Late Jurassic–Early Cretaceous hydrocarbon seep boulders from Novaya Zemlya and their faunas

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ABSTRACT

The paper describes Late Jurassic–Early Cretaceous seep carbonate boulders from the Russian Arctic island of Novaya Zemlya, collected in 1875 by A.E. Nordenskiöld during his expedition to Siberia. The carbonates are significantly depleted in heavy carbon isotopes (δ^{13}C values as low as ca. −40‰) and show textures typical for carbonates formed under the influence of hydrocarbons, such as fibrous carbonate cements and corrosion cavities. The rocks contain index fossils of Late Oxfordian–Early Kimmeridgian, Late Tithonian (Jurassic) and latest Berriasian–Early Valanginian (Cretaceous) age. The fossil fauna is species rich and dominated by molluscs, with subordinate brachiopods, echinoderms, foraminifera, serpulids and ostracods. Most of the species, including two chemosymbiotic bivalve species, likely belong to the 'background' fauna. Only a species of a hokkaidoconchid gastropod, and a possible abyssochrysoid gastropod, can be interpreted as restricted to the seep environment. Other seep faunas with similar taxonomic structure are suggestive of rather shallow water settings, but in case of Novaya Zemlya seep faunas such structure might result also from high northern latitude.

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1. Introduction

The chemosynthetic environments grouped around deep marine hydrocarbon emissions, known as hydrocarbon seeps (e.g. Paull et al., 1984; Campbell, 2006; Judd and Hovland, 2007), together with hydrothermal vents (e.g. Lonsdale, 1977; Van Dover, 2000) and whale falls (Smith and Baco, 2003) are characterized by distinct biota, largely different from that of the surrounding marine environments (Levin, 2005). The large concentrations of reduced compounds available at these sites, chiefly sulphides and to a lesser extent methane, sustain mass accumulations of chemosymbiotic fauna, such as solemyid, lucinid, thyasirid and vesicomyid clams, and bathymodiolin mussels (Métiver and von Cosel, 1993; Sibuet and Olu, 1998; Fujikura et al., 1999; Glover et al., 2004; Taylor and Glover, 2010; Krylova et al., 2011), large abyssochrysoid gastropods (Kojima et al., 2001; Sasaki et al., 2010) and siboglinid tubeworms (Hilário et al., 2011). Additionally, exposed hard substrates provide attachment opportunities for hard-substrate dwellers, such as serpulid polychaetes, and sea anemones (e.g. Ten Hove and Zibrovius, 1986; Fabri et al., 2011; Vinn et al., 2013). Shallower water (~300 m and less) chemosynthetic communities have few, or no seep and vent specialists, and their fauna is composed of background species (i.e., species typical for the surrounding 'normal' seabed) (Levin et al., 2000; Sahling et al., 2003; Dando, 2010).

Fossil hydrocarbon seep faunas are known since the Devonian (Peckmann et al., 1999) and possibly Silurian (Barbieri et al., 2004). The scarcity of sites older than late Mesozoic means that knowledge of pre-Cretaceous hydrocarbon seep faunas is poor (Gischler et al., 2003; Campbell, 2006; Peckmann et al., 2011, 2013). It has been suggested that since at least the Late Devonian until the Early Cretaceous, seeps were largely dominated by dimerelloid rhynchonellid brachiopods (Peckmann et al., 2007; Sandy, 2010; Kiel et al., 2014), with molluscs also present, although often subordinate (e.g. Peckmann et al., 1999, 2001, 2011); the younger seep sites are populated almost exclusively by molluscs (Kiel et al., 2008a, b; Kaim et al., 2009). However, the oldest known mollusc-dominated seep faunas known are Late Jurassic (Oxfordian) in age (Gaillard et al., 1992) and there are some other Late Jurassic and Early Cretaceous seep sites which are dominated both in abundance and diversity by molluscs (e.g. Campbell et al., 1993; Kaim and Kelly, 2009; Hammer et al., 2011). At least some of mollusc-dominated seep sites formed in relatively shallow water (Hryniewicz et al., 2015). Irrespective of the bathymetrical setting and their faunal composition, the seep carbonates display a set of characters allowing their straightforward interpretation in the fossil record (Campbell, 2006), such as significant contribution of isotopically light

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carbon (e.g. Kelly et al., 1995; Campbell et al., 2002; Peckmann et al., 2003; Campbell, 2006), textures suggesting formation under the influence of gaseous or liquid hydrocarbons (e.g. Peckmann et al., 2002; Campbell et al., 2008; Krause et al., 2009) and lipid biomarkers suggestive of microbial processes accompanying methane oxidation (e.g. Peckmann and Thiel, 2004; Birgel et al., 2008; Peckmann et al., 2009).

This paper presents three new Mesozoic seep deposits and associated fossils from the Arctic island of Novaya Zemlya, Russia. Two of the faunas are Late Jurassic in age (Oxfordian/Kimmeridgian and Tithonian, respectively) and one is Early Cretaceous (latest Berriasian–Valanginian). All three fossil assemblages are composed almost exclusively of molluscs, with very few brachiopods, serpulids and echinoderms, and associated microfauna. In this paper we establish the seep origin of the Novaya Zemlya material using stable C and O istope analyses and petrography. We also re-figure fauna described from these deposits by Tullberg (1881) with preliminary new identifications.

2. Locality

The material used for this study is stored in the Naturhistoriska Riksmuseet in Stockholm (prefix NRM), Sweden and was collected on the 14th of July, by Adolf Erik Nordenskiöld during his 1875 expedition to the mouth of Yenisei river and to Siberia on board the ship *Pröven* (Fig. 1; Nordenskiöld, 1877). It was initially studied and described by Tullberg (1881) and some of the gastropods were later re-described by Kaim et al. (2004) and Kaim and Biesel (2005), although their seep origin was not suspected at the time. The material was most likely collected at the base of a cliff formed of Silurian rocks in 'Skodde Bay' on Novaya Zemlya (Nordenskiöld, 1877; Stuxberg, 1877; Tullberg, 1881). The locality name does not exist on any past or recent topographic map of Novaya Zemlya; further, there are no Jurassic rocks marked on any geological map of the area. To track the origin of the material, we analysed the timeline of the *Pröven* expedition using unpublished materials (the log book and weather report) stored in the Royal Swedish Academy of Sciences in Stockholm, together with official published reports (Nordenskiöld, 1877; Stuxberg, 1877). There are only written accounts of fossils collected in 'Skodde Bay' on the 14th of July, 1875, but the bay and the landing site are not indicated on any map. Tullberg (1881) also discusses fossil material collected further south in Bezymyannaya Bay (Besimennaya Bay in Tullberg (1881) and on NRM labels; literally means No-name Bay in Russian), but stable C

isotope values between −3.7 to −1.7 δ^{13}C) suggest this material is most likely not of a seep origin and will not be discussed further here.

The Nordenskiöld expedition used the small 43-ton Norwegian yacht *Pröven*. The team of 17 men boarded ship in Tromsø, Norway, and left for the sea on the 14th of June, 1875, entering the Barents Sea on the 17th. After crossing the Barents Sea, *Pröven* reached the Southern Island of Novaya Zemlya near the northern shores of Goose Land on 22nd of June, stayed there for four days (Fig. 1) and proceeded northwards towards Matochkin Shar, which was reached on the 6th of July (Stuxberg, 1877). The attempt to cross the strait was unsuccessful and after six days, on the 13th the ship turned back into a severe SW wind. According to Nordenskiöld (1877), the ship proceeded only a short distance towards the SW and then, as the wind died down, drifted close to shore on the 14th and anchored close to a cape noted as 'Säulen C.' in a shallow bight named as 'Skodde Bay'. 'Säulen' ('pillars') is written as 'Столбы' ('Stolbi') in Russian. If such direct translation is applied, then it seems likely that on the 14th of July *Pröven* anchored close to Cape Stolbovoi west of the mouth of Matochkin Shar. 'Skodde Bay' represents an informal 19th Century name given, presumably, to Bakan Bay by Norwegian hunters (Nordenskiöld, 1877). It is also possible that the expedition anchored in Pomorskaya Bay close to Cape Matochkin (Fig. 2), misidentified in bad weather as 'Säulen C.'.

The area west of the mouth of Matochkin Shar is known to contain Late Jurassic and Early Cretaceous fossils from erratic boulders spread out over a relatively large area (Holtedahl, 1924; Salfeld and Frebold, 1924; Bodylevsky, 1936a, b, 1967; Dibner, 1962) and we postulate that the studied material is also erratic in origin and therefore ex-situ. The source for the erratic boulders is uncertain. The lithology of the Jurassic–Cretaceous rocks on Spitsbergen (Birkenmajer et al., 1982) and Franz Josef Land (Dibner and Shulgina, 1998) is different from the inferred host rocks of the seep carbonate boulders and it is unlikely that they come from these islands. They might have come from the Jurassic rocks cropping out in the Northern Siberia, which are more coarse-grained (e.g. Wierzbowski and Rogov, 2013a, 2013b and references therein).

3. Materials and methods

Blocks of fossil seep carbonates collected during Nordenskiöld's expedition at 'Skodde Bay' are up to 20 cm in diameter. All blocks are fragments of larger boulders which were broken up, presumably in the field,
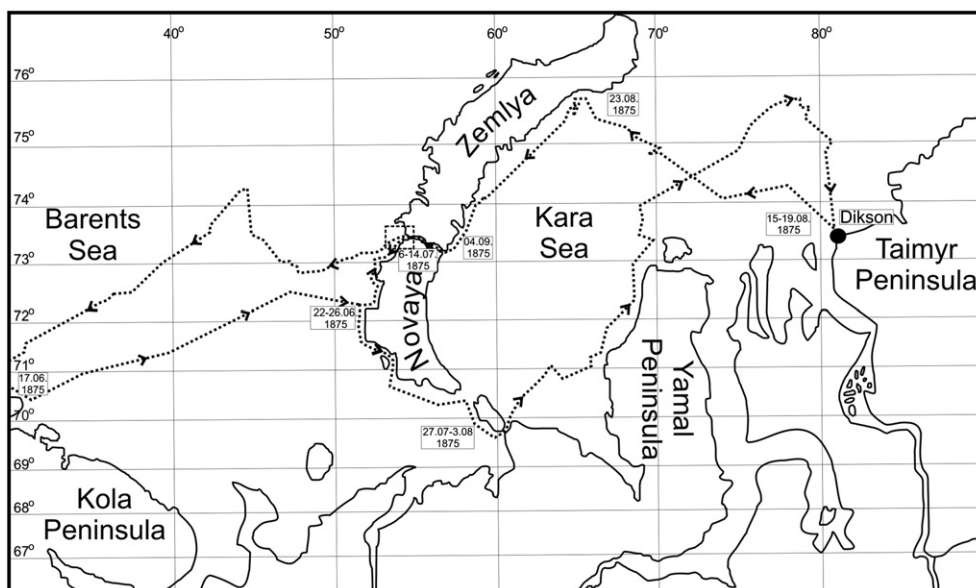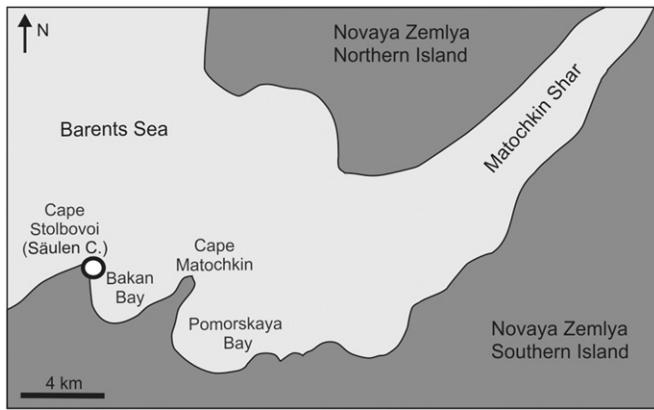

Fig. 1. The path of the 1875 *Pröven* expedition of A.E. Nordenskiöld to Novaya Zemlya and Siberia. Inset marks the approximate position of map from Fig. 2. Modified from Nordenskiöld (1877) and Stuxberg (1877).

Fig. 2. The map of western mouth of Matochkin Shar. The white circle marks a possible anchorage of *Pröven* on 14th of July, 1875. Based on Holtedahl (1922).

Fig. 3. Stratigraphic position of the seep carbonate boulders from Novaya Zemlya. Length of bars indicates dating uncertainties, not the duration of seepage. Dates after Ogg et al. (2012).

to recover the fossils. The few weathered surfaces available are polished, possibly due to glacial action, and pitted due to dissolution of carbonate. The material can be grouped into three main lithologies: calcareous sandstones, black limestones and sandy limestones (Tullberg, 1881, p. 6). All fossils are very well preserved, with some shells still retaining an original aragonitic structure. Mechanical preparation of most of the fossils from their matrices was necessary.

Carbonate samples from all the lithologies were analysed for their stable isotope compositions (δ^{13}C and δ^{18}O) at the Department of Earth Science, University of Bergen, Norway. Fragments of calcareous sandstones and sandy limestones were removed from larger blocks using pliers; the black limestone proved to be tougher and had to be hand-drilled. The samples were analysed using Finnigan MAT251 and MAT253 machines coupled to automated Kiel devices; the data are reported to VPDB standard; the long-term analytical precision is 0.05‰ with respect to δ^{13}C and 0.1‰ with respect to δ^{18}O. A few blocks were cut on a rock saw and polished to investigate their macroscopic textures, and smaller fragments were used to prepare petrographic thin sections. These sections were investigated in plane-polarized and cross-polarized light using a Leica DMLB microscope; when necessary, the whole thin-sections were scanned using a Nikon LS4000 slide scanner. The definitions of different carbonate phases follow that of Folk (1959).

4. Results

4.1. Seep carbonate ages

The lithological subdivision of Tullberg (1881) can be further supported by age differences shown by index fossils extracted from the boulders. The calcareous sandstones contain numerous specimens of the ammonite *Amoeboceras* sp., and therefore can be dated as Late Oxfordian–Early Kimmeridgian (Fig. 3; Sykes and Callomon, 1979; Zeiss, 2003; Wierzbowski and Rogov, 2013a, 2013b). Species-level identification of *Amoeboceras* found in the current material and thus potentially narrowing down the age of the calcareous sandstone blocks is currently not possible due to lack of individuals with well preserved ventral margin. The black limestones contain ammonites, preliminarily identified as belonging to the earliest Late Volgian species *Craspedites okensis*. The Late Volgian is roughly correlable with the Late Tithonian–earliest Berriasian, and the black limestones can therefore be dated as Late Tithonian (Fig. 3; Zakharov and Rogov, 2008; Wierzbowski et al., 2011). The sandy limestones do not contain any ammonites, therefore, precise dating is problematic. The blocks do contain abundant specimens of the bivalve *Buchia*, which is most similar to the morphology of specimens of *Buchia inflata* that occur in the latter part of the temporal
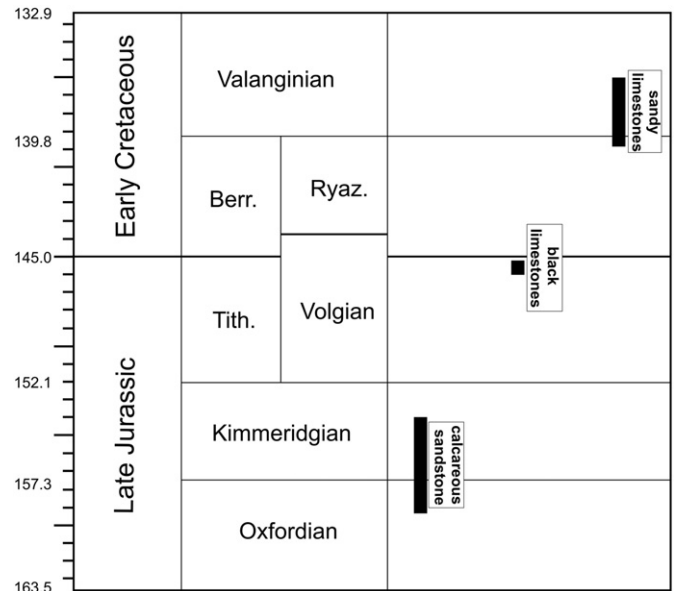
range of this species, or to *Buchia keyserlingi* (Zakharov, 1981; Surlyk and Zakharov, 1982); this suggests a latest Ryazanian–Early Valanginian age for the sandy limestone blocks (Fig. 3). A latest Ryazanian age can be correlated with latest Berriasian in the standard stratigraphy (Wierzbowski et al., 2011) and the latter age is used in this paper.

4.2. Petrography and stable isotopes

Carbonate fabrics in all the investigated facies are fairly simple and homogenous, although some carbonate authigenetic phases are present.

The Late Oxfordian–Early Kimmeridgian calcareous sandstones are dark grey, highly fossiliferous, homogenous and devoid of any macroscopically visible primary cavities filled with cements (Fig. 4A). The rock is mostly composed of fine to medium-grained quartz grains. The pore space is occluded by calcitic microspar (ms) with clotted micritic aggregates (Fig. 4B). Up to 10% of the grains are volcanic glass clasts, up to 2 mm in diameter, which in some cases are replaced by aggregates of phyllosilicate minerals (Fig. 4C). These grains are often covered and impregnated with pyrite (Fig. 4C). The bioclastic content comprises bivalve (Fig. 4D), scaphopod (Fig. 4E) and ammonite shells, rare calcareous foraminifera (Fig. 4F), echinoderm skeletal fragments (Fig. 4G) and serpulid worm tubes (Fig. 4H). The only cavities filled with fine fibrous cements are those within some serpulid tubes (Fig. 4H).

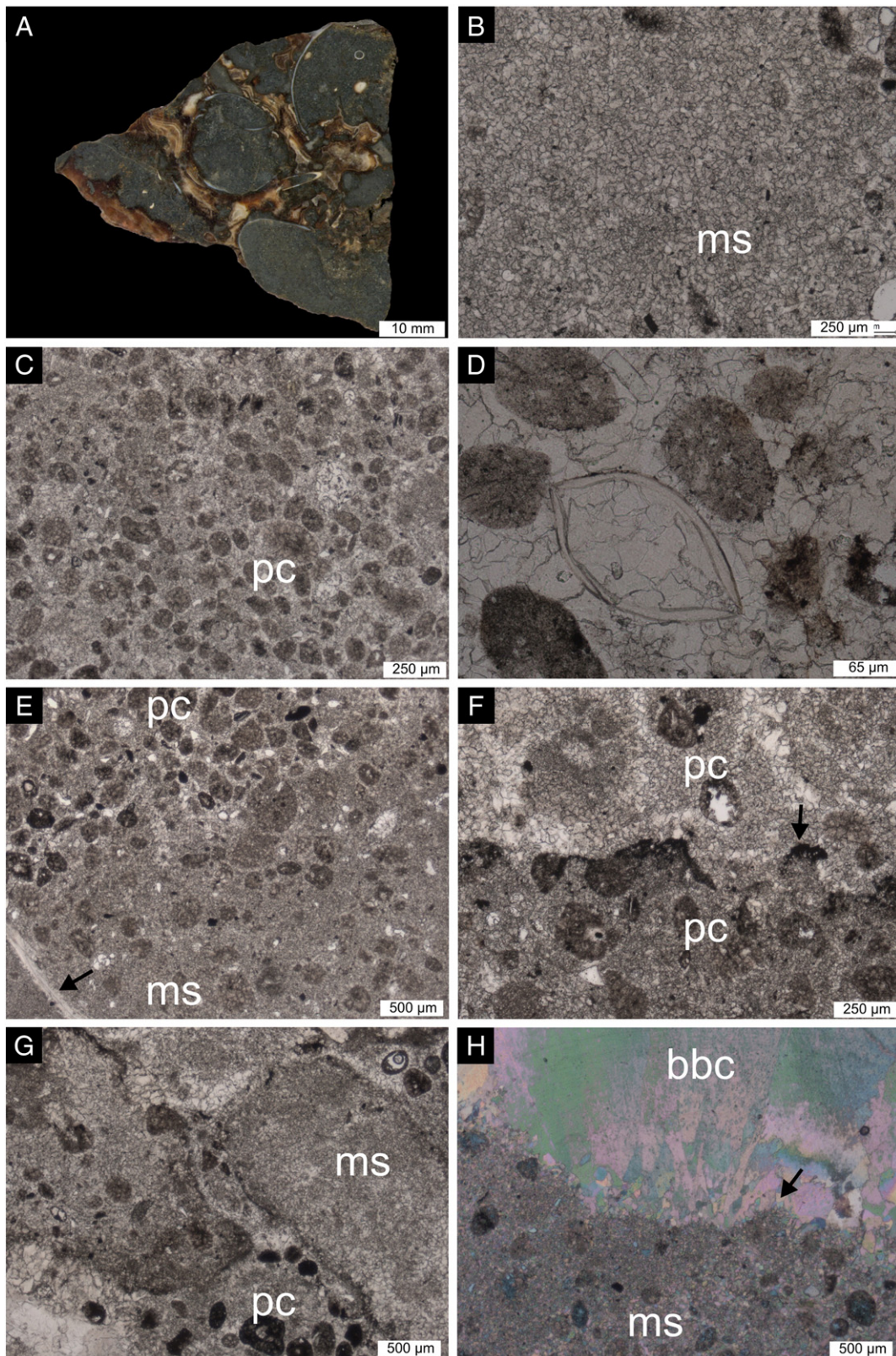The Late Tithonian black limestones are rich in macroscopically visible cavities, filled with banded botryoidal cements (Fig. 5A). The rock is composed of several carbonate phases. Of these, the two most common are brown microspar with rare bioclasts (ms; Fig. 5B) and peloidal carbonate (pc) composed of possible fecal pellets (pc; Fig. 5C). The most common clasts within both microspar and peloidal carbonate are ostracods (Fig. 5D), and bivalve shells (Fig. 5E). Rare pyrite framboids are dispersed within the microspar and may impregnate some of the peloids. Both phases occur together, and gradational or rapid change can be observed from microspar, through microspar with rare peloids, to peloidal wackestone and peloidal packstone (Fig. 5E). Microspar and peloidal carbonates are truncated by corrosion surfaces, often associated with the impregnation of the corroded surface with pyrite (Fig. 5F). Several corrosion events can be seen, followed by recurring formation of microspar/peloidal carbonate phases (Fig. 5F). Some corrosion resulted
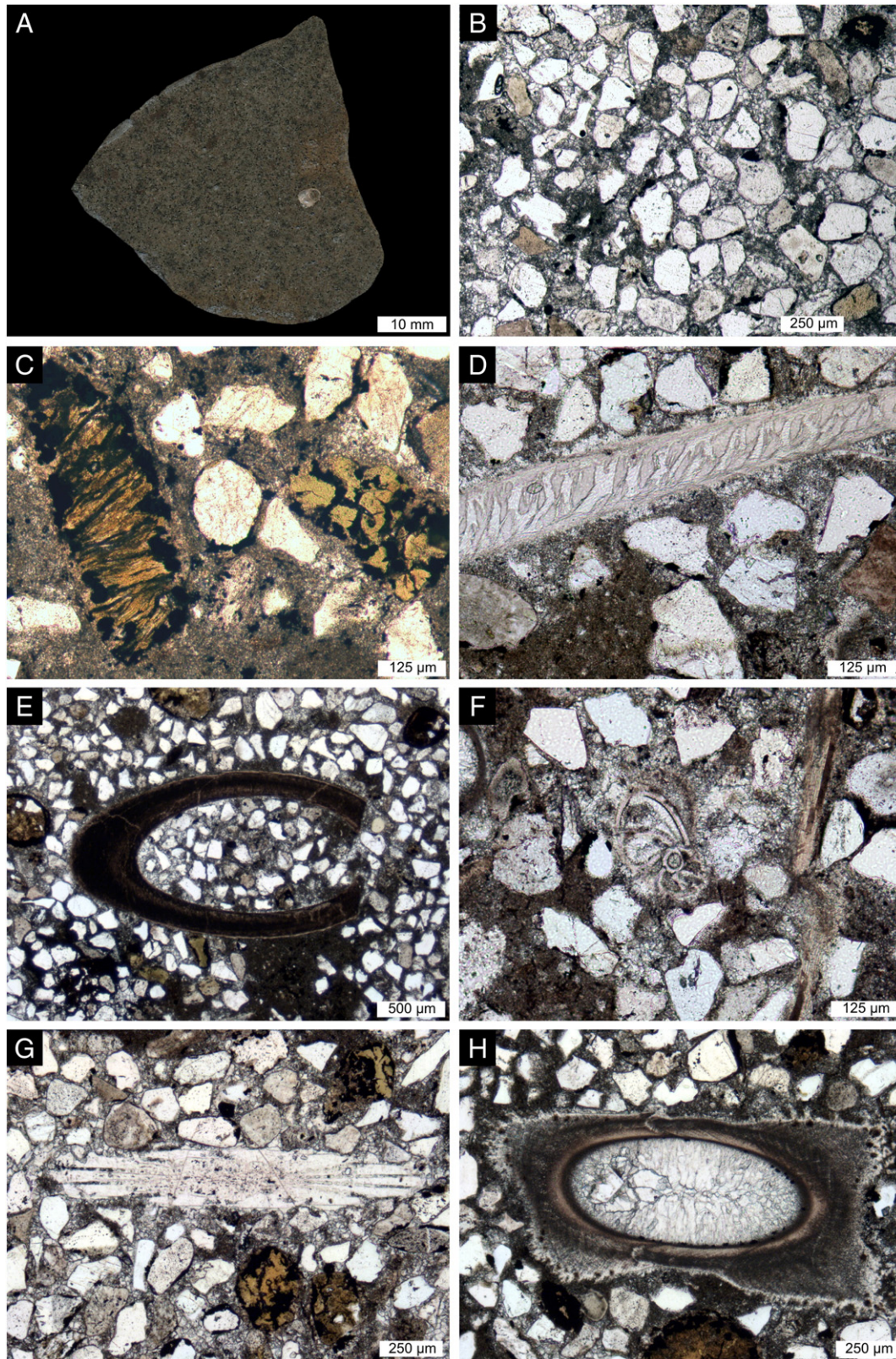
Fig. 4. Late Oxfordian–Early Kimmeridgian calcareous sandstone petrography. A) Polished hand specimen with gastropod. NRM Mo1322a. B) Fine to medium quartz sand grains cemented by micritic carbonate. C) Unidentified green fractured clasts of possible volcanogenic origin (right) and (left) grain of the same material, here totally replaced by phyllosilicates. D) Well-preserved bivalve shell bioclast. E) Oblique cross-section of a possible scaphopod tube. F) Calcareous foraminiferan, enclosed in carbonate matrix. G) Echinoderm skeletal fragment, partially replaced by blocky calcite. H) Serpulid worm tube, filled by acicular cement (right) and blocky calcite (left). B–H NRM Mo2593x. All images in plane polarized light.

in the formation of a brecciated fabric (Fig. 5G). The last corrosion event is usually not associated with pyrite but followed by formation of banded botryoidal carbonate (bbc), lining the cavities (Fig. 5H). Unlike many other fossil seep carbonates, there is no late stage blocky calcite present. The idealized paragenetic sequence can thus be presented as follows: ms–pc → corrosion(pyrite) → ms–pc → corrosion → bbc.

Fig. 5. Late Tithonian black limestone petrography. A) Polished hand specimen showing nodules and cavities filled with banded botryoidal cements. Mo167763. B) Calcareous microspar with rare dispersed fecal peloids. NRM PZ X 5312. C) Peloidal carbonate composed of an accumulation of fecal pellets. NRM PZ X 5312. D) Ostracod between peloids. NRM PZ X 5313. E) Gradual change from microspar with fecal peloids to more condensed peloidal carbonate. NRM PZ X 5314. F) Corrosion surface covered with iron oxyhydroxides, followed by microspar formation. NRM PZ X 5312. G) Corroded carbonate fragments, coated with iron oxyhydroxides and encased in microspar–peloidal carbonate association. NRM PZ X 5315. H) Fans of banded botryoidal cements nucleating on corroded carbonate surface. NRM PZ X 5312. A–G plane polarized light, H cross polarized light.
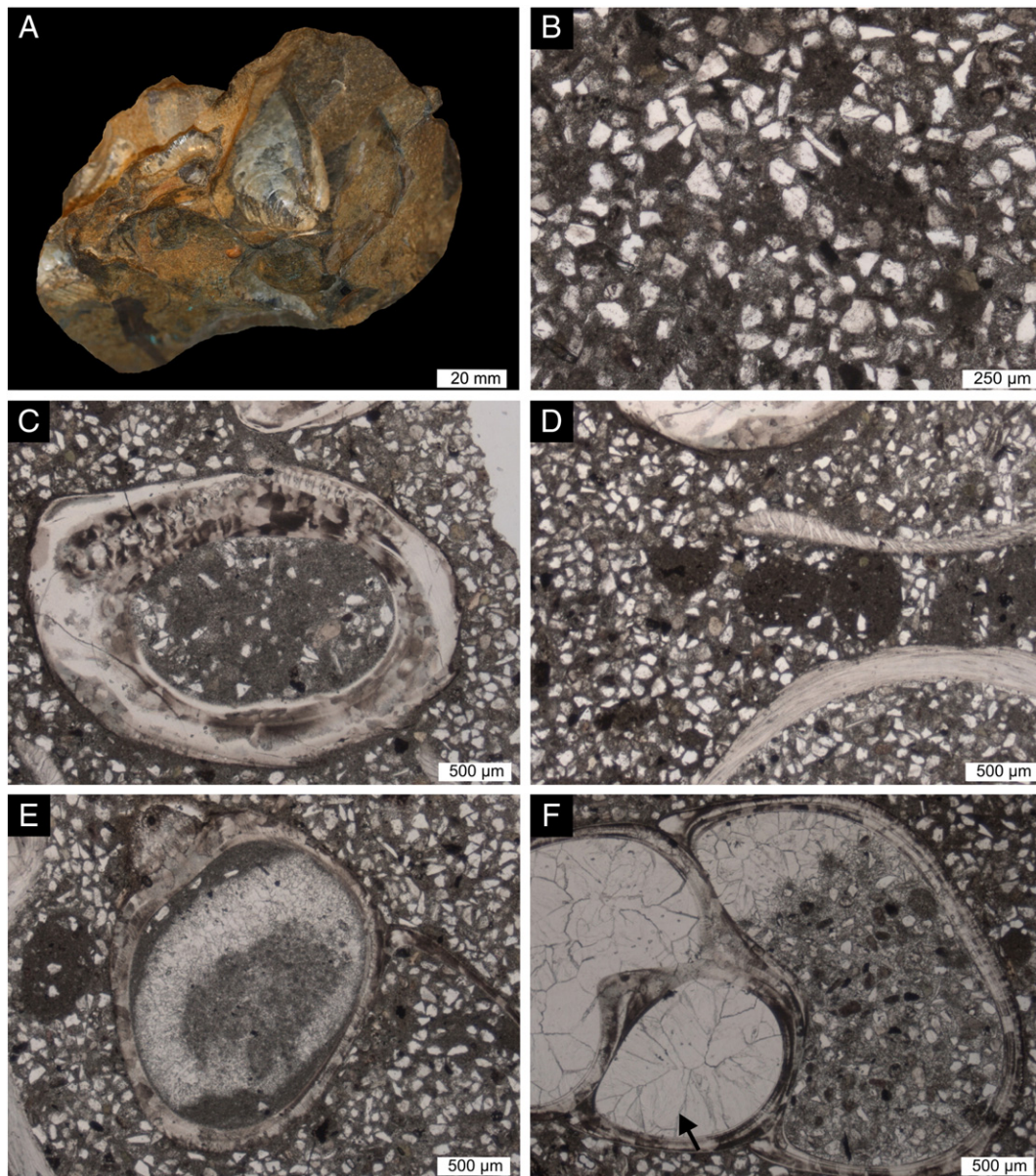
Fig. 6. Latest Berriasian–Early Valanginian sandy limestones petrography. A) Weathered block with abundant fossils and yellow-gray coloration. NRM Mo167817. B) Fine grained quartz sand grains cemented by micritic carbonate. C) Well-preserved protobranch bivalve shell, showing taxodont dentition. D) Well-preserved carbonate fecal peloids enclosed by fine sand matrix. E) Gastropod shell infilled by fine gray micrite and clotted micrite. F) Gastropod shell with last whorl geopetally filled with clastic-carbonate mixture, and earlier whorls filled with acicular carbonate cement, which nucleates on the inner walls of the shell. B–F NRM Mo167817x. All images in plane polarized light.

The latest Berriasian–Early Valanginian sandy limestones are yellowish-grey, highly fossiliferous and without any macroscopically visible cavities (Fig. 6A). They are predominantly composed of fine, poorly rounded quartz grains (Fig. 6B). The pore space is filled with gray to brown micrite (Fig. 6B). The most common grains are bioclasts, predominantly bivalve (Fig. 6C) and gastropod shell fragments, and possible fecal peloids (Fig. 6D), with a small admixture of wood fragments. The gastropod shells are often complete and have fills of clotted grey micrite (Fig. 6E) and geopetal fine sand (Fig. 6F). Some of the early whorls are filled with fibrous cements (Fig. 6F).

The stable C and O isotope values of all three lithologies show fairly narrow groupings (Table 1, Fig. 7). All the Late Oxfordian–Early Kimmeridgian $\delta^{13}C$ values come from calcitic microspar cementing the pore space and are low; between −31.0‰ and −40.1‰. The $\delta^{18}O$ isotope values are between 0.1‰ and −0.4‰, thus having a seawater signature. The Late Tithonian black limestones show a wider range of $\delta^{13}C$ values (from −16.7‰ to −41.3‰), but with most being below −30‰.

The $\delta^{18}O$ values plot between −3.1‰ and 0.0‰, which is close to a normal marine signature; $\delta^{18}O$ values greater than −1.2‰ are more common. The latest Berriasian–Early Valanginian sandy limestones are the isotopically heaviest of all the Novaya Zemlya seep lithologies with respect to $\delta^{13}C$ (values between −21.8‰ and −26.0‰). The $\delta^{18}O$ values are close to normal marine (between 0.2‰ and −1.0‰, respectively).

4.3. Fossil content

All three lithologies contain diverse macrofauna, comprising predominantly molluscs, with subordinate echinoderms and brachiopods. The faunal list, with original identifications of Tullberg (1881), and preliminary re-interpretations, is given in Table 2. We plan a detailed taxonomic redescription of all of the taxa in a subsequent paper, to supplement the work by Kaim et al. (2004) and Kaim and Beisel (2005) on some of the gastropods from the fauna.

Table 1
Stable isotopes values from Late Jurassic–Early Cretaceous seep carbonate boulders from Novaya Zemlya.

Sample name	Lithology	$\delta^{13}C$	$\delta^{18}O$	Age
Mo 1185a	Calcareous sandstone	−35.2	−0.3	Late Oxfordian–Early Kimmeridgian
Mo 1185b	Calcareous sandstone	−34.4	−0.4	Late Oxfordian–Early Kimmeridgian
Mo 1185c	Calcareous sandstone	−37.4	−0.4	Late Oxfordian–Early Kimmeridgian
Mo 1185d	Calcareous sandstone	−31.0	−0.2	Late Oxfordian–Early Kimmeridgian
Mo 1329a	Calcareous sandstone	−39.1	0.1	Late Oxfordian–Early Kimmeridgian
Mo 167816a	Calcareous sandstone	−36.6	0.1	Late Oxfordian–Early Kimmeridgian
Mo 167816b	Calcareous sandstone	−40.1	0.1	Late Oxfordian–Early Kimmeridgian
SB 2	Black limestone	−40.5	−0.7	Late Tithonian
SB 3	Black limestone	−30.3	−0.6	Late Tithonian
SB 4	Black limestone	−41.3	−0.2	Late Tithonian
SB 5	Black limestone	−32.0	−0.8	Late Tithonian
SB 6	Black limestone	−32.6	−0.5	Late Tithonian
SB 7	Black limestone	−32.0	−0.5	Late Tithonian
SB 8	Black limestone	−38.6	−0.3	Late Tithonian
SB 9	Black limestone	−36.0	−0.4	Late Tithonian
SB 10	Black limestone	−38.3	0.0	Late Tithonian
SB 11	Black limestone	−16.7	−3.1	Late Tithonian
SB 12	Black limestone	−32.0	−1.0	Late Tithonian
SB 13	Black limestone	−31.8	−0.6	Late Tithonian
SB 14	Black limestone	−27.1	−1.3	Late Tithonian
SB 15	Black limestone	−37.9	0.0	Late Tithonian
SB 16	Black limestone	−34.2	−0.7	Late Tithonian
SB 17	Black limestone	−30.2	−0.8	Late Tithonian
SB 18	Black limestone	−28.1	−1.2	Late Tithonian
SB 19	Black limestone	−36.1	−0.1	Late Tithonian
Mo 167187	Sandy limestone	−22.8	−0.9	latest Berriasian–Early Valanginian
Mo 167817Z	Sandy limestone	−25.3	−0.6	latest Berriasian–Early Valanginian
Mo 167817Y	Sandy limestone	−26.0	−0.2	latest Berriasian–Early Valanginian
Mo 167817X	Sandy limestone	−22.7	−1.0	latest Berriasian–Early Valanginian
Mo 167817V	Sandy limestone	−21.8	−1.0	latest Berriasian–Early Valanginian
Mo 167817Q	Sandy limestone	−24.2	−0.6	latest Berriasian–Early Valanginian
Mo 149380X	Sandy limestone	−25.0	−0.5	latest Berriasian–Early Valanginian

The Late Oxfordian–Early Kimmeridgian calcareous sandstones contain 11 species of invertebrate macrofauna, nine of which are molluscs (Fig. 8; Table 2). The fossils are mostly uncrushed and have their original shell structure preserved, including nacre. The most numerous species is the ammonite *Amoeboceras* sp., preserved as both mature specimens (Fig. 8A) and juveniles. Gastropods are represented by two species. One is a eucyclid (ascribed to two species of *Turbo* by Tullberg (1881)) (Fig. 8B); the other (*Cerithium elatum* of Tullberg (1881)) is a hokkaidoconchid (Fig. 8C) and is much more common. Bivalves are fewer in number than the gastropods. These include
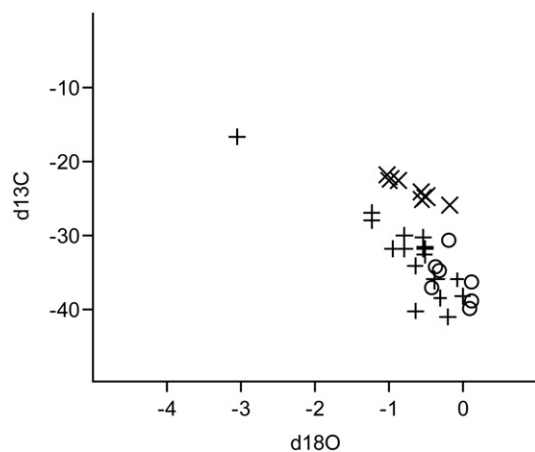
Fig. 7. Cross plot of $\delta^{13}C$ and $\delta^{18}O$ composition of all of the three Novaya Zemlya seep carbonates. Open circle indicates Late Oxfordian–Early Kimmeridgian calcareous sandstones, cross indicates Late Tithonian black limestones, X indicates latest Berriasian–Early Valanginian sandy limestones.

disarticulated specimens of the epifaunal genus *Oxytoma* (*Avicula muensteri* of Tullberg (1881)) (Fig. 8D) and disarticulated specimens of a thick-shelled astartiid bivalve, not figured in Tullberg (1881) (Fig. 8E). The only semi-articulated bivalve specimens belong to the deep-burrowing species *Goniomya elegantula* of Tullberg (1881) (Fig. 8F). There are also numerous large (>20 mm in the longest axis) shell fragments of unidentified bivalves. Other fossils comprise belemnoid guards, scaphopods and serpulid tubes, echinoderm skeletal plates (identified in thin section), and numerous fragments of sunken driftwood.

The Late Tithonian black limestones contain at least 13 macrofossil species, which are well preserved, retaining much original shell structure, but rather sparse (Fig. 9, Table 2). There is a single species of ammonite: *Craspedites okensis* (Fig. 9A). Gastropods are represented by *Eulima undulata* of Tullberg (1881), reindentified as the rissoid *Hudlestoniella* by Kaim et al. (2004) (Fig. 9B). The black limestones seep fauna is the only one from the Stockholm Novaya Zemlya collections to contain chemosymbiotic bivalves. These comprise *Solenomya costata* of Tullberg, 1881, which we interpret as a species of an as yet unidentified solemyid genus (Fig. 9C), and *Ptychostolis nordenskioeldi* of Tullberg (1881) which is a species of the shallow burrowing genus *Nucinella* (Fig. 9D). Specimens of shallow burrowing nuculid protobranch bivalves belong to *Nucula* sp. (Fig. 9E) (*Nucula borealis* of Tullberg (1881)), and *Dacromya* sp. (Fig. 9F) (*Leda zieteni* of Tullberg (1881)). Another protobranch is a species of malletiid (Fig. 9G) (*Leda galathea* of Tullberg (1881)). Epifaunal bivalves are represented by three species: an arcoid (Fig. 9H) (*Cucullaea novaesemlyae* of Tullberg (1881)), a few poorly preserved specimens of *Oxytoma* (*Avicula muensteri* of Tullberg (1881)), and a single internal mould of *Pseudolimea* sp. (Fig. 9I) (*Limea duplicata* of Tullberg (1881)). The most numerous bivalve in the fauna (>10 specimens) is the epifaunal bivalve *Buchia obliqua* (Fig. 9J) (*Aucella keyserlingiana* f. *obliqua* of Tullberg (1881)). The only heterodont in the fauna is a single specimen

Table 2
List of the macrofossils from Late Jurassic–Early Cretaceous seep boulders from Novaya Zemlya, with identifications of Tullberg (1881) and our preliminary re-interpretation of their systematic position. The x indicates species in Tullberg (1881); a number in brackets is number of specimens discovered during the study; '?' marks species in Tullberg (1881) not confirmed by us in this study.

	calcareous sandstones	black limestone	sandy limestones	
Age proposed herein	Late Oxfordian–Early Kimmeridgian	Late Tithonian	latest Berriasian–Early Valanginian	
Age based on	*Amoeboceras* sp.	*Craspedites okensis*	*Buchia* cf. *inflata*	
Faunal list of Tullberg (1881)				Identification proposed herein
Ammonites alternans	x (many)			*Amoeboceras* sp.
Ammonites okensis		x (2)		*Craspedites okensis*
Belemnites magnificus	x (few)			Belemnoid guard
Dentalium subanceps	x (few)	x (2)		Scaphopod sp.
Turbo unicostatus n. sp.	x (?)			Eucyclid sp.
Turbo micans n. sp.	x (3)		x (3)	Eucyclid sp.
Turbo capitaneus			x (4)	Eucyclid sp.
Cerithium elatum n. sp.	x (many)			Hokkaidoconchid sp.
Turitella novaesemljae n. sp.			x (2)	High-spired gastropod sp.
Eulima pusilla n. sp.	x (?)		x (many)	*Huddlestoniella pusilla*
Eulima undulata n. sp.		x (1)		*Huddlestoniella undulata*
Acteon exsculptus n. sp.			x (1)	Bullinid sp.
Acteon Frearsianus n. sp.			x (1)	Bullinid sp.
-			x (1)	Maturifusid sp.
Ptychostolis nordenskioeldi gen. et sp. nov.		x (7)		*Nucinella* sp.
Solenomya costata n. sp.		x (2)		Solemyid sp.
Nucula borealis n. sp.		x (5)		Nuculid sp.
Nucula sp.			x (1)	Nuculid sp.
Leda zieteni		x (5)		*Dacromya* sp.
Leda angulata			x (1)	Protobranch sp. A
Leda galathea		x (1)	x (2)	Malletiid sp.
Leda subovalis			x (1)	Protobranch sp. B
Cucullaea novaesemljae n. sp.		x (1)		Arcoid sp.
Aucella Keyserligniana Trautsch. f. *obliqua*		x (many)		*Buchia obliqua*
Aucella Keyserligniana Trautsch. f. *majuscula*			x (many)	*Buchia* cf. *inflata*
Inoceramus revelatus Keyserling		x (?)	x (?)	-
Pecten lindstroemi n. sp.		x (?)	x (1)	*Camptonectes* sp.
Avicula muensteri	x (2)	x (1)	x (1)	*Oxytoma* sp.
Limea duplicata		x (1)	x (1)	*Pseudolimea* sp.
Ostrea sp.			x (?)	-
Astarte voltzii			x (3)	Astartiid sp.
-	x (4)			Astartiid sp.
Crastasella? sp.		x (?)		-
Cardium concinnum		x (?)		-
Cardium sp.		x (?)		-
Tellina subalpina			x (3)	Heterodont bivalve sp.
Cyprina polaris		x (1)		Arcticid sp.
Goniomya elegantula	x (3)		x (1)	*Goniomya* sp.
-	x (many)			Bivalve sp.
-			x (1)	Rhynchonellide sp.
-			x (5)	Terebratulide sp.
-	x (many)			Echinoderm sp.
-	x (many)			Serpulid sp.
-	x (common)	x (common)	x (common)	Sunken driftwood

of arcticid (Fig. 9K) (*Cyprina polaris* of Tullberg (1881)). There are also a few scaphopods in the black limestones, as well as fragments of sunken driftwood.

The latest Berriasian–Early Valanginian sandy limestones are highly fossiliferous and contain well-preserved specimens, with shell material mostly preserved (Fig. 10) (Table 2). The gastropods comprise common specimens of the rissoid *Hudlestoniella pusilla* as identified by Kaim *et al.* (2004) (Fig. 10A) (*Eulima pusilla* of Tullberg (1881)), which occur as accumulations of dozens of specimens in individual blocks. The four other gastropod species are far less common. These are a few specimens of a eucyclid gastropod (*Turbo capitaneus* of Tullberg, 1881)), a maturifusid (Fig. 10B), a bullinid (Fig. 10C) (identified as *Acteon* by Tullberg (1881)), and two specimens of a large high-spired gastropod (Fig. 10D) identified by Tullberg (1881) as *Turitella novaesemljae*. This gastropod almost certainly does not belong to the turitellids, and requires more taxonomic work; for now we refer to it as a 'high-spired gastropod' though most likely it is an abyssochrysoid and might be another seep-restricted gastropod next to the hokkaidoconchid (AK unpublished data). There are 11 bivalve species in the sandy limestones material (Table 2). Four of them are protobranchs: a poorly preserved

nuculid; a malletiid (Fig. 10E) and two unidentified species, sp. A (Fig. 10F), and sp. B (Fig. 10G). Other bivalves in the fauna include *Buchia* cf. *inflata* (*Aucella keyserlingiana* f. *majuscula* of Tullberg (1881) (Fig. 10H), *Oxytoma* sp. (Fig. 10I) a single fragmentary preserved specimen of *Pseudolimea*, and a pectinid, possibly a species of *Camptonectes* (Fig. 10J). Infaunal bivalves comprise a small astartiid, identified by Tullberg (1881) as *Astarte voltzii*, and a small heterodont bivalve (Fig. 10L), as yet unidentified. *Goniomya elegantula* is another infaunal bivalve present in the material. The sandy limestones are the only investigated lithology to host rhynchonellate brachiopods. These are one rhynchonellide (Fig. 10M) and one terebratulide species (Fig. 10N). The sandy limestones also contain abundant sunken driftwood fragments.

5. Discussion

5.1. Seep origin of the Novaya Zemlya boulders

The textures found in all the boulders are typical for authigenically precipitated carbonates (e.g. Peckmann and Thiel, 2004), and the
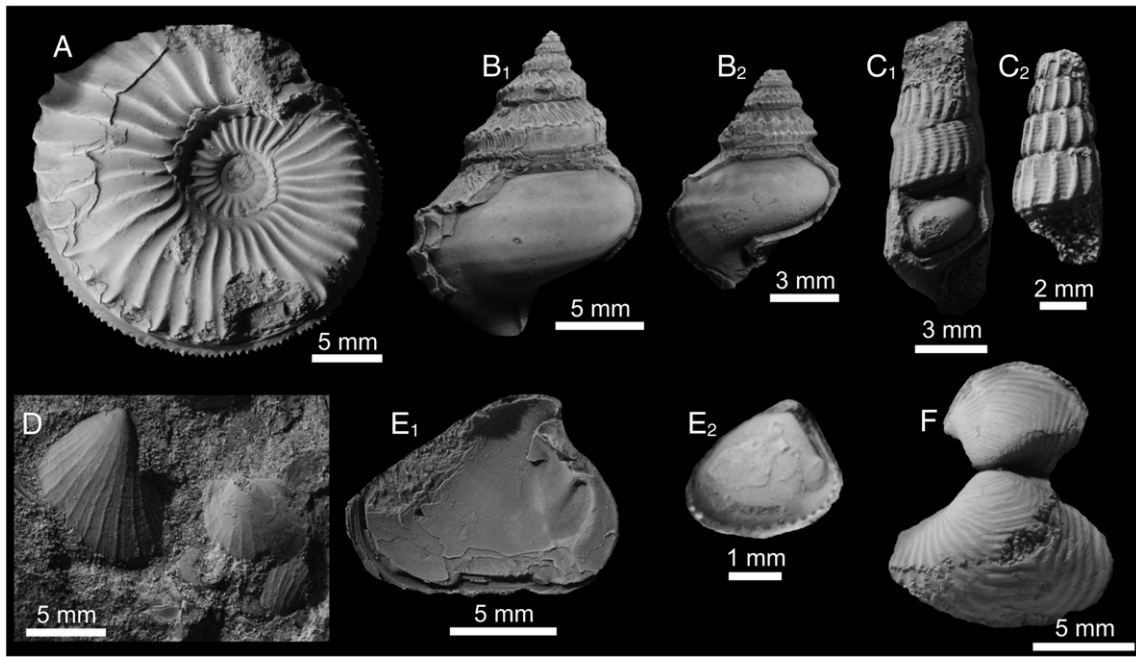
Fig. 8. Fossils from the Late Oxfordian–Early Kimmeridgian calcareous sandstones. A) *Amoeboceras* sp., NRM Mo 2593a. B) Eucyclid sp., B_1) NRM Mo2593b, B_2) NRM Mo167816a. C) Hokkaidoconchid sp. (*Cerithium elatum* of Tullberg (1881)), C_1) NRM Mo 2593d, C_2) NRM Mo2593e. D) Small accumulation of disarticulated shells of *Oxytoma* sp., NRM Mo1185a. E) Astartiid sp., E_1) an inner shell surface of a large specimen showing deeply impressed anterior adductor muscle scar, NRM Mo1185b, E_2) internal mould of a small specimen showing crenulated ventral shell margin, NRM Mo167816b. F) *Goniomya* sp., NRM Mo167817c.

^{13}C-depleted composition of all three investigated lithologies shows that the authigenic carbonates were formed under the influence of the anaerobic oxidation of methane (AOM; Boetius et al., 2000). The Late

Oxfordian–Early Kimmeridgian calcareous sandstones were formed mostly by cementation of quartz sand in authigenic seep carbonate (Fig. 4). Recent seep carbonates are mostly formed of fibrous aragonite
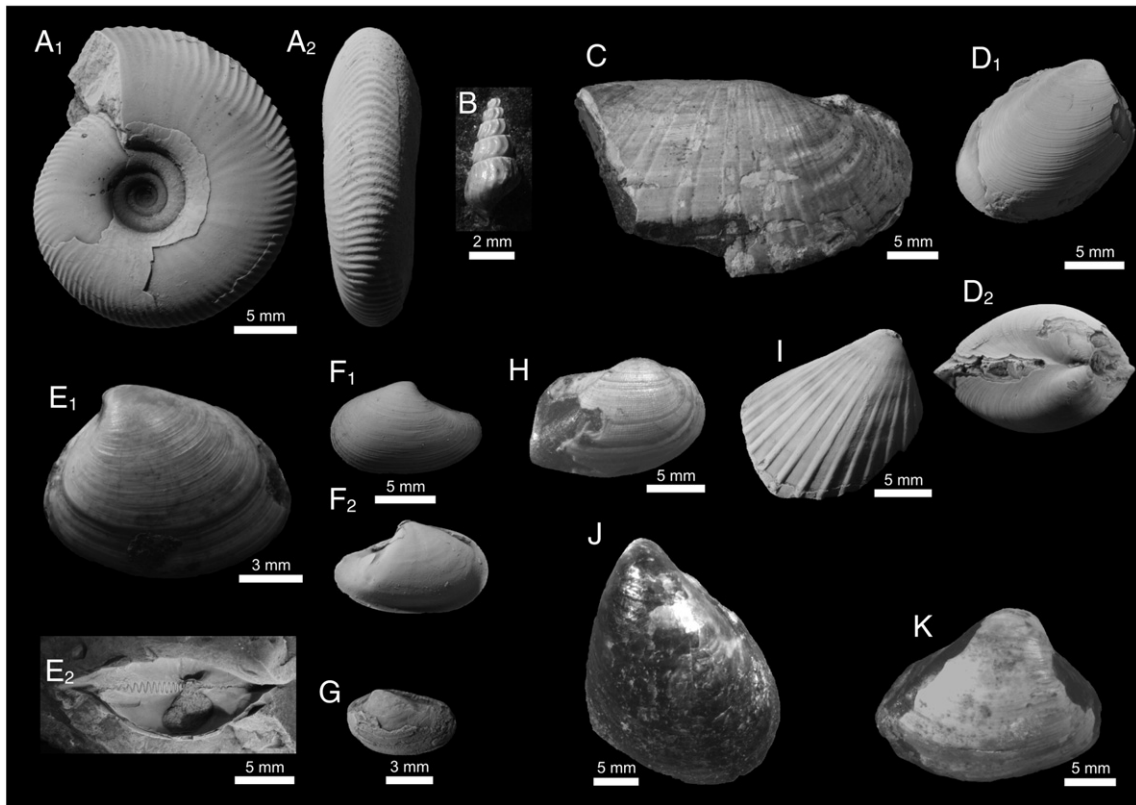
Fig. 9. Fossils from the Late Tithonian black limestones. A) *Craspedites okensis*, Mo1226, A_1) lateral view, A_2) ventral view. B) *Hudlestoniella undulata*, NRM Mo1182. C) Solemyid sp., NRM Mo1319. D) *Nucinella* sp., NRM Mo 152372, D_1) left-lateral view, D_2) dorsal view. E) Nuculid sp., E_1) right-lateral view, NRM Mo152374, E_2) internal view of the dorsal margin showing taxodont dentition, NRM Mo1194a. F) *Dacromya* sp., NRM Mo 1301a, F_1) left-lateral view showing the external ornament, F_2) right-lateral view of an internal mould. G) Malletiid sp., NRM Mo167815a. H) Arcoid sp., NRM Mo1309a. I) *Pseudolimea* sp., internal mould, NRM Mo 1215b. J) *Buchia obliqua*, NRM Mo1205. K) Arcticid sp., NRM Mo1313.
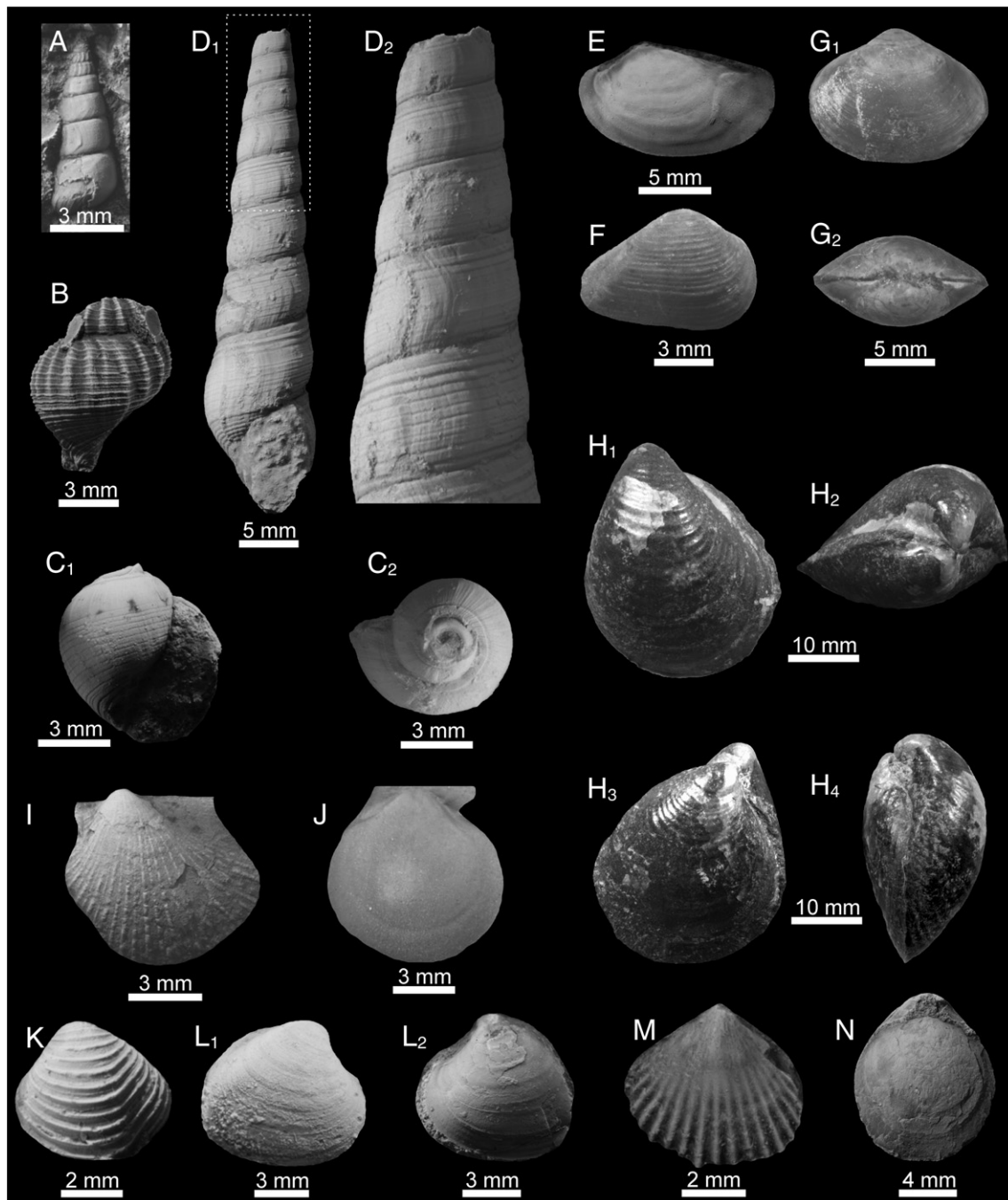
Fig. 10. Fossils from the latest Berriasian–Early Valanginian sandy limestones. A) *Hudlestoniella pusilla*, NRM Mo 149380a-1. B) Maturifusid sp., NRM Mo 149371c-1. C) Bullinid sp., NRM Mo 1189, C_1) apertural view, C_2) apical view. D) high-spired gastropod sp., NRM Mo 167817a. D_1) whole specimen, D_2) younger teleoconch view. E) Malletiid sp., NRM Mo 14929a. F) Protobranch sp. A, NRM Mo 1198. G) Protobranch sp. B, NRM Mo 1199a, G_1) left lateral view, G_2) dorsal view. H) *Buchia* cf. *inflata*, NRM Mo 1206, H_1) left-lateral view, H_2) dorsal view, H_3) right-lateral view, H_4) anterior view. I) *Oxytoma* sp., NRM Mo 14929b. J) *Camptonectes* sp., plasticine cast, NRM Mo 1218. K) Astartiid sp., NRM Mo 149380b. L) Heterodont bivalve sp., L_1) right-lateral view of a delaminated valve, NRM Mo 149380c, L_2) left lateral view of an internal mould, NRM Mo 149497. M) Rhynchonellide brachiopod sp., NRM Mo 149572. N) Terebratulide brachiopod, NRM Mo 102390.

(e.g. Aloisi et al., 2000, 2002; Teichert et al., 2005), which usually forms when marine sulphate is present (e.g. Bayon et al., 2009). Calcite is less commonly reported from Recent seep carbonates (Reitner et al., 2005). In contrast, fossil seep carbonates are predominantly calcitic, as fibrous aragonite is not stable during burial, although its former presence is often reconstructed based on ghost textures (e.g. Savard et al., 1996; Peckmann et al., 2007; Kiel and Peckmann, 2008). Although our XRD investigation reveals that the Novaya Zemlya seep carbonate is now calcite, the carbonate cementation of pore space in calcareous sandstones and the preservation of aragonitic mollusc shells suggest that the intial mineralogy of this phase was aragonite. The character of fibrous carbonate cement filling cavities within fossils (Fig. 4H) is typical for an aragonite precursor (Aïssaoui, 1985). The textures suggest homogenous cementation of the quartz sand, rather than the formation of concretions (e.g. Peckmann and Thiel, 2004; Kaim et al., 2013; Kiel et al., 2013) or tubular conduit structures (e.g. Campbell et al., 2008; Krause et al., 2009), characteristic of localized AOM reactions. The carbon isotope values are very depleted (Table 1, Fig. 7) and this indicates

precipitation during active seepage of methane (e.g. Campbell et al., 2002; Campbell, 2006). The sediment was probably charged with gas, and some cavities within fossils were likely also partially filled with gas, as shown by asymmetrical cement fills (Fig. 4H). This is all suggestive of diffusive rather than advective seepage (e.g. Campbell, 1992; Peckmann et al., 2009; Haas et al., 2010; Natalicchio et al., 2015).

The Late Tithonian black limestones have more complex carbonate fabrics. They are very similar to those from latest Jurassic–earliest Cretaceous hydrocarbon seep carbonates from Spitsbergen, Svalbard (Hryniewicz et al., 2012). Microspar and peloidal carbonate most likely represent cemented fine grained and peloidal sediment, respectively, with the latter possibly additionally winnowed along fluid flow paths. Such peloidal carbonates are especially common in fossil seep sites (e.g. Beauchamp and Savard, 1992; Krause et al., 2009; Kiel et al., 2013). Nodular fabrics, seen in some carbonate blocks (Fig. 4A), suggest localized centers of AOM (e.g. Peckmann and Thiel, 2004). The origin of the cavities filled with cements was probably related to episodes of increased acidity (Himmler et al., 2011), either by the aerobic oxidation of methane or by sulphide oxidation. The first process can be linked to exposure of the carbonate to the bottom water, for example due to an erosional episode (e.g. Matsumoto, 1990). Some corrosion surfaces, especially those without mineral coatings, might have been associated with this process. Sulphide oxidation can be associated, for example, with development of *Beggiatoa* or *Thioploca* bacterial mats (Himmler et al., 2011). These bacteria are able to oxidize large volumes of sulphide-charged sediment using free or bound oxygen, leading to lowered pH in the underlying sediments and corrosion of authigenic carbonates (Joye et al., 2004; Cai et al., 2006). The corrosion surfaces in the Novaya Zemlya carbonates associated with black oxyhydroxide coatings may have been the result of this process. Cavities resulting from either of these processes would have been filled with botryoidal carbonate, as AOM became locally active again. The $\delta^{13}C$ isotope values, ranging from $-41.3‰$ to $-16.7‰$ (Table 1, Fig. 7) suggest precipiation under the influence of methane and diverse fluid circulation patterns, with the more depleted values representing phases formed under a constant supply of methanogenic carbon, possibly closer to active fluid conduits (e.g. Campbell et al., 2002; Peckmann et al., 2003; Campbell et al., 2008; Himmler et al., 2008). The more negative values indicate biogenic rather than thermogenic methane (Peckmann and Thiel, 2004). The heavier values may imply precipitation from a small pool of carbonate in sealed cavities, or precipitation influenced by sedimentary organic matter, heavier hydrocarbons or significant mixing with seawater bicarbonate (e.g. Kiel and Peckmann, 2008).

The latest Berriasian–Early Valanginian sandy limestones have a fairly simple paragenetic sequence, roughly comparable to that of the Late Oxfordian–Early Kimmeridgian calcareous sandstones (Fig. 6). Fine quartz sand and related fecal peloids and fossils are cemented by calcitic micrite, which is likely to have initially been aragonite, diagenetically recrystallized to calcite. The homogenous rock textures are suggestive of diffusive rather than advective flux, with no localized centres of AOM, or formation of fluid conduits. Microbial clotted micrite (Fig. 6E), filling some fossils, is fairly common in other fossil seep carbonates (e.g. Kiel and Peckmann, 2007, 2008; Kuechler et al., 2012; Kiel et al., 2013) and most likely represents cemented organic membranes (Flügel, 2004). The micrite is accompanied by fans of fibrous cements, possibly former aragonite (Fig. 6F), suggesting rapid precipitation of carbonate, perhaps due to active AOM within hydrocarbon-filled shells. The carbon isotopes are much less depleted than in the other Novaya Zemlya seep lithologies, with values roughly between $-22‰$ and $-26‰$ $\delta^{13}C$ (Table 1, Fig. 7). These values can be interpreted in three ways. First, they could have been associated with oxidation of heavier hydrocarbons (e.g. Kiel and Peckmann, 2007), as the $\delta^{13}C$ values between $-15‰$ and $-25‰$ $\delta^{13}C$ are similar to the values found in carbonates formed at oil seeps (e.g. Joye et al., 2004). However, the absence of impsonite (biodegraded oil; e.g. Peckmann et al., 2001) argues against an oil seepage origin. The second and third explanation could be the oxidation of either thermogenic

or biogenic methane (Sackett, 1978; Schoell, 1988; Whiticar, 1999). Assuming that methane was involved in the formation of the latest Berriasian–Early Valanginian sandy limestones, then the $\delta^{13}C$ composition of around $-20‰$ to $-25‰$ suggests significant mixing of methanogenic carbon with heavier source, such as seawater bicarbonate (Peckmann and Thiel, 2004).

5.2. Ecological structure

The Novaya Zemlya seep boulders contain a fauna which – based on the current state of knowledge – is mostly comparable with that of non-seep Jurassic–Early Cretaceous shelf environments (e.g. Zakharov, 1966, 1970; Duff, 1978; Fürsich, 1982; Kelly, 1984, 1992) and represents the 'background' fauna, which have taken advantage of the enhanced nutrient availability and increased amount of hard substrate for attachment at seep (e.g. Dando, 2010; Kiel, 2010). Out of the 33 species identified in the material (Table 2), only one can be currently interpreted as being closely tied to the seep environment. This is the seep-restricted hokkaidoconchid gastropod in the Late Oxfordian–Early Kimmeridgian calcareous sandstones identified by Tullberg (1881) as *Cerithium elatum* (Fig. 8C) (e.g. Kaim et al., 2008, 2009; Kiel et al., 2013). The only chemosymbiotic bivalves found in the Novaya Zemlya material are a solemyid bivalve and *Nucinella* from the Late Tithonian black limestones (e.g. Stewart and Cavanaugh, 2006; Oliver and Taylor, 2012). These taxa are, however, not restricted to seep environments and are found in normal marine settings with high redox potential (e.g. Reid, 1980; Taylor and Glover, 2010; Glover and Taylor, 2013). Similarly structured seep faunas, with a large number of 'background' species and few seep-restricted species, are also found in the geographically and stratigraphically near Late Tithonian–latest Berriasian seeps from Svalbard (Hammer et al., 2011). As these formed in shallow water (Hryniewicz et al., 2015) and a paucity of seep-restricted species is a general feature of shallow-water vent and seep faunas (Dando, 2010 and references therein), a similar palaeobathymetric setting is likely to have influenced the structure of Novaya Zemlya seep boulder faunas. The Svalbard seeps contain only four seep-restricted species, out of over 50: a lucinid and thyasirid bivalves (Hryniewicz et al., 2014), hokkaidoconchid gastropods, and possible 'vestimentiferan' worm tubes (Hammer et al., 2011). Except for the hokkaidoconchids, these taxa are unknown from the Novaya Zemlya seep boulders, which is intriguing, considering they could have formed in relative proximity (Hryniewicz et al., 2015, fig. 8). It could be that the paucity of seep-restricted species in the Novaya Zemlya seep fauna was also to some extent a function of palaeogeography, as Recent Arctic seep (e.g. Gebruk et al., 2003) and vent faunas (e.g. German et al., 2012) also contain few obligate species, for reasons that are yet not well understood.

5.3. Relationships with other Late Mesozoic seep faunas

There are a few other Mesozoic seeps known from the Boreal area. The palaeobiogeographically closest are the Late Tithonian–latest Berriasian seeps from Svalbard (Hammer et al., 2011; Wierzbowski et al., 2011). Cretaceous Boreal occurrences include the Barremian Kuhnpasset seeps from Wollaston Forland, East Greenland (Kelly et al., 2000) and the Albian Ellef Ringnes and Prince Patrick Islands seeps from Arctic Canada (Beauchamp and Savard, 1992), both younger than the latest Berriasian–Early Valanginian occurrence reported here. Therefore, the Novaya Zemlya seep boulders record one of four currently known areas of seepage from the Mesozoic high northern latitudes, with the Late Oxfordian–Early Kimmeridgian calcareous sandstone boulders being the oldest known examples from this area. Jurassic seeps are in general not well known and there are currently only seven other sites of this age recognized. Three of these are Early Jurassic: the Sinemurian Kilve seeps, UK (Alisson et al., 2008), the Sinemurian seep from Seneca, Oregon, USA (Peckmann et al., 2013) and the

Toarcian Los Molles seep in Argentina (Gómez-Perez, 2003). The remaining four are Late Jurassic. These are the Oxfordian seeps in Beauvoisin, southern France (Gaillard et al., 1992; Kiel et al., 2010; Gaillard et al., 2011), the Tithonian seep in Alexander Island, Antarctica (Kelly et al., 1995; Kaim and Kelly, 2009), the Tithonian seeps in Paskenta and NW Berryessa, California, USA (e.g. Campbell et al., 2002; Kiel et al., 2008b; Jenkins et al., 2013), and the Late Tithonian seeps of Svalbard. The Cretaceous seeps are more common than those of the Jurassic and a fair number of both Early and Late Cretaceous aged seeps have been found (e.g. Campbell, 2006; Kiel and Peckmann, 2008; Kiel, 2010; Kaim et al., 2013; Kiel et al., 2013).

The highly diverse fossil molluscan fauna from the Late Jurassic–Early Cretaceous Novaya Zemlya seep boulders is composed mostly of 'background' taxa. Some of these taxa had rather narrow palaeobiogeographical ranges. This is especially true for the arcticid bivalves, *Dacromya* and the gastropod *Hudlestoniella* (Table 2), which are shared only with the geographically and temporarily adjacent Svalbard seeps and Boreal 'normal' marine sediments, and are unknown from Late Mesozoic deep water seeps (Hryniewicz et al., 2014 and references therein). Some 'background' taxa show preference towards seep environments. For example, the chemosymbiotic protobranch bivalve genus *Nucinella*, which occur in Late Tithonian bituminous limestones, is known from some of Triassic?–Cretaceous seep sites worldwide, for example in fairly deep-water Late Cretaceous (Campanian) seeps in Hokkaido (Amano et al., 2007) and in Early Cretaceous (Valanginian–Albian) seeps in California (Kaim et al., 2014). The eucyclid gastropods, which are present in the Late Oxfordian–Early Kimmeridgian calcareous sandstones, are shared with Late Jurassic–Early Cretaceous (Tithonian–Valanginian) deep-water seep faunas in California (Kiel et al., 2008b). Those 'background' taxa were likely to occur in Late Mesozoic seep faunas worldwide, as their respective families are rather common constituents of the deep-water faunas and had broad palaeobiogeographic ranges (e.g. Oliver and Taylor, 2012; Ferrari et al., 2014). Interestingly, the latest Berriasian–Early Valanginian sandy limestones lack the seep-restricted dimerelloid brachiopod *Peregrinella*, which are very common in some Late Berriasian–Early Hauterivian seeps elsewhere (Kiel et al., 2014). This brachiopod is also absent from Late Berriasian seeps in Svalbard (Hammer et al., 2011). This argues against the spread of *Peregrinella* towards the high-northern latitudes (Biernat, 1957).

The only seep-restricted species in the Novaya Zemlya seep boulders is the hokkaidoconchid gastropod. Hokkaidoconchids range from the Late Jurassic to the Eocene–Oligocene (Gill et al., 2005; Kaim et al., 2014). The oldest known species is *Hokkaidoconcha novacula* from the Late Jurassic (Oxfordian) Beauvoisin hydrocarbon seep site (Kiel et al., 2010), with '*Cerithium elatum*' from Novaya Zemlya (this study) being coeval or slightly younger. Other Late Jurassic species include *Hokkaidoconcha occidentalis* from the Paskenta Tithonian seep (Kiel et al., 2008b; Kaim et al., 2014) and *Hokkaidoconcha hignalli* from the Tithonian Gateway Pass Limestone of Antarctica (Kaim and Kelly, 2009). Poorly preserved high-spired gastropods identified as hokkaidoconchids have also been found in Late Tithonian seeps from Spitsbergen, Svalbard (A. Kaim, unpublished data). Thus, out of five Late Jurassic seep sites known, hokkaidoconchid gastropods occur in four, or possibly five of them. Broad palaeobiogeographic ranges are typical for fossil seep molluscs (e.g. Jenkins et al., 2013; Kiel, 2013; Kaim et al., 2014). By their first appearance in the Late Jurassic, hokkaidoconchids are already widely distributed and occur in geographically disparate basins; this suggests a pre-Late Jurassic origin and dispersal for the hokkaidoconchids (cf. Johnson et al., 2010).

6. Conclusion

The Novaya Zemlya seep boulders provide a new record of the ancient hydrocarbon seepage in the Boreal area. The boulders represent some of the few Jurassic seep rocks from Mesozoic high latitudes, and

Late Oxfordian–Early Kimmeridgian calcareous sandstones record the oldest known seep environment in the Boreal realm. The boulders contain common fragments of sunken driftwood and a very diverse fauna of at least 32 species, the great majority of which are 'background' species, with no special preference towards the seep environment. Some of those species, for example the gastropod *Hudlestoniella*, are high-Boreal elements and are unknown from deep-water Late Mesozoic seeps world-wide. Others, such as the eucyclid gastropod species, belong to deep-water group which had broad palaeobiographic range and occurred in other Late Mesozoic seeps, also including those from deep water. The only species which is currently interpreted as seep-restricted is a hokkaidoconchid gastropod, accompanied by a possible second seep-restricted abyssochrysoid gastropod. Faunas structured similarly to those of Novaya Zemlya seep boulders are known from palaeogeographically nearby latest Jurassic–earliest Cretaceous shallow water seeps from Svalbard, which also contain few seep-restricted species, although these are not the same as those in the Novaya Zemlya seeps.

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