Lower Permian bryozoans from southern and central Spitsbergen, Svalbard

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Bryozoans from the Lower Permian Treskelodden and Wordiekammen formations of southern and central Spitsbergen respectively, Svalbard, have been studied. Twenty species are identified, including one new genus, *Toulapora* gen. nov., with *Toulapora svalbardense* as type species and one new species, *Ascopora birkenmajeri* sp. nov. The taxonomic composition is typical Lower Permian, with species in common with Timan-Pechora and the Urals (Russia) and Ellesmere Island (the Canadian Arctic). Growth habits reflect a moderately to deeper shelf environment.

Key words: Bryozoa, Permian, Spitsbergen, Arctic.

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Introduction

The bryozoans described here are from strata representing the two Lower Permian marine formations on Spitsbergen (Svalbard): the Treskelodden Formation and Wordiekammen Formation (Figs. 1, 2).

The Treskelodden Formation in the Hornsund area (south Spitsbergen) is 120 m thick succession of fossiliferous shallow-marine clastic sediments deposited under relatively dynamic-water conditions on the continental shelf, as indicated by palaeontological and sedimentological data (Birkenmajer 1979, 1984; Fedorowski 1982; see also Dallmann 1999).

The studies of foraminifers and bryozoans were carried out using thin sections from samples collected through the Treskelen and Hyrnefjellet sections (Figs. 3, 4).

Foraminiferal assemblages consisting of 23 genera and 58 species were recovered in the formation and three biostratigraphical assemblage zones: *Pseudofusulinella occidentalis*, *Midiella ovata–Calcitornella heathi*, and *Hemigordius arcticus–Hemigordius hyrnensis* were recognised for regional and interregional correlation (Błażejowski 2008, 2009).

Detailed taxonomic and stratigraphic analysis of foraminifers dated the Treskelodden Formation as Gzhelian–Artinskian (Błażejowski et al. 2006; Błażejowski and Gaździcki 2007; Błażejowski 2009).

Additional material from the time-equivalent Wordiekammen Formation of central Spitsbergen has also been prepared for the current study to aid identification of bryozoan species. The Gipsvika section (Figs. 1, 2), inner Isfjorden area (Asselian–Sakmarian, Tyrrellfjellet Member), sampled by Mari Skaug for a university thesis work in the early 1980s (Skaug 1982), yielded a bryozoan fauna with many components similar to the Hornsund material. The Tyrrellfjellet Member here – the "Limestone B" – see Skaug (1982: 22) and Gee et al. (1953) contains 10–14 fining-upwards sequences each 0.5 to 7 m thick. Bioturbation is common, and the carbonate texture varies from mudstone to grainstone, with common crinoid and brachiopod grains. Well preserved brachiopods, like *Tornquistia forbesi* (Gobbett 1963) and *Cancrinella singletoni* Gobbett 1963 are locally common (Skaug 1982), often in life position. Other brachiopods are present with their spines preserved. The depositional environment is considered to reflect near-shore migrating carbonate shoal sands outside more lagunal settings.

The Gipsvika material is well dated by fusulinaceans (Nilsson 1988, 1993) and conodonts (Nakrem et al. 1992). A rich bryozoan fauna from this area was described by Nakrem (1994a) and some material from that publication has been re-investigated in the current work.

The bryozoans from the Treskelodden Formation were collected in 1997 by AG and Andrzej Kaim and in 2005 by BB and AG.

Institutional abbreviations.—PMO, palaeontological collection Natural History Museum, University of Oslo, Norway; ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

Other abbreviations.—CV, coefficient of variation (SD*100/X); MAX, maximal value; MIN, minimal value; N, number of zoaria measured; n, number of measurements taken; SD, sample standard deviation; X, mean value.

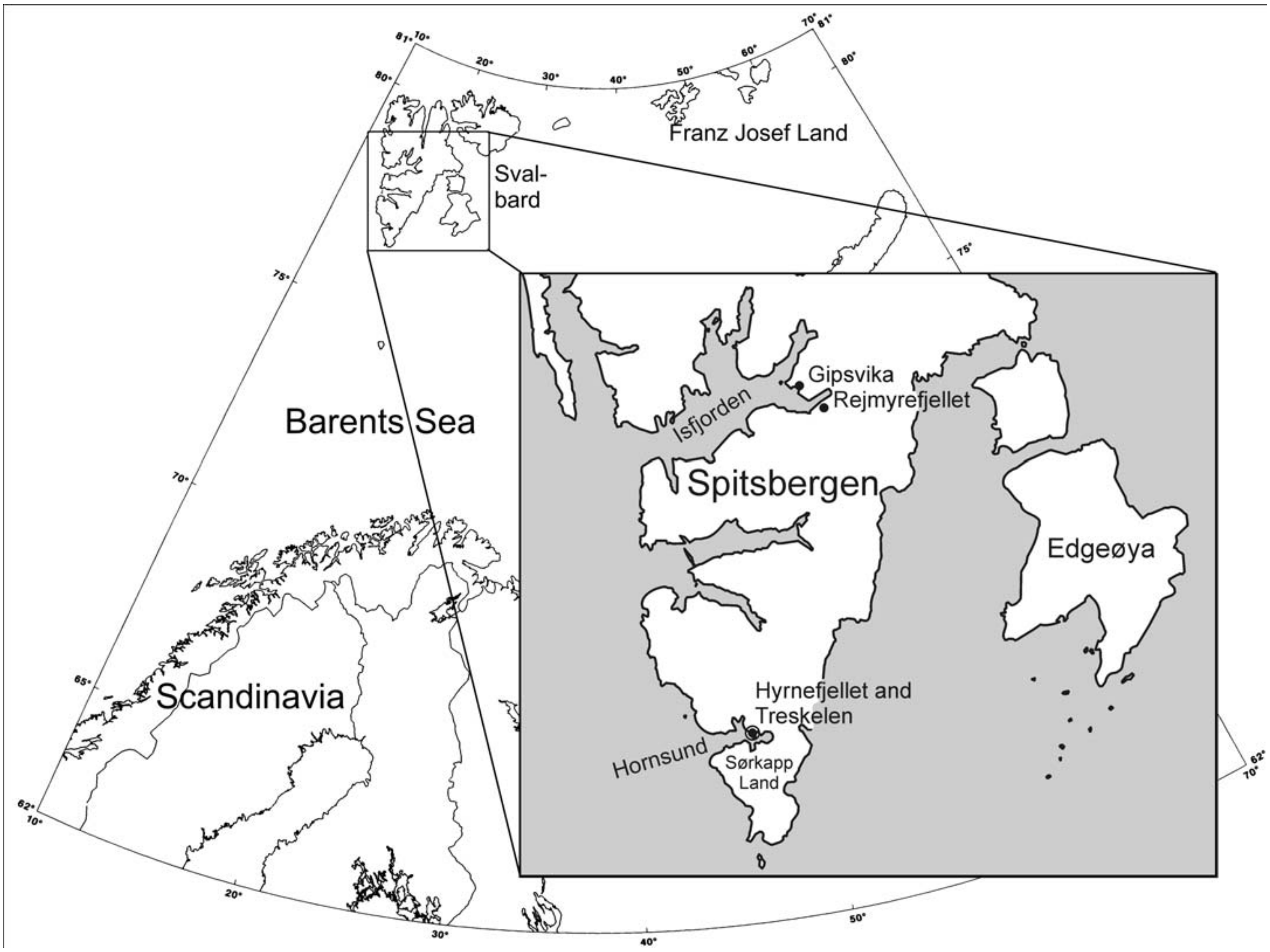

Fig. 1. Map of Svalbard with localities mentioned in the text.

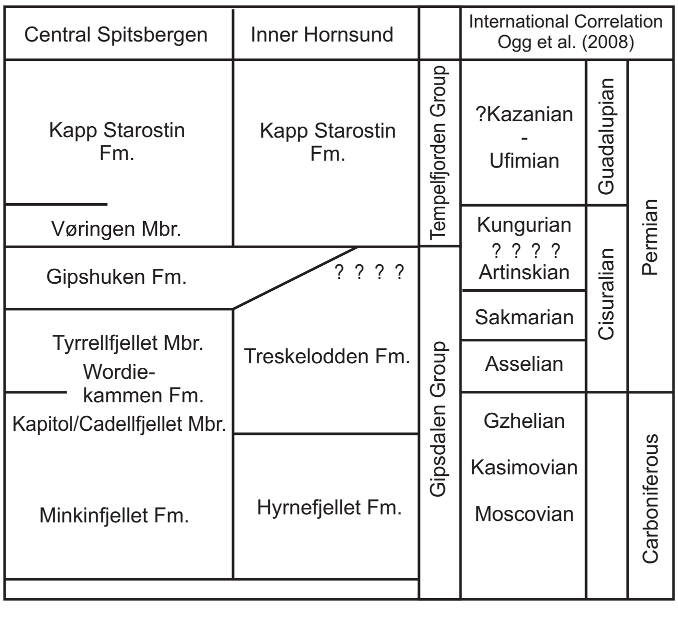

Fig. 2. Lithostratigraphy of Hornsund area and inner Isfjorden area (emended from Dallmann 1999).

Material and methods

The majority of information used in this study comes from field observations and descriptions of two outcrop localities, Hyrnefjellet and Treskelen, representing approximately 150 m of strata, along the fjord Hornsund. More than 50 samples were collected for laboratory examination. Stratigraphic placement of samples is indicated in Figs. 3 and 4 (lithostratigraphic logs for Treskelen and Hyrnefjellet); these sample numbers are also used in the systematic description of individual taxa. Samples Br.12/G14–G16 are scree samples (loose material) from Hyrnefjellet.

Bryozoans were identified from standard petrographic thin sections, in many cases not providing the desired orientations for proper bryozoan identification. Some samples were subsequently thin sectioned in Oslo to obtain oriented views of the bryozoans. 46 thin sections were made from these samples. Acetate peels were made initially from most samples, but did not always give enough details due to partly silicification of the fossil contents.

Samples from Gipsvika were thin-sectioned after preparation of acetate peels revealed problematic dolomitisation and silicification of some of the bryozoans. 73 oriented thin sections were made from a carbonate rich interval with visible, but rock embedded bryozoans.

Bryozoan distribution

Treskelen.—The lowermost part of the Treskelen section (see Fig. 3) contains only two bryozoans identifiable to species level, *Rectifenestella submicroporata* and a species questionably identified as *Rhombotrypella* cf. *arbuscula*. The former species has an Asselian distribution in Russia, whereas the latter has a younger Artinskian–Kungurian distribution. Slightly higher in the same section Sakmarian species like *Coscinium cyclops* and *Ascopora sterlitamakensis* are present. The bryozoans in general support the biostratigraphic dating for this unit based on small foraminiferans (Błażejowski 2008).

Hyrnefjellet.—As for the Treskelen section, Sakmarian species like *Coscinium cyclops* and *Ascopora sterlitamakensis* are present in lower part of the Hyrnefjellet section. These bryozoans support the biostratigraphic dating for this part based on small foraminiferans. *Ascopora magniseptata*, occurring near the Sakmarian–Artinskian transition in the Hyrnefjellet section has a Gzhelian distribution in its type area in the Urals, and thus has a significantly younger distribution in Svalbard.

Gipsvika.—The bryozoans identified from the Gipsvika section have a general Sakmarian affinity. *Coscinium cyclops* has its first appearance in the late Asselian (Nenets Horizon), but is more common in the Sakmarian–Artinskian (Komichan Horizon) of Timan-Pechora and the Urals (Morozova and Kruchinina 1986). *Ascopora grandis* and *Ascopora sterlitamakensis* have a Sakmarian distribution of Timan-Pechora and the Urals, whereas *Ascopora magniseptata* has a Gzhelian distribution. *Rectifenestella submicroporata* is known from the Asselian of the Urals, *Fabifenestella quadratopora* is known from the Sakmarian of the Urals, whereas *Rectifenestella nikiforovae* has a Sakmarian– Artinskian distribution of northern Urals and Timan-Pechora, Russia. This species is also known from the Lower Permian of China. Nakrem (1994a) reported the following additional species from the Gipsvika section: *Rectifenestella microporata* (known from the Sakmarian of the Urals and the Artinskian of Ellesmere Island) and *Polypora martis* (known to have a wide Late Carboniferous–Early Permian distribution).

Systematic palaeontology

Order Cystoporida Astrova, 1964

Family Fistuliporidae Ulrich, 1882

Fistuliporidae indet.

Fig. 5A–C.

Material examined.—Treskelen, sample ZPAL Br. 12/Cr. 55, PMO 170.908A-D.

Remarks.—Varying parts of encrusting zoaria of *Fistulipora*-like bryozoans were observed in several thin sections. Morphological characters include short tubular autozooecia budding from substrate and bending at their bases towards the colony surface, slightly oval apertures with well developed lunaria, and small vesicles arranged usually in 2–3 rows between autozooecia. Due to insufficient material a more precise identification cannot be presented.

Family Hexagonellidae Crockford, 1947

Genus *Coscinium* Keyserling, 1846

Type species: *Coscinium cyclops* Keyserling, 1846, Early Permian of Timan, Russia.

Coscinium cyclops Keyserling, 1846

Figs. 6A–E, 8A, 10H.

Material examined.—Measurements based on 10 zoaria in the following samples: Hyrnefjellet (scree), thin sections PMO 170.892A-B, as well as 11 thin sections from samples ZPAL Br. 12/H10, G16; Treskelen, sample ZPAL Br. 12/Cr. 55, thin section PMO 170.908B and one thin section ZPAL Br. 12/Cr. 55; Gipsvika, thin sections PMO 170.919A-G.

Description.—Bifoliate frondescent colonies with oval and circular fenestrules and anastomosing branches with zooecia opening on both sides of branches. The branches are lens-shaped in cross section being bifoliate compressed perpendicular to branch surfaces. Width of branches varies between 2.86 and 3.00 mm, thickness 1.53–2.51 mm. The fenestrules are 2.00–2.81 mm long and 1.66–1.92 mm wide. Vesicular, blister-like tissue is developed between autozooecial tubes. Massive stereom is developed near colony surface. Apertures are ovate in outline being 0.22–0.23 mm long and 0.16–0.20 mm wide. The apertures carry a weakly developed lunarium. There are about 3.5–5 apertures along colony per 2 mm and 4.5–5 diagonally. Distance between apertural centers is about 0.40–0.55 mm.

Remarks.—The current material, as well as previously described material from Gipsvika (Nakrem 1994a) closely resemble the description and measurements of *C. cyclops* from the Asselian–Artinskian of Timan (Morozova and Kruchinina 1986). *Coscinium hermidensis* Ernst and Minwegen 2006, from the Late Carboniferous of Spain (Ernst and Minwegen 2006) differs from *C. cyclops* only in having slightly narrower fenestrules (0.9 mm wide) and may be a synonym of *C. cyclops*.

Measurements.—See Table 1.

Stratigraphic and geographic range.—First appearance in the late Asselian, more common in the Sakmarian–Artinskian of Timan-Pechora, Russia and Lower Permian the Urals (Morozova and Kruchinina 1986). Occurrence on Svalbard:

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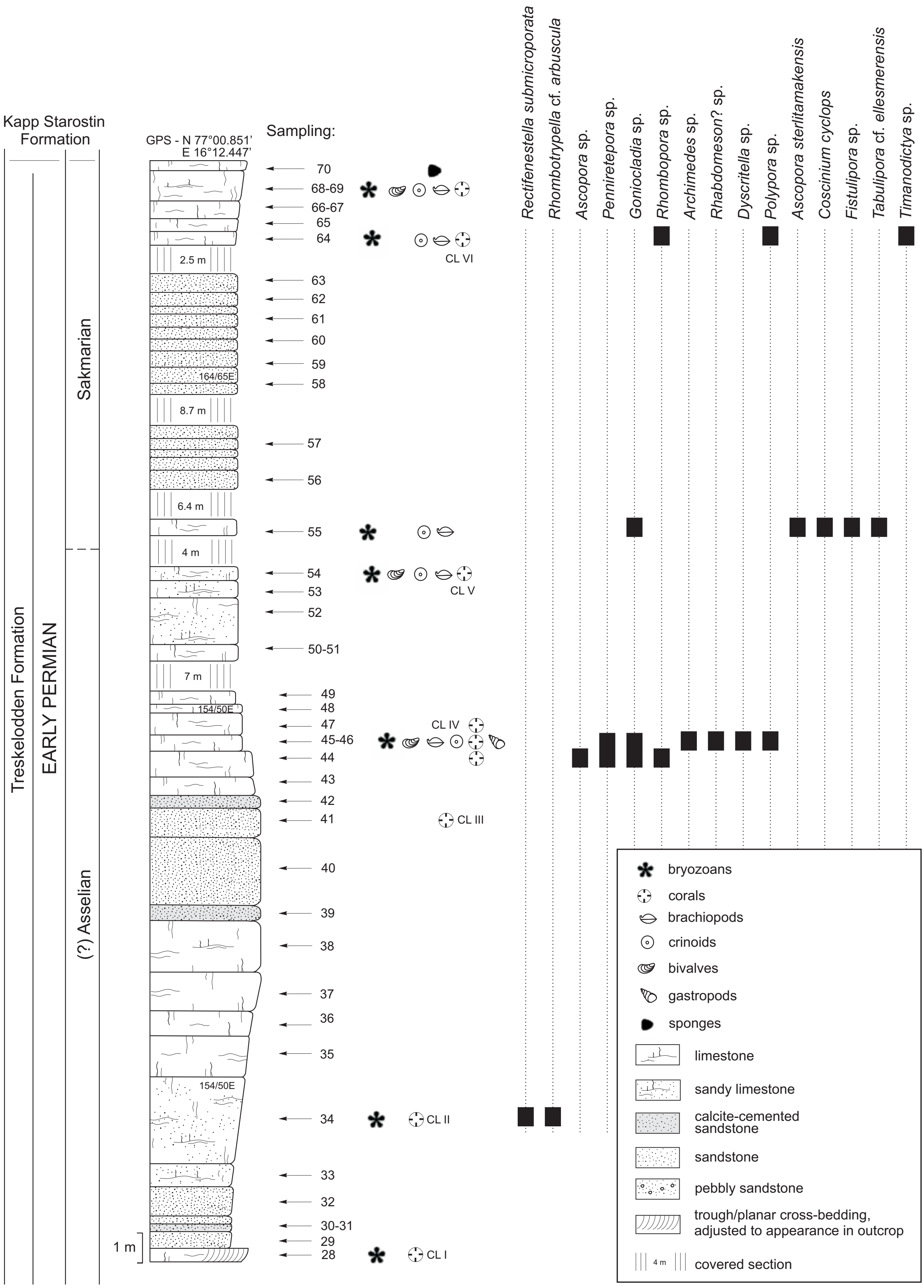


Fig. 3. Lithological log and distribution of bryozoans through the Treskelen section.

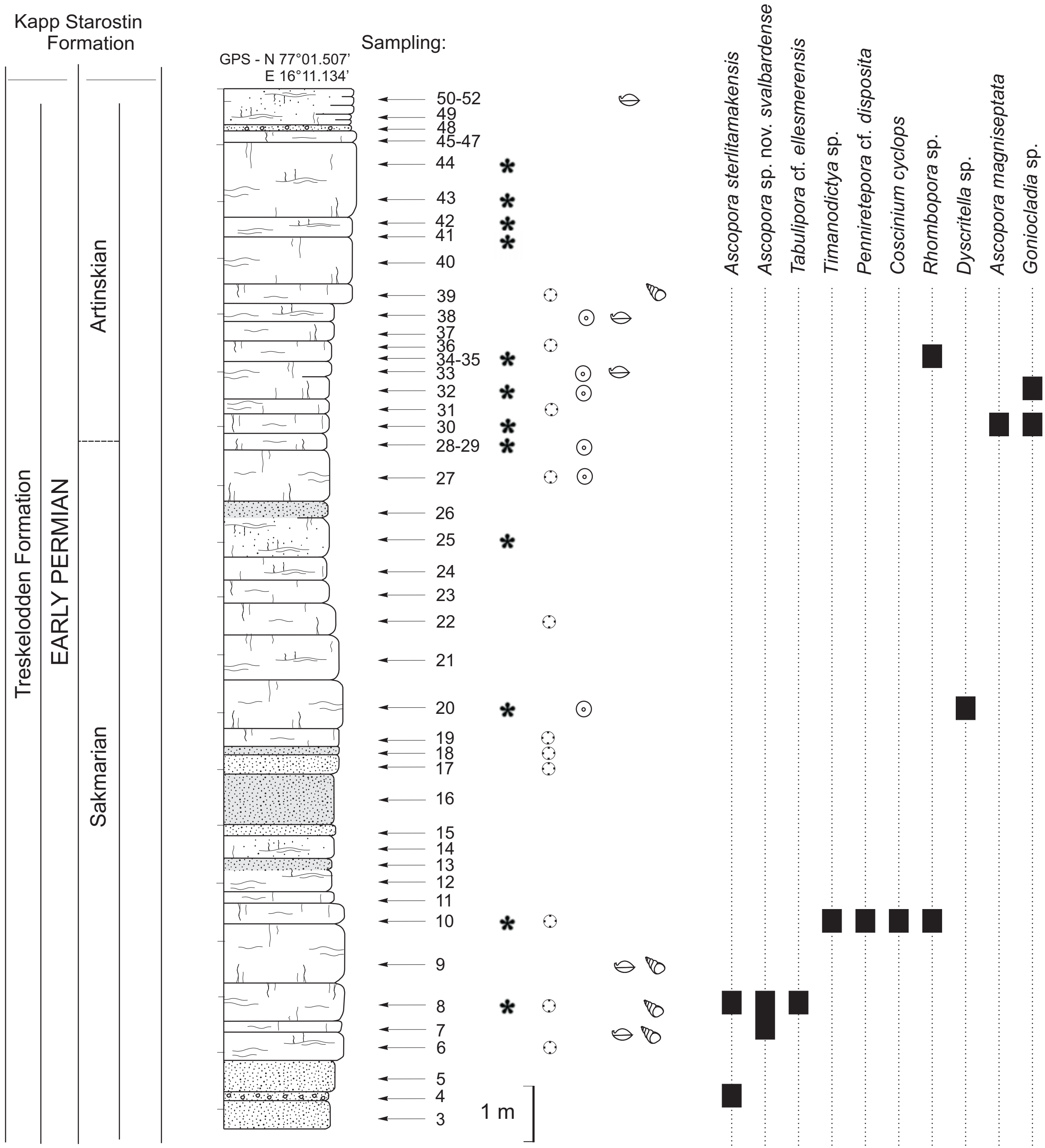


Fig. 4. Lithological log and distribution of bryozoans through the Hyrnefjellet section. Legend as in Fig. 3.

Asselian–early Sakmarian, middle-upper part of the Tyrrellfjellet Member, and the Treskelodden Formation.

Genus *Goniocladia* Etheridge, 1876

Goniocladia sp.

Fig. 5D–E.

Material examined.—Hyrnefjellet, samples and three thin sections ZPAL Br. 12/H10, H30, H32, ; Treskelen, samples and three thin sections ZPAL Br. 12/Cr. 44, Cr. 45, Cr. 55.

Remarks.—Fragments of *Goniocladia* are only observed in oblique sections, and specific identification is not possible

Order Trepostomida Ulrich, 1882

Family Crustoporidae Dunaeva and Morozova, 1967

Diagnosis (from Astrova 1978, translation by D.A. Brown).—Zoaria laminar, unilamellar, sometimes bilamellar-symmetrical, tabulate, and branching. Zooecial orifices rounded-polygonal, circular or oval. Walls in the exozone weakly, and sometimes unevenly thickened, fused, with longitudinally-fibrous and obliquely-laminar microstructure. Diaphragms incomplete, less frequently complete. Exilazooecia numerous, their accumulation frequently forming maculae. Acanthozoocia uniform, commonly small, sometimes absent.

Table 1. Measurements of *Coscinium Cyclops*. Abbreviations: CV, coefficient of variation (SD*100/X); MAX, maximal value; MIN, minimal value; N, number of zoaria measured; n, number of measurements taken; SD, sample standard deviation; X, mean value.

Coscinium cyclops (N = 10)	n	X	SD	CV	MIN	MAX
Branch width	12	2.879	0.440	15.265	2.24	3.50
Branch thickness	28	1.895	0.521	27.496	1.20	2.90
Fenestrule length	23	2.712	0.426	15.728	2.00	3.75
Fenestrule width	23	1.889	0.270	14.281	1.55	2.60
Aperture spacing along	24	0.482	0.081	16.751	0.34	0.60
Aperture spacing diagonally	24	0.404	0.049	12.053	0.34	0.50
No. apertures/2 mm along					3.3	5.9
No. apertures/2 mm diagonally					4.0	5.9
Aperture length	22	0.225	0.011	4.883	0.20	0.24
Aperture width	22	0.165	0.010	6.132	0.15	0.20
No. of zooecial rows on branch	12	10.3	0.9	8.6	9	12

Genus *Toulapora* nov.

Etymology: The genus name is erected in honour of the Austrian palaeontologist Franz Toula (1845–1920), who conducted the first thorough investigation and description of fossil Bryozoa from Svalbard. Through the years 1873–1875 he published three papers on "Permo-Carbon-Fossilien" from southern and western Spitsbergen, and he described many new species.

Type species: *Toulapora svalbardense* (Nakrem, 1994a) from the Asselian–early Sakmarian, middle-upper part of the Tyrrellfjellet Member, Rejmyrefjellet, Spitsbergen.

Diagnosis.—Encrusting unilamellar zoaria. Zooecial walls evenly thickened, not beaded, at places crenulated. Autozooecial apertures oval, rounded, indented by a row of small acanthostyles. Diaphragms thin, usually absent, or extremely rare. Exilazooecia, without diaphragms, commonly distributed around each autozooecium. Acanthostyles of two sizes; sparcely distributed large ones, and a row of regularly distributed small ones inflecting each zooecial aperture; both types with a clear central calcitic rod. Zooecial walls laminated.

Comparison.—*Toulapora* is superficially similar to *Hinaclema* Sakagami and Sugimura, 1987 first described from the Early Carboniferous (Viséan) of Japan, subsequently reported from the Viséan of Uzbekistan (Schastlivtseva 1991) and the Tournaisian of Mongolia (Gorjunova 1996). Diagnostic characters of *Hinaclema* include lamellar or multilamellar encrusting zoarium with hollow axial area, thin endozone and absence of diaphragms in auto- and exilazooecial tubes, (large) acanthostyles of one size present (Sakagami and Sugimura 1987). Sakagami and Sugimura (1987) also mention "Other very small 'acanthoecia' (micropore?) … nearly not observable" in the type species *Hinaclema hinaensis* Sakagami and Sugimura, 1987, but these are not visible in their illustrations, and if present are clearly different from the row of small acanthostyles bordering each aperture in *Toulapora*.

Remarks.—*Toulapora* is tentatively placed in family Crustoporidae Dunaeva and Morozova, 1967, as suggested for *Hinaclema* by Schastlivtseva (1991), but contrary to the original placement of *Hinaclema* in family Heterotrypidae Ulrich, 1890 by Sakagami and Sugimura (1987). *Toulapora* deviates from the diagnosis of Crustoporidae in having both large and small acanthostyles and in the scarcity of zooecial diaphragms.

It can be added that Gorjunova (1996) in a revision of *Hinaclema* placed that genus within the order Cystoporida, suborder Ceramoporina. In the same publication she also pointed out that the Svalbard material published as *Hinaclema svalbardensis* Nakrem, 1994a should not be placed within genus *Hinaclema*.

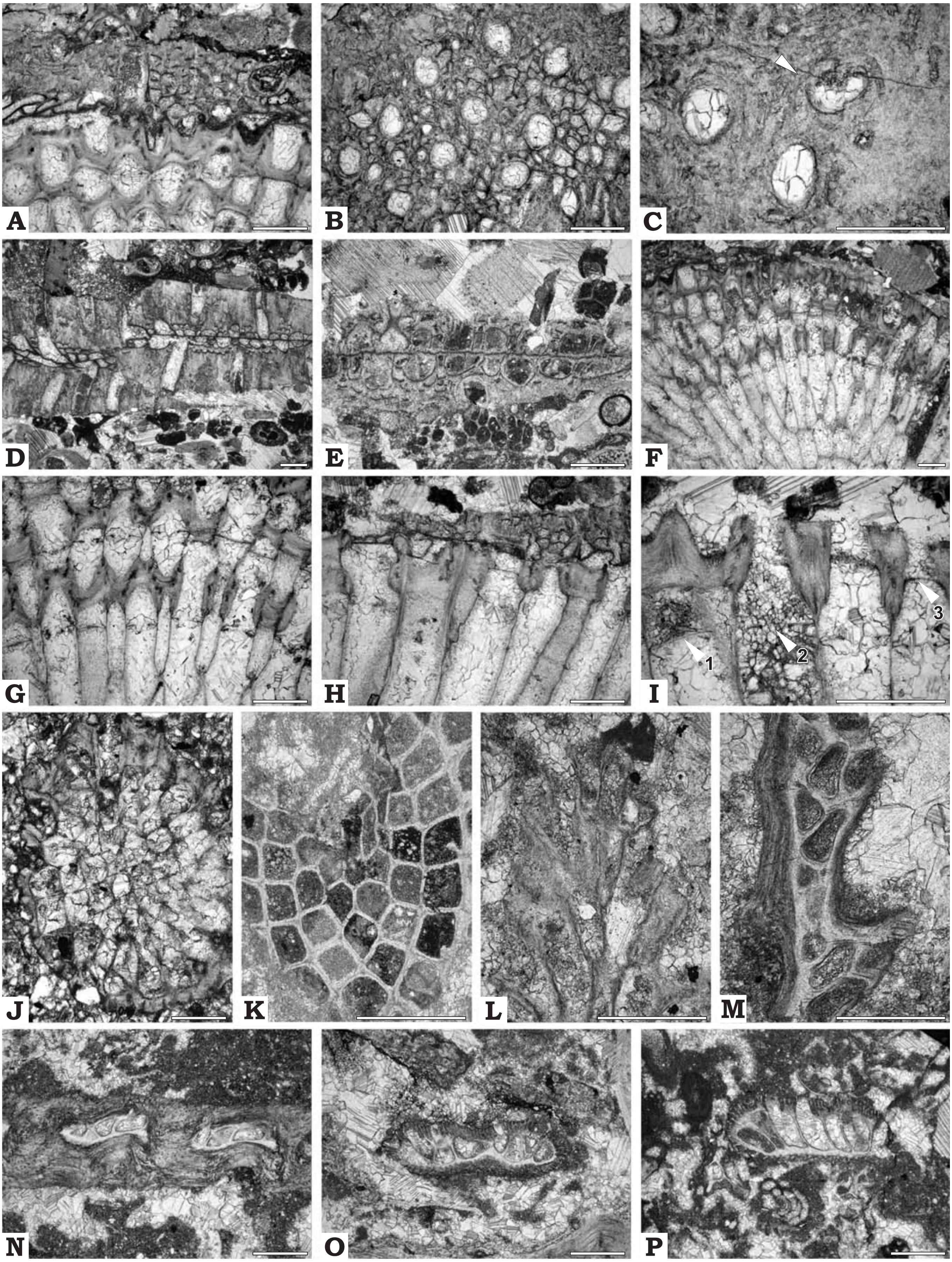
Stratigraphic and geographic range.—Lower Permian of central Spitsbergen (Svalbard): Tyrrellfjellet Member (Wordiekammen Formation) of Sakmarian age, and upper part of the Gipshuken Formation of late Artinskian age.

Toulapora svalbardense (Nakrem, 1994a)

Fig. 9A–I.

1994a *Hinaclema svalbardensis* sp. nov.; Nakrem 1994a: 65–66, figs. 8D–H, 9.

Fig. 5. Lower Permian bryozoan from Treskelen, Svalbard. **A**–**C**. Fistuliporidae indet. **A**. Encrusting colony on *Tabulipora* sp. Sample ZPAL Br. 12/Cr. 55, PMO 170.908C. **B**. Tangential section, encrusting colony on *Tabulipora* sp. Sample ZPAL Br. 12/Cr. 55, PMO 170.908B. **C**. Tangential section, arrow head points at lunarium. Sample ZPAL Br. 12/Cr. 55, PMO 170.908B. **D**, **E**. *Goniocladia* sp. **D**. Transverse section. Sample ZPAL Br. 12/Cr. 55, PMO 170.908B. **E**. Transverse section. Sample and thin section ZPAL Br. 12/Cr. 55a. **F**–**I**. *Tabulipora* sp. **F**. Transverse section. Sample ZPAL Br. 12/Cr. 55, PMO 170.908C. **G**. Transverse section. Sample ZPAL Br. 12/Cr. 55, PMO 170.908C. **H**. Transverse section. Sample ZPAL Br. 12/Cr. 55, PMO 170.908D. **I**. Oblique longitudinal sections. White arrow heads point at basal diaphragm (1), perforation in basal diaphragm (2), and terminal diaphragm (3). Sample ZPAL Br. 12/Cr. 55, PMO 170.908D. **J**. *Rhombotrypella* sp. Transverse section. Sample and thin section ZPAL Br. 12/Cr. 34. **K**. *Rhabdomeson*? sp. Oblique section. Sample and thin section ZPAL Br. 12/Cr. 46. **L**. *Rhombopora* sp. Longitudinal section near colony growth tip. Sample and thin section ZPAL Br. 12/Cr. 44. **M**. Penniretepora sp. A. Deep tangential sections. Sample and thin section ZPAL Br. 12/Cr. 44. **N**. *Archimedes* sp. Transverse section. Sample and thin section ZPAL Br. 12/Cr. 45. **O**. *Polypora* sp. Transverse section. Sample and thin section ZPAL Br. 12/Cr. 45. **P**. *Polypora* sp. Oblique longitudinal section. Sample and thin section ZPAL Br. 12/Cr. 45. Scale bars 0.4 mm. →



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1994b ?*Hinaclema* sp.; Nakrem 1994b: fig. 2d.

Type material: Holotype REF-4–15.0m, PMO A42600/1 (petrographic thin section); paratypes REF-4–15.0m, PMO 138.126 (rock specimen) and PMO A42600/2-4 (petrographic thin sections) all from the Rejmyrefjellet locality; thin sections PMO 170.941 and 170.942 from the Gipsvika (Sakmarian) locality.

Type locality: Rejmyrefjellet, Spitsbergen.

Type horizon: Gipshuken Formation, 15 m below the top of the formation, late Artinskian.

Material examined.—Measurements based on 9 zoaria in the following samples: Gipsvika (Sakmarian), thin sections PMO 170.929, 170.941, 170.942; Rejmyrefjellet (Artinskian), 15 m below top of the Gipshuken Formation, thin sections PMO A42600/1-4, 138.126. Oblique zoaria in a sample from the Tyrrellfjellet Member at Rejmyrefjellet were not measured (thin section 138.124).

Diagnosis.—As for genus.

Description (emended from Nakrem 1994a).—Zoarium encrusting, encrusting layer 0.44–0.80 mm in thickness. The endozone is indistinguishable from the exozone. The autozooecia meet zoarial surface at about 90° in longitudinal section (exozonal part); proximal (endozonal) portion of zooecia sometimes are oriented parallel to zoarial growth direction. Rare diaphragms observed in autozooecia, not in exilazooecial tubes. Zooecial walls are evenly thickened, not beaded, but at places crenulated; a dark central zone is visible in deep tangential section. The zooecial apertures are oval, 0.17–0.24 mm long and 0.13–0.17 mm wide. Distance between centers of adjacent apertures usually 0.24–0.30 mm in all directions. Abundant exilazooecia, average 0.038 mm long and 0.033 mm wide are developed between autozooecia. 12–16 small acanthostyles, average 0.014 mm in diameter are developed around each autozooecial aperture. Scattered larger acanthostyles average 0.075 mm in diameter; but up to 0.10 mm in shallowest section, are also developed, 0–3 per autozooecial aperture.

Measurements.—See Table 2.

Stratigraphic and geographic range.—Sakmarian–late Artinskian, upper part of the Tyrrellfjellet Member of the Gipsvika section, and the upper part of the Gipshuken Formation of the Rejmyrefjellet section.

Family Stenoporidae Waagen and Wentzel, 1886

Genus *Tabulipora* Young, 1883

Type species: *Cellepora urii* Fleming, 1828, Early Carboniferous of Scotland.

Tabulipora sp.

Fig. 5F–I.

Material examined.—Hyrnefjellet, sample ZPAL 12/H8, thin section PMO 170.950A; Treskelen, sample ZPAL Br. 12/Cr. 55, thin sections PMO 170.908A-D.

Remarks.—The identification is based on one fairly large zoarium displaying irregular branching growth with a colony diameter <10 mm. The exozone is very narrow, 0.40–0.57 mm wide. There is constantly one (rarely two) perforated diaphragm in the inner exozone. Both large and small acanthostyles are present. Measurements resemble those presented for *Tabulipora ellesmerensis* Sakagami, 1998, described from the Lower Permian of Ellesmere Island (Arctic Canada).

Genus *Rhombotrypella* Nikiforova, 1933

Type species: *Rhombotrypella astragaloides* Nikiforova, 1933, Middle Carboniferous of the Donetz Basin, Ukraine.

Rhombotrypella sp.

Fig. 5J.

Material examined.—Treskelen, sample and one thin section ZPAL Br. 12/Cr. 34.

Remarks.—Only a single oblique cross section of a *Rhombotrypella* colony was observed being 1.7 mm in diameter with an exozone width of 0.28 mm and an endozone 1.10 mm in diameter. Zooecial apertures may be estimated from the oblique section to be about 0.20 × 0.14 mm. Square zooecial tubes in

Table 2. Measurements of *Toulapora svalbardense*. Abbreviations: CV, coefficient of variation (SD*100/X); MAX, maximal value; MIN, minimal value; N, number of zoaria measured; n, number of measurements taken; SD, sample standard deviation; X, mean value.

Toulapora svalbardense (N = 9)	n	X	SD	CV	MIN	MAX
Encrusting layer thickness	16	0.656	0.111	16.874	0.44	0.80
Aperture length	22	0.207	0.027	12.870	0.17	0.24
Aperture width	22	0.148	0.014	9.558	0.13	0.17
Distance between aperture centers along	24	0.295	0.038	12.899	0.24	0.36
Distance between aperture centers across	24	0.233	0.021	8.901	0.20	0.26
Exozone wall thickness	22	0.054	0.009	16.554	0.04	0.07
Endozone wall thickness	10	0.012	0.001	6.050	0.01	0.01
Exilazooecia length	10	0.038	0.014	38.039	0.02	0.06
Exilazooecia width	10	0.033	0.008	23.381	0.02	0.04
Large acanthostyle diameter	24	0.075	0.010	13.239	0.06	0.10
Central calcitic rod diameter	15	0.025	0.001	2.822	0.02	0.03
Small acanthostyle diameter	22	0.014	0.003	20.547	0.01	0.02
No. large acanthostyles per aperture					0	3
No. small acanthostyles per aperture	24	15	0.83	5.56	12	16

the endozone number 2–2.5 per 1 mm. These insufficient observations cannot provide a species identification, but the measurements are closest to *Rhombotrypella arbuscula* (Eichwald, 1860) known from the Artinskian–Kungurian of Timan-Pechora (Russia) (Morozova and Kruchinina 1986) and the Kungurian Vøringen Member (Kapp Starostin Formation) of Spitsbergen (Nakrem 1995).

Family Dyscritellidae Dunaeva and Morozova, 1967

Genus *Dyscritella* Girty, 1911

Type species: *Dyscritella robusta* Girty, 1911, Early Carboniferous (Mississippian, Chester) of Arkansas, North America.

Dyscritella sp.

Fig. 6F.

Material examined.—Treskelen, sample and one thin section ZPAL Br. 12/Cr. 45, Hyrnefjellet, sample and one thin section ZPAL Br. 12/H20.

Remarks.—Fragmented zoaria with oval apertures 0.21 × 0.18 mm with an irregular outline due to bordering acanthostyles. Exilazooecia are commonly developed between autozooecia. Acanthostyles of only one size, 0.043–0.057 mm in diameter. Diaphragms not observed.

Order Rhabdomesida Astrova and Morozova, 1956

Family Rhabdomesidae Vine, 1884

Genus *Rhabdomeson* Young and Young, 1874

Type species: *Rhabdomeson progracile* Wyse Jackson and Bancroft, 1995, Lower Carboniferous, England.

Rhabdomeson sp.

Fig. 8B.

Material examined.—Gipsvika, thin section PMO 170.911A. See also occurrences listed in Nakrem (1994a: 72).

Remarks.—Specimens of *Rhabdomeson* were encountered in some randomly oriented sections, and identified due to the characteristic hollow central canal. Zoaria about 0.65 mm in diameter; hollow canal about 0.40 mm in diameter. Lack of properly oriented sections has prevented identification to species level.

Rhabdomeson? sp.

Fig. 5K.

Material examined.—Treskelen, sample and two thin sections ZPAL Br. 12/Cr. 46.

Remarks.—Oblique sections through an endozonal fragment is tentatively placed in the genus *Rhabdomeson*. The genus identification is based on the regular development of zooecia, and the possible presence of a central hollow canal in a zoarium being about 1 mm in diameter.

Genus *Ascopora* Trautschold, 1876

Type species: *Ceriopora nodosa* Fischer von Waldheim, 1837, Carboniferous, Russia, by subsequent designation (ICZN 1994, Wyse Jackson 1993).

Remarks.—Kruchinina (1980) erected the genus *Ascoporella* with *Geintzella borealis* Stuckenberg, 1895, from the Sakmarian of Belaya River, Timan, Russia as type species. *Ascoporella* is incorrectly described as a new genus in Morozova and Kruchinina (1986: 65), and *Ascopora grandis* Kruchinina, 1973 is erroneously assigned as type species. In the original description of *Ascoporella* by Kruchinina in 1980, and the repeated description by Morozova and Kruchinina in 1986 *Ascoporella* is distinguished from *Ascopora* in having thicker branches, a wider bundle of parallel zooecial in the endozone and often unevenly thickened or beaded exozonal zooecial walls. The number of parallel zooecial in the central bundle ranges from 15 to 30 as observed in longitudinal thin sections. It is difficult to accept these characters as being diagnostic for *Ascoporella* as the illustrated specimens in Kruchinina (1980) and Morozova and Kruchinina in (1986) deviate strongly from the definitions. In these publications the following can be observed from the illustrations: *Ascoporella grandis* (Kruchinina, 1973) has 10–13 parallel zooecial in the central bundle and the walls are not beaded. *Ascopora borealis* (Stuckenberg, 1895) has indeed beaded walls, 13–15 parallel zooecial in the central bundle, but a zoarium diameter of 13–18 mm (measured from the original material in Nikiforova 1938: pl. III, VI) instead of 30–40 mm as given by Morozova and Kruchinina (1986). *Ascoporella enormis* Kruchinina, 1980 is the only species that fulfills the diagnostic characters being 40–45 mm in diameter, having 20–22 parallel zooecial in the central bundle and having thickened or beaded exozonal zooecial walls.

Ascopora magniseptata Shul'ga-Nesterenko, 1955

Fig. 6G.

Material examined.—Measurements based on 5 zoaria in the following samples: Hyrnefjellet, sample ZPAL Br. 12/H10, thin section PMO 170.906; sample and two thin sections ZPAL Br. 12/H30; Gipsvika, thin sections PMO 170.911A, 170.932B, C.

Description.—Cylindrical dichotomically branching colonies averaging 2 mm in diameter. Exozone 0.52 mm wide. Axial bundle of parallel zooecia about 0.52 mm in diameter with 4 to 5 parallel zooecial tubes as observed from longitudinal sections. One distinct proximal hemiseptum is present in zooecial tubes in the transition between the exozone and the endozone. Apertures elongated oval, about 0.28 mm long and 0.12–0.13 mm wide. There are 3.5–4 apertures per 2 mm along colony and 6.3–7.1 diagonally. Distance between apertures longitudinally average 0.53 mm. Large acanthostyles 0.10–0.14 mm in diameter, stylets are present in ridges between apertural rows. Zooecial wall in exozone is about 0.10–0.12 mm in thickness; endozonal wall about 0.006–0.010 mm.

Measurements.—See Table 3.

Stratigraphic and geographic range.—Occurrence on Svalbard: Asselian, middle part of the Tyrrellfjellet Member, and the Treskelodden Formation. Gzhelian of the Urals, Russia (Shul'ga-Nesterenko 1955).

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Table 3. Measurements of *Ascopora magniseptata*. Abbreviations: CV, coefficient of variation (SD*100/X); MAX, maximal value; MIN, minimal value; N, number of zoaria measured; n, number of measurements taken; SD, sample standard deviation; X, mean value.

Ascopora magniseptata (N = 5)	n	X	SD	CV	MIN	MAX
Branch diameter	5	2.03	0.935	46.167	1.15	3.25
Exozone width	5	0.52	0.107	20.810	0.40	0.65
Endozone diameter	5	1.11	0.741	66.767	0.35	1.95
Axial bundle diameter	3	0.52	0.104	20.145	0.40	0.60
No. axial zooecial (longitudinal section)	5	4.20	0.447	10.648	4.00	5.00
Aperture spacing along	5	0.53	0.029	5.501	0.50	0.57
Aperture spacing diagonally	5	0.30	0.016	5.270	0.28	0.32
No. apertures/2 mm along					3.5	4.0
No. apertures/2 mm diagonally					6.3	7.1
Aperture length	6	0.277	0.005	1.866	0.27	0.28
Aperture width	6	0.127	0.005	4.077	0.12	0.13
Acanthostyle diameter (macro)	6	0.115	0.015	13.188	0.10	0.14

Ascopora sterlitamakensis Nikiforova, 1939

Figs. 6H–K, 8F, K, 10E–G.

Material examined.—Measurements based on 9 zoaria in the following samples: Treskelen, sample and one thin section ZPAL Br. 12/Cr. 55; Hyrnefjellet, samples ZPAL Br. 12/H4 (thin section PMO 170.893A), ZPAL Br. 12/H8 (thin section PMO 170.904B), ZPAL Br. 12/H11 (thin section PMO 170.896); Gipsvika, thin sections PMO 170.911D, 170.911E, 170.914, 170.928, 170.945.

Description.—*Ascopora* with cylindrical bifurcating branches of varying diameter (2.25–4.75 mm). Exozone about 0.40–1.20 mm wide, axial bundle of parallel zooecial tubes 0.75–1.00 mm in diameter containing 6–7 parallel tubes as observed in longitudinal sections. Two proximal hemisepta are usually present in zooecial tubes in exozone. Apertures elongated oval, sometimes slit-like, 0.26–0.32 mm long and 0.09–0.15 mm wide. The apertures are arranged in rows with ridges between; 3.1–4.5 per 2 mm along colony and 5.9–6.7 diagonally. Distance between apertural centers longitudinally average 0.50 mm. Two large acanthostyles are present adjacent to each aperture. A row of stylets, as observed in shallow tangential section, is present on the ridges between apertural rows. Zooecial wall in exozone is 0.13–0.14 mm in thickness; endozonal wall about 0.010 mm.

Remarks.—Nikiforova's original material was re-investigated by Morozova and Kruchinina (1986) and the identification herein is mainly based on their revision. Accordingly, *A. sterlitamakensis* is distinguished from *A. magniseptata* in having larger and more spaced apertures, a wider axial bundle of parallel zooecia, and also acanthostyles of greater diameter.

One 20 mm long specimen was identified with growth basis preserved, but no visible hard substrate (Fig. 6K). A possible hard substrate may have been dissolved or lost otherwise, or more likely, this specimen grew in a soft bottom sediment. This unusual preservation indicates deposition in calm low-energy waters.

Measurements.—See Table 4.

Stratigraphic and geographic range.—Occurrence on Svalbard: Asselian, middle part of the Tyrrellfjellet Member, and the Treskelodden Formation. Sakmarian of Timan-Pechora and the Urals, Russia (Morozova and Kruchinina 1986).

Ascopora cf. *sterlitamakensis* Nikiforova, 1939

Fig. 6L–N.

Material examined.—Five partial zoaria in the following samples: Hyrnefjellet, samples ZPAL Br. 12/G14 (thin sections PMO 170.895A-C), ZPAL Br. 12/G15 (thin section PMO 170.891), and sample and one thin section ZPAL Br. 12/G14. For measurements, see Table 5.

Ascopora cf. *sterlitamakensis* is distinguished in displaying multiple regenerated growth layers, with an exozone up to 3.3 mm wide, but in many other charcters similar to *A. sterlitamakensis*. This growth pattern is very much like the description of *Tabulipora borealis* (Stuckenberg, 1895) by

Fig. 6. Lower Permian bryozoans from Hyrnefjellet, Svalbard. **A**–**E**. *Coscinium cyclops* Keyserling, 1846. **A**. Tangential section showing one fenestrule. Scree sample, PMO 170.892A. **B**. Tangential section. Scree sample, PMO 170.892A. **C**. Longitudinal sections. Scree sample, PMO 170.892B. **D**. Oblique transverse section close to anastomosis. Scree sample, ZPAL Br.12/G16-17. **E**. Transverse section. Scree sample, ZPAL Br.12/G16-07. **F**. *Dyscritella* sp. Oblique transverse to tangential section. Sample and thin section ZPAL Br. 12/H20. **G**. *Ascopora magniseptata* Shul'ga-Nesterenko, 1955. Longitudinal section. Sample ZPAL Br. 12/H10, PMO 170.906. **H**–**K**. *Ascopora sterlitamakensis* Nikiforova, 1939. **H**. Tangential section. Sample ZPAL Br. 12/H4, PMO 170.893. **I**. Very shallow tangential section displaying large acanthostyles protruding into surrounding sediment. Sample ZPAL Br. 12/H4, PMO 170.893. **J**. Transverse section close to level of bifurcation. Sample ZPAL Br. 12/H8, PMO 170.904B. **K**. Longitudinal section of large colony with growth basis preserved. Sample ZPAL Br. 12/H11, PMO 170.896. **L**–**N**. *Ascopora* cf. *sterlitamakensis* Nikiforova, 1939. **L**. Transverse section. Cavities (predatory borings?) (four arrow heads) in the exozonal walls. Sample Br. 12/G14, PMO 170.895B. **M**. Basal attachment (on crinoid fragment). Sample Br. 12/G14, PMO 170.895C. **N**. Sample Br. 12/G14, PMO 170.895C. Abbreviations: Co, encapsulated coral; Cr, crinoid fragment. **O**. Fenestellid basal attachment. Sample and thin section ZPAL Br. 12/H35. **P**. *Penniretepora* cf. *disposita* (Trizna, 1939). Deep tangential to longitudinal sections. Sample and thin section ZPAL Br. 12/H10. Scale bars 0.4 mm except for K which represents 5 mm. →

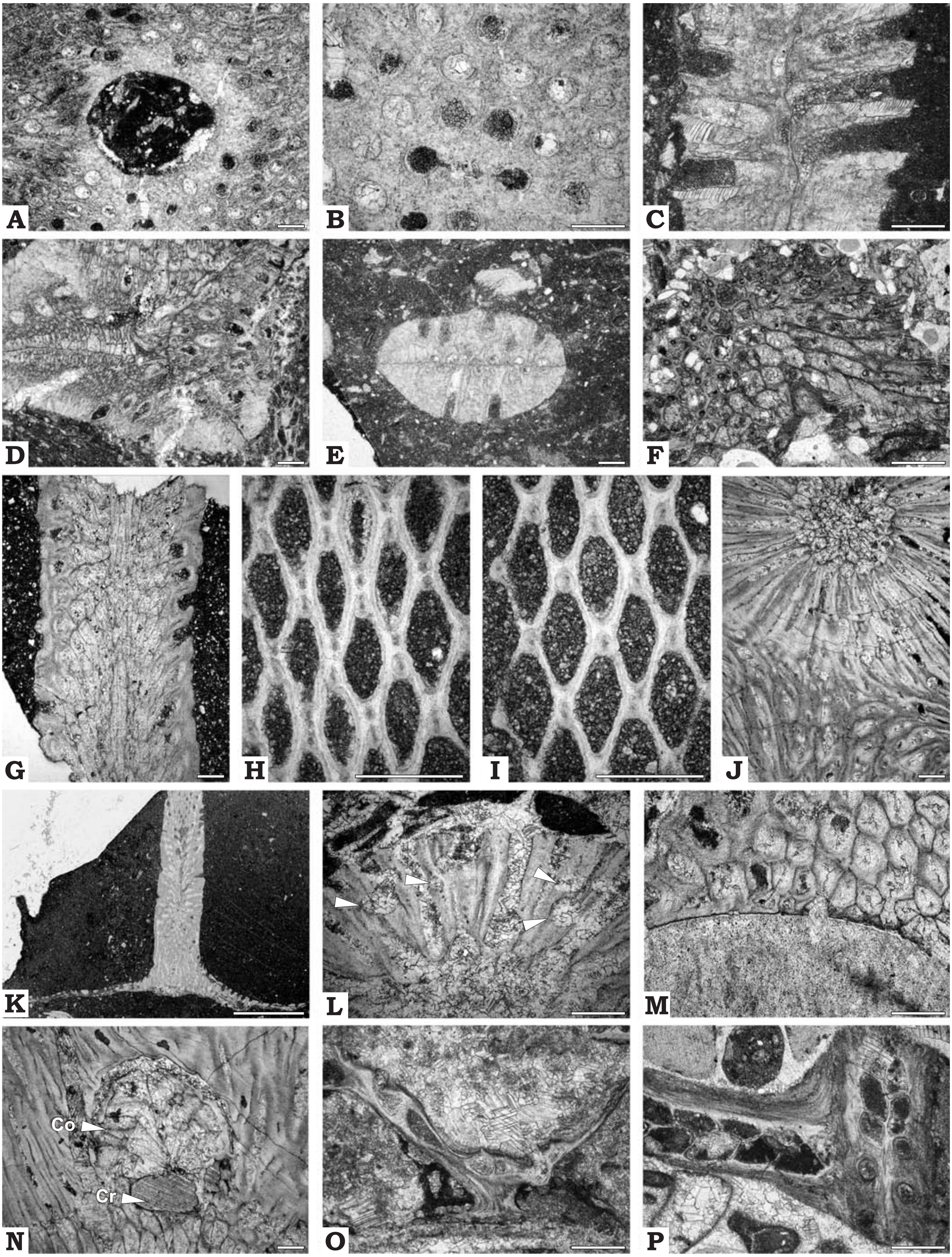

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Table 4. Measurements of *Ascopora sterlitamakensis*. Abbreviations: CV, coefficient of variation (SD*100/X); MAX, maximal value; MIN, minimal value; N, number of zoaria measured; n, number of measurements taken; SD, sample standard deviation; X, mean value.

Ascopora sterlitamakensis (N = 9)	n	X	SD	CV	MIN	MAX
Branch diameter	11	3.59	0.775	21.558	2.25	4.75
Exozone width	10	0.83	0.245	29.725	0.40	1.20
Endozone diameter	10	2.07	0.312	15.072	1.45	2.40
Axial bundle diameter	10	0.91	0.118	12.990	0.75	1.00
No. axial zooecial (longitudinal section)	10	6.60	0.516	7.824	6.00	7.00
Aperture spacing along	17	0.50	0.071	14.350	0.44	0.64
Aperture spacing diagonally	17	0.33	0.010	3.151	0.30	0.34
No. apertures/2 mm along					3.1	4.5
No. apertures/2 mm diagonally					5.9	6.7
Aperture length	18	0.282	0.014	4.945	0.26	0.32
Aperture width	18	0.111	0.016	14.707	0.09	0.15
Acanthostyle diameter (macro)	10	0.110	0.009	8.571	0.10	0.12
Exozonal walls (thickness)	15	0.193	0.019	10.092	0.18	0.24
Endozonal walls (thickness)	15	0.010	0.001	7.559	0.01	0.01

Table 5. Measurements of *Ascopora sterlitamakensis*. Abbreviations: CV, coefficient of variation (SD*100/X); MAX, maximal value; MIN, minimal value; N, number of zoaria measured; n, number of measurements taken; SD, sample standard deviation; X, mean value.

Ascopora cf. *sterlitamakensis* (N = 5)	n	X	SD	CV	MIN	MAX
Branch diameter	4	7.63	3.987	52.288	4.00	12.00
Exozone width	4	3.28	1.641	50.119	1.85	5.25
Endozone diameter	4	1.65	0.436	26.418	1.10	2.00
Axial bundle diameter	7	0.69	0.150	21.807	0.50	0.90
No. axial zooecial (longitudinal section)	3	6.33	1.528	24.119	5.00	8.00
Aperture spacing along	30	0.46	0.069	14.968	0.36	0.60
Aperture spacing diagonally	30	0.33	0.041	12.716	0.28	0.41
No. apertures/2 mm along					3.3	5.6
No. apertures/2 mm diagonally					4.9	7.1
Aperture length	10	0.254	0.005	2.033	0.25	0.26
Aperture width	10	0.142	0.012	8.657	0.13	0.16
Acanthostyle diameter (macro)	10	0.084	0.012	13.974	0.07	0.10

Nikiforova (1938: 221–222, pl. 4: 1, 2), subsequently re-assigned as *Ascoporella borealis* by Morozova and Kruchinina (1986). Some specimens have an unusually widened exozone, up to 5.25 mm wide with no signs of overgrowth. Circular cavities/openings, up 0.17–0.20 mm in diameter, are observed in the exozone of these colonies with extraordinary exozone. These holes are herein interpreted as being the results of bioerosion by unknown parasites drilling into the calcitic exozone of the bryozoan zoaria (Fig. 6L). Some cavities are later filled in with sediments and skeletal debris, e.g., coral and echinoderm fragments (Fig. 6N).

Ascopora grandis Kruchinina, 1973

Fig. 8C–E, J.

Material examined.—Measurements based on 12 zoaria (including material from Nakrem 1994a) in the following samples: Gipsvika, thin sections PMO 170.933, 170.936. See also occurrences listed in Nakrem (1994a: 80).

Description.—Zoarium ramose with thick branches averaging 6.8 mm in diameter. Exozone average 1.08 mm wide; endozone average 4.11 mm in diameter. Axial bundle diameter 1.75–2.35 mm. The axial bundle comprises 9–10 parallel zooecial tubes as viewed in longitudinal section. Zooecial apertures elongated, 0.26–0.36 mm long and 0.12–0.16 mm wide. There are 3.3–3.8 zooecial apertures in 2 mm along colony; 5.6–6.7 diagonally. There are 2–3 hemisepta present in exozonal zooecial tubes (Fig. 8J). One large acanthostyle is developed in the area between zooecial apertures protruding above colony surface (Fig. 8E); diameter 0.08–0.13 mm. Small, infrequent pores are also present in exozonal walls. Exozonal walls are generally 0.11–0.12 mm thick as measured between adjacent apertures in tangential section. Endozonal walls are 0.11–0.12 mm thick.

Remarks.—The described specimens compare well with the illustrations and descriptions given by Kruchinina (1973) and Morozova and Kruchinina (1986) in branch diameter and number of parallel zooecia in the central bundle, but the Spitsbergen material has a significantly narrower axial bundle diameter. It should be remarked that the axial bundle was described as containing 15–22 parallel zooecial tubes, but the illustrations given (Kruchinina 1973: pl. 28: 1c, identical to Morozova and Kruchinina 1986: pl. 22: 1c) display a maximum of 11 parallel zooecia. The number of parallel zooecial

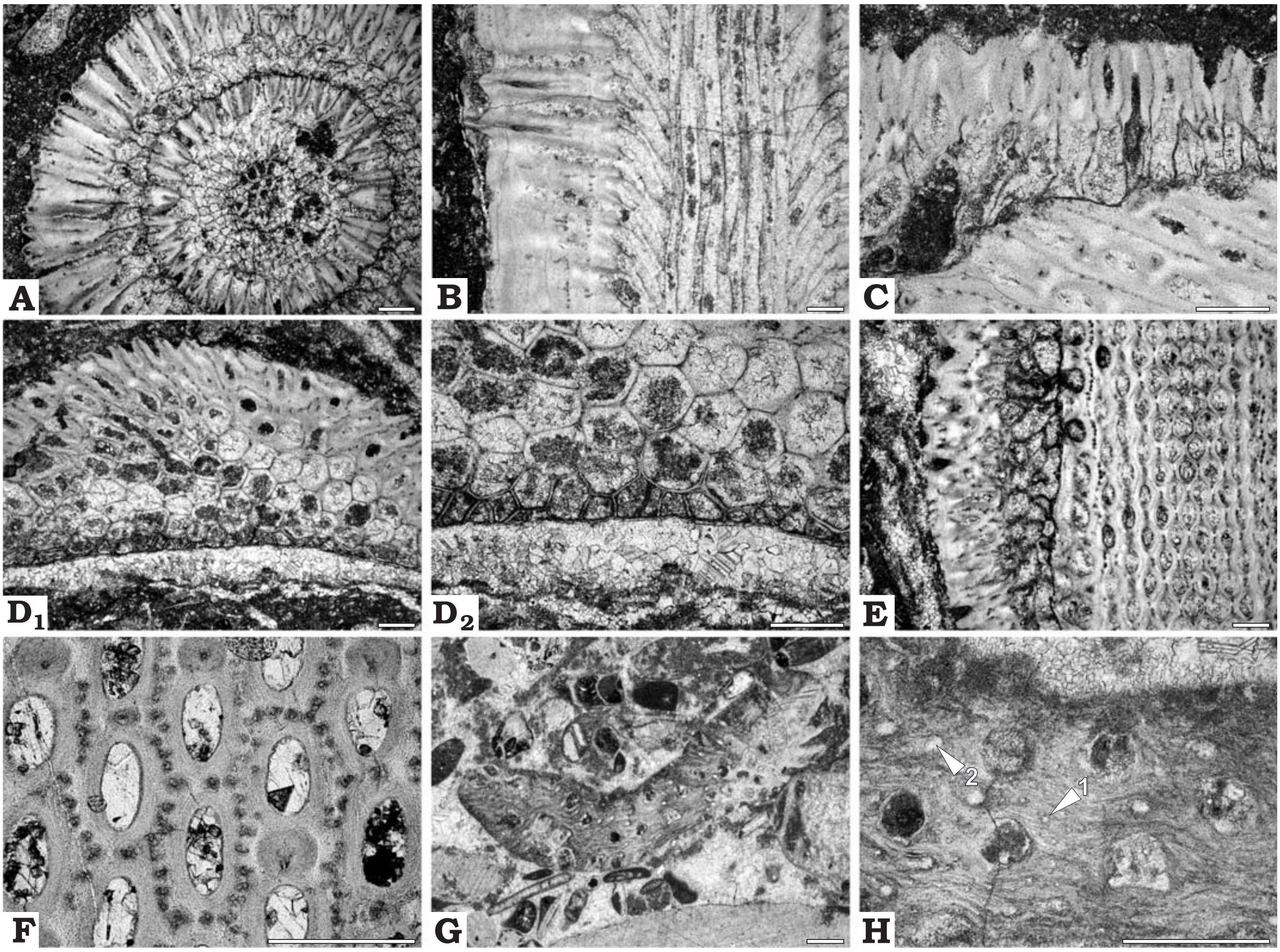

Fig. 7. Lower Permian bryozoans from Hyrnefjellet, Svalbard. **A**–**F**. *Ascopora birkenmajeri* sp. nov. **A**. Transverse section showing completely regenerated growth (cylindrical self-encrustation). Sample H7, PMO 170.903A. **B**. Longitudinal section showing central canal with parallel zooecia. Regenerated growth. PMO 170.903H. **C**. Regenerated growth. Sample H7, PMO 170.903E. **D**. Sample H7, PMO 170.903C. Colony growth basis (D_1) and colony growth basis displaying unusual thich endozonal walls (D_2). **E**. Sample H7, PMO 170.903D. Regenerated growth. **F**. Tangential section showing zooecial apertures, large acanthostyles between apertures, and a row of small stylets bordering each aperture. Sample Br.12/G15, PMO 170.899. **G**, **H**. *Timanodictya* sp. **G**. Oblique tangential section. Sample H10, ZPAL thin section. **H**. Tangential section showing apertures, and scattered small (1) and large (2) tubercles on colony surface between apertures. Sample H10, ZPAL thin section. Scale bars 0.4 mm.

tubes counted from these illustrations is actually lower than the minimum figure given in the generic diagnosis of their genus *Ascoporella* and we have chosen to place this species in *Ascopora*.

Comparison.—*A. grandis* is distinguished from *A. borealis* (Stuckenberg, 1895) and *A. enormis* Kruchinina, 1986 (both Artinskian species from Timan) in having smaller branch diameter, and fewer parallel zooecia in the axial bundle. *A. grandis* is distinguished from all other species in the current study in its wide axial bundle and number of parallel zooecia in the axial bundle.

Measurements.—See Table 6.

Stratigraphic and geographic range.—Occurrence on Svalbard: Late Asselian, middle part of the Tyrrellfjellet Member. Sakmarian (Ilibei Horizon) of Timan-Pechora, Russia (Morozova and Kruchinina 1986).

Ascopora birkenmajeri sp. nov.

Figs. 7A–F, 8G–H, 10A, C.

1994a? *Ascoporella* sp. A; Nakrem 1994a: 80, figs. 13C, 17A–C.

Etymology: The species name is in honour of Professor Krzysztof Birkenmajer (Institute of Geological Sciences of the Polish Academy of Sciences, Kraków) in recognition of his scientific achievements in the geology of Svalbard.

Type material: Holotype PMO 170.913, paratype PMO 170.913.

Type locality: Gipsvika, Spitsbergen, Svalbard.

Type horizon: Wordiekammen Formation, Tyrrellfjellet Member. Permian, Cis-Uralian, late Asselian–early Sakmarian.

Material examined.—Measurements based on 15 zoaria in the following samples: Hyrnefjellet, sample ZPAL Br.12/G15 (thin section PMO 170.899), sample ZPAL Br. 12/H7 (thin sections PMO 170.903A-G), sample ZPAL Br. 12/H8 (thin section PMO 170.949); Gipsvika, thin sections PMO 170.911B, 170.911C, 170.911F, 170.912, 170.913.

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Table 6. Measurements of *Ascopora grandis*. Abbreviations: CV, coefficient of variation (SD*100/X); MAX, maximal value; MIN, minimal value; N, number of zoaria measured; n, number of measurements taken; SD, sample standard deviation; X, mean value.

Ascopora grandis (N = 12)	n	X	SD	CV	MIN	MAX
Branch diameter	10	6.77	1.226	18.115	4.75	9.45
Exozone width	10	1.08	0.316	29.355	0.50	1.60
Endozone diameter	10	4.11	0.423	10.288	3.50	4.80
Axial bundle diameter	10	2.07	0.168	8.155	1.75	2.35
No. axial zooecial (longitudinal section)	9	9.56	0.527	5.516	9.00	10.00
Aperture spacing along	9	0.56	0.025	4.423	0.52	0.60
Aperture spacing diagonally	9	0.33	0.019	5.739	0.30	0.36
No. apertures/2 mm along					3.3	3.8
No. apertures/2 mm diagonally					5.6	6.7
Aperture length	7	0.317	0.032	10.089	0.26	0.36
Aperture width	7	0.144	0.015	10.478	0.12	0.16
Acanthostyle diameter (macro)	9	0.107	0.016	14.823	0.08	0.13
Exozonal walls (thickness)	15	0.116	0.011	9.666	0.10	0.14
Endozonal walls (thickness)	15	0.011	0.001	7.762	0.01	0.01

Diagnosis.—Robust zoaria with a wide endozone and axial bundle, up to 8 parallel zooecia in the axial bundle.

Description.—Robust branching species of *Ascopora* with branch diameter verying between 3.75 and 7.00 mm. Exozone width varies between 0.80 and 1.75 mm. There are usually 2 hemisepta present in exozonal zooecial tubes.Variation in branch diameter and exozone width is generally caused by several growth generations. Endozone average 2.50 mm, with an axial bundle varying between 0.75 and 1.25 mm. There are 5 to 8 parallel zooecia in the axial bundle as viewed in parallel section. Zooecial apertures are elongated being 0.24–0.30 mm long and 0.10–0.14 mm wide. Distance between aperture centers along colony is 0.40–0.60 mm and 0.30–0.40 diagonally. There are 3.3 to 5 apertures along colony per 2 mm and 5 to 6.7 diagonally. Acanthostyles are sometimes up to 0.15–0.16 mm in diameter, averaging 0.11 mm. Stylets, 0.02–0.04 mm in diameter, are developed in the walls between apertures (Fig. 7H).

Comparison.—*A. birkenmajeri* is distinguished from all other species in the current study by the diameter of the axial bundle and the number of parallel zooecia in the axial bundle. The endozone shows great variation in diameter, but is on average narrower than the one in *A. grandis*, and wider than the endozones of the other species described in the current study.

Remarks.—Several growth generations can be observed in many zoaria (170.903A-G). Locally the exozone is developed as solid stereom without apertures, or very small ("dwarfed") or closed off apertures.

Measurements.—See Table 7.

Stratigraphic and geographic range.—Occurrence on Svalbard: Asselian, middle part of the Tyrrellfjellet Member, Gipsvika, and the Treskelodden Formation, Hyrnefjellet.

Family Rhomboporidae Simpson, 1895

Genus *Rhombopora* Meek, 1872

Type species: *Rhombopora lepidodendroides* Meek, 1872 Late Carboniferous, Nebraska, USA.

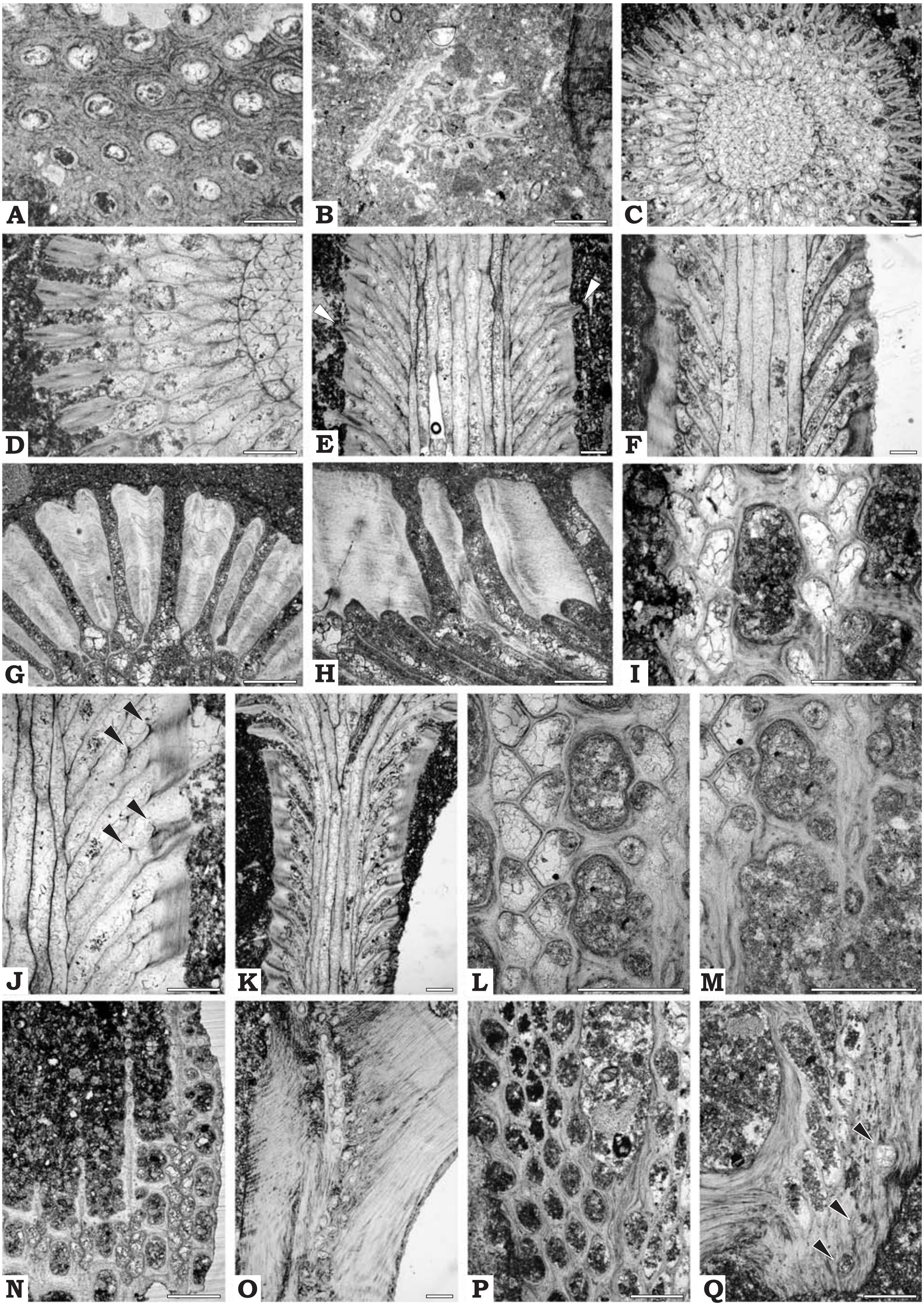
Rhombopora sp.

Fig. 5L.

Material examined.—Treskelen, sample and two thin sections ZPAL Br. 12/Cr. 44; Hyrnefjellet, samples and two thin sections ZPAL Br. 12/H10 and H34; Gipsvika, thin section PMO 170.911B.

Remarks.—Fragments of *Rhombopora* occur in many thin sections, but reliable orientations are lacking and rather few measurements could be made. Colonies have diameters ranging between 0.88 and 1.07 mm and exozones widths 0.28 and 0.30 mm. Zooecia in endozone observed in transverse section have a rather square outline. The most similar species is

Fig. 8. Lower Permian bryozoans from Gipsvika, Svalbard. **A**. *Coscinium cyclops* Keyserling, 1846. Tangential section. PMO 170.919A. **B**. *Rhabdomeson* sp. Transverse section showing well visible hollow central canal. PMO 170.911A. **C–E**, **J**. *Ascopora grandis* Kruchinina, 1973. **C**. Transverse section. PMO 170.933. **D**. Transverse section. PMO 170.933. **E**. Longitudinal section showing central bundle of parallel zooecia. Arrows point at acanthostyles protruding into enclosing sediment. PMO 170.936. **J**. Longitudinal section. Black arrow heads point at hemiseptae. PMO 170.936. **F**, **K**. *Ascopora sterlitamakensis* Nikiforova, 1939. **F**. Longitudinal section. PMO 170.945. **K**. Longitudinal section. PMO 170.945. **G**, **H**. *Ascopora birkenmajeri* sp. nov. **G**. Transverse section. Holotype. PMO 170.913A. **H**. Longitudinal section. Holotype. PMO 170.913B. **I**. *Fabifenestella* cf. *quadratopora* (Shul'ga-Nesterenko, 1939). Tangential section showing zooecial chamber shape. PMO 170.935. **L**, **M**. *Rectifenestella nikiforovae* (Shul'ga-Nesterenko, 1936). **L**. Shallow to deep tangential section. PMO 170.943. **M**. Shallow tangential section showing row of large carinal tubercles. PMO 170.943. **N**. *Rectifenestella submicroporata* (Shul'ga-Nesterenko, 1952). Shallow to deep tangential section. 170.938B (acetate peel). **O**. *Archimedes* sp. Oblique longitudinal section through central axis of colony with zooecia visible close to fenestrate meshwork. PMO 170.929. **P**, **Q**. *Shulgapora* cf. *porosa* (Eichwald, 1860). **P**. Tangential section. PMO 170.944. **Q**. Oblique longitudinal section displaying cyclozooecia on reverse side (black arrow heads). PMO 170.944. Scale bars 0.4 mm. →



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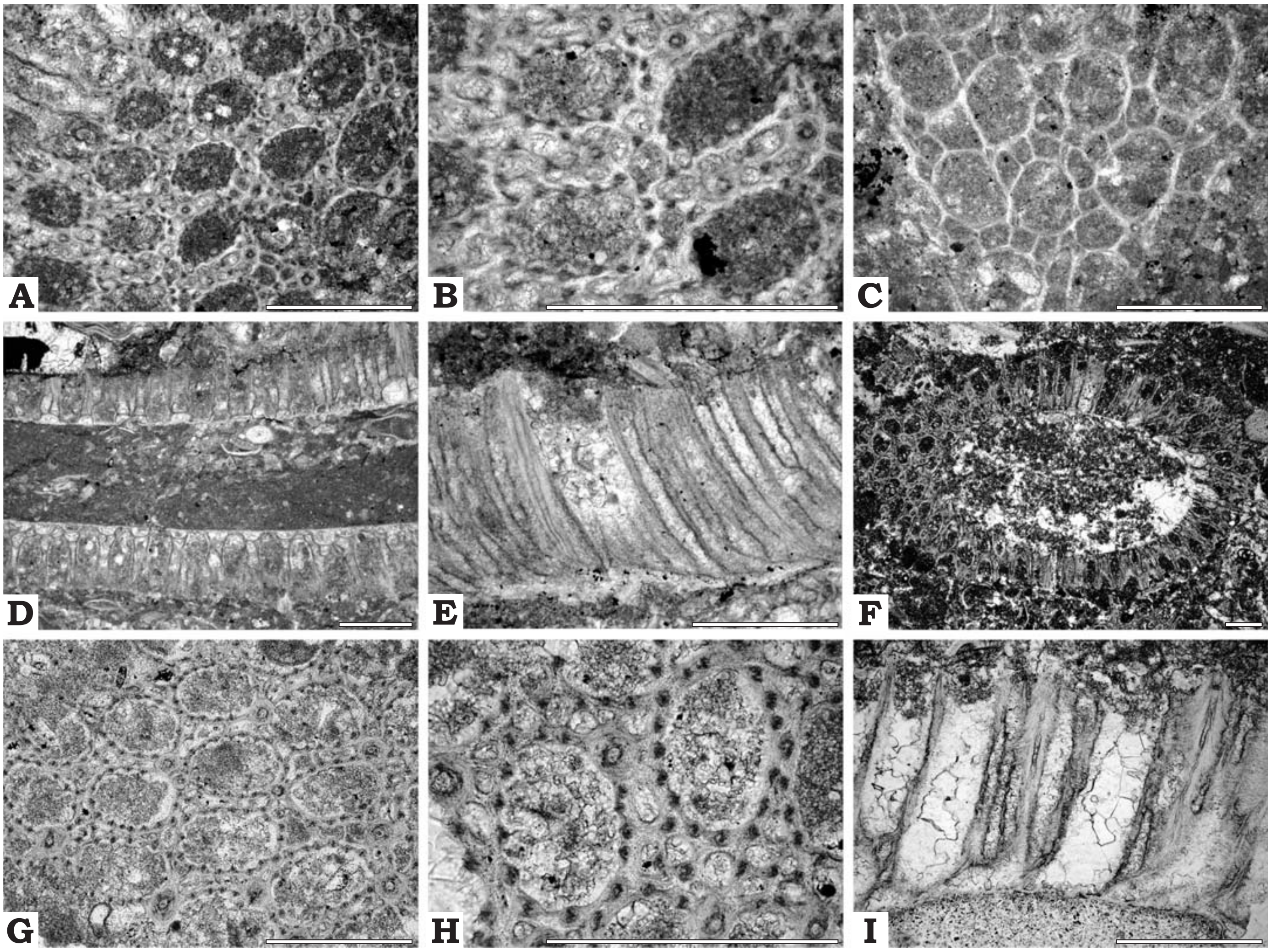

Fig. 9. Lower Permian bryozoans from Gipsvika, Svalbard. *Toulapora svalbardense* (Nakrem, 1994a). **A**. Tangential section. Rejmyrefjellet, Artinskian, PMO A42600/1 (holotype). **B**. Tangential section. Rejmyrefjellet, Artinskian, PMO A42600/1 (holotype). **C**. Tangential section. Rejmyrefjellet, Artinskian, PMO A42600/1 (holotype). **D**. Longitudinal section. Cylindrical colony with now decayed ephemeral encrustation substrate ("hollow tubes"). Rejmyrefjellet, Artinskian, PMO A42600/4 (paratype). **E**. Longitudinal section. Rejmyrefjellet, Artinskian, PMO A42600/2 (paratype). **F**. Transverse section of cylindrical colony. Gipsvika, Sakmarian, PMO 170.929. **G**. Tangential section. Gipsvika, Sakmarian, PMO 170.929. **H**. Tangential section. Gipsvika, Sakmarian, PMO 170.929. **I**. Longitudinal section. Gipsvika, Sakmarian, PMO 170.941. Scale bars 0.4 mm.

Rhombopora optima Gorjunova, 1975, from the Artinskian of Pamir, but better material is required for a more conclusive identification.

Order Timanodictyida Morozova, 1966

Family Timanodictyidae Morozova, 1966

Genus *Timanodictya* Nikiforova, 1938

Type species: *Coscinium dichotomum* Stuckenberg, 1895, Early Permian of Timan, Russia.

Timanodictya sp.

Fig. 7G–H.

Material examined.—Treskelen, sample and one thin section ZPAL Br. 12/Cr. 64; Hyrnefjellet, sample and two thin sections ZPAL Br. 12/H10.

Remarks.—Fragments of *Timanodictya* colonies are observed in oblique orientations. The genus identification is based on the presence of a median lamina and the abundant small microstylets in the extrazooidal skeleton. Branch width is about 1 mm with slightly oval zooecial apertures 0.12 × 0.13 mm. Aperture center distance is about 0.29–0.31 mm along colony, 0.35–0.36 mm diagonally. These measurements are not sufficient for specific identifications.

Order Fenestellida Astrova and Morozova, 1956

Family Fenestellidae King, 1849

Genus *Fabifenestella* Morozova, 1974

Type species: *Fenestella praevirgosa* Shul'ga-Nesterenko, 1951, Gzhelian of the East European Platform, Russia.

Fabifenestella cf. *quadratopora* (Shul'ga-Nesterenko, 1939)

Fig. 8I.

Table 7. Measurements of *Ascopora birkenmajeri* sp. nov. Abbreviations: CV, coefficient of variation (SD*100/X); MAX, maximal value; MIN, minimal value; N, number of zoaria measured; n, number of measurements taken; SD, sample standard deviation; X, mean value.

Ascopora birkenmajeri sp. nov (N = 15)	n	X	SD	CV	MIN	MAX
Branch diameter	15	5.12	0.879	17.174	3.75	7.00
Exozone width	16	1.24	0.266	21.438	0.80	1.75
Endozone diameter	15	2.50	0.605	24.228	1.75	4.00
Axial bundle diameter	12	1.05	0.145	13.785	0.75	1.25
No. axial zooecial (longitudinal section)	13	6.62	0.870	13.147	5.00	8.00
Aperture spacing along	35	0.48	0.043	8.953	0.40	0.60
Aperture spacing diagonally	35	0.35	0.022	6.247	0.30	0.40
No. apertures/2 mm along					3.3	5.0
No. apertures/2 mm diagonally					5.0	6.7
Aperture length	15	0.278	0.017	6.111	0.24	0.30
Aperture width	15	0.115	0.010	8.588	0.10	0.14
Acanthostyle diameter (macro)	20	0.108	0.025	22.960	0.07	0.16
Acanthostyle diameter (micro)	15	0.029	0.007	23.991	0.02	0.04
Exozonal walls (thickness)	15	0.147	0.012	7.893	0.12	0.16
Endozonal walls (thickness)	15	0.012	0.001	11.247	0.01	0.01

Table 8. Measurements of *Fabifenestella* cf. *quadratopora*. Abbreviations: CV, coefficient of variation (SD*100/X); MAX, maximal value; MIN, minimal value; N, number of zoaria measured; n, number of measurements taken; SD, sample standard deviation; X, mean value.

Fabifenestella cf. *quadratopora* (N = 1)	n	X	SD	CV	MIN	MAX
Branch width	12	0.297	0.010	3.319	0.28	0.31
Disseppiment width	12	0.143	0.006	4.362	0.13	0.15
Fenestrule length	14	0.514	0.016	3.205	0.50	0.56
Fenestrule width	14	0.282	0.021	7.509	0.26	0.32
Distance between branch centers	15	0.593	0.052	8.750	0.53	0.68
Distance between dissepiment centers	15	0.680	0.011	1.667	0.66	0.70
Aperture diameter	15	0.109	0.007	6.382	0.10	0.12
Aperture spacing along branch	15	0.284	0.011	3.948	0.26	0.30
Node dimension (diameter, length × width)		0.10 × 0.03				
Branches / 10 mm	12	16.8	1.46	8.72	14.7	18.9
Fenestrules / 10 mm	12	14.7	0.24	1.66	14.3	15.2
Apertures / 5 mm	14	17.9	0.70	3.93	16.7	19.2

Material examined.—Gipsvika, thin section PMO 170.935.

Description.—*Fabifenestella* with relatively small fenestrules and robust branches and dissepiments as compared with other species of this genus. There are 14–19 branches per 10 mm across colony and 14–15 dissepiments per 10 mm along colony. Branches 0.28–0.31 mm wide carrying scattered nodes (0.10 mm × 0.03 mm). Dissepiments 0.13–0.15 mm wide. Fenestrules 0.50–0.56 mm long and 0.26–0.32 mm wide. Apertures circular 0.10–0.11 mm in diameter. There are 17–19 apertures per 5 mm along branch; 2–2.5 bordering each fenestrule. Distance between apertural centers 0.26–0.30 mm along branch. Zooecial chambers fabiform in shallow tangential section; elongated-pentagonal in median to deep section. *F. quadratopora* occurs in the Sakmarian of the Russian Platfdorm, Russia (Shul'ga Nesterenko 1936).

Measurements.—See Table 8.

Genus *Rectifenestella* Morozova, 1974

Type species: *Fenestella medvedkensis* Shul'ga-Nesterenko, 1951, Kasimovian of the East European Platform, Russia.

Rectifenestella nikiforovae (Shul'ga-Nesterenko, 1936)

Figs. 8M, 10D.

Material examined.—Gipsvika, thin section PMO 170.943, 170.915B.

Description.—*Rectifenestella* with minute meshwork and narrow branches and dissepiments. There are 20–22 branches per 10 mm across colony and 18–20 dissepiments per 10 mm along colony. Branches 0.24–0.30 mm wide carrying 4–5 nodes (0.05 mm × 0.10 mm) per 1 mm. Distance between node centers 0.18–0.26 mm. Dissepiments 0.12–0.18 mm wide. Fenestrules 0.38–0.44 mm long and 0.18–0.24 mm wide. Apertures circular 0.10–0.12 mm in diameter or slightly oval measuring 0.10 mm × 0.12 mm. There are 18–22 apertures per 5 mm along branch; 2–2.5 bordering each fenestrule. Distance between apertural centers 0.22–0.28 mm along branch. Zooecial chambers fabiform in shallow tangential section; pentagonal in median to deep section.

Measurements.—See Table 9.

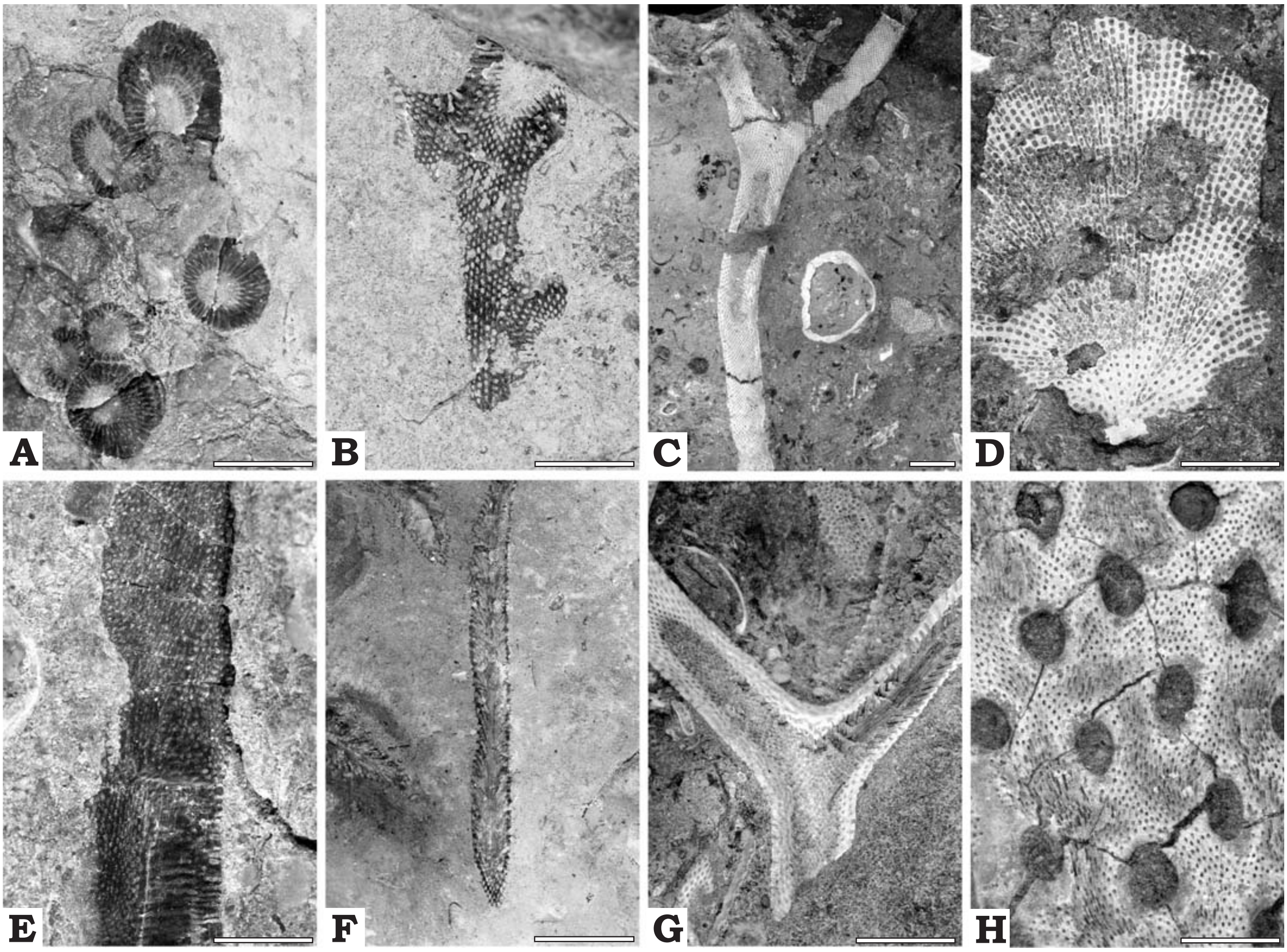

Fig. 10. External views of selected bryozoan growth forms. **A**, **C**. *Ascopora birkenmajeri* sp. nov. A. Cross-sections of zoaria. Hyrnefjellet, sample ZPAL Br. 12/H7, PMO 170.903. **C**. Large zoarium. Holotype. Gipsvika, PMO 170.913. **B**. *Ascopora* sp. Zoarium surface. Hyrnefjellet, sample ZPAL Br. 12/H24, PMO 170.907. **D**. *Rectifenestella nikiforovae* (Shul'ga-Nesterenko, 1936). Gipsvika, PMO 170.915B. **E**–**G**. *Ascopora sterlitamakensis* Nikiforova, 1939. **E**. Oblique cut abnormal thick zoarium displaying regenerated growth (bottom). Hyrnefjellet, sample Br.12/G15, PMO 170.891. **F**. Oblique longitudinal section of regular thin zoarium displaying zooecial apertures (bottom). Hyrnefjellet, sample ZPAL Br. 12/H4, PMO 170.893. **G**. Longitudinal section near point of bifurcations displaying thick endozone (dark) and slightly silicified exozone (white). Gipsvika, PMO 170.911 (original for thin sections 170.911D and E). **H**. *Coscinium cyclops* Keyserling, 1846. Zoarium surface showing large fenestrules and numerous rows of apertures on branches. Gipsvika, PMO 170.919. Scale bars 5 mm.

Stratigraphic and geographic range.—Occurrence on Svalbard: Asselian, middle part of the Tyrrellfjellet Member. Sakmarian–Artinskian of the Russian Platform, Russia (Morozova and Kruchinina 1986); Lower Permian of China (Yang and Lu 1983).

Rectifenestella submicroporata (Shul'ga-Nesterenko, 1952)

Fig. 8N.

Material examined.—Treskelen, sample and one thin section ZPAL Br. 12/Cr. 34; Gipsvika, thin sections PMO 170.915A and B, 170.938B. See also occurrences listed in Nakrem (1994a: 93).

Description.—Delicate meshwork with 21–28 fenestrules along colony and 25–29 branches across colony per 10 mm. Branches about 0.21 mm thick and 0.23 mm wide with a straight low carina carrying 5–6 nodes per 1 mm. Nodes are about 0.05 mm long and 0.03 mm wide being 0.16–0.21 mm apart. Dissepiments 0.07–0.12 mm wide. Fenestrules 0.26–0.34 mm long and 0.12–0.20 mm wide. Apertures circular in outline, 0.06–0.09 mm in diameter. There are usually 25–27 apertures per 5 mm along branch. Distance between apertural centers along colony 0.17–0.22 mm; 2 or 2.5 apertures border each fenestrule. Zooecial chambers are pentagonal in outline in median tangential section.

Remarks.—*R. submicroporata* is distinguished from *R. microporata* by smaller apertures (0.06–0.09 vs. 0.07 mm in diameter) and narrower and more closely spaced branches and dissepiments. A fragmentary specimen assigned as *Rectifenestella* cf. *submicroporata* (Shul'ga-Nesterenko 1952) (one ZPAL thin section from Hyrnefjellet) is separated by having more robust branches and dissepiments and the follow-

Table 9. Measurements of *Rectifenestella nikiforovae*. Abbreviations: CV, coefficient of variation (SD*100/X); MAX, maximal value; MIN, minimal value; N, number of zoaria measured; n, number of measurements taken; SD, sample standard deviation; X, mean value.

Rectifenestella nikiforovae (N = 2)	n	X	SD	CV	MIN	MAX
Branch width	7	0.281	0.023	8.315	0.24	0.30
Disseppiment width	7	0.154	0.024	15.813	0.12	0.18
Fenestrule length	7	0.417	0.024	5.825	0.38	0.44
Fenestrule width	7	0.207	0.019	9.123	0.18	0.24
Distance between branch centers	15	0.481	0.017	3.587	0.45	0.50
Distance between dissepiment centers	15	0.534	0.014	2.629	0.51	0.55
Aperture diameter	7	0.107	0.008	7.055	0.10	0.12
Aperture spacing along branch	13	0.255	0.015	5.695	0.22	0.28
Node dimension (diameter, length × width)		0.10 × 0.05				
Node spacing	16	0.22	0.02	9.42	0.18	0.26
Branches / 10 mm	7	21.1	0.75	3.58	20.0	22.2
Fenestrules / 10 mm	7	18.9	0.50	2.64	18.2	19.6
Apertures / 5 mm	7	20.3	1.18	5.81	17.9	22.7

Table 10. Measurements of *Rectifenestella submicroporata*. Abbreviations: CV, coefficient of variation (SD*100/X); MAX, maximal value; MIN, minimal value; N, number of zoaria measured; n, number of measurements taken; SD, sample standard deviation; X, mean value.

Rectifenestella submicroporata (N = 4)	n	X	SD	CV	MIN	MAX
Branch width	20	0.233	0.011	4.602	0.21	0.25
Disseppiment width	24	0.100	0.018	17.937	0.07	0.12
Fenestrule length	22	0.309	0.025	8.141	0.26	0.34
Fenestrule width	22	0.161	0.026	16.036	0.12	0.20
Distance between branch centers	24	0.391	0.024	6.126	0.35	0.44
Distance between dissepiment centers	32	0.413	0.033	7.884	0.36	0.46
Aperture diameter	12	0.078	0.009	11.967	0.06	0.09
Aperture spacing along branch	30	0.195	0.013	6.550	0.17	0.22
Node dimension (diameter, length × width)		0.05 × 0.03				
Node spacing	24	0.17	0.02	10.81	0.14	0.21
Branches / 10 mm	20	25.6	1.61	6.27	22.7	28.6
Fenestrules / 10 mm	24	24.8	1.90	7.69	21.7	27.8
Apertures / 5 mm	22	26.1	1.73	6.64	22.7	29.4

ing measurements: 23–25 branches per 10 mm, width of branch 0.28–0.30 mm, width of dissepiments 0.25–0.26 mm.

Measurements.—See Table 10.

Stratigraphic and geographic range.—Occurrence on Svalbard: Late Asselian–early Sakmarian, middle and upper part of the Tyrrellfjellet Member, and late Artinskian-early Kungurian, Vøringen Member of the Kapp Starostin Formation. Asselian of the Urals, Russia (Shul'ga-Nesterenko 1952).

Genus *Archimedes* Owen, 1842, SD by Hall 1857

Type species: *Fenestella wortheni* Hall, 1857, Mississippian (Warsaw) of Illinois, USA.

Archimedes sp.

Figs. 5N, 8O.

Material examined.—Treskelen, sample and one thin section ZPAL Br. 12/Cr. 45, Gipsvika, thin section PMO 170.929.

Remarks.—The current material of *Archimedes* is distinguished from other fenestellids by the growth shape of the zoarium. Zooecial measurements are insufficient for a detailed description. Czarniecki (1964) described *Archimedes* aff. *magnus* Condra and Elias, 1944 from coral horizon IV, Treskelen, but it is not possible to tell whether the current specimens can be attributed to the same taxon. Czarniecki (1964) did not provide zooecial observations, and it is not possible to revise his identification. Nakrem (1994a: 98–100) described other occurrences of *Archimedes* from the Upper Carboniferous of the inner Isfjorden area, not considered to be con-specific with the material from Treskelen.

Genus *Penniretepora* d'Orbigny, 1849

Type species: *Retepora pluma* Phillips, 1836, Early Carboniferous of Yorkshire, England.

Penniretepora cf. *disposita* (Trizna, 1939)

Fig. 6P.

Material examined.—Hyrnefjellet, sample and one thin section ZPAL Br. 12/H10.

Remarks.—Main branch 0.71 mm wide, secondary branches 0.61 mm wide. Zooecial apertures oval, 0.12–0.13 × 0.15–0.16 mm. Distance between aperture centers along main branch is 0.37–0.39 mm equaling 12.8–13.5 per 5 mm. Zooecial chamber is elongated parallelogram shaped, no internal septa are observed. Nodes are present along main branch,

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Table 11. Measurements of *Shulgapora* cf. *porosa*. Abbreviations: CV, coefficient of variation (SD*100/X); MAX, maximal value; MIN, minimal value; N, number of zoaria measured; n, number of measurements taken; SD, sample standard deviation; X, mean value.

Shulgapora cf. *porosa* (N = 1)	n	X	SD	CV	MIN	MAX
Branch width	2	1.375	0.177	12.856	1.25	1.50
Disseppiment width	2	0.625	0.177	28.284	0.50	0.75
Fenestrule length	5	1.540	0.238	15.469	1.15	1.80
Fenestrule width	5	0.950	0.190	20.042	0.75	1.15
Distance between branch centers	6	2.427	0.272	11.215	2.00	2.80
Distance between dissepiment centers	6	2.083	0.144	6.900	1.90	2.25
Aperture dimension (diameter, length × width)		0.20–0.22 × 0.15–0.16				
Aperture spacing along branch	10	0.380	0.027	7.018	0.34	0.42
Branches / 10 mm	2	4.3	0.54	12.68	3.6	5.0
Fenestrules / 10 mm	2	4.9	0.37	7.59	4.4	5.3
Apertures / 5 mm	5	13.3	4.97	37.39	11.9	14.7

0.25–0.26 mm apart. Material and measurements are not sufficient to establish a conclusive specific identification, but the most similar species is *Penniretepora disposita* (Trizna, 1939) known from the Sakmarian–Artinskian of Bashkiria, Russia (Trizna 1939).

Penniretepora sp. A.

Fig. 5M.

Material examined.—Treskelen, sample and one thin section ZPAL Br. 12/Cr. 44.

Description.—Main branch 0.26 mm wide. 13–14 secondary branches (0.24 mm wide) per 10 mm. 20–21 zooecial apertures per 5 mm on both main and secondary branches. Circular zooecial aperture with a diameter of 0.07–0.08 mm.

Remarks.—The investigated material is too rare to establish a specific identification. The dimensions are most similar to different Carboniferous species, e.g., some species described by Shishova (1959).

Family Septoporidae Morozova, 1962

Genus *Shulgapora* Termier and Termier, 1971

Type species: *Polypora helenae* Shul'ga-Nesterenko, 1951, Moscovian of the East European Platform, Russia.

Shulgapora cf. *porosa* (Eichwald, 1860)

Fig. 8P, Q.

Material examined.—Gipsvika, thin section PMO 170.916, acetate peel 170.944.

Description.—*Shulgapora* with large, elongated fenestrules and slender branches producing a relatively open meshwork. There are 4–5 branches per 10 mm across colony and most commonly 4.5–5 fenestrules per 10 mm along colony. Branches bearing 5–6 rows of apertures are 1.25–1.50 mm wide. Branch surfaces are pierced by numerous small stylets. Dissepiments are 0.50–0.75 mm wide. Fenestrules are 1.15–1.80 mm long and 0.75–1.15 mm wide. Apertures are distinctly ovate, measuring 0.20–0.22 × 0.15–0.16 mm. There are 5–6 apertures per fenestrule. Distance between apertural centres is 0.34–0.42 along branch. Autozooecial chambers are rhomboid or less commonly hexagonal in median to deep tangential section.

Cyclozooecia (heterozooecia) up to 0.16 mm in diameter as measured deeper into the zooarium with an aperture diameter of 0.10 mm; these open on reverse side on branch. Cyclozooecia are locally also developed on obverse side of branches. *S. porosa* occurs in Sakmarian–Artinskian of Timan-Pechora (Morozova and Kruchinina 1986).

Measurements.—See Table 11.

Family Acanthocladiidae Zittel, 1880

Genus *Polypora* M'Coy, 1844

Type species: *Polypora dendroides* M'Coy, 1844, Viséan of Ireland.

Polypora sp.

Fig. 5O, P.

Material examined.—Treskelen, samples and two thin sections ZPAL Br. 12/Cr. 45 and Cr. 46; Hyrnefjellet, samples and three thin sections ZPAL Br. 12/H8, H10, H20; Gipsvika, thin sections PMO 170.916, 170.927, 170.944, 170.947.

Remarks.—Fragments of *Polypora*, too small for measurements or identification are observed in most samples. The genus identification is based mainly on cross-sections where more than two rows of zooecia are developed.

Discussion

Most bryozoans identified in the current study support the ages for the investigated horizons as previously dated by fusulinaceans and conodonts (Nakrem et al. 1992). Some taxa, however, have a deviating older and/or younger distribution elsewhere. During the late Palaeozoic Spitsbergen was a central part of an extensive carbonate platform, which was located on the northwestern margin of the Pangea (Stemmerik et al. 1999; Hüneke et al. 2001). Distribution and migration of bryozoans in the Boreal seas in Permian time have recently been discussed by Reid et al. (2007) and Sørensen et al. (2007) with focus on occurrences in the northern margins of Pangaea (Canadian Arctic and North Greenland respectively). The species diversity during the Early Permian is higher in those areas than in Svalbard, especially regarding rhabdomesid taxa. Notably the distribution of the genus

Ascopora is of special interest. This genus is present throughout the Permian in the Tethys realm, as well as in North Greenland (Sørensen et al. 2007), but is confined to the Early Permian of Svalbard, the Canadian Arctic and the Russian Platform. It is also well known from the Late Carboniferous of the Tethys Realm as well as the boreal seas. This genus seems to have disappeared from most parts of the boreal seas during the Permian cooling period (Reid et al. 2007), but continued diversification in the Tethyan seas (Ross 1995).

The genus *Coscinium* has a Late Carboniferous occurrence in Spain (Ernst and Minwegen 2006), but is only known from the Early Permian of the Svalbard and the Russian Platform. It is so far not reported from either the Canadian Arctic nor from North Greenland and seems to have preferred the environmental conditions available in the eastern part of the boreal sea and the Uralian sea during the Asselian through the Artinskian. This genus disappeared from the cooling boreal waters by the Artinskian and has its youngest occurrence in the Late Permian of the Tethys (Primory region, Russia) (Kiseleva 1982).

The bryozoans' adaptation to the more local (Spitsbergen) depositional settings is characterised by medium to robust branching in the rhabdomesid species of *Ascopora*, up to 10 mm in diameter, and the robust frondescent development of *Coscinium*. The fenestrates are characterised by fenestellid colonies with robust branches and small fenestrules, and occurrence of *Shulgapora* cf. *porosa* with large fenestrules and robust branches and dissepiments. These growth forms are commonly associated with moderately strong currents and waves of a shallow shelf environment (e.g., Nakrem 1994b).

Bryozoans from the Hornsund sections are characterised by more finely-branched colonies like *Dyscritella* and *Rhombopora*, but also moderately robust colonies of *Ascopora* (less than 5 mm in diameter). Bryozoan growth forms indicate that the depositional environment was here characterised by more quiet waters (more off-shore) than sediments through the Gipsvika section. The Hornsund sections are partly dominated by siliciclastic sedimentation, and the bryozoans embedded in siliciclastic matrix were perhaps washed out from a more near-shore environment.

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