59, pl. 18, figs 2, 3.

2008 *Spiriferella keilhavii* (von Buch); Angiolini & Long: 93, fig. 9A–H.

2008 *Spiriferella loveni* (Diener); Angiolini & Long: 96, figs 9I, J, 10A.

2008 *Eridmatus* sp. Angiolini & Long: 96, fig. 10B–F.

Diagnosis. Shell medium to large for genus, commonly elongate in outline, with strongly incurved ventral beak. Lateral slopes steep, with weakly costate plicae. Ventral interarea generally high, delthyrium commonly covered by pseudodeltidium. Sulcus relatively wide, anteriorly extensively broadening, bearing single median costa and several lateral costae. Fold narrow, with distinct median groove starting from dorsal beak and extending anteriorly. Dental plates relatively high, composed of strongly thickened dental flanges and short adminicula. Ventral apical callus strongly developed. Ventral muscle platform elevated.

Lectotype. Gobbett (1964) selected a single specimen (ventral valve) collected from Akseløya in Spitsbergen and illustrated by Toula (1875, pl. 7, fig. 4a–c) as the lectotype of *S. draschei*. According to our inspection of the single syntype specimen stored at NHMW, Toula's original illustrations appear to be composite drawings. However, as the illustrated features are matched with the characteristics of the syntype specimen (NHMW 1875/0041/0020; Fig. 15A–D), it is here considered as the lectotype.

Other material. Fifteen specimens, all from the the Kapp Starostin Formation in Spitsbergen (PMO A26116, PMO 234.049–234.052, NMV P340467–340473, KOPRIF10010–10012), comprising two conjoined shells and 13 ventral valves.

Description. Shell medium to large for genus, 39.0 mm wide and 45.0 mm long in lectotype, 36.1–58.1 mm in width and 43.0–70.5 mm in length (Fig. 9A). Outline mostly elongate, with width/length ratio reaching 0.752 in most elongate specimen; lateral profile strongly ventribiconvex. Maximum width generally located at middle of shell length; hinge line slightly narrower than maximum width, normally with obtuse cardinal extremities. Shell material strongly thickened, particularly in ventral umbonal area.

Ventral valve moderately to strongly convex, with maximum convexity on umbonal region; ventral beak strongly incurved. Ventral interarea generally high (occupying around one-fifth to one-quarter of valve length) and concave, bearing weakly developed horizontal striations. Delthyrium triangular, with delthyrial angle of 50– 60°, largely covered by pseudodeltidium (Fig. 14G–J). Sulcus broad, shallow to moderately deep, starting anterior to beak, quickly broadening anteriorly to form transversely extended 'V'-shaped commissure line, ornamented by single median costa and 10 or more lateral costae; median costa narrow to broad, distinctly developed, originating near beak; lateral costae less distinct, branching on middle to anterior of valve. Ventral lateral slopes relatively steep, with five to six pairs of plicae; plicae distinct, broad, weakly rounded, with narrow interspaces; costae weakly developed, only distinct on anterior of valve.

Dorsal valve weakly convex, much thinner than ventral valve, with maximum convexity on umbonal region. Fold narrow, low to moderately high, relatively angular, with costate lateral sides (four costae in each side), divided by distinct median groove commencing from dorsal beak and anteriorly extending. Dorsal lateral slopes nearly flat, ornamented by four to six simple plicae on each side of valve; dorsal plicae narrower than ventral plicae, rarely branched, with interspaces of similar width.

Micro-ornamentation composed of numerous concentric growth lamellae, capillae and pustules; pustules minute, 0.05–0.15 mm in diameter; growth lamellae and capillae forming reticulated structure, bearing 15–20 pustules per 1 mm^2 on intersections of mid-valve (Fig. 5C, D). Shell material strongly thickened in posterior part but thin in lateral and anterior of valve.

Ventral interior with strong teeth supported by largely thickened dental plates; dental plates relatively high, composed of swollen dental flanges and relatively short adminicula; ventral adminicula fully buried by apical callus. Ventral muscle platform considerably elevated.

Dorsal interior with rounded ctenophoridium; spiralia generally developed posterolaterally.

Remarks. *Spiriferella draschei* is characterized by an elongate outline with maximum width at the mid-valve, a high interarea, a broad sulcus with numerous costae, and a narrow fold with a distinct median groove, though the width of costae appears to be variable among individuals. In addition, all of our specimens assigned to *S. draschei* consistently exhibit a median costa within the sulcus that is more distinct than its lateral costae. The presence of a well-defined median costa was also expressed in the original figure of Toula (1875, pl. 7, fig. 4a; see also Fig. 4J), and it seems to be uniformly developed in most specimens from the Kapp Starostin Formation in Spitsbergen. The micro-ornamentation of *S. draschei* is represented by growth lamellae and capillae that together form a reticulate structure from which

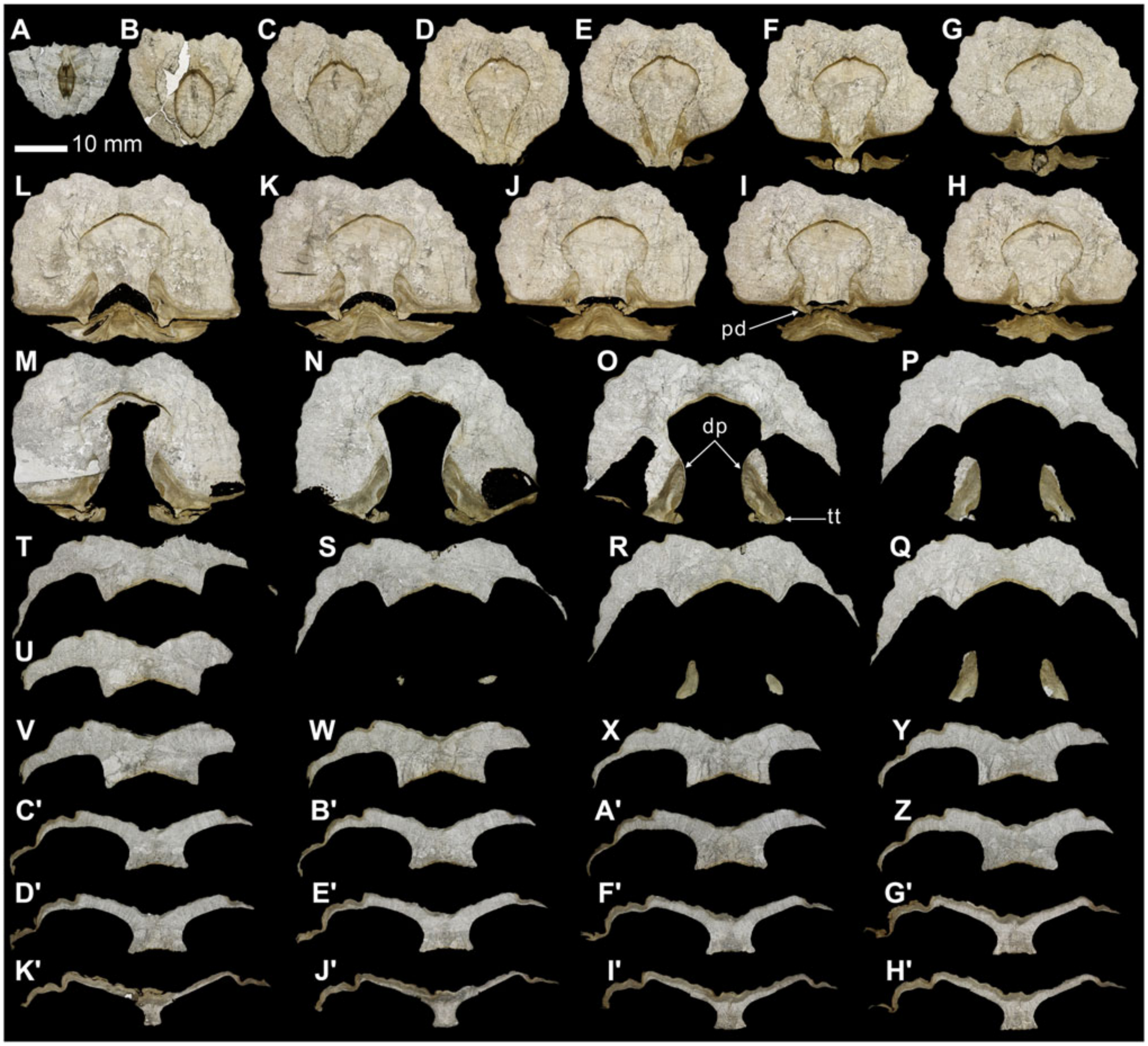

Figure 14. Serial sections of *Spiriferella draschei* (Toula, 1875), NMV P340468. The interval between adjacent sections is approximately 1 mm. **Abbreviations: dp**, dental plates; **pd**, pseudodeltidium; **tt**, tooth.

minute pustules arise at the junctions (Fig. 5C, D). This micro-ornamentation feature is evidently shared with *S. protodraschei* and *T. wilczeki* (Fig. 5A, B, G, H), supporting a close relationship among these species (Fig. 6).

Similar to the case of *S. loveni*, *S. draschei* has often been synonymized with *S. keilhavii*. However, *S. draschei* is distinguished from *S. keilhavii*, as it is from *S. loveni*, by its more elongate outline, strongly incurved ventral beak, high interarea, and broad sulcus. A considerable number of spiriferellid specimens from the Permian of Arctic Canada were previously assigned to *S. keilhavii* by Harker & Thrsteinsson (1960) and Waterhouse & Waddington (1982). Many of these specimens are characterized by an elongate outline, a broad sulcus with numerous fine costae, and a relatively narrow fold with a distinct median groove, all of which are also characteristics of *S. draschei* (see the synonymy list). The Canadian specimens differ slightly from the typical *S. draschei* from Spitsbergen in having more frequently branched lateral plicae on the dorsal valve, but this subtle alteration could be considered intraspecific variation. The similar branching pattern on the dorsal plicae is also observed in *S. draschei* from the Kozhim

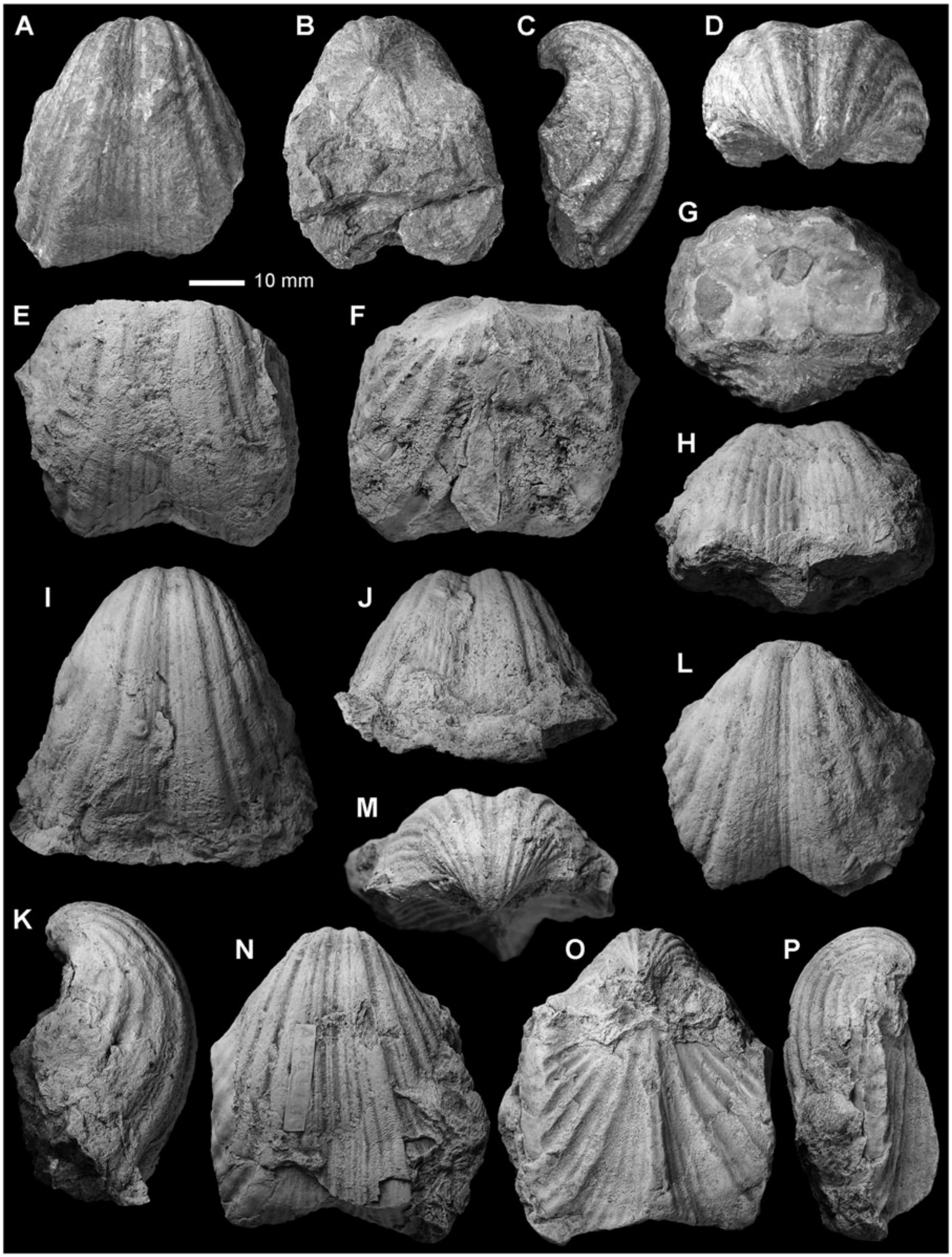

Figure 15. *Spiriferella draschei* (Toula, 1875) from the Kapp Starostin Formation in Spitsbergen. **A**–**D,** lectotype, NHMW 1875/0041/0020, ventral, dorsal, lateral and posterior views of a ventral valve (photographed by Andreas Kroh); **E**–**H,** PMO 234.049, ventral, dorsal, posterior and anterior views of a conjoined shell; **I**–**K,** PMO 234.050, ventral, anterior and lateral views of a ventral valve; **L,** PMO 234.051, ventral view of a ventral valve; **M**–**P,** PMO A26116, ventral, dorsal and lateral views of a conjoined shell.

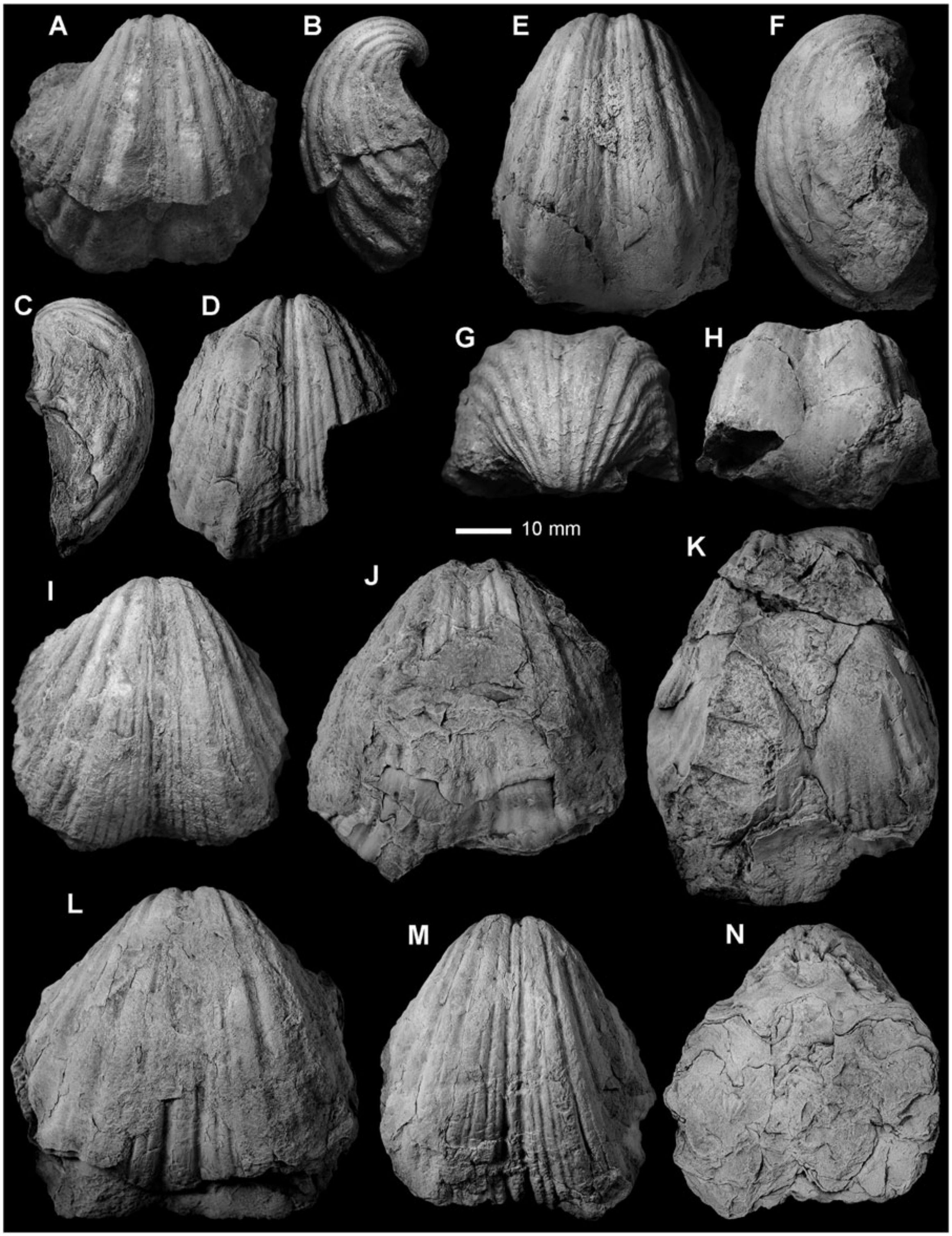

Figure 16. *Spiriferella draschei* (Toula, 1875) from the Kapp Starostin Formation in Spitsbergen. **A, B,** KOPRIF10010, ventral, and lateral views of a ventral valve; **C, D,** NMV P340471, lateral and ventral views of a ventral valve; **E–H,** PMO 234.052, ventral, lateral, posterior and anterior views of a ventral valve; **I,** KOPRIF10011, ventral view of a ventral valve; **J,** NMV P340469, ventral view of a ventral valve; **K,** NMV P340473, ventral view of a ventral valve; **L,** NMV P340470, ventral view of a ventral valve; **M, N,** NMV P340468, ventral and dorsal views of a ventral valve.

Rudnik Formation in the Subpolar Urals (Kalashnikov 1990, pl. 5, fig. 3b).

Angiolini & Long (2008) identified an elongate *Spiriferella* form from the Vøringen Member in central Spitsbergen as *S. keilhavii*. However, these specimens seem to be more similar to *S. draschei* in having numerous costae on a wide sulcus and relatively high interarea, as well as a distinct median groove on the fold. Additionally, other specimens figured as *S. loveni* and *Eridmatus* sp. by Angiolini & Long (2008) similarly demonstrate a strong morphological resemblance to *S. draschei*, having a distinct median costa on the sulcus and a weakly convex dorsal valve with a narrow fold. *Spiriferella rajah* var. *saranaeformis* from the Sedovskaya Formation (Sakmarian?) of northern Novaya Zemlya shown in Licharew & Einor (1939) is likewise assigned to *S. draschei* as these species share an elongate outline, a relatively broad sulcus with costation, and a high interea.

Eridmatus erjakhensis Kalashnikov, 1998 from the Talata Formation (Kungurian) in the Pai-Khoy Range, Russia, resembles *S. draschei* in the elongate outline, high interarea, distinct median costa and less distinct lateral costae on the sulcus, and narrow fold with a deep median groove. But *E. erjakhensis* is distinguished by its deeper and more anteriorly extending sulcus as well as by its smaller shell size. The morphological resemblance between these two species might suggest that *S. draschei* is more closely related to *Eridmatus*. However, the status of *Eridmatus* remains problematic as its identity as a separate genus has been questioned by Waterhouse & Waddington (1982, p. 29).

Two spiriferellid subspecies from the Permian of Yukon (*S. rajah* subsp. A and *S. rajah* subsp. B), reported by Nelson & Johnson (1968), are both comparable with *S. draschei* in outline and costation pattern, but their dorsal fold lacks a median groove that is distinctly present in *S. draschei*. This comparison may imply that the fold morphology is easily modified in some spiriferellid lineages. If so, it is likely that *S. draschei* evolved from another *Spiriferella* species with a narrower sulcus and weak median groove on the fold (most probably *S. protodraschei*) (Fig. 6).

Occurrence. Kapp Starostin Formation (late Artinskian–Capitanian) in Spitsbergen; Kim Fjelde Formation (Kungurian–Capitanian) in Amdrup Land, north-east Greenland; Great Bear Cape (Artinskian), Assistance (Roadian), and Trold Fiord (Wordian–Wuchiapingian) formations in the Canadian Arctic Archipelago; Middle Recessive (Sakmarian?–Artinskian) and Tahkandit formations (Kungurian–Guadalupian) in Yukon and Alaska; Kozhim and Kozhim Rudnik formations (Kungurian) in Subpolar Urals; Sedovskaya Formation (Sakmarian?) of Novaya Zemlya.

Spiriferella protodraschei sp. nov. Lee & Shi
(Figs 5A, B, 9A, 17, 18A–G)

Etymology. Latin, *proto-* (primitive) and *draschei*, referring to this species being a more primitive form of *S. draschei*.

Diagnosis. Shell slightly transverse, with strongly ventribiconvex lateral profile. Ventral interarea very low; delthyrium mostly covered by pseudodeltidium. Sulcus narrow and shallow, with a few timid costae. Ventral lateral slopes steep, with four to five plicae on each side. Fold narrow, with slightly angular crest; median groove less distinctly developed on fold crest. Lateral plication rounded to slightly angular, unequally costate; costae mostly limited to middle to anterior of shell. Micro-ornamentation with numerous small pustules developed along both growth lamellae and capillae. Dental plates relatively high; ventral apical callus strongly thickened. Ctenophoridium relatively narrow; spiralia ventrally directed.

Holotype. Conjoined shell collected from the Vøringen Member of the Kapp Starostin Formation in the southern part of Dickson Land, central Spitsbergen (NMV P340474; Fig. 18A–E). The locality section (Skansbukta A section in this study) is exposed along a small creek that is directed south-easterly from Høgskulefjellet. It is also south-westward around 1 km from the western border of Skansbukta (see Supplementary material 1, Fig. S5). The Vøringen Member of the section forms a cliff about 5 m high (at GPS point 78.50397°N, 16.00434°E). The holotype specimen was serially thin sectioned to identify its internal structure, and all of the thin-sections (Fig. 17) are currently stored at NMV P.

Other material. A fragmentary ventral valve from the Vøringen Member of the Kapp Starostin Formation in Idodalen, Spitsbergen (NMV P340475).

Description. Shell medium sized for genus, 52.7 mm wide, 47.2 mm long and 41.8 mm thick in holotype (Fig. 9A). Outline slightly transverse; lateral profile strongly ventribiconvex. Hinge line equal to maximum width; cardinal extremities slightly acute.

Ventral valve strongly convex, with gently incurved short beak. Ventral interarea very low, slightly concave; delthyrium covered by solid pseudodeltidium (Fig. 17E–H). Sulcus indistinctly developed, relatively narrow and shallow, commencing from ventral beak, anteriorly forming 'V'-shaped commissure line, weakly

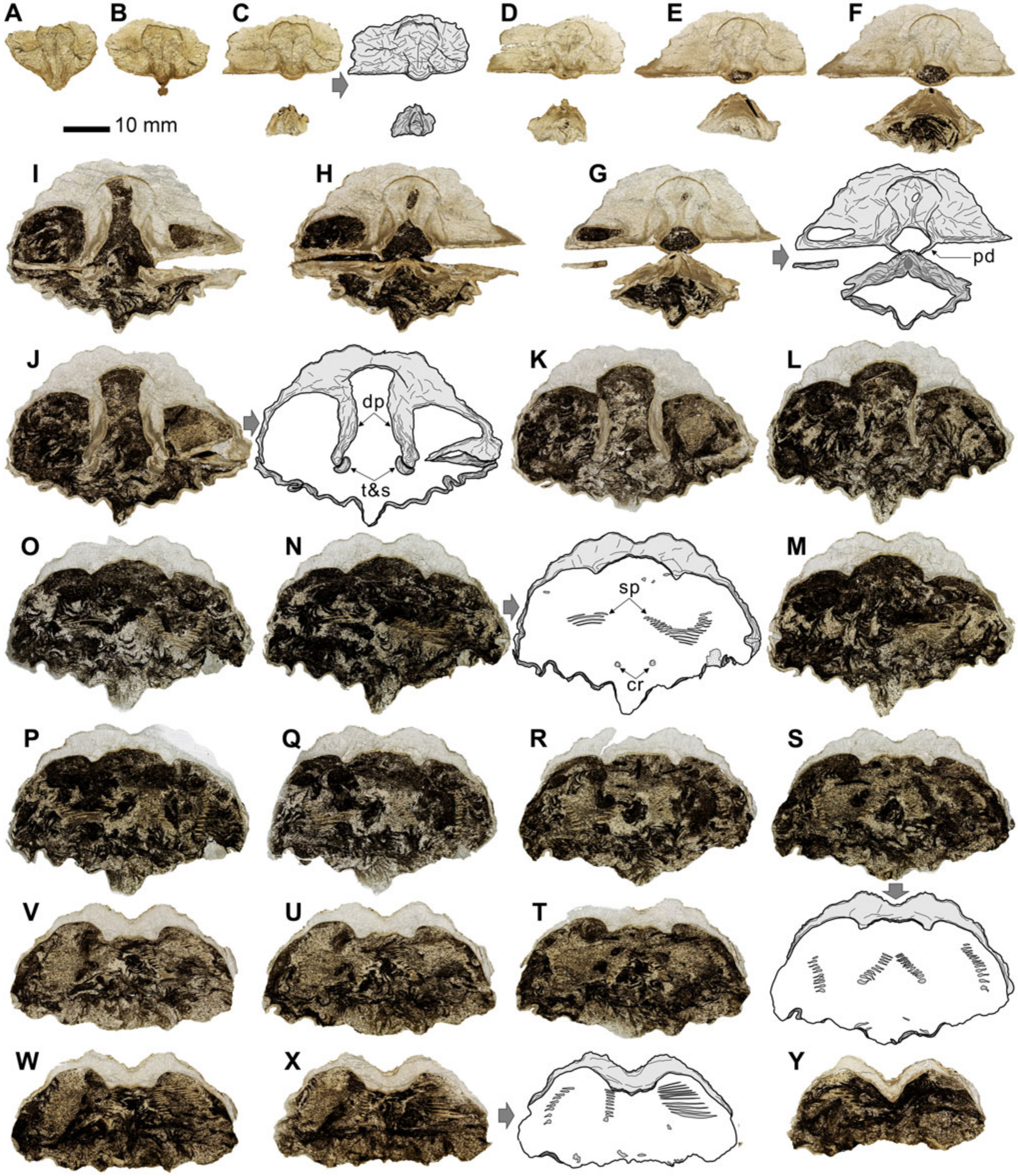

Figure 17. Serial sections of *Spiriferella protodraschei* sp. nov. Lee & Shi, NMV P340474. The interval between adjacent sections is approximately 1 mm. **Abbreviations: cr**, crura; **dp**, dental plates; **pd**, pseudodeltidium; **sp**, spiralia; **t&s**, teeth and sockets.

ornamented with about four costae. Ventral lateral slopes considerably steep, bearing four to five plicae on each side; plicae rounded or slightly angular, much broader than interspaces, with indistinct costation; costae slightly rounded to flat, unequally developed, recognizable only on middle to anterior part of valve.

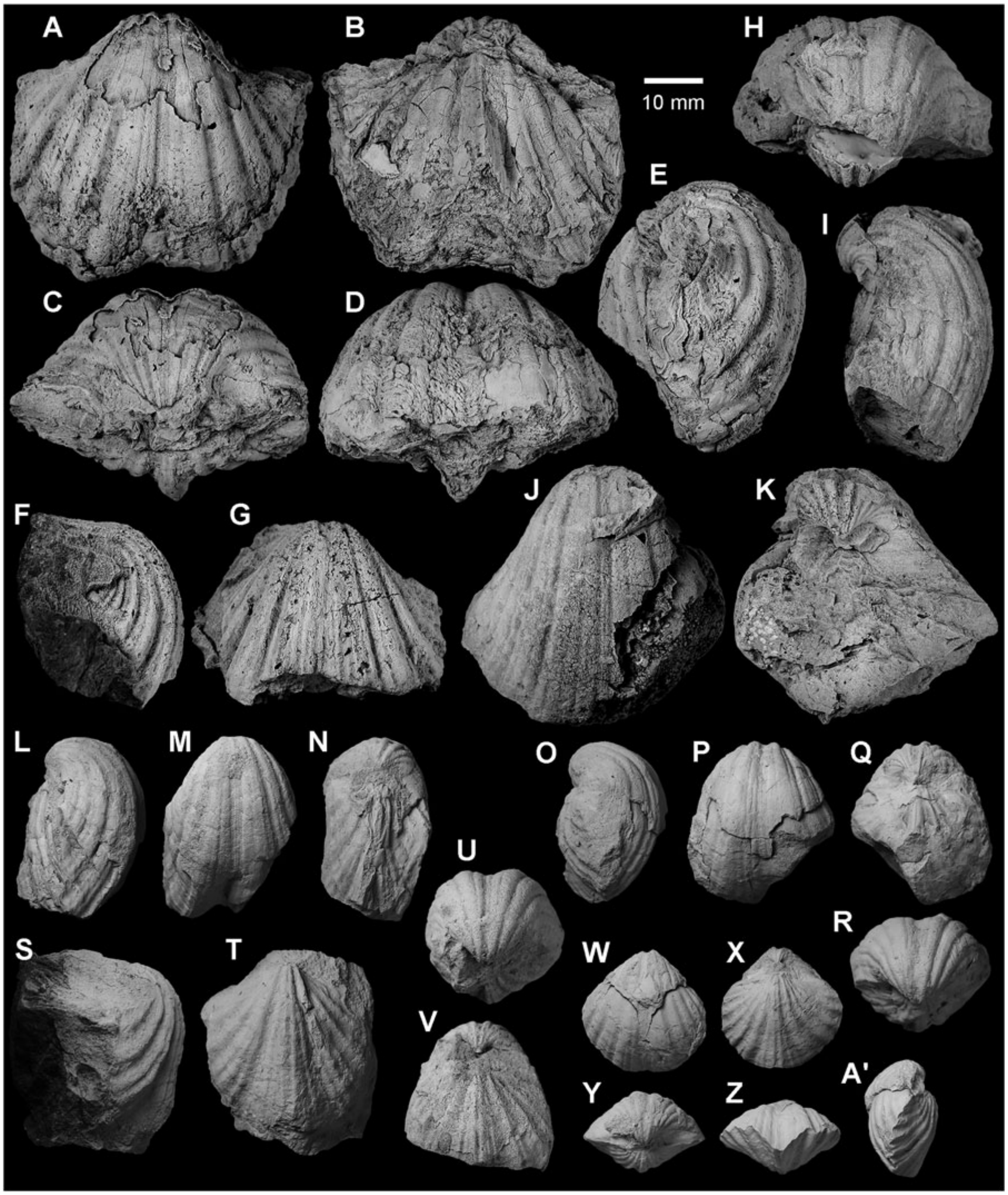

Figure 18. **A**–**G,** *Spiriferella protodraschei* sp. nov. Lee & Shi from the Kapp Starostin Formation in Spitsbergen. **A**–**E,** holototype, NMV P340474, ventral, dorsal, posterior, anterior and lateral views of a conjoined shell; **F, G,** NMV P340475, lateral and ventral views of a ventral valve. **H**–**K,** *Spiriferella* sp. from the Kapp Starostin Formation in Spitsbergen, NMV P340477, posterior, lateral, ventral and dorsal views of a ventral valve. **L**–**V,** *Eridmatus talbeicus* (Ifanova, 1972) from the Kozhim Rudnik Formation in the Subpolar Urals (**L**–**T**), from the Hambergfjellet Formation in Bjørnøya (**U**–**V**). **L**–**N,** NMV P340479, lateral, ventral and dorsal views of a conjoined shell; **O**–**R,** NMV P340480, lateral, ventral, dorsal and posterior views of a conjoined shell; **S, T,** NMV P340481, lateral and dorsal views of a dorsal valve. **U, V,** PMO 234.053, posterior and dorsal views of a conjoined shell. **W**–**A',** *Spiriferella* cf. *S. interplicata* (Rothpletz, 1892) from the Kozhim Rudnik Formation in the Subpolar Urals, NMV P340476, ventral, dorsal, posterior, anterior and lateral views of a conjoined shell.

Dorsal valve very weakly convex except fold, much thinner than ventral valve. Fold relatively high and narrow, with slightly angular crest, ornamented by median groove and a few lateral costae; median groove on fold very faintly developed, originating from posterior tip anteriorly. Dorsal lateral slopes nearly flat, with three or four lateral plicae on each side; plicae slightly more angular than those of ventral valve, weakly costate; interspaces narrower than plicae, but broader than those on ventral valve.

Micro-ornamentation comprising growth lamellae, capillae and pustules; pustules 0.05–0.15 mm in diameter, 15–20 per 1 mm^2 on mid-valve, distributed on intersections of capillae and concentric growth lamellae (Fig. 5A, B). Shell material strongly thickened in posterior of ventral valve, thinning anteriorly.

Ventral apical callus strongly thickened, occupying considerable space below delthyrium; teeth strongly developed, supported by thickened dental plates; ventral adminicula relatively low and short, buried by shell thickening; median septum probably present on posterior part of valve floor, but mostly buried by apical callus (Fig. 17I). Ventral muscle field somewhat elevated above valve floor.

Dorsal interior with ctenophoridium small, longer than wide, with around 15 platelets (Fig. 17G). Spiralia posteroventrally directed, asymmetrical along plane of symmetry (one spiralium with 10 whorls but another bearing 13 whorls) (Fig. 17M–Y); each spiralium shaped like an inclined cylinder; whorls more or less uniform, densely positioned, each about 20 mm in diameter.

Remarks. Although the new species *S. protodraschei* is represented by only two specimens, they clearly show some unique characteristics, including an indistinct narrow sulcus, costate lateral plication, a high and narrow fold with a sharp crest and faint median groove, and posteroventrally directed spiralia. These shells look superficially like the drawings of *S. keilhavii* given in von Buch (1847, fig. 2a, b; see also Fig. 4A, B), in having a nearly isometric outline with slightly extended cardinal extremities, a short ventral beak, a low ventral interarea and a weak median groove on the fold. However, the new species is clearly characterized by its strongly convex ventral valve, a less distinct sulcus, and fewer but conspicuously costate ventral plicae. In addition, compared to *S. keilhavii* the fold of *S. protodraschei* is evidently higher and narrower, with an angular crest.

It seems that *S. protodraschei* is more closely related to *S. draschei* than to *S. keilhavii*. Although there is certainly a morphological gap between these two species (e.g. height of ventral interarea and width of sulcus), they resemble one another both externally and internally. Both species exhibit fewer costate lateral plications and a slightly more convex dorsal valve and a narrower fold, in comparison with *S. keilhavii*. The presence of a solid pseudodeltidium as well as the development of strongly thickened dental plates is also fully shared between the new species and *S. draschei*; likewise, they are nearly identical in their micro-ornamentation patterns (Fig. 5A–D).

The morphology of the new species is, to some degree, compatible with that of *T. wilczeki*, including the common costation on the lateral plicae as well as a narrow sulcus and fold. The arrangement of pustules in *T. wilczeki* (Fig. 5G, H) is also comparable to those of both *S. protodraschei* and *S. draschei.* These morphological similarities among the three species suggest that they might have a phylogenetically close relationship. In spite of the fact that all three species have been collected mainly from the same stratigraphical horizon in Spitsbergen (Vøringen Member), it is most likely that the morphology of *S. protodraschei* represents the primitive characteristics (as plesiomorphies). In particular, the primitive features might include the weakly transverse outline, less distinct sulcus, and narrow fold with an indistinct median groove. Under this scenario, *S. protodraschei* is here depicted to form a monophyletic group with *S. draschei*, whereas *Timaniella*'s clade is interpreted to have branched out a little earlier through the development of a more transverse outline (Fig. 6).

Spiriferella protodraschei is here understood to be a rather primitive taxon among the spiriferellids studied in this paper, but its posteroventrally directed spiralia (Fig. 17M–Y) are unique. It is known that the spiralia of spiriferides (including the spiriferellids) are directed laterally (or posterolaterally) within their mantle cavity (Williams *et al.* 1997). All the other spiriferellid taxa examined in this study consistently exhibit posterolaterally directed spiralia. The functional role and phylogenetic implications of the peculiar spiralia in *S. protodraschei* are under investigation.

Occurrence. Vøringen Member (late Artinskian–early Kungurian) of the Kapp Starostin Formation.

Spiriferella cf. ***S. interplicata*** (Rothpletz, 1892)
(Figs 9A, 18W–A')

1990 *Spiriferella*? *talbeica* Ifanova; Kalashinikov: pl. 5, fig. 2; *non* pl. 5, fig. 1.

Material. A conjoined shell from the Kozhim Rudnik Formation in the Subpolar Urals (NMV P340476).

Description. Shell small, 22.1 mm wide, 21.6 mm long and 13.0 mm thick (Fig. 9A); outline relatively circular, slightly ventribiconvex in lateral profile. Maximum width at mid-valve, hinge line evidently narrower, cardinal extremities rounded.

Ventral valve moderately convex, with weakly incurved short beak. Ventral interarea low, around 3 mm high, slightly concave. Sulcus relatively narrow, shallow but deepening in anterior part of valve, commencing from beak and anteriorly forming a 'V'-shaped commissure line. Ventral lateral slopes gently steep, with four plicae on each slope.

Dorsal valve slightly less convex than ventral valve. Fold low and narrow, distinctly separated from lateral slopes, with distinct median groove, additionally grooved on lateral sides. Dorsal lateral slopes weakly steep, bearing four plicae in each slope.

Plication in both valves similar, rounded to slightly angular, bounded by narrower interspaces, distinctly branched only on anterior part of shell. Micro-ornamentation composed of growth lamellae, capillae and pustules; capillae more distinct than growth lamellae; pustules tiny, arranged along both growth lamellae and capillae, about 25 per 1 mm^2 on mid-valve.

Remarks. This small spiriferellid shell is characterized by a circular outline, a narrow hinge line and a relatively narrow sulcus and fold. Kalashnikov (1990) considered this species to be *Eridmatus talbeicus* (Ifanova, 1972), as they were discovered from the same horizon of the Kozhim Rudnik Formation in the Subpolar Urals and share relatively small size and a hinge narrower than the maximum width, as well as a distinct median groove on the fold. However, in our view, *E. talbeicus* can be differentiated from these shells by its circular outline, as the former is elongate and has a deep sulcus, an anteriorly diverging fold, and more fasciculate costation.

Among all known *Spiriferella* species, the present specimen is most compatible with *S. interplicata* (Rothpletz, 1892) from the Permian of West Java, Indonesia, in its overall features, but its full identification with the latter species cannot be confirmed with confidence at this point due to insufficient material.

On the other hand, this single shell appears to bear some similarities to species of *Elivina* Fredericks, 1924. In particular, *E. tibetana* (Diener, 1897) from the Lopingian of the Himalayas looks very close, because both of them are characterized by small size, a hinge that is much narrower than the maximum width, and a relatively narrow fold. However, our specimen is semicircular in outline, rather than elongate as in *E. tibetana*, and lacks costation on the shell surface.

Occurrence. Kozhim Rudnik Formation (late Kungurian) in the Subpolar Urals.

***Spiriferella* sp.**

(Figs 9A, 18H–K)

Material. Two ventral valves (NMV P340477–340478) from the Kapp Starostin Formation in Spitsbergen.

Description. Ventral valve with relatively narrow width and possibly elongate outline. Ventral umbonal region strongly incurved; beak short, acute, incurved. Ventral interarea high with horizontal striation; delthyrium triangular, with delthyrial angle of 50°, posteriorly covered by solid pseudodeltidium. Sulcus shallow and narrow, indistinctly developed even in anterior part of valve, ornamented by median costa and three pairs of lateral costae; median costa starting near beak, lateral costae originating from middle to anterior of valve. Ventral lateral slopes steep, with four plicae on each side; plicae rounded, broad, bounded by very narrow interspaces, with anteriorly branched or weakly costate.

Micro-ornamentation poorly preserved but presenting wavy growth lamellae and weak capillae with small pustules on valve anterior.

Remarks. These two incomplete ventral valves with a narrow hinge are mostly comparable with *S. draschei*, due to their strongly incurved ventral umbonal region, high interarea, steep lateral slopes, and a median costa on the sulcus, implying that they might represent a variety of *S. draschei*. Nevertheless, these shells are differentiated in having fewer costae within the sulcus. Moreover, although their micro-ornamentation is not fully preserved, the pattern seems to be more similar to that of *S. loveni*, characterized by the weak capillae and pustules arranged along the growth lamellae. These facts suggest that this, potentially new, species might be a representative of a transitional form between *S. draschei* and *S. loveni*. However, this interpretation needs to be clarified through the study of more corresponding specimens.

Occurrence. Svenskeegga and Hovtinden members of the Kapp Starostin Formation (late Kungurian–Capitanian) in Spitsbergen.

Genus ***Eridmatus*** Branson, 1966

Type species. *Spirifer* (?*Trigonotreta*) *texanus* Meek, 1871, p. 179.

Remarks. *Eridmatus* bears many similarities to *Spiriferella* but can be differentiated by the presence of a high fold and a deep sulcus, both 'V'-shaped. The type species, *E. texana*, from Carboniferous strata is additionally characterized by an extended hinge line, although the Permian species of this genus from northern Pangaea appear to lack these characteristics.

Cooper & Grant (1976) suggested that *Eridmatus* might be a phylogenetically transitional genus between *Neospirifer* and *Spiriferella*, emphasizing the former's strong affinity to *Neospirifer*. On the other hand, others have interpreted *Eridmatus* as closer to *Spiriferella* than to *Neospirifer* (Waterhouse & Waddington 1982; Kalashnikov 1998). Furthermore, Kalashnikov (1998) suggested that *Eridmatus* might represent an intermediate form between *Spiriferella* and *Arcullina*. In this study, it is not possible for us to judge the phylogenetic relationships among these genera, due to the limited material of *Eridmatus* in our hands. Nevertheless, it is worth noting that the development of pustules on the shell surface of *Eridmatus* is closer to that in *Spiriferella* species than it is to that in *Arcullina*, implying that *Eridmatus* might not represent a transitional form between any two of the distinct genera but rather a minor split within *Spiriferella*.

Eridmatus talbeicus (Ifanova, 1972)
(Figs 9A, 18L–V)

1972 *Spiriferella talbeica* Ifanova: 140, pl. 13, figs 3, 4.
1990 *Spiriferella*? *talbeica* Ifanova; Kalashnikov: pl. 5, fig. 1; *non* pl. 5, fig. 2.
1998 *Eridmatus talbeicus* (Ifanova); Kalashnikov: 61, pl. 20, figs 7, 8.

Material. Two specimens (a conjoined shell and a ventral valve) from the Hambergfjellet Formation in Bjørnøya (PMO 234.053–234.054); three specimens (two conjoined shells and a dorsal valve) from the Kozhim Formation in the Subpolar Urals (NMV P340479–340481).

Description. Shell small for genus, ranging from 24.0 to 28.2 mm in width and around 30.0 mm long (Fig. 9A); outline elongate, ventribiconvex in lateral profile, generally with obtuse cardinal extremities; hinge line slightly narrower than maximum width; maximum width generally at anterior to mid-valve.

Ventral valve considerably convex, umbonal region strongly incurved, with shortly developed beak. Ventral interarea moderately high, occupying around one-seventh of valve length. Sulcus distinct, relatively narrow, generally deep in mid-valve but further deepening anteriorly, ornamented by indistinct costae. Ventral lateral slopes generally steep, with three to four plicae on each slope; plicae anteriorly branched, divided by narrower interspaces.

Dorsal valve weakly convex, except relatively high fold; fold anteriorly widened and elevated, distinctly forming reversed 'V'-shape (Fig. 18T), with distinct median groove, additionally grooved in middle to anterior part of lateral sides. Dorsal lateral slopes gently steep, with three plicae in each slope; dorsal plicae more angular than ventral ones, distinctly branched in middle to anterior part of valve.

Micro-ornamentation composed of growth lamellae and capillae, forming reticulate structure; capillae more distinct than growth lamellae; pustules small, arranged along both growth lamellae and capillae, around 20 per 1 mm^2 on mid-valve.

Remarks. The morphology of these shells is well matched with that of the holotype material of *S. talbeica* Ifanova, 1972 (pl. 13, fig. 3) as well as that of the conspecific specimens illustrated by Kalashnikov (1998, pl. 20, figs 7, 8). Although our specimens appear to be slightly more elongate than the holotype, they all share the maximum width at the anterior part of the shell, anteriorly deepening sulcus, and relatively angular dorsal plication. More importantly, the presence of the strongly defined fold with an inverted 'V'-shape in all of the dorsal valves indicates that they are definitely conspecific.

Although the morphological characteristics of this species are well defined, its generic identity seems to be problematic. Kalashnikov (1998) re-assigned this species to the genus *Eridmatus*, without sufficient explanation. A pentagonal outline was emphasized as the diagnostic feature of the genus, but the outline of the present species is close to oval. The narrow hinge line in this species also contrasts with the extended hinge line of the type species, *E. texanus*. Moreover, the pattern of micro-ornamentation observed in our specimens is very similar to those of some *Spiriferella* species (particularly, *S. draschei* and *S. protodraschei*; see Fig. 5A–D). Nevertheless, we decided to provisionally leave the species within *Eridmatus*, as the unique fold morphology of *E. talbeicus* seems to be similarly expressed by the type species.

Eridmatus erjakhensis Kalashnikov, 1998 from the Talata Formation in the Pai-Khoy Range is similar to *E. talbeicus* in the oval outline, maximum width at the anterior part of shell, a distinctly developed sulcus/fold, and a deep median groove on the fold. But the former is sufficiently discriminated by its larger shell size and high intearea. *Spiriferella draschei* appears to be the most similar to *E. talbeicus* among the various *Spiriferella* species. Both of these species are characterized by an elongate outline, hinge slightly narrower than maximum width, steep ventral lateral slopes, and relatively angular dorsal plications. However, the former species is distinguished by its large shell size, high interarea, broad sulcus, and much less convex dorsal valve.

Occurrence. Kozhim Rudnik Formation (late Kungurian) in the Subpolar Urals; Hambergfjellet Formation (Artinskian) in Bjørnøya.

Genus *Arcullina* Waterhouse, 1986

Type species. *Spiriferina polaris* Wiman, 1914, p. 39.

Diagnosis. Shell variable in size, generally with slightly elongate outline; hinge line commonly narrower than maximum width. Sulcus deep, smooth or occasionally costate, commencing from umbonal region. Ventral lateral slopes steep, with broad plicae. Fold generally highly developed with sharp crest; median groove on fold principally absent, but possibly developed in younger species. Lateral plication simple, distinctly developed. Delthyrium posteriorly closed by solid pseudodeltidium. Shell surface covered with very densely arranged coarse pustules.

Remarks. *Arcullina* is readily distinguished from other spiriferellid genera by the absence of a median groove on the dorsal fold, as originally noted by Waterhouse (1986). The deeply incised sulcus as well as the absence or scarcity of costae on lateral plicae is also a typical feature of the genus. In addition, the coarse pustules densely arranged on the shell external surface appear to be clearly distinguished from the small, less densely populated pustules of *Spiriferella* species, at least in the northern margin of Pangaea (Fig. 5).

In addition to the type species from the Permian of Svalbard, two Permian species from North Timan, Russia, *S. digna* Barchatova, 1968 and *S. timanica* Barchatova, 1970, which seem to be very closely related to the type species, can be assigned to *Arcullina*. Kalashnikov (1998) assigned two additional species, both from the Permian of Russia, *A. editiareatus* (Einor, 1939) and *A. mica* (Barchatova, 1968), to this genus. Also, the new species *A.*? *enokiani* from the Subpolar Urals is provisionally assigned to the genus in this study. Meanwhile, Waterhouse (2001, 2004) assigned several species from the Permian of New Zealand and the Himalayas to the genus, but their relationships with *Arcullina* from the Arctic region have not been clarified. *Spiriferella rajah* subsp. B of Nelson & Johnson (1968) from the Yukon in western Canada lacks a median groove on the fold, but it should remain in *Spiriferlla* due to its striking affinity to *S. draschei.*

Arcullina polaris (Wiman, 1914)
(Figs 5I, J, 7A, 19–21)

?1855 *Spirifer keilhavii* von Buch; Salter: 386, pl. 36, fig. 11; *non* pl. 36, figs 9, 10.
1914 *Spiriferina polaris* Wiman: 39, pl. 4, figs 1–25, pl. 5, figs 1–5.
1937 *Spiriferella polaris* (Wiman); Stepanov: 150, pl. 8, figs 7, 8; *non* pl. 8, figs 5, 6.
1937 *Spiriferella polaris* (Wiman); Frebold: 47, pl. 11, fig. 1, 1a, 1b.
?1960 *Spiriferella saranae* (de Verneuil) *sensu lato*; Harker & Thorsteinsson: 71, pl. 23, fig. 8; *non* pl. 22, figs 1–8, pl. 23, figs 3, 4.
1964 *Spiriferella polaris* (Wiman); Gobbett: 150.
1968 *Spiriferella saranae* (de Verneuil); Nelson & Johnson: 729, pl. 93, figs 3–10, pl. 96, fig. 9; *non* pl. 93, figs 1, 2.
1970 *Spiriferella polaris* (Wiman); Barchatova: 176, pl. 20, fig. 7.
1986 *Spiriferella polaris* (Wiman); Kalashnikov: 93, pl. 123, figs 3–5.
1986 *Arcullina polaris* (Wiman); Waterhouse: 4.
1992 *Spiriferella polaris* (Wiman); Nakamura, Tazawa & Kumon: pl. 1, fig. 8.
1998 *Arcullina polaris* (Wiman); Kalashnikov: 61, pl. 16, figs 1, 2, pl. 17, figs 5–7, pl. 18, fig. 1.

Diagnosis. Slightly elongate spiriferellid shell. Delthyrium mostly covered by solid pseudodeltidium. Sulcus deep and angular, smooth or rarely costate. Fold highly developed with sharp crest; median groove absent. Lateral plicae simple and broad, with very narrow interspaces on ventral valve, more angular with broader interspaces on dorsal valve. Pustules swollen, densely arranged on shell surface. Dental plates highly developed; short median septum present.

Lectotype. When Wiman (1914) first proposed this species, he did not select a type specimen. Later, two different specimens of Wiman were chosen as lectotypes, by Gobbett (1964) and Kalashnikov (1998), respectively. We here accept the specimen that was figured by Wiman (1914, pl. 4, figs 23–25) and then selected by Gobbett (1964) as the lectotype, because it was nominated earlier and displays the typical characteristics in both valves (unlike Kalashnikov's lectotype, which is represented only by a ventral valve). This lectotype was originally collected from the Vøringen Member in Bjonahamna, Spitsbergen.

Material. Thirty-six specimens from the Kapp Starostin Formation (Vøringen Member) in Spitsbergen (PMO

A26051, PMO A9885, PMO 234.060, NMV P340482–340506, KOPRIF10013–10020), comprising 34 ventral valves and two dorsal valves; five ventral valves from the Hambergfjellet Formation in Bjørnøya (PMO 234.055–234.059).

Description. Shell medium in size for genus, 18.1–56.1 mm in width and 18.0–54.0 mm in length (Fig. 19); outline generally ovate, 0.935 width/length ratio on average; lateral profile moderately to strongly biconvex. Hinge line slightly narrower than maximum width, with rounded cardinal extremities; maximum width commonly at middle of shell.

Ventral valve with slender umbo and short beak. Ventral interarea moderately high and apsacline; delthyrium, at least, posteriorly covered by pseudodeltidium, with delthyrial angle around 60°; pseudodeltidium arched, solidly attached along lateral edges of delthyrium (Figs 7A, 20D–H). Sulcus distinctly developed, angular, normally bold, mostly originating from umbonal region, deepening and widening anteriorly, then forming strong 'V'-shaped anterior commissure line with fold. Ventral lateral slopes generally steep, with five to seven plicae on each slope; plicae simple, broad, rounded to slightly angular, bounded by very narrow interspaces, anteriorly forming zigzagging commissure line.

Dorsal valve moderately convex, much thinner than ventral valve, hardly preserved. Fold highly developed, having sharp crest without median groove. Dorsal lateral slopes gently steep, with four to five plicae; dorsal plicae simple and angular, divided by broader interspaces than ventral ones.

Micro-ornamentation characterized by numerous granular pustules; pustules relatively large, reaching 0.1–0.2 mm in diameter, developed along fine capillae and wavy growth lamellae, showing very dense distribution on whole shell surface (Fig. 5I, J). Shell material strongly thickened in ventral valve, particularly at umbonal region, dorsal valve much thinner.

Ventral interior with strong teeth and highly developed dental plates; ventral apical region strongly thickened; median septum shortly developed on ventral floor (Fig. 20M).

Remarks. Although the most distinctive character of this species is the absence of a median groove on the dorsal fold, our collection provides only two small dorsal valves (Fig. 21I, J). These two dorsal valves show a somewhat weaker convexity than those of the lectotype as well as a specimen figured by Frebold (1937, pl. 11, fig. 1, 1a), but the relatively angular fold without a median groove strongly indicates their affinity with *Arcullina*. The external features of the ventral valve that are represented by a relatively large number of specimens are mostly identical to those of the type material figured by Wiman (1914). In particular, the present species is distinctly separated from other *Spiriferella* species of Permian Spitsbergen in having a deep and angular sulcus starting from the umbonal region (or anterior to that) and steep lateral slopes, as well as in the absence of costae on plicae. Licharew & Einor (1939) commented that *A. polaris* is restricted to specimens with a sulcus starting from the ventral beak according to Wiman's original description. However, all ventral valves figured by Wiman commonly show that their sulcal depressions originate from the umbonal region where the sulcus appears as a deep groove.

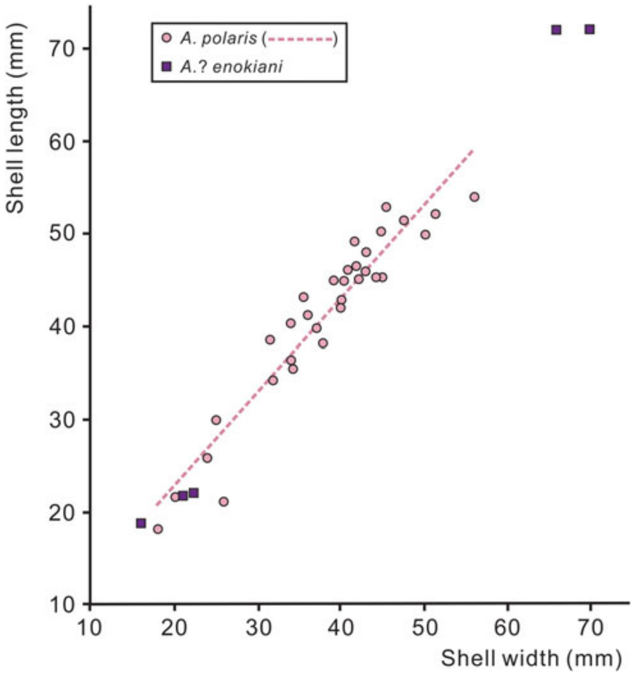

Figure 19. Shell measurements of two *Arcullina* species included in this study (fragmentary shells and only dorsal valves were excluded; see also Supplementary material 2).

Kalashnikov (1998) synonymized two species from the Permian of North Timan, *S. digna* Barchatova, 1968 and *S. timanica* Barchatova, 1970, with *A. polaris*. It is true that these two former species may be assignable to *Arcullina* in view of the shared absence of a median groove on the fold and other strong morphological similarities to *A. polaris*. However, *A. digna* is distinguished by having its maximum shell width at the hinge line and by its acute cardinal extremities. *Arcullina timanica* can also be differentiated, by the possession of pronouncedly angular lateral plicae.

Spiriferella vaskovskii Zavodowsky, 1968 from the Permian of north-eastern Siberia is similar to *A. polaris* in its ovate outline, posteriorly narrow sulcus, and broad lateral plicae, but the former differs in possessing a

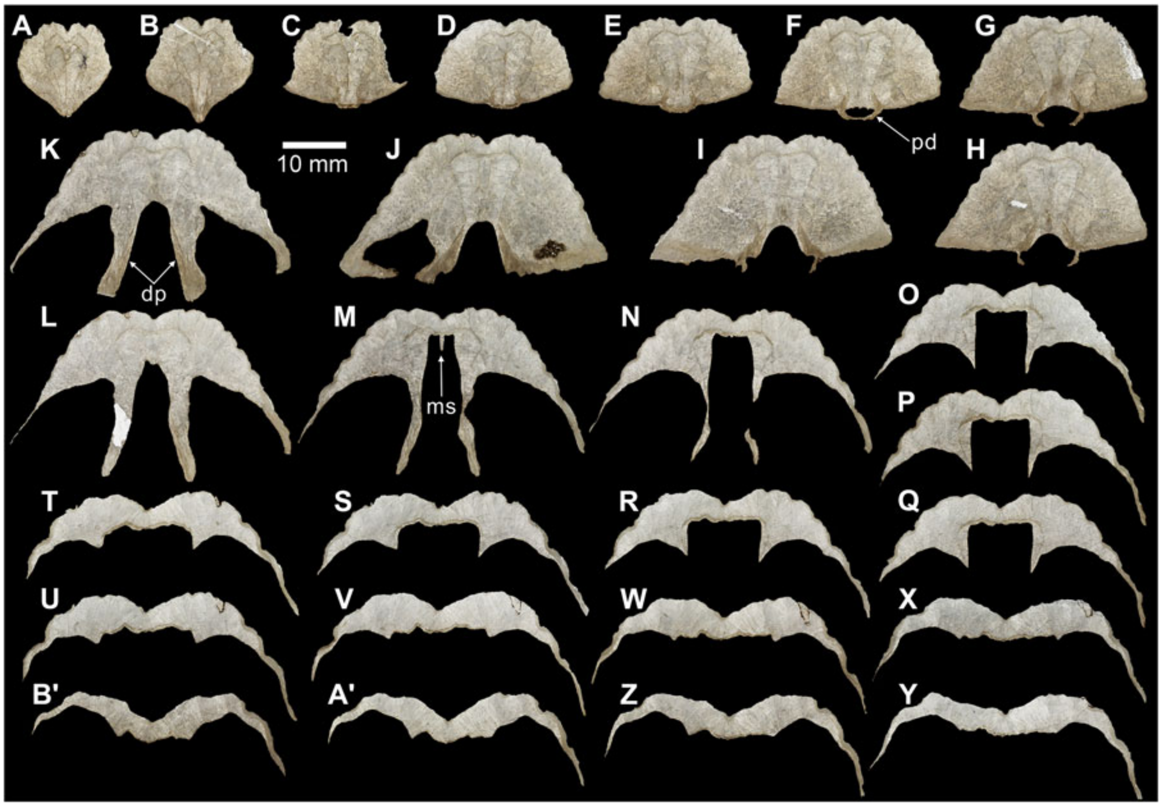

Figure 20. Serial sections of *Arcullina polaris* (Wiman, 1914), NMV P340482. The interval between adjacent sections is approximately 1 mm. **Abbreviations: dp**, dental plates; **ms**, median septum; **pd**, pseudodeltidium.

distinct median costa on the sulcus and an anteriorly retained narrow sulcus, as well as a median groove on the fold.

As pointed out by several authors (Wiman 1914; Stepanov 1937; Licharew & Einor 1939; Nelson & Johnson 1968), *A. polaris* seems to be closely related to some specimens regarded as *S. saranae* (de Verneuil). In particular, the existence of intermediate forms between the two species, such as *A. polaris* with weakly developed costae on sulcus (e.g. Wiman 1914, pl. 4, fig. 18; Nelson & Johnson 1968, pl. 93, figs 3, 7, 10) and *S. saranae* having a rounded fold without median groove (e.g. Tschernyschew 1902, pl. 40, fig. 7), appears to suggest that *A. polaris* might have originated directly from *S. saranae* through the loss of costation as well as the development of a more angular fold. However, in spite of their morphological similarities, the relationship between *A. polaris* and genuine *S. saranae* is still unclear owing to the fact that the identity of the type specimen of *S. saranae* has not been properly understood. As noted by Waterhouse & Waddington (1982) and Waterhouse (2004, 2016), the original illustration of *S. saranae* by de Verneuil (1845, pl. 6, fig. 15b) is not correctly matched with most other specimens assigned to *S. saranae*, even including the figures by Tschernyschew (1902).

Gobbett (1964) reported that *A. polaris* is common in the lower beds of the Brachiopod Chert, a rock unit possibly equivalent to the Svenskeegga member of the Kapp Starostin Formation. However, according to our biostratigraphical examination of spiriferellid species, this species is confined to the Vøringen Member in Spitsbergen and to the Hambergfjellet Formation in Bjørnøya, possibly providing a biostratigraphical and palaeoclimatic signal. In this sense, it is also noteworthy that Grunt *et al.* (1998) established a biozone of late Kungurian age, mainly based on the occurrence of *A. polaris* and *T. festa* in the East European Platform. On the other hand, a probable conspecific specimen (Harker & Thorsteinsson 1960, pl. 23, fig. 8) has been reported from the Belcher Channel Formation (Asselian–Sakmarian) in Arctic Canada.

Occurrence. Vøringen Member (late Artinskian–early Kungurian) of the Kapp Starostin Formation in Spitsbergen; Hambergfjellet Formation (Artinskian) in Bjørnøya; Kungurian strata in North Timan; Middle

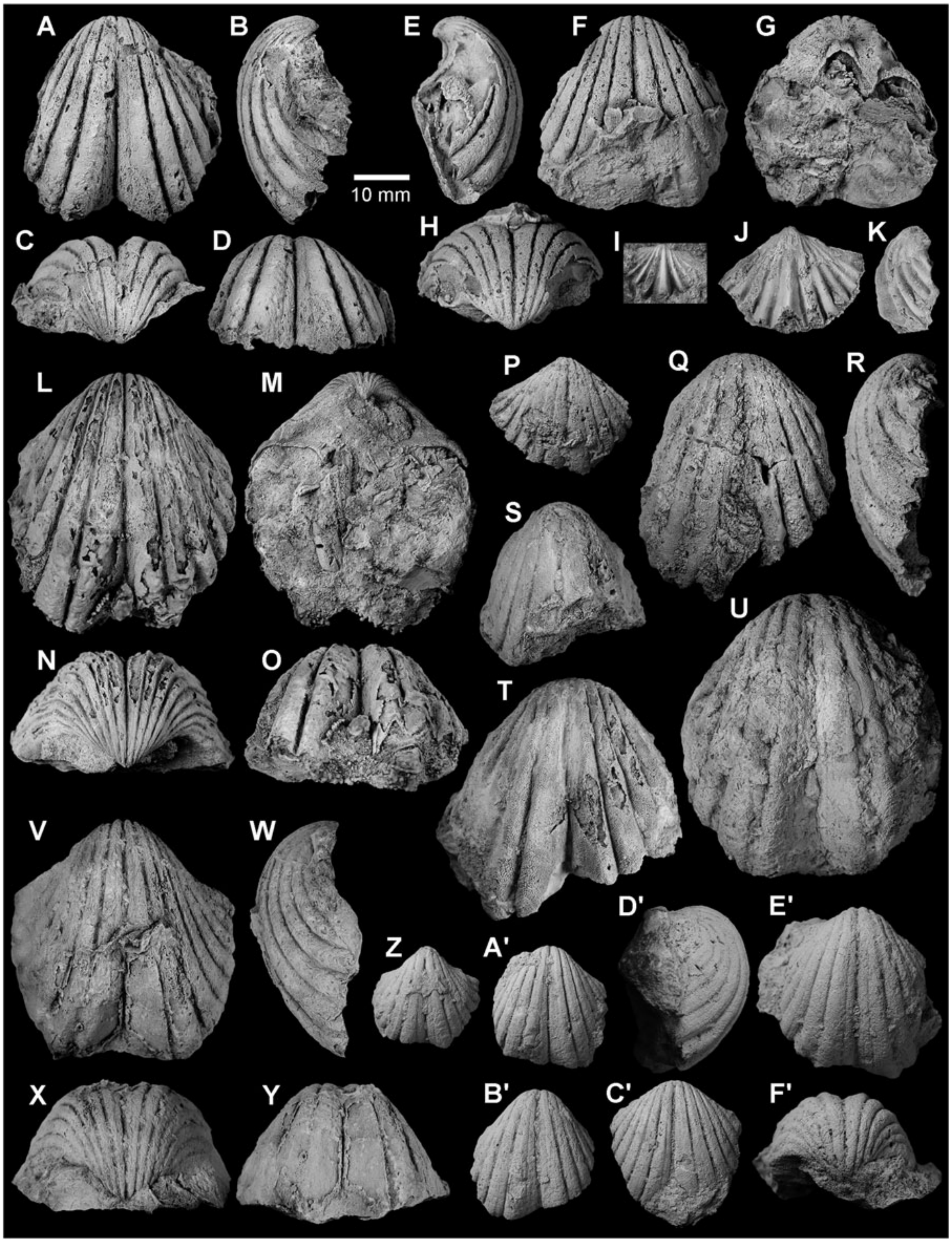

Figure 21. *Arcullina polaris* (Wiman, 1914) from the Kapp Starostin Formation in Spitsbergen (**A**–**Y**) and the Hambergfjellet Formation in Bjørnøya (**Z**–**F'**). **A**–**D,** NMV P340498, ventral, lateral, posterior and anterior views of a ventral valve; **E**–**H,** NMV P340490, lateral, ventral, dorsal and posterior views of a ventral valve; **I,** PMO A9885, dorsal view of a dorsal valve; **J, K,** NMV P340506, dorsal and lateral views of a dorsal valve; **L**–**O,** NMV P340499, ventral, dorsal, posterior and anterior views of a ventral valve; **P,** KOPRIF10013, ventral view of a ventral valve; **Q, R,** NMV P340484, ventral and lateral views of a ventral valve; **S,** NMV P340483, ventral view of a ventral valve; **T,** NMV P340503, ventral view of a ventral valve; **U,** NMV P340487, ventral view of a ventral valve; **V**–**Y,** NMV P340482, ventral, lateral, posterior and anterior views of a ventral valve; **Z,** PMO 234.055, ventral view of a ventral valve; **A',** PMO 234.056, ventral view of a ventral valve; **B',** PMO 234.057, ventral view of a ventral valve; **C',** PMO 234.058, ventral view of a ventral valve; **D'**–**F',** PMO 234.059, lateral, ventral and posterior views of a ventral valve.

Recessive (Sakmarian?–Artinskian) and Tahkandit formations (Kungurian to Guadalupian) in Yukon.

Arcullina*? *enokiani sp. nov. Lee & Shi
(Figs 5K, L, 19, 22)

2016 *Spiriferella gigantea* Enokian; Yurievich: a–c.

Etymology. Named after the famous Russian geologist and palaeontologist Ninel Enokian, in honour of her contribution to the discovery of this species from the Kozhim River.

Diagnosis. Large shell with variable pentagonal outline; hinge line extended, equal to maximum width. Ventral interarea very high in adult stage. Sulcus narrow and deep, indistinctly costate; sulcal tongue short in juvenile, but strongly extended in adult. Ventral lateral slopes steep in adult, with five to six plicae on each slope; plicae broad, rounded to slightly angular, costae absent. Fold low and narrow, with distinct median groove. Capillae distinct; pustules relatively large and densely populated.

Holotype and paratype. Two conjoined shells collected from the Kozhim Formation in the Subpolar Urals are designated as the holotype (NMV P340507; Fig. 22I, K) and paratype (NMV P340508; Fig. 22G, H). The locality section of these type materials on the Kozhim River is the type section of the Kozhim Formation. Both specimens were obtained stratigraphically from layers 463–461 of the section marked in Grunt *et al.* (1998, fig. 25).

Other material. A ventral valve from the Kozhim Formation in the Subpolar Urals (NMV P340509); four specimens consisting of three ventral valves and a dorsal valve from the Kozhim Rudnik Formation in the Subpolar Urals (NMV P340510–340513). All of these specimens are provisionally considered to represent juvenile forms of the species.

Description. Shell very large in adult stage, reaching 66.0 mm in width and 72.0 mm in length in holotype (Fig. 19); outline variably pentagonal, from transverse in juvenile to elongate in adult; hinge line extended, equal to maximum width, with acute cardinal extremities, at least in juvenile stage.

Ventral valve moderately to strongly convex, with higher convexity in adult stage. Ventral interarea low in juvenile, but very high reaching to more than one-third of valve length in adult, concave, with horizontal striations. Sulcus relatively narrow, very deep and sharp, commencing near ventral beak, weakly ornamented by costae; sulcal tongue short in juvenile, but strongly extended in adult, anteriorly forming sharp ‘V’-shaped commissure line. Ventral lateral slopes gentle in juvenile, but steeply developed in adult, with five to six plicae on each slope; plicae broad, rounded to slightly angular, divided by narrower interspaces; costae absent on lateral slopes.

Dorsal valve only observed in juvenile, less convex than ventral valve. Fold low and narrow, with distinct median groove. Dorsal lateral slopes weakly steep, with five plicae on each side.

Micro-ornamentation dominated by distinct capillae and pustules; growth lamellae wavy, indistinct in posterior to middle part of shell, but anteriorly becoming more distinct (Fig. 22J); pustules relatively large, reaching about 0.1 mm in diameter, densely populated and developed along both capillae and growth lamellae (Fig. 5K, L).

Remarks. Intriguingly, some large shells that are evidently conspecific with this species (also from the Kozhim River section) were referred to as ‘*Spiriferella gigantea* Enokian’ in a few Russian publications without any citation (e.g. Grunt *et al.* 1998; Yurievich 2016). It is now known that this species was originally recognized from the type section and informally named *S. gigantea* by N. Enokian. However, we confirm that the species has never been published according to the requirements of the International Code of Zoological Nomenclature (T. Grunt, pers. comm. 2017). Therefore, we formally erect the species as *Arcullina*? *enokiani.*

This species is characterized by its unique morphological features, such as its very large size as well as a deep ‘V’-shaped sulcus with an anteriorly elongate sulcal tongue, particularly in the adult stage. Both the broad plication on the lateral slopes and well-developed pustules on the shell surface strongly indicate that this species represents a spiriferellid taxon. However, its generic assignment is somewhat uncertain, due to the odd combination of its morphological characteristics. We provisionally place this species in *Arcullina*, because these shells show some typical features of this genus, including the deeply incised sulcus, simple lateral plication, and relatively large pustules on the shell surface. On the other hand, a few characteristics are incompatible with this genus. For example, the transversely extended hinge line combined with a low fold bearing a median groove suggests a strong resemblance to *Spiriferella* or *Timaniella*. The ambiguity of its generic identity might imply that this species represents an intermediate form, possibly a new genus, between *Spiriferella* and *Arcullina*.

On the other hand, it must be noted that the specimens assigned to the new species are composed of two distinct size clusters of shells that also demonstrate

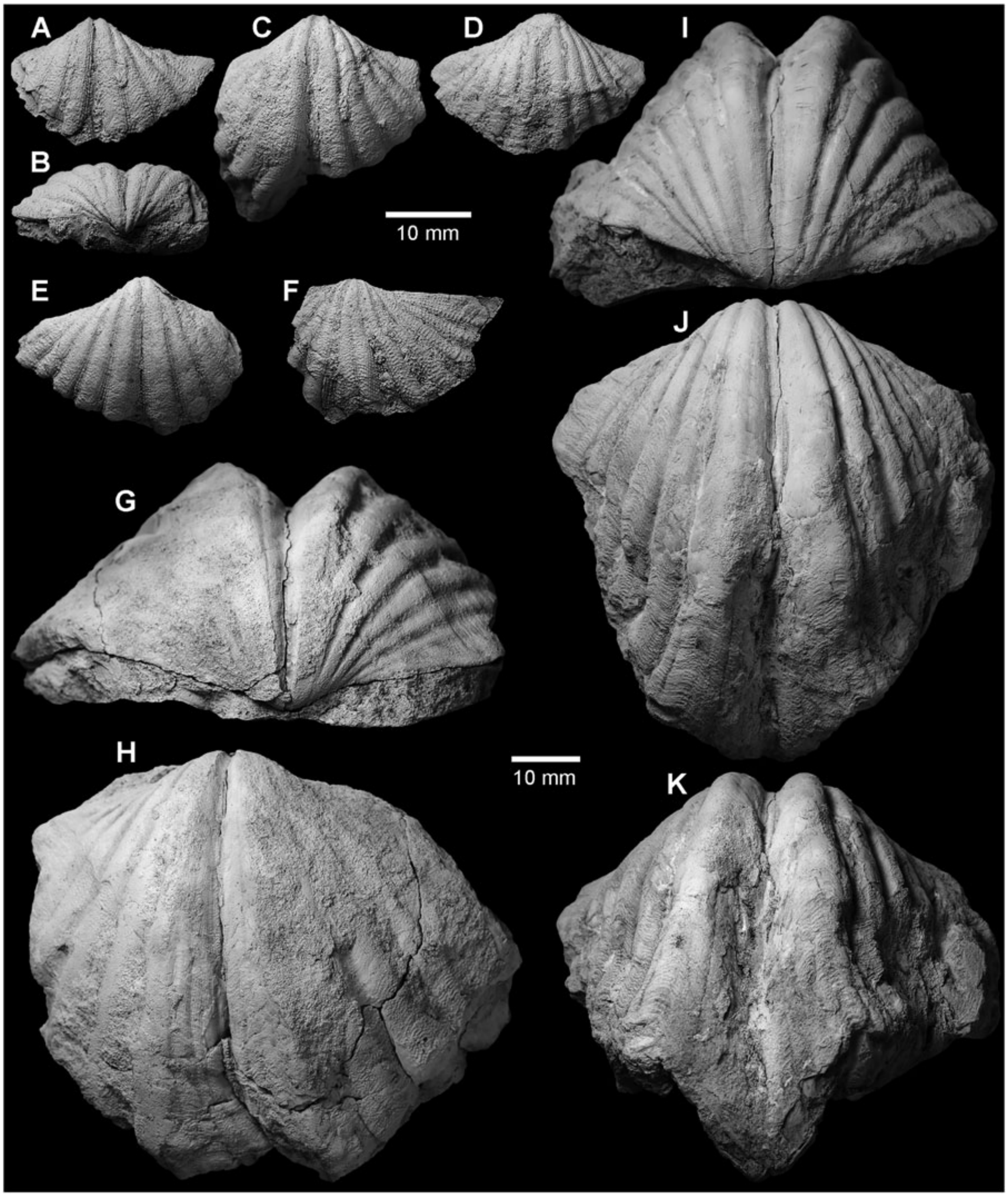

Figure 22. *Arcullina*? *enokiani* sp. nov. Lee & Shi from the Kozhim Rudnik Formation (**A–F**) and the Kozhim Formation (**G–K**) in the Subpolar Urals. **A, B,** NMV P340509, ventral and posterior views of a ventral valve; **C,** NMV P340510, ventral view of a ventral valve; **D,** NMV P340511, ventral view of a ventral valve; **E,** NMV P340512, ventral view of a ventral valve; **F,** NMV P340513, dorsal view of a ventral valve; **G, H,** paratype, NMV P340508, posterior and ventral views of a ventral valve; **I, K,** holotype, NMV P340507, posterior, ventral and anterior views of a ventral valve. Please note that the juvenile specimens (**A**–**F**) are scaled differently from the adult specimens (**G**–**K**).

certain morphological disparities: the small specimens show a transverse outline with a relatively low shell convexity accompanied by a low ventral intearea (Fig. 22A– E), whereas the large shells have an elongate outline, high ventral convexity and a much higher interarea (Fig. 22G–K). Otherwise, the shells are very similar, especially in the deeply incised sulcus as well as the micro-ornamentation composed of distinct capillae and coarse pustules. At this point, the size-related differences are considered possible ontogenetic changes, but the possibility that they represent different species or genera cannot be ruled out. This uncertainty is due to the limited material available for this study.

The type species, *A. polaris*, is most similar to the adult specimens of *A.*? *enokiani* among known *Arcullina* species, but is very different to the new species in having an ovate outline with a short sulcal tongue. Like the new species, *Arcullina dinga* also has its maximum shell width placed at the hinge line, but in the latter the hinge line is much more extended. Compared to any other known *Arcullina* species, the new species is distinguished by its low and medially grooved dorsal fold. *Timaniella harkeri* from the Assistance Formation in Arctic Canada resembles the smaller specimens of *A.*? *enokiani* in outline and sulcus, but it is clearly distinguished by its much weaker lateral plicae.

Occurrence. Kozhim and Kozhim Rudnik formations (Kungurian) in the Subpolar Urals.

Genus ***Timaniella*** Barchatova, 1968

Type species. *Timaniella festa* Barchatova, 1968, p. 162.

Diagnosis. Shell medium to large for family, transverse with acute to alate cardinal extremities, broadly ventribiconvex. Ventral interarea low to moderately high, flat to weakly concave; delthyrium covered by variable delthyrial coverings. Sulcus and fold relatively narrow, costate. Ventral lateral slopes gently steep, moderately to strongly plicate; plicae rounded to angular, costate, with distinct fasciculation. Fold variably elevated by species, but always with median groove starting near dorsal beak. Ventral interior greatly thickened with apical callus; teeth stout, supported by strong dental flanges; ventral adminicula short, low, buried by shell thickening. Micro-ornamentation generally composed of capillae and growth lamellae, forming fine pustules.

Remarks. This spiriferellid genus with a transverse outline is readily distinguished from *Spiriferella* Tschernyschew, 1902 by having a much less convex ventral valve and a less elevated muscle field, as well as a distinctively transverse outline. The transverse outline and fasciculated plicae of *Timaniella* have sometimes led some authors to consider it a neospiriferine genus (e.g. Wiman 1914, *Spirifer fasciger* Keyserling, pl. 5, figs 14–16; Stepanov 1937, *Spirifer moosakhailensis* Davidson, pl. 7, fig. 2). However, *Timaniella* is different from neospiriferine genera in the presence of a strongly thickened apical callus and a distinct median groove on the fold, both features suggesting strong affinity with spiriferellids. *Rhombospirifer* Duan & Li, 1985 from the Permian of Inner Mongolia in north-eastern China is very similar to *Timaniella* in having a transverse outline, plicated lateral slopes and costate plicae, but the former differs in the presence of stegidia as well as weakly developed costae and median groove.

As indicated by Stepanov (1937) and Barchatova (1968, 1970), many spiriferellid species with a transverse outline from the Arctic region have commonly been identified as *S. keilhavii*. We here reassign them to *T. wilczeki* (see the synonymy list below). The close morphological similarity between *Timaniella* and *Spiriferella* suggests some ancestral relationship between them. Interestingly, although the species of *Timaniella* have been mainly compared with *S. keilhavii*, *Timaniella* (particularly *T. wilczeki*) appears to be more compatible with *S. draschei* and *S. protodraschei* due to their similarity in both macro- and micro-ornamentation. Consequently, it is believed that *Timaniella* might have evolved from one of the earlier forms in the *S. draschei* lineage by attaining a much wider hinge line (Fig. 6).

On the other hand, several other spiriferellid species that have been assigned to *Timaniella* solely due to their transverse outline may prove to belong to other genera. For example, *T. magniplicata*, proposed by Abramov & Grigorieva (1988, p. 159, pl. 29, figs 1–3) from the Permian of western Verkhoyan in Russia, has a slightly transverse outline and narrow sulcus that can be regarded as characteristic features of *Timaniella*, but this species differs in having strong plicae and a deep sulcus, unlike typical *Timaniella*. Spirifellid specimens from the Permian of northern Yukon in Canada, referred to *T. convexa* Shi & Waterhouse (1996, p. 135, pl. 25, figs 16–28), are also characterized by a wide hinge line, bearing a strong similarity to *T. harkeri* Waterhouse in Bamber & Waterhouse, 1971. It is of interest to note that both *T. magniplicata* and *T. convexa* co-existed with elongate spiriferellids having similar shell ornamentation. This may suggest that *Timaniella* with extended hinges may have evolved from spiriferellids with a shorter hinge line. If this is true, *T. harkeri*, which seems to be closely related to *T. convexa*, might have originated from a different lineage to that of the type species of *Timaniella*.

Transverse shells from the Permian of the Pechora Basin in Russia, assigned to *T. vasjagensis* (Ifanova, 1972) by Kalashnikov (1998, p. 64, pl. 24, figs 1–5), differ from the other genuine species of *Timaniella* in shell ornamentation composed of weak plicae and reticulated structure formed of strong costae and growth lamellae. This reticulate structure suggests an affinity with trigonotretid species rather than spiriferellid forms.

Wang & Zhang (2003) assigned *S. grandis* Kotlyar in Licharew & Kotlyar (1978, p. 73, pl. 18, figs 7, 8) from the Permian of southern Primorye, Russia, to *Timaniella*. This species is similar to *Timaniella* in its wide outline and costation both in the sulcus and on lateral plicae, but its median groove seems to develop only on the anterior part of the fold, indicating its resemblance to *Rhombospirifer*.

Except for the type species and the two other species described below, *T. pseudocamerata* (Girty, 1920), reported from the Permian of the United States by Wardlaw (1977), is here regarded as the only other valid species of *Timaniella* because it displays the typical features of the genus including a transverse outline, costate sulcus, narrow fold with a distinct median groove, and pustules as micro-ornamentation, in spite of some minor differences in the costation of lateral plicae.

Timaniella wilczeki (Toula, 1873)
(Figs 4K, L, 5G, H, 23–26)

1873 *Spirifer wilczeki* Toula: 271, pl. 1, fig. 3a, b.

1875 *Spirifer wilczeki* Toula; Toula: 241.

1914 *Spirifer fasciger* Keys; Wiman: 41, pl. 5, figs 14–16; *non* pl. 5, figs 6–13.

1937 *Spirifer moosakhailensis* Davidson; Stepanov: 140, pl. 7, fig. 2; *non* pl. 7, fig. 1.

1937 *Spiriferella keilhavii* var. *wilczeki* (Toula); Stepanov: 148, pl. 7, fig. 8.

1937 *Spiriferella keilhavii* (von Buch); Frebold: 46, pl. 11, fig. 9.

1964 *Spiriferella keilhavii* (von Buch); Gobbett: 152, pl. 20, figs 8–10.

Diagnosis. Shell large for genus, transversely semicircular in outline, with acute to weakly alate cardinal extremities. Ventral interarea moderately high, nearly flat; delthyrium generally covered by pseudodeltidium. Sulcus shallow, mostly ornamented by median plica and lateral costae; fold narrow, highly elevated from lateral slopes, with median groove developing from dorsal beak. Lateral plicae relatively angular, generally costate and fasciculate. Micro-ornamenation composed of growth lamellae, capillae and minute pustules.

Lectotype. When *Spirifer wilczeki* was first proposed by Toula (1873), Toula did not select any specimen as the type material. Unfortunately, it has been confirmed that the only specimen figured by Toula (1873, pl. 1, fig. 3a, b; see also Fig. 4K, L) is missing. Therefore, we select a ventral valve (NHMW 2017/0119/0001) from among the seven syntypes remaining from the original collection as the lectotype. This specimen was originally collected from the Tokrossøya Formation in Sørkapp, Spitsbergen.

Other material. Forty-seven registered specimens from the Kapp Starostin Formation (Vøringen Member) in Spitsbergen (PMO A9880, PMO 227.384, NMV P340514–340555, KOPRIF10021–10023), comprising six conjoined shells, 37 ventral valves and four dorsal valves.

Description. Shell large for genus, 38.0–82.4 mm in width and 22.1–49.5 mm in length, 45.7 mm wide and 23.4 mm long in lectotype (Fig. 23). Outline transversely semicircular; shell width/length ratio variable, ranging from 1.337 to 2.275 with an average of 1.692. Maximum width always at hinge line; cardinal extremities acute to weakly alate.

Ventral valve weakly to moderately convex, with broad umbo and gentle lateral slopes. Ventral interarea moderately low and wide, slightly concave; delthyrium triangular, with delthyrial angle around 70°, generally covered by pseudodeltidium. Sulcus narrow to moderately wide, shallow, starting from beak and anteriorly forming ‘V’-shaped commissure line with fold, having weak to distinct median costa and less distinct lateral costae; sulcal tongue generally short but occasionally long and frequently geniculated. Ventral lateral slopes with five to six plicae on each side; plicae relatively angular and wide, originating from beak, each plica composed generally of three distinct costae (one median costa and two lateral costae); costae unequal in width, rounded, normally appearing at slightly anterior to umbonal region, forming distinct fascicles, lateral costae bifurcating on anterior part.

Dorsal valve relatively thin, less convex than to equally convex to ventral valve. Fold narrow, relatively angular, highly elevated, with median groove and anteriorly lateral costae; median groove distinct, starting at slightly anterior to beak. Dorsal lateral plicae angular, narrower than those of ventral valve, with relatively indistinct costae.

Micro-ornamentation rarely remained, composed of faintly developed capillae and concentric growth lamellae; pustules minute, 0.05–0.15 mm in diameter, 15–20 per 1 mm^2 on mid-valve, arranged on intersections of growth lamellae and capillae (Fig. 5G, H).

Ventral interior with strongly thickened posterior part; teeth stout, supported by strong dental plates; ventral adminicula buried by thickened apical callus.

Ctenophoridium transversely elliptical, with more than 30 platelets (Fig. 24C). Spiralia laterally directed, around 24 whorls in each side (Fig. 24F–Q).

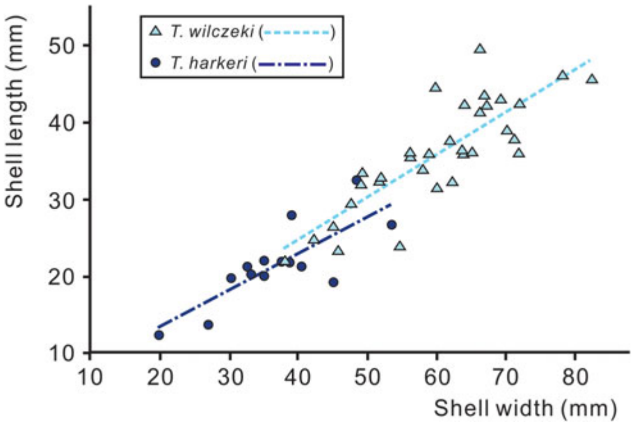

Figure 23. Shell measurements of two *Timaniella* species included in this study (fragmentary shells and only dorsal valves were excluded; see also Supplementary material 2).

Remarks. These large transverse shells sufficiently demonstrate all the key features of the genus *Timaniella*. In particular, both the transverse outline and costate plication are nearly identical to those in the type species, *T. festa* Barchatova, 1968. The morphological resemblance may indicate that *T. wilczeki* could be conspecific with *T. festa*. However, despite this possibility, we here separate these two species since the detailed morphology of the dorsal fold in *T. festa* has yet not been fully identified.

Spirifer wilczeki has been regarded as a junior synonym of *S. keilhavii* by most previous studies (Wiman 1914; Stepanov 1937; Gobbett 1964; Waterhouse & Waddington 1982). However, according to our re-examination of type specimens of both species, *T. wilczeki* is considerably different from genuine specimens of *S. keilhavii*, especially in having a much more transverse outline, higher interarea, more angular lateral plicae with common costation, and a single median costa in the sulcus.

Spiriferina keilhavii figured by Wiman (1914, pl. 2, figs 25–27, pl. 3, fig. 1) seems to be more similar to *T. wilczeki* in outline and the dorsal median groove; however, Wiman's specimen has more numerous (nine on each side) plicae but each is only feebly costate. In this regard, Wiman's specimen may be conspecific with *Timaniella* aff. *T. magniplicata* (not *magniplica*) of Angiolini & Long (2008) because both have relatively simple and narrow plicae, and further, these two species may indicate a possible transition from *T. wilczeki* to *T. harkeri* through the loss of plication and costation.

Timaniella wilczeki is stratigraphically limited to the Vøringen Member (late Artinskian–early Kungurian) in Spitsbergen, together with *A. polaris*. Interestingly, the morphologically closest species, *T. festa*, also occurs exclusively in a short stratigraphical interval (of late Kungurian age), thus pointing to a possible close ecological association and stratigraphical co-existence between *A. polaris* and *T. festa* in North Timan (Kalashnikov 1998). On the other hand, *T. wilczeki* has not been reported from the western part of the northern margin of Pangaea (e.g. Yukon and Canadian Arctic islands), contrasting with the common records of *A. polaris* across the region.

Occurrence. Vøringen Member (late Artinskian–early Kungurian) of the Kapp Starostin Formation as well as the Tokrossøya Formation in Spitsbergen.

Timaniella harkeri Waterhouse in Bamber & Waterhouse, 1971
(Figs 23, 27, 28)

1960 *Pterospirifer* sp. A Harker & Thorsteinsson: 69, pl. 21, figs 1–14.
1971 *Timaniella harkeri* Waterhouse in Bamber & Waterhouse: 220, pl. 26, figs 10–22.
1982 *Timaniella harkeri* Waterhouse; Waterhouse & Waddington: 32, pl. 8, figs 9–18.

Material. Fourteen specimens (NMV P340556–340569) comprising four conjoined shells and 10 ventral valves from the GSC locality 26406 on the Grinnell Peninsula, Devon Island.

Description. Shell medium in size, 19.8–53.4 mm in width and 12.2–32.4 mm in length (Fig. 23). Outline transversely pentagonal, with width/length ratio of 1.491–2.356, generally becoming more transverse in adult stage. Hinge line corresponding to maximum width; cardinal extremities relatively rounded in early growth stages but acute to alate in adults.

Ventral valve moderately convex, with maximum convexity at umbo. Ventral interarea relatively wide and high (occupying around one-third of ventral length), slightly concave, vertically striated; delthyrium triangular with delthyrial angle of 50–60°; pseudodeltidium commonly very rudimentary, only covering posterior tip of delthyrium, sometimes fused with apical callus. Sulcus narrow and shallow, weakly costate, with median groove, originating near beak; sulcal tongue mostly short, anteriorly forming very gentle commissure line. Ventral lateral slopes with four to five plicae on each slope; plicae slightly angular to rounded, weakening laterally, originating from beak, each plica with one to three costae; costae rounded, weakly developed.

Dorsal valve relatively thin, less convex than ventral valve. Fold moderately wide, relatively low and flat,

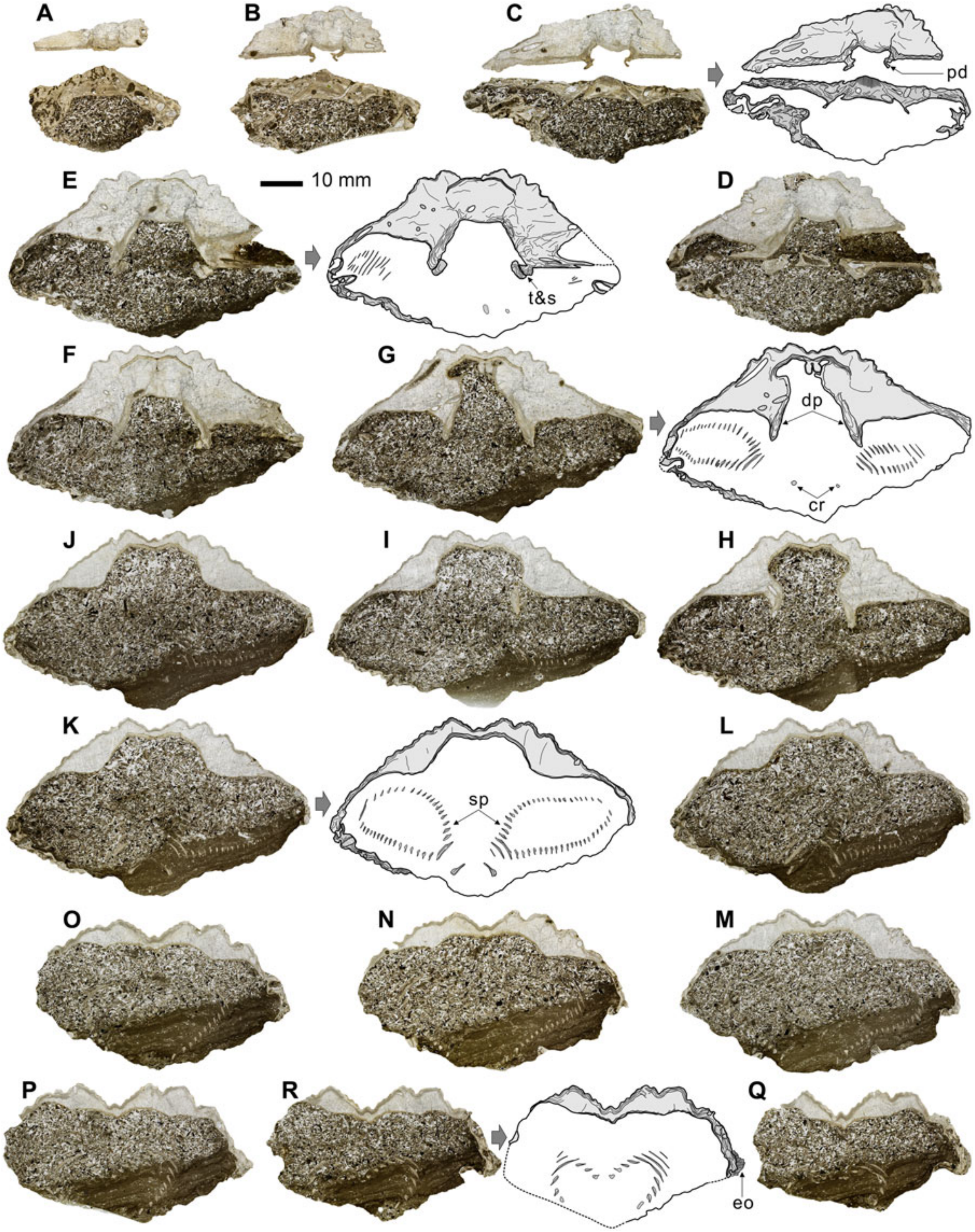

Figure 24. Serial sections of *Timaniella wilczeki* (Toula, 1873), NMV P340515. The interval between adjacent sections is approximately 1 mm. **Abbreviations: cr**, crura; **dp**, dental plates; **eo**, encrusting other organisms (coral?) on the lateral edge of the ventral valve; **pd**, pseudodeltidium; **sp**, spiralia; **t&s**, tooth and socket.

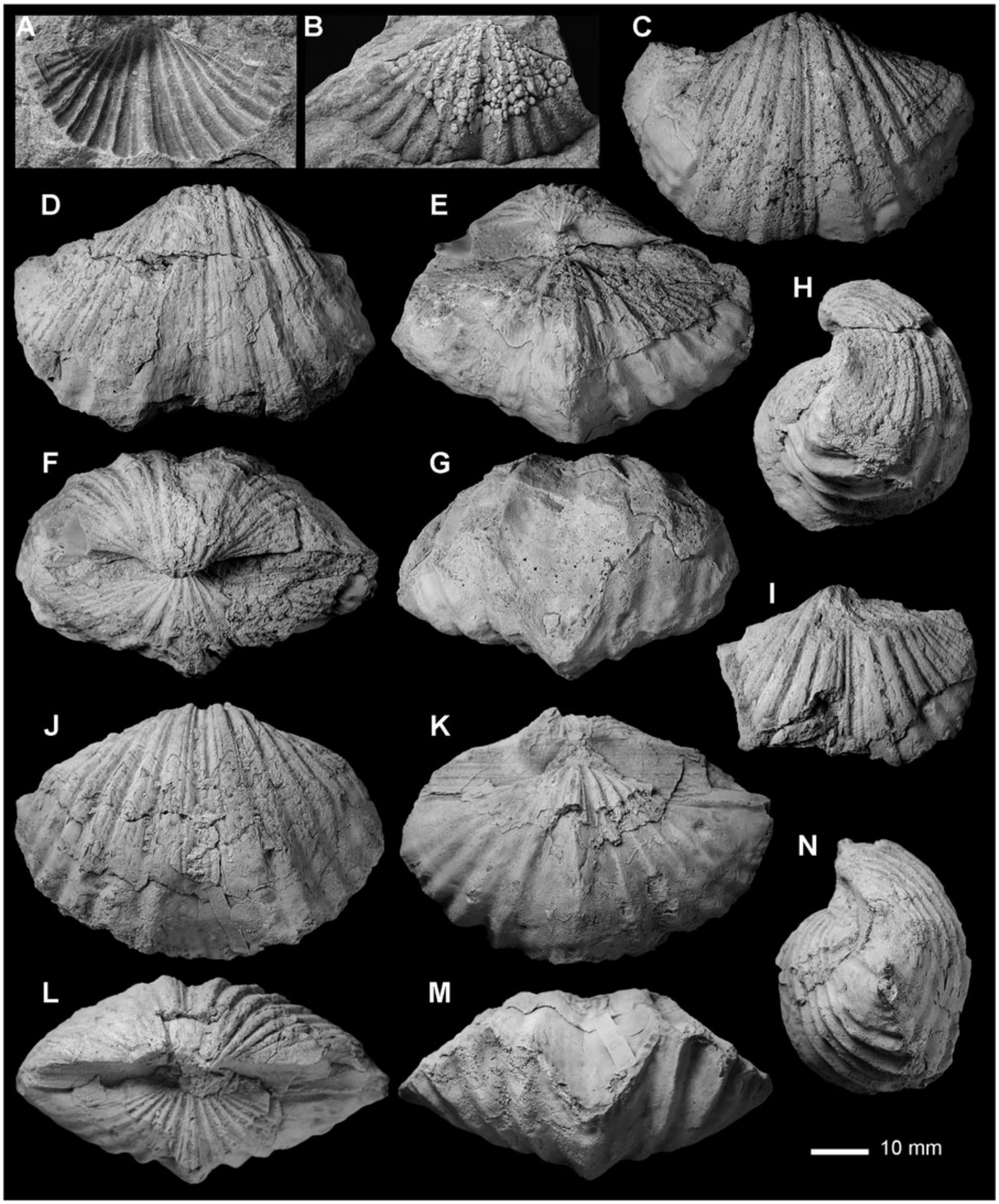

Figure 25. *Timaniella wilczeki* (Toula, 1873) from the Kapp Starostin Formation in Spitsbergen. **A,** lectotype (selected here), NHMW 2017/0119/0001, external mould of a ventral valve (photographed by Andreas Kroh); **B,** NHMW 2017/0119/0002, internal mould of a ventral valve, counterpart to NHMW 2017/0119/0001; **C,** NMV P340526, ventral view of a ventral valve; **D**–**H,** NMV P340514, ventral, dorsal, posterior, anterior and lateral views of a conjoined shell; **I,** NMV P340524, ventral view of a ventral valve; **J**–**N,** PMO A9880, ventral, dorsal, posterior, anterior and lateral views of a conjoined shell.

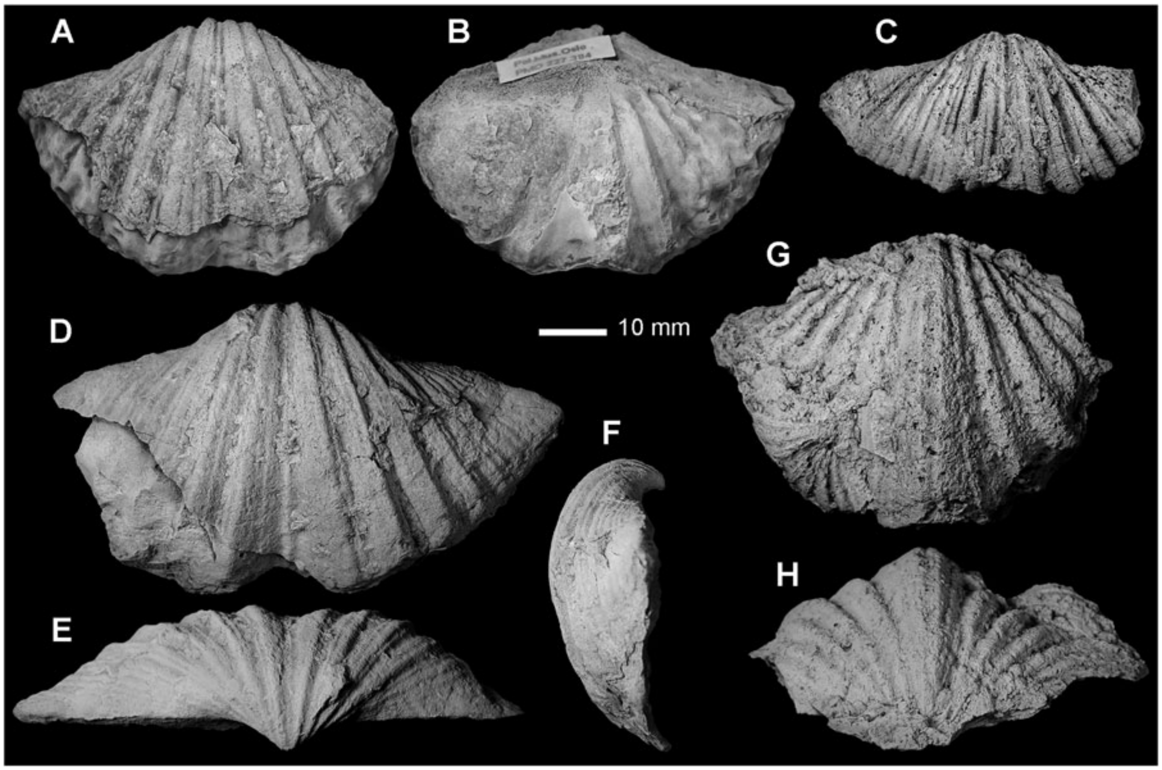

Figure 26. *Timaniella wilczeki* (Toula, 1873) from the Kapp Starostin Formation in Spitsbergen. **A, B,** PMO 227.384, ventral and dorsal views of a conjoined shell; **C,** NMV P340546, ventral view of a ventral valve; **D–F,** NMV P340520, ventral, posterior and lateral views of a ventral valve; **G, H,** NMV P340554, dorsal and posterior views of a dorsal valve.

smooth except median groove; median groove distinctly developed on fold crest; dorsal lateral plication and costation same as ventral ones.

Micro-ornamentation mostly indicated by growth lamellae, particularly on anterior of valve; pustules not preserved or absent.

Ventral interior with strongly thickened apical callus; teeth relatively strong, supported by short and low dental plates; dental flanges relatively large, divergent, ventral adminicula very low and usually buried by apical callus. Ventral muscle area semicircular and large (occupying around two-thirds of valve length), posteriorly bounded with thickened callus and adminicula, comprising narrow adductor scars medially located and wide and laterally located diductor scars; vascular markings radially developed around muscle area with numerous pits.

Dorsal interior with low crural plates and subhorizontal socket plates. Spiralia developed posterolaterally, with 17 whorls in each side (Fig. 27).

Remarks. The present species seems to be well matched with *Timaniella* in general morphological features including the strongly transverse outline, plicate shell surface with costation, and a distinct median groove on fold. Nevertheless, it displays several characteristics that distinctly separate it from other species of *Timaniella* (*T. festa* and *T. wilczeki*), such as simple to weakly costate lateral plicae, a median groove on the sulcus instead of a median plica, and absence of costation on the fold. *Timaniella convexa* Shi & Waterhouse, 1996 from northern Yukon, Canada, is identical to this species in these characteristics. As discussed above, *T. convexa* seems to have originated from another spiriferellid rather than from genuine *Timaniella*. If this scenario is followed, it is possible that *T. harkeri* might also have evolved from a different lineage. However, as discussed above, there are specimens that show a transition between *T. harkeri* and *T. wilczeki* (as well as *T. festa*), supporting a close relationship between these two species. One example of this possible transitional form is illustrated by the specimen figured as *S. keilhavii* by Wiman (1914, pl. 2, figs 25–27, pl. 3, fig. 1). This material has relatively simple lateral plicae, similar to those of *T. harkeri*, but a fold with lateral costae like those of *T. wilczeki*.

On the other hand, the strongly thickened apical callus and a convexly developed structure occupying at least the posterior part of the delthyrium in *T. harkeri* suggests considerable similarities to *Trigonotreta* König, 1825. Kalashnikov (1998) noted the strong similarity between *Timaniella* and *Trigonotreta* and regarded *Timaniella* as a trigonotretin genus. However, trigonotretine genera do not have pustules on their shell

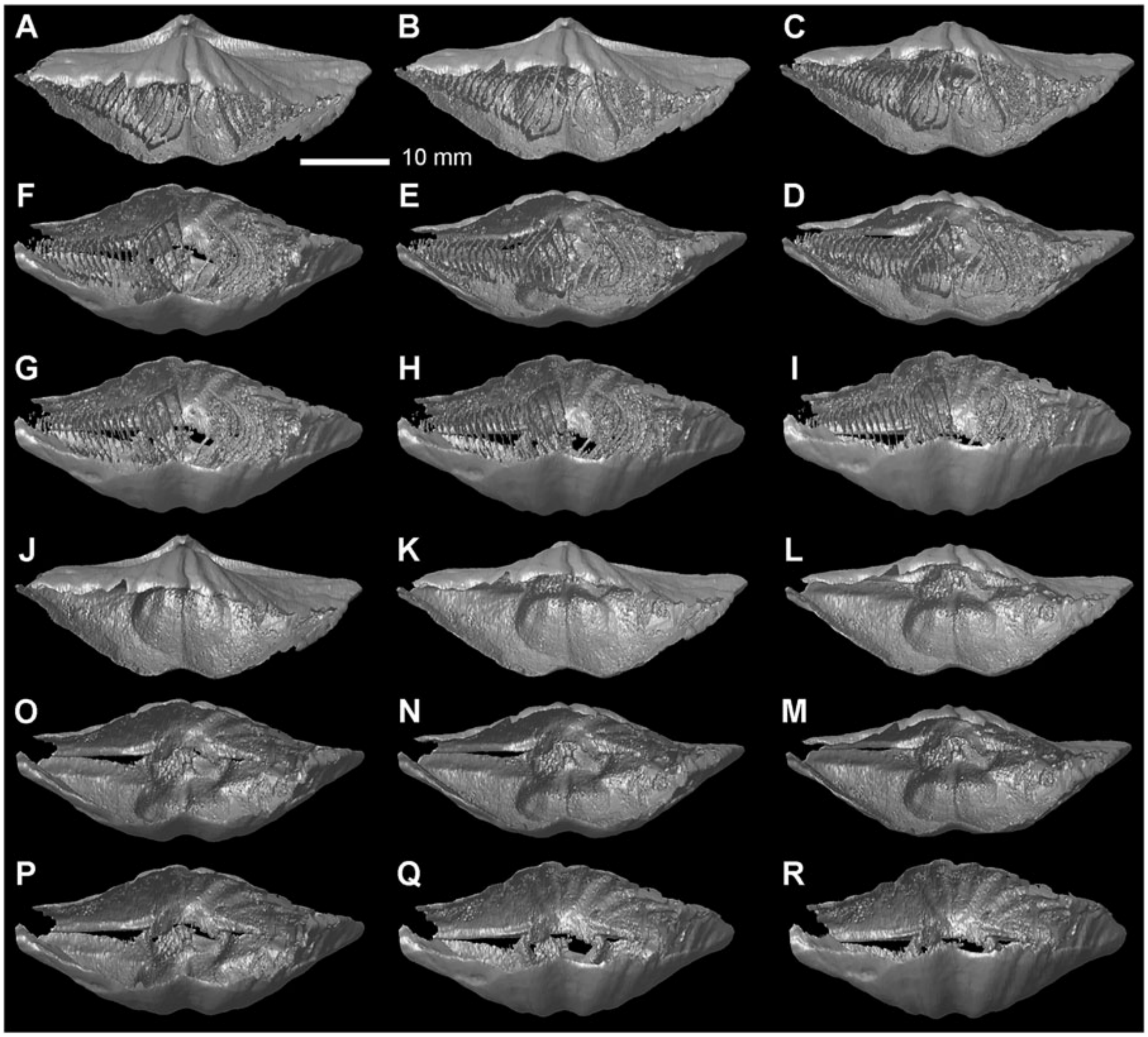

Figure 27. Reconstruction of the three-dimensional internal shell structure of *Timaniella harkeri* Waterhouse in Bamber & Waterhouse, 1971 (NMV P340556) through X-ray microtomographic scanning (see Lee *et al.* 2017). The anterior part of the shell is virtually eliminated to show the internal structure. **A**–**I,** dorsal and anterior views of the whole shell interior through posteriorly continuous rotation; **J**–**R,** dorsal and anterior views of the shell interior without spiralia through posteriorly continuous rotation.

surface, which is a feature unique to all spiriferellids including *Timaniella*.

Occurrence. Assistance Formation (Roadian), Canadian Arctic Archipelago; Saddlerochit Formation (Roadian), Yukon.

Conclusions

The study of the Permian spiriferellid brachiopods from Svalbard and adjacent regions, all located in the northern marginal shelf areas of Pangaea, has provided a significant opportunity to systematically revise and modernize the taxonomy of this diverse clade, along with the discovery of two new species: *Spiriferella protodraschei* and *Arcullina*? *enokiani*. Most notably, the taxonomic revision of all the important spiriferellid taxa from Svalbard, including *S. keilhavii*, *S. loveni*, *S. draschei*, *A. polaris* and *Timaniella wilczeki*, has revealed that both the types and distribution of shell micro-ornamentation (especially pustules) and the development of delthyrial coverings (pseudodeltidium and stegidia) are crucial features for tracing the evolutionary pathways of spiriferellid species in the Boreal Realm. This revision also suggests that *S. keilhavii* was an endemic species restricted to Bjørnøya and, possibly, central East Greenland, and was phylogenetically closest to *S. loveni*, a species that had attained a much wider distribution along the northern margin of Pangaea.

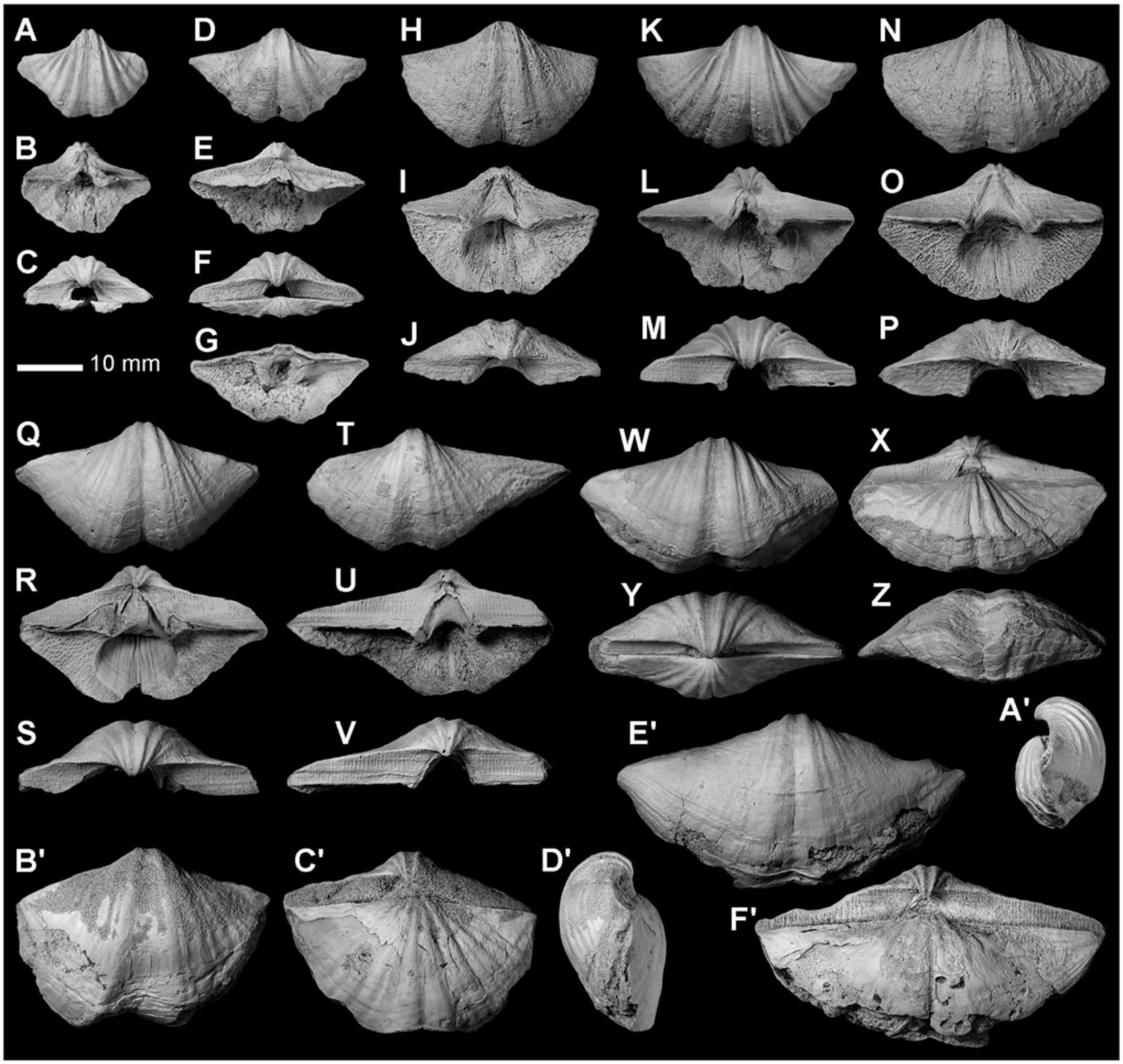

Figure 28. *Timaniella harkeri* Waterhouse in Bamber & Waterhouse, 1971 from the Assistance Formation of Devon Island, Arctic Canada. **A–C,** NMV P340560, ventral, dorsal and posterior views of a ventral valve; **D–G,** NMV P340561, ventral, dorsal, posterior and anterodorsal views of a ventral valve with posterior part of dorsal valve; **H–J,** NMV P340562, ventral, dorsal and posterior views of a ventral valve; **K–M,** NMV P340563, ventral, dorsal and posterior views of a ventral valve; **N–P,** NMV P340565, ventral, dorsal and posterior views of a ventral valve; **Q–S,** NMV P340566, ventral, dorsal and posterior views of a ventral valve; **T–V,** NMV P340567, ventral, dorsal and posterior views of a ventral valve; **W–A',** NMV P340556, ventral, dorsal, posterior, anterior and lateral views of a conjoined shell; **B'–D',** NMV P340557, ventral, dorsal and lateral views of a conjoined shell; **E', F',** NMV P340558, ventral and dorsal views of a conjoined shell.

The biostratigrapy of the spiriferellid species from the Kapp Starostin Formation in Spitsbergen displays two distinct spiriferellid assemblages stratigraphically bounded by the upper boundary of the Vøringen Member. The lower assemblage is represented by *A. polaris*, *T. wilczeki* and *S. protodraschei*, whereas the upper one is dominated by abundant *S. loveni*. This abrupt transition between the spiriferellid assemblages seems to be strongly linked to a palaeoclimatic shift from cool to cold conditions between the Vøringen Member and the overlying Svenskeegga member, and this climatic shift is inferred to have occurred most likely during the Kungurian. Similar transitions in spiriferellid assemblages have been detected from other areas along the northern margin of Pangaea, suggesting that the Kungurian cooling episode occurred extensively in the Boreal region.

It is evident that *S. loveni* flourished in northern Pangaea under the cold climate regime until the whole spiriferellid clade was wiped out by the end-Permian catastrophe. The abundance of this species in the Lopingian strata of central East Greenland indicates that the species migrated southward through the Zechstein seaway. The population of *S. loveni* in Greenland can be morphologically distinguished from its counterpart from Spitsbergen by its more costate shell surface. This modification in shell ornamentation is explained as a reponse (adaptation) to climatic warming as it migrated southward.

Supplemental material

Supplemental material for this article is available here: http://dx.doi.org/10.1080/14772019.2019.1570569.

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