A Boreal serpulid fauna from Volgian-Ryazanian (latest Jurassic-earliest Cretaceous) shelf sediments and hydrocarbon seeps from Svalbard

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ABSTRACT
Serpulid polychaete tubes are described from Volgian-Ryazanian sediments (?*Pyrgopolon decorata* (Stolley, 1912), ?*Pyrgopolon* aff. *nodulosum* (Lundgren, 1883)) and four contemporaneous hydrocarbon seep deposits (?*Pyrgopolon* aff. *nodulosum*, ?*Pyrgopolon* sp. A, *Propomatoceros* sp. A, *Nogrobs* aff. *quadricarinata* Münster *in* Goldfuss, 1831) from Spitsbergen, Svalbard. These are the oldest serpulid tubes yet described from fossil hydrocarbon seep deposits, and comprise the most diverse fossil seep serpulid fauna known to date. The genera *Propomatoceros* Ware, 1975 and *Nogrobs* de Montfort, 1808 have their first fossil occurrence elsewhere in the Early Jurassic and then appear in the Svalbard seeps much later. This is the first report of ?*Pyrgopolon* de Montfort, 1808 from a fossil seep site.

KEY WORDS
Serpulidae,
Spitsbergen,
Volgian,
Ryazanian,
hydrocarbon seeps.

RÉSUMÉ
Une faune boréale de Serpulidés des sédiments de plateaux et des suintements d'hydrocarbure du Volgien-Ryazanien de Svalbard (Jurassique terminal-Crétacé basal).
Des tubes de serpules (annélides polychètes) sont décrits à partir de sédiments du Volgien-Ryazanien (?*Pyrgopolon decorata* (Stolley, 1912), ?*Pyrgopolon* aff. *nodulosum* (Lundgren, 1883)) et à partir de quatre dépôts contemporains riches en hydrocarbure (?*Pyrgopolon* aff. *nodulosum*, ?*Pyrgopolon* sp. A, *Propomatoceros* sp. A, *Nogrobs* aff. *quadricarinata* Münster *in* Goldfuss, 1831) du Spitsberg, Svalbard. Ce sont les plus anciens tubes de serpules décrits, mais aussi la faune de serpules la plus diversifiée connue de dépôts riches en hydrocarbure. Les genres *Propomatoceros* Ware, 1975 et *Nogrobs* de Montfort, 1808 ont leur première occurrence ailleurs au Jurassique inférieur et apparaissent beaucoup plus tard dans des suintements à hydrocarbures du Svalbard. C'est la première citation de ?*Pyrgopolon* de Montfort, 1808 dans un site fossile de suintements à hydrocarbure.

MOTS CLÉS
Serpulidae,
Spitsbergen,
Volgien,
Ryazanien,
suintements d'hydrocarbures.

INTRODUCTION

Serpulids are cosmopolitan sedentary polychaetes that form variously shaped calcareous tubes (ten Hove & Kupriyanova 2009). They are known from a range of water depths, from intertidal settings down to the abyssal plains (ten Hove & Kupriyanova 2009; Kupriyanova *et al.* 2011). Since their first occurrence in the Mid-Triassic (Vinn & Mutvei 2009) and diversification during the Jurassic (Parsch 1956), serpulids have colonized a wide variety of Mesozoic environments (Ware 1975; Jäger 1983, 1993, 2005, 2011; Jäger & Schubert 2008; Schlögl *et al.* 2008; Vinn *et al.* 2012; Sklenář *et al.* 2013), including, from the Late Mesozoic, hydrocarbon seep environments, where serpulids are frequent but a relatively understudied faunal element (Campbell 2006; Vinn *et al.* 2013). Serpulids have been also recorded in recent seeps (Olu *et al.* 1996a, b), but do not show any specific adaptations to this environment, probably simply taking advantage of the abundant hard carbonate substrate available for colonization (Vinn *et al.* 2013).

This work is part of a wider taxonomic and palaeoecological study of the fauna found in Volgian-Ryazanian shallow water seep deposits from Spitsbergen, Svalbard, as part of the research carried out by the Svalbard Jurassic Research Group (SJRG). The fauna is rich and diverse, and includes abundant bivalves, gastropods, and brachiopods, in addition to the serpulids described here (Hammer *et al.* 2011). Serpulids have been known from Jurassic and Cretceous non-seep sediments from Svalbard for a long time (Lindström 1865; Lundgren 1883; Stolley 1912). Lindström (1865) described *Serpula* Linnaeus, 1758 from undivided Jurassic rocks of Svalbard, but these records are difficult to confirm since no illustration of this material was given. Lundgren (1883) noted the presence of finely ribbed tubes and smooth, free *Ditrupa*-like tubes in Jurassic rocks of the western Isfjorden area of Spitsbergen, which he described as the scaphopods *Dentalium lindstroemi* Lundgren, 1883 and *Dentalium nodulosum* Lundgren, 1883. Here we reinterpret tubes of *D. nodulosum* as having a serpulid origin. Stolley (1912) described tubes with fine regular perpendicular ornamentation as *Ditrupa decorata* Stolley, 1912 from the Aptian-Albian Carolinefjellet Formation of the west side of Adventfjorden close to the city of Longyearbyen, Spitsbergen. These form mass accumulations known as "Ditrupen-Arten" or "Dentalien-Schichten" (Nathorst 1910; Różycki 1959). Birkenmajer *et al.* (1982) also described *Serpula* (*Cycloserpula*) cf. *subcrispa* Parsch, 1956

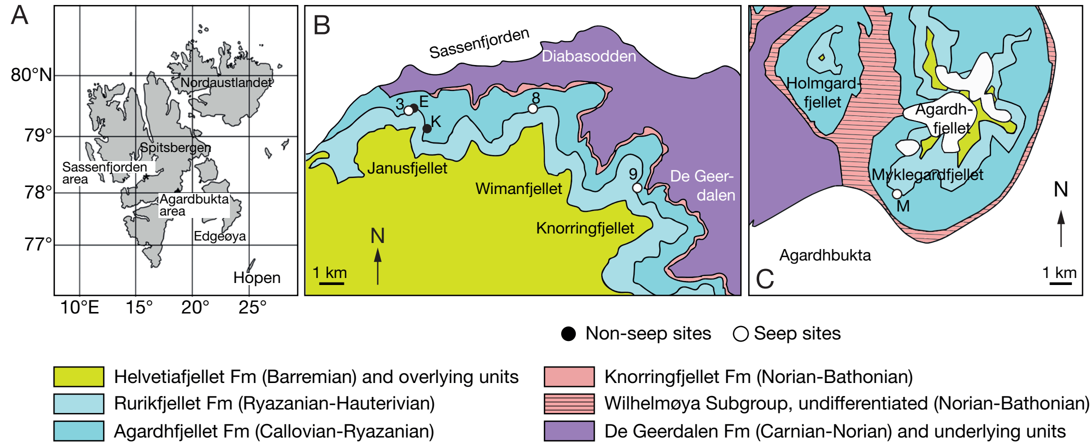

Fig. 1. — Map showing the location of study areas (**A**), geological map of Sassenfjorden (**B**) and Agardhbukta (**C**) areas of Spitsbergen, Svalbard with the serpulid-bearing localities in the paper marked; **K**, locality with ?*Pyrgopolon decorata* in Konusdalen; **E**, mass accumulation of ?*Pyrgopolon* aff. *nodulosum* from the Echinoderm bed; **M**, Myklegardfjellet seep; **3**, **8**, **9**, seep numbers. Modified from Dallmann *et al.* (2001).

and an unidentified serpulid specimens from the Volgian of Svalbard, which we here synonymize with *Ditrupa decorata* of Stolley (1912).

The aim of the paper is to: 1) systematically describe serpulids from the latest Jurassic-earliest Cretaceous seeps and shelf sediments of Svalbard; 2) investigate the ecology of Svalbard seep serpulids; 3) discuss palaeobiogeographic affiliations of the Svalbard serpulid fauna; 4) compare the Svalbard seep and shelf serpulid from the latest Jurassic-earliest Cretaceous; and 5) investigate their evolutionary links with later seep serpulids.

GEOLOGICAL BACKGROUND

All the described fossils come from the Agardhfjellet Formation (Dypvik *et al.* 1991a) cropping out in the Agardhbukta and Sassenfjorden areas of Spitsbergen, Svalbard (Fig. 1). A single serpulid fossil was collected from Myklegardfjellet in the Agardhbukta area from a hydrocarbon seep carbonate hosted by dark gray mudstones of the upper part of the Agardhfjellet Formation (see Dypvik *et al.* 1991b: fig. 6 for lithostratigraphic section). This part of the unit was deposited on a middle to outer shelf (Nagy *et al.* 1988, 1990) and is thought to be Volgian in age (Birkenmajer *et al.* 1982; Nagy & Basov 1998; Rogov 2010).

The serpulid fossils collected in the Sassenfjorden area come from the Slottsmøya Member of the uppermost Agardhfjellet Formation (Fig. 2). The Slottsmøya Member is up to 90 m thick and is a relatively homogenous unit, developed as black, organic-rich mudstones, with some coarser sediments present, mostly close to the base and top of the unit. The unit contains diagenetic carbonates, which accentuate depositional bedding and allow local correlations in an otherwise homogenous succession. The Slottsmøya Member was deposited in a middle to outer shelf environment with high organic matter supply (Nagy *et al.* 1988; Dypvik *et al.* 1991b; Reolid *et al.* 2010), with a reduction of sedimentation rates in the uppermost part of the member (Wierzbowski *et al.* 2011; Hryniewicz *et al.* 2012).

Due to strong provincialism of ammonite faunas around the Jurassic-Cretaceous boundary (Rogov & Zakharov 2009), only Boreal realm stratigraphic subdivisions can be applied in Svalbard, as in the rest of the Arctic region. Here the Tithonian and Berriasian standard stages equate roughly to the Boreal Volgian and Ryazanian stages, respectively (e.g., Zakharov & Rogov 2008). The Tithonian-Berriasian boundary and hence the boundary between the Jurassic-Cretaceous is positioned within the Upper Volgian Taimyrensis zone, so the Volgian-Ryazanian

Table 1. — Localities and stratigraphy of serpulid species from Jurassic-Cretaceous seeps and background sediments from Svalbard. Abbreviations: **Fm**, Formation; **spec.**, specimen.

Species	PMO number	Locality and number of specimens	Stratigraphy (this study)	Occurrence and stratigraphy elsewhere	References
?*Pyrgopolon decorata*	217.355 A, B	Konusdalen; 2 spec.	Middle Volgian, 5-7 m below Dorsoplanites bed	Jurassic (Western Spitsbergen), Jurassic-Cretaceous (Greenland), Aptian-Albian (Central Spitsbergen)	Stolley (1912) Donovan (1957) Birkenmajer *et al.* (1982)
?*Pyrgopolon* aff. *nodulosum*	217.357 217.366 numerous specimens on 226.601	Janusfjellet (numerous); seep 3; one spec., seep 9; one spec.	Echinoderm bed, Lower-Middle Volgian (background), Upper Volgian (seep 3), uppermost Ryazanian (seep 9)	Jurassic (Western Spitsbergen), Jurassic-Cretaceous (Greenland)	Lundgren (1883) Donovan (1957) Birkenmajer *et al.* (1982)
?*Pyrgopolon* sp. A	217.365	Seep 8; one specimen	Upper Volgian	–	–
Propomatoceros sp. A	217.354 A-F 225.171 A, B	Seep 3; eight specimens	Upper Volgian	genus widespread in Jurassic (Europe, Russia) and Lower Cretaceous (Europe)	Parsch (1956) Ware (1975) Ippolitov (2007b)
Nogrobs aff. *quadricarinata*	217.356	Myklegardfjellet seep, one specimen	Volgian, 40-50 m below the top of the Agardhfjellet Fm	Upper Jurassic (Germany)	Parsch (1956)

boundary occurs above the Jurassic-Cretaceous boundary (Houša *et al.* 2007). This indicates that all the Volgian seeps from Svalbard are of latest Tithonian age (Wierzbowski *et al.* 2011) and in the discussed succession Volgian roughly correlates with Tithonian.

LOCALITY INFORMATION

Details on serpulid-bearing localities are given in Table 1. The described non-seep specimens were discovered during prospecting for and excavation of fossil marine reptiles (Hurum *et al.* 2012) in Konusdalen and on the northern slopes of Janusfjellet (Fig. 1). Unidentified serpulid tubes, not included into the systematic part of this paper, are visible in thin sections from several seep carbonate bodies. Detailed descriptions of the seep localities are in Hammer *et al.* (2011), Wierzbowski *et al.* (2011) and Hryniewicz *et al.* (2012). The Myklegardfjellet seep carbonate was discovered on the southwestern slopes of Myklegardfjellet in the Agardhbukta area by Snorre Olaussen from the University of Svalbard in 2011. This seep carbonate is preserved *in situ* as a series of stacked carbonate lenses, occurring 40 to 50 m below the top of the formation. All fossil specimens described below are housed in the palaeontological collection of the Natural History Museum, University of Oslo, Norway (PMO).

SYSTEMATIC PALAEONTOLOGY

Class POLYCHAETA Grube, 1850
Order SABELLIDA Dales, 1962
Family Serpulidae Rafinesque, 1815
Genus *Pyrgopolon* de Montfort, 1808

Type species. — *Pyrgopolon mosae* de Montfort, 1808 by original designation.

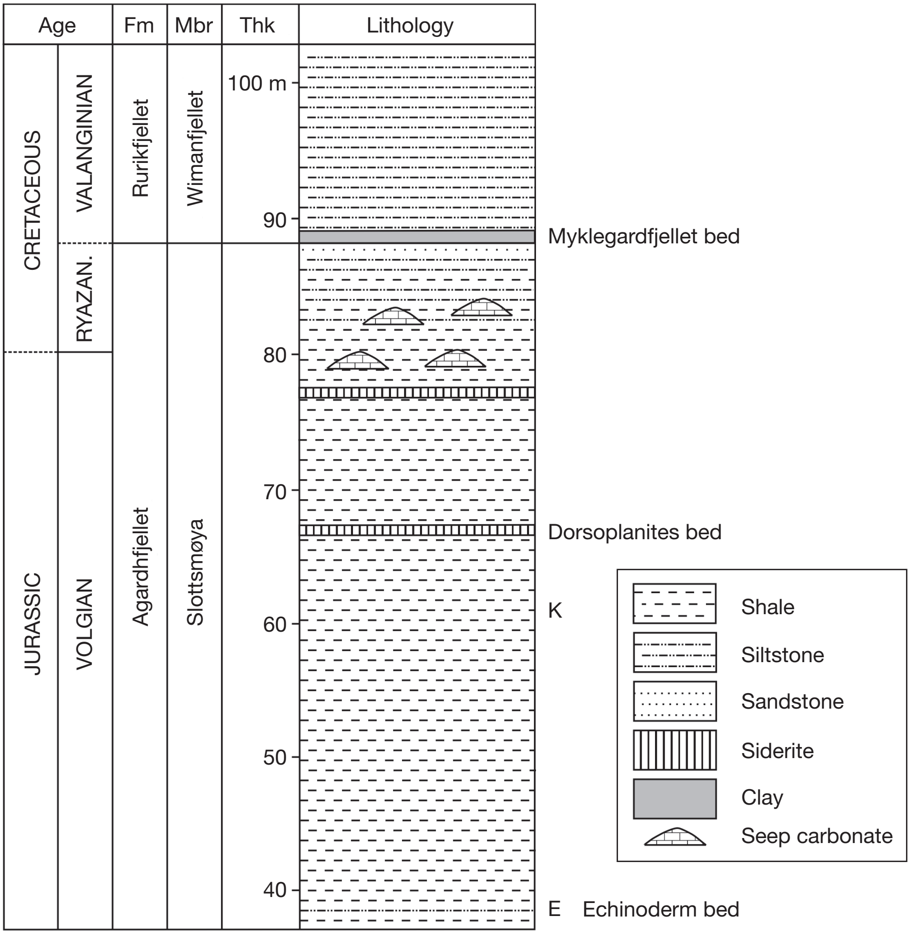

Fig. 2. — Simplified profile of the Slottsmøya Member, Agardhfjellet Formation at the Janusfjellet section. "K" marks the approximate stratigraphic position of the locality with *Pyrgopolon*? *decorata* in Konusdalen, "E" marks the stratigraphic position of the mass accumulation of ?*Pyrgopolon* aff. *nodulosum* from the Echinoderm bed. Modified from Wierzbowski *et al.* (2011).

?*Pyrgopolon decorata* (Stolley, 1912) (Fig. 3A-C)

Ditrupa decorata Stolley, 1912: 23-26, pl. 2, figs 5, 6, pl. 3.

Serpula (*Cycloserpula*) cf. *subcrispa* Parsch, 1956: 28, pl. 21, fig. 3. — Birkenmajer *et al.* 1982: 118, pl. 38, fig. 7.

Material and locality. — see Table 1.

Description

Tubes curved, with circular cross section. Tube wall rather thick, 0.7 mm at tube diameter 3.2 mm. Entire tube covered with extremely regular fine perpendicular rings, 8 to 9 per 1 mm at tube diameter of 5.0 mm. Several weakly developed thin, but regularly shaped ampullacea-type peristomes present, about 0.5 mm wide. Tube double-layered, with chevron-shaped growth lamellae.

Discussion

The specimens are assigned to ?*P. decorata*, due to their characteristic fine perpendicular tube ornamentation. ?*Pyrgopolon decorata* is a serpulid because of the chevron-shaped growth lamellae, and we tentatively ascribe this species to the genus *Pyrgopolon* because of its relatively thick walled and large tubes. ?*Pyrgopolon decorata* differs from ?*P.* aff. *nodulosum* by the presence of fine regular perpendicular ornamentation. ?*Pyrgopolon decorata* differs from ?*Pyrgopolon* sp. A in having fine regular perpendicular ornamentation and ampullacea-type peristomes.

?***Pyrgopolon*** aff. ***nodulosum*** (Lundgren, 1883) (Fig. 3D-G)

Dentalium nodulosum Lundgren, 1883: 10, 11, pl. 2, figs 7-9.

Serpula sp. indet. – Birkenmajer *et al.* 1982: 119, pl. 38, fig. 8; pl. 43, fig. 8.

MATERIAL AND LOCALITY. — See Table 1.

DESCRIPTION
Tube smooth, cross section circular, straight, with weakly developed regularly shaped ampullacea-type peristomes, about 1 mm wide. Tube wall moderately thick, about 0.5 mm at 3.0 mm tube diameter of free tube part, two-layered, inner layer granular, outer layer prismatic; relative thickness difficult to estimate due to corrosion. Chevron-shaped growth lamellae visible.

DISCUSSION
The specimens presumably belong to *Dentalium nodulosum* Lundgren, 1883, because they have a similar general appearance and lack of fine perpendicular ornamentation. *Dentalium nodulosum* is a serpulid, not a scaphopod, because of the chevron-shaped growth lamellae. The species is tentatively assigned to the genus *Pyrgopolon* because of the relatively large tubes.

?*Pyrgopolon* sp. A (Fig. 4A-E)

MATERIAL AND LOCALITY. — See Table 1.

DESCRIPTION
Maximum tube diameter 4.8 mm. Free tube part smooth, circular in cross section, without any ornamentation, slightly meandering. Tube wall rather thick, 0.7 to 1.0 mm at 4.8 mm tube diameter, two-layered, inner layer microgranular, occupying about half of the tube thickness, outer layer prismatic.

DISCUSSION
The specimen is tentatively assigned to *Pyrgopolon* because of its relatively thick walls.

Genus *Propomatoceros* Ware, 1975

TYPE SPECIES. — *Propomatoceros sulcicarinata* Ware, 1975 by original designation.

Propomatoceros sp. A (Fig. 4F)

MATERIAL AND LOCALITY. — See Table 1.

DESCRIPTION
Free tube part short, up to 3 mm long, with circular cross section and well-developed and relatively thick keel (1.0 mm thick at the base). Tube wall moderately thick, 0.75-1.0 mm at 4.5 mm tube diameter. Cementing part more than 15 mm long, keeled, poorly preserved.

DISCUSSION
The specimen is assigned to the genus Propomatoceros due to its characteristic single, well-developed longitudinal keel. The fragmentary state of preservation precludes species identification.

Genus *Nogrobs* de Montfort, 1808

TYPE SPECIES. — *Nogrobs vermicularis* de Montfort, 1808 by original designation.

Nogrobs aff. ***quadricarinata*** Münster *in* Goldfuss, 1831 (Fig. 4G, H)

MATERIAL AND LOCALITY. — See Table 1.

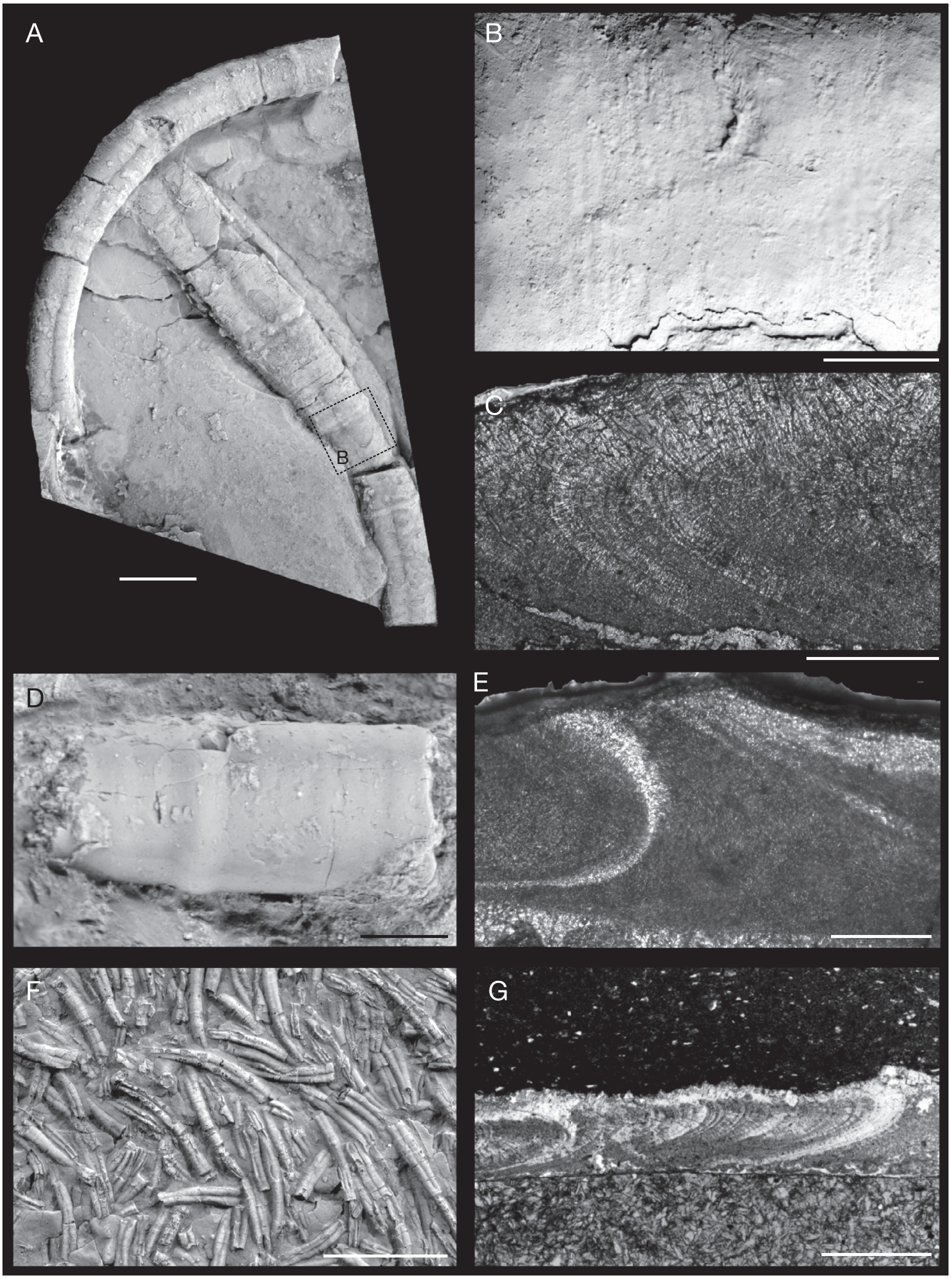

FIG. 3. — Serpulids from background sediments and seep carbonate bodies, Spitsbergen, Svalbard: **A**-**C**, ?*Pyrgopolon decorata* (Stolley, 1912): **A**, two large specimens showing the shape and external ornament of the tube (PMO 217.355A, B), Konusdalen; **B**, details of the external ornament of ?*Pyrgopolon decorata* (PMO 317.355 A); **C**, acetate peel of the tube wall of ?*Pyrgopolon decorata* (PMO 217.355 B). **D**-**G**, ?*Pyrgopolon* aff. *nodulosum* (Lundgren, 1883): **D**, fragment of a tube (PMO 217.357), seep 3; **E**, acetate peel of the tube wall (PMO 217.357), seep 3; **F**, mass accumulation of ?*Pyrgopolon* aff. *nodulosum* (PMO 226.601), Echinoderm bed, Janusfjellet; **G**, thin section of the tube wall of ?*Pyrgopolon* aff. *nodulosum* (PMO 214.847), Echinoderm bed, Janusfjellet. Scale bars: A, 5 mm; B, 1 mm; C, E, G, 200 µm; D, 2 mm; F, 15 mm.

Description

Tube free part curved, with quadrangular cross section, edges rounded, tube surface slightly concave between edges. Tube entirely covered with well-developed perpendicular ornament of fine ridges, which do not form complete rings. Tube wall much thicker at edges than between them.

Discussion

The specimen is assigned to the genus *Nogrobs* because of its characteristic quadrangular cross section. The rounded cross-sectional edges, and the concave surfaces between them are features seen in the tube of *Nogrobs quadricarinata*. However, the fragmentary nature of our material precludes exact species determination.

DISCUSSION

Ecology of Svalbard seep serpulids.

The poor state of preservation of the Svalbard seep serpulid material, being mostly free tube fragments, does not allow us to reconstruct to what most of the tubes were originally attached. Only in case of *Propomatoceros* sp. A from seep 3 it can be seen that the tubes were attached directly to seep carbonates (Fig. 5A). Therefore, these serpulids must have populated the site after seepage started and some seep carbonates had formed and were exposed (e.g., Vinn *et al.* 2013). On the other hand, some unidentified, unkeeled serpulids seen in thin section from seep 9 and probably representing one of the species of ?*Pyrgopolon*, were attached to bioclasts, or to each other (Fig. 5B), indicating some local hard substrate deficiency and the necessity of utilizing smaller hard surfaces. As ?*Pyrgopolon decorata* and ?*Pyrgopolon* aff. *nodulosum* occur in the surrounding shales, where no hard carbonate substrate other than shells is available, the seep ?*Pyrgopolon* specimens could represent background fauna cemented by the seep carbonate after seepage had commenced. Other unidentified serpulid tubes visible in thin sections are covered with microinfestation traces (Fig. 5C) which are filled by micritic seep carbonate. All of the seep serpulid tubes studied here are filled with authigenic carbonate, either as micrite (Fig. 5C), or in some cases botryoids (Fig. 5D), indicating at least some seepage activity and anaerobic oxidation of methane after the death of the serpulids. All the above observations suggest that the Svalbard seep serpulids were not restricted to any particular stage of seep evolution.

Palaeobiogeography

Late Jurassic-Early Cretaceous serpulids from Europe are relatively well known (Parsch 1956; Jäger *et al.* 2001; Jäger 2011; Ippolitov 2007a, b), particularly those from lower latitudes. The Svalbard Volgian serpulid fauna contains Boreal serpulid species that are not known from elsewhere in Europe. ?*Pyrgopolon decorata* and ?*Pyrgopolon* aff. *nodulosum* are species occurring in high latitudes only. In addition to their occurrence in Svalbard (Table 1), ?*P. decorata* and ?*P.* aff. *nodulosum* have been reported from Jurassic-Cretaceous deposits of Greenland (Donovan 1957) and may have been Boreal species. However, there are species with similar morphology from lower latitudes of Europe (e.g., Parsch 1956; Ware 1975). An alternative is that they represent species with high climatic tolerance. *Nogrobs* aff. *quadricarinata* is very similar in morphology to the *Nogrobs* species from the Late Jurassic of Germany (Table 1; Parsch 1956). It is likely that this genus may have had a wide climatic distribution, from warm waters of Europe to cooler waters of Svalbard. Species of *Propomatoceros* are known from the Jurassic (Parsch 1956) and the Early Cretaceous (Ware 1975) normal marine sediments of Europe and Jurassic of Russia (Ippolitov 2007b). The current study indicates that this genus also occurs in higher latitudes. As based on this the Svalbard serpulid genera are rather cosmopolitan considering their known occurrences.

Comparison of Svalbard seep and shelf faunas

The Jurassic background sediments of Svalbard contain a rather low diversity association of serpulids (two species) compared to Mesozoic shelf serpulid faunas in general (Table 2; e.g., Parsch 1956; Ware 1975; Jäger 1983, 1993, 2005, 2011), and modern Boreal serpulid faunas (Kupriyanova & Jirkov 1997). This may partially reflect sampling bias, as latest Jurassic-earliest Cretaceous background sediments from Svalbard have been subjected to only limited

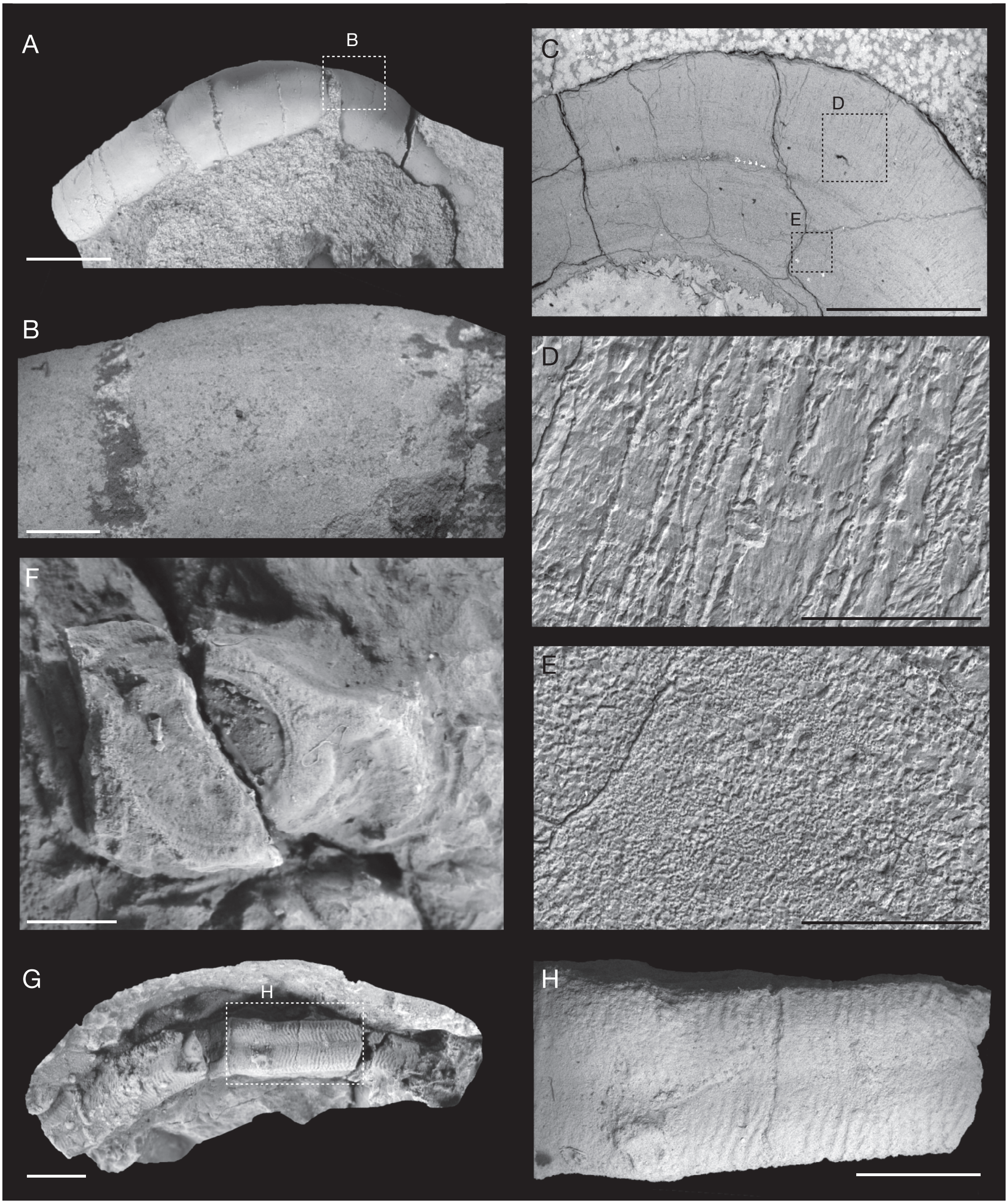

FIG. 4. — Serpulids from seep carbonate bodies, Spitsbergen, Svalbard: **A**-**E**, ?*Pyrgopolon* sp. A: **A**, large specimen showing the shape and external surface of the tube (PMO 217.365), seep 8; **B**, details of the outer surface of ?*Pyrgopolon* sp. A, showing the smooth outer surface (PMO 217.365), seep 8; **C**, cross-section of the tube showing the thickness relation of inner and outer layers (PMO 217.365), seep 8; **D**, details of the outer prismatic layer (PMO 217.365), seep 8; **E**, details of the inner microgranular layer (PMO 217.365), seep 8. **F**, *Propomatoceros* sp. A, apertural view (PMO 217.354), seep 3. **G**, **H**, *Nogrobs* aff. *quadricarinata* Münster *in* Goldfuss, 1831: **G**, specimen showing shape and external ornament of the tube (PMO 217.356), Myklegardfjellet seep; **H**, details of the outer surface showing ornament composed of incomplete rings and concave surface of the tube (PMO 217.356), Myklegardfjellet seep. Scale bars: A, 5 mm; B, C, H, 1 mm; D, 200 µm; E, 100 µm; F, G, 2 mm.

TABLE 2. — List of studied taxa occurring in background and seep environments.

Background environment	**Seep environment**
?*Pyrgopolon decorata* ?*Pyrgopolon* aff. *nodulosum*	?*Pyrgopolon* aff. *nodulosum* ?*Pyrgopolon* sp. A *Propomatoceros* sp. A *Nogrobs* aff. *quadricarinata*

palaeontological study (Lundgren 1883; Birkenmajer *et al.* 1982). ?*Pyrgopolon decorata* and ?*Pyrgopolon* aff. *nodulosum* represent forms with long erect free tubes, which reflects the overall low-energy setting and scarcity of the available hard substrate (Dypvik *et al.* 1991b). No attached sections have been found so far. The mass-accumulations of ?*Pyrgopolon* aff. *nodulosum* found in the Echinoderm bed on Janusfjellet probably represent current-sorted material, indicated by the similar size and orientation of the specimens (Fig. 3F). In contrast to the background serpulid fauna from Svalbard, the seep serpulid fauna is twice as diverse (four species), making it the most diverse fossil seep serpulid fauna known to date (Table 2; cf. Vinn *et al.* 2012, 2013). Three of the species are represented by fragments of free erect tubes, which is in accordance with the generally low-energy setting for most of the Svalbard seeps (e.g., Hryniewicz *et al.* 2012). *Propomatoceros* sp. A represents a cementing form with a long attached tube section, probably reflecting increased availability of hard substrate in the seep environment as compared to the surrounding background environment (Ware 1975; Ippolitov 2007b; Hryniewicz *et al.* 2012). A higher diversity of serpulids in the Svalbard seeps in comparison to surrounding sediments is unlike the situation encountered in modern vents (ten Hove & Zibrowius 1986; Kupriyanova *et al.* 2010) and seeps (Olu *et al.* 1996a, b), where serpulids are less diverse than in the surrounding environment (Vinn *et al.* 2013). Serpulids in general are considered as seep colonists (e.g., Olu *et al.* 1996a), meaning that they represent taxa from surrounding areas that have subsequently populated the seep environment. In the Svalbard context, the increased diversity at seeps may reflect an increased availability of hard carbonate substrate for larval settlement, compared to the overall soupy and organic-rich surrounding soft sediment (e.g., Ippolitov 2007a, b; Hryniewicz *et al.* 2012). Taking into account the limited sampling, especially in the lower part of the Volgian sucession, the actual diversity of the background serpulids may be greater and hence the difference between the fossil seep and background serpulids assemblages may be not so large.

EVOLUTIONARY IMPLICATIONS

The Volgian seeps of Svalbard contain the earliest known seep serpulid fauna. The fauna is surprisingly diverse (three genera, four species) compared to later Mesozoic seeps in North America and Japan (Tables 2, 3; e.g., Vinn *et al.* 2013). The genus ?*Pyrgopolon* is recorded here for the first time in the seep of Late Volgian age and the Early to Mid-Volgian occurrence in the surrounding background sediments, together with occurences of similar forms in Late Kimmeridgian of Europe, could be the oldest record of the genus (Table 3; e.g., Jäger 2005; Pillai 2009). Two of the Svalbard genera are shared with Valanginian seeps from California (*Propomatoceros* and ?*Nogrobs*) and one from the Campanian-Maastrichtian of Japan (*Propomatoceros*) (Table 3; Vinn *et al.* 2012, 2013). The genus *Propomatoceros* has its oldest occurrences in the Toarcian of Europe (*Serpula* (*Dorsoserpula*) sensu Parsch 1956) and colonizes seeps no later than Late Volgian (Table 3). The genus *Nogrobs* is known from the Late Pliensbachian (Jäger 2005) and, like *Propomatoceros*, occurs in seeps in the Volgian (Table 3). A pattern of some time lag between the first fossil occurrence and first occurrence at seep observed among the serpulids in this paper is similar to pattern noted among some seep molluscs (Warén & Bouchet 2001; Kiel 2010a, b; Kiel & Little 2006).

Modern serpulids form two large clades, one containing species with more plesiomorphic characters and another containing species with more apomorphic characters. *Pyrgopolon* belongs to the apomorphic clade (Vinn & Kupriyanova 2011) and the position of *Nogrobs* is not known in the serpulid phylogeny (E. Kupriyanova pers. comm. 2013). It is possible that *Propomatoceros* is an ancestor of *Spirobranchus* and thus also belongs to the apomorphic clade. Thus,

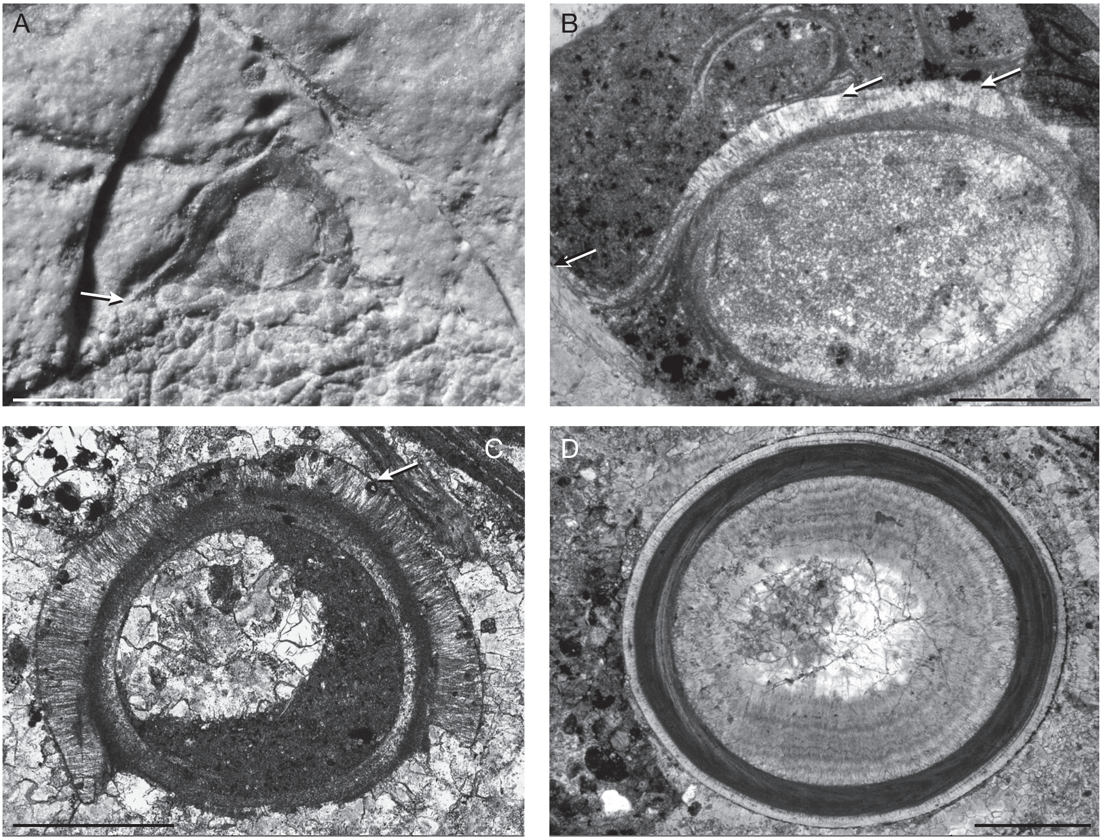

FIG. 5. — Ecology of serpulids from latest Jurassic-earliest Cretaceous seep carbonates from Spitsbergen, Svalbard: **A**, specimen of *Propomatoceros* sp. attached to exposed carbonate surface (**white arrow**) (PMO 225.171), seep 3; **B**, serpulid tube attached to bioclast (**black arrow**) with surface covered with smaller serpulid tubes (**white arrows**) (PMO 214.757), seep 9; **C**, serpulid tube partially filled with dark authigenic micrite; some microborings visible close to the surface (**white arrow**) are filled with dark authigenic micritie (PMO 214.723), seep 9; **D**, serpulid tube filled with authigenic botryoidal cement (PMO 171.023B), seep 13. Scale bars: A, B, 2 mm; C, D, 1 mm.

the species of the apomorphic clade were among the first serpulid colonizers of seep environments.

One could ask whether later Mesozoic seep serpulids evolved from the early seep species or they belong to later colonists. It is possible, though rather unlikely, that later seep species may have evolved from early seep *Propomatoceros*, but most likely species of *Propomatoceros* could have been opportunistic and colonized seeps multiple times during the geological past. The same applies for *Nogrobs* which is known both from the Volgian seeps of Svalbard and later Valanginian seeps of California. Among the chaetopterids (a group of annelids with organic tubes), which apparently are colonists, there seems to be a distinct group that colonizes chemosynthetic ecosystems (Morineaux *et al.* 2010).

CONCLUSION

Five species of serpulids, distributed in three genera are described from Volgian-Ryazanian sediments and seeps from Svalbard. The fauna is in general characteristic of low-energy environments. The seep fauna is more diverse than that in the background sediments, which probably reflects the greater availability of hard carbonate substrates in the seeps, but may also reflect sampling bias.

TABLE 3. — Oldest occurrences of the studied serpulid genera in other seeps and other environments.

Genus	Oldest seep occurrence	Other seep occurrences	Oldest occurrence	Reference
?*Pygopolon*	Late Volgian (this study)	–	Late Kimmeridgian?	Jäger (2005), Pillai (2009), Vinn *et al.* (2012), Vinn *et al.* (2013).
Propomatoceros	Late Volgian (this study)	Valanginian; Campanian-Mastrichtian	Toarcian	Parsch (1956), Vinn *et al.* (2012), Vinn *et al.* (2013).
Nogrobs	Volgian (this study)	Valanginian	Late Pliensbachian	Jäger (2005), Vinn *et al.* (2012), Vinn *et al.* (2013).

A single species is shared between the background sediments and seeps, but the overall seep fauna is composed of different taxa than the background fauna. The Svalbard seep serpulids are the oldest seep occurrences known to date. They are all younger than the oldest evolutionary occurrences of the same genera from background sediments elsewhere, which is a pattern also recorded for other seep fossil groups.

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