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Cryoconite – From minerals and organic matter to bioengineered sediments on glacier's surfaces

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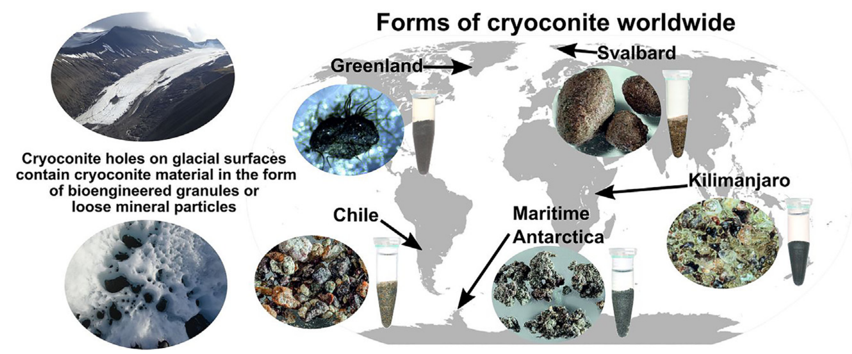
HIGHLIGHTS

- The morphology of cryoconite varies greatly between regions.
- Cryoconite consists of loose mineral material or various types of granules.
- Colour of cryoconite depends on organic matter content and its interplay with minerals.
- Cryoconite is a complex structure providing various ecological niches for glacial microbes.

GRAPHICAL ABSTRACT



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ABSTRACT

Cryoconite is a mixture of mineral and organic material covering glacial ice, playing important roles in biogeochemical cycles and lowering the albedo of a glacier surface. Understanding the differences in structure of cryoconite across the globe can be important in recognizing past and future changes in supraglacial environments and ice-organisms-minerals interactions. Despite the worldwide distribution and over a century of studies, the basic characteristics of cryoconite, including its forms and geochemistry, remain poorly studied. The major purpose of our study is the presentation and description of morphological diversity, chemical and photoautotrophs composition, and organic matter content of cryoconite sampled from 33 polar and mountain glaciers around the globe. Observations revealed that cryoconite is represented by various morphologies including loose and granular forms. Granular cryoconite includes smooth, rounded, or irregularly shaped forms; with some having their surfaces covered by cyanobacteria filaments. The occurrence of granules increased with the organic matter content in cryoconite. Moreover, a major driver of cryoconite colouring was the concentration of organic matter and its interplay with minerals. The structure of cyanobacteria and algae communities in cryoconite differs between glaciers, but representatives of cyanobacteria families Pseudanabaenaceae and Phormidiaceae, and algae families Mesotaeniaceae and Ulotrichaceae were the most common. The most of detected cyanobacterial taxa are known to produce polymeric substances (EPS) that may cement granules. Organic matter content in cryoconite varied between glaciers, ranging from 1% to 38%. The geochemistry of all the investigated samples reflected local sediment sources, except of highly concentrated Pb and Hg in cryoconite collected from European glaciers near industrialized regions, corroborating cryoconite as element-specific collector and potential environmental indicator of anthropogenic activity. Our work supports a notion that cryoconite may be more than just simple sediment and instead exhibits complex structure with relevance for biodiversity and the functioning of glacial ecosystems.

1. Introduction

Cryoconite is a fine, usually dark material found on glacier surfaces around the world. The term originates from ancient Greek and combines two words: κρύος – cold and κόνις – dust. It was firstly introduced by the Finnish-Swedish explorer Adolf Erik Nordenskiöld during the exploration of Greenland interior in 1870 (Nordenskiöld, 1872, 1875), at the time sediment was inspected and described by the author as a little, granular structures on glacier (Fig. 1). The mineral matter covering ice surface originates from various sources, such as local moraines (Porter et al., 2010), surrounding valley walls (Reznichenko et al., 2011), in-situ melting of englacial material (Kirkbride and Deline, 2013; Lewandowski et al., 2020), long-range atmospheric transport from distant deserts or volcanoes (Takeuchi and Li, 2008; Kalińska-Nartiša et al., 2017), anthropogenic activity (Kang et al., 2020) and even extra-terrestrial matter (e.g., micro-meteorites) (Maurette et al., 1987).

Already in the nineteenth century, cryoconite was considered to be partly of biogenic origin (Nordenskiöld, 1875; Von Drygalski, 1897; Nansen, 1906). The first petrographic analysis (Bayley, 1891) revealed that cryoconite was an aggregation of local crystalline schist particles and organic matter. Since then, studies on cryoconite have focused on their biogeochemistry, taxonomic diversity, mineral composition, size, and even cryoconite mineral's micromorphology (e.g. Hodson et al., 2008; Takeuchi et al., 2001a, 2010; Takeuchi, 2002; Nagatsuka et al., 2014; Anesio et al., 2017; Uetake et al., 2019; Zawierucha et al., 2019a). However, despite the rapidly increasing knowledge (Cook et al., 2015), detailed data on cryoconite morphology and colouring, which are crucial for lowering albedo and glacier biogeochemistry, are scarce and available only for a few glaciers (Takeuchi, 2002; Takeuchi et al., 2001a, 2014; Tedesco et al., 2013; Langford et al., 2014).

Mineral particles on the ice surface have been suggested to play important roles for glacial organisms as a source of nutrients in harsh, nutrient-poor glacial ecosystems as well as a physical platform for growth (Smith et al., 2016; Zawierucha et al., 2019a). It is thought that the interaction between organisms and abiotic particles leads to the formation of oval structures, called cryoconite granules, thanks to the production of organic compounds (mostly by cyanobacteria) like extracellular polymeric substances (EPS), which agglutinate together with the mineral fraction (Takeuchi et al., 2010; Langford et al., 2014; Supplementary Fig. 1). Particles deposited on the glaciers as well as autochthonous and allochthonous organic matter are darker than ice and they reduce its albedo. By changing the optical properties of ice, dark sediments facilitate increased input of energy to the glacier radiative balance (Takeuchi, 2002; Di Mauro et al., 2017). Indeed, the presence of cryoconite on ice may reduce ice albedo by 5–30% depending on the colour and spatial distribution (Kohshima et al., 1993; Takeuchi, 2002).

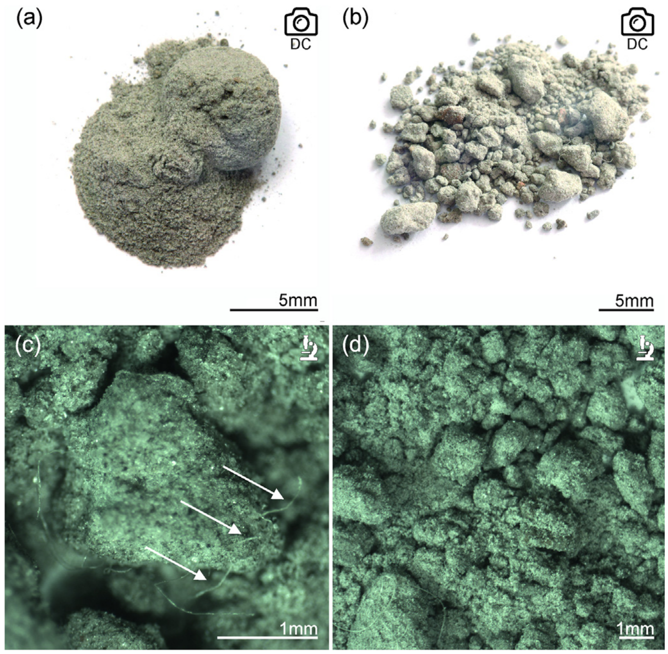

Fig. 1. Original cryoconite collected by A. Nordenskiöld during Greenland expedition in the XIX century. (a), (b) cryoconite granules under high resolution camera. (c), (d) cryoconite granules with thin filaments, which are most probably old cyanobacteria. (Courtesy Patrick Pwiniger). DC - dry cryoconite.

The reduction of ice albedo due to the presence of cryoconite leads to the formation of cryoconite holes — water-filled reservoirs (during ablation season) on the surface of glaciers (Wharton et al., 1985; Macdonell and Fitzsimons, 2008; Cook et al., 2015). Cryoconite holes are regarded as biodiversity hotspots on glaciers, with a number of organisms (algae, bacteria, archaea, fungi, ciliates, and invertebrates) represented by unique species and assemblages (Stibal et al., 2015; Franzetti et al., 2017; Zawierucha et al., 2019b; Stibal et al., 2020).

Cryoconite holes and cryoconite granules support diverse microbial communities in both aerobic and anaerobic microenvironments (Poniecka et al., 2018; Žárský et al., 2013; Uetake et al., 2019; Segawa et al., 2020); the size and shape of the granules affect the community structure (Uetake et al., 2019). Therefore, knowledge of the variation in cryoconite's physical structure is essential for understanding the biogeochemistry, biodiversity, ecology and dynamics of supraglacial ecosystems worldwide.

Takeuchi (2002) and Takeuchi et al. (2001a, 2001b, 2010) showed that cryoconite is a very diversified material in terms of particle size and amount of organic matter. Moreover, specific components of organic matter like fulvic or humic acids may influence cryoconite's colour (Takeuchi, 2002; Macdonell and Fitzsimons, 2008; Langford et al., 2014). Nevertheless, there is still a lack of basic visualisation and description of cryoconite on a global scale, highlighting how the key components of supraglacial systems are still largely overlooked. The major goal of our study is to compare the morphological and colour tones diversity of cryoconite collected from glacier surfaces worldwide and highlight their relationship with glacier bedrock geology, organic matter content, composition of cyanobacteria and algae, and geochemistry. This is the first study to compare supraglacial sediments worldwide (from polar to tropical regions) and to provide baseline for future biological, geological and glaciological studies towards understanding the interplay between biotic and abiotic components and their impact on the darkening of glaciers worldwide.

2. Materials & methods

2.1. Sampling

Cryoconite material was collected from cryoconite holes and from the surface of the glaciers. In order to investigate how the mineralogy, organic matter content (OM), and primary producer communities influence the morphology of cryoconite, a wide range of glacier locations were selected. A total of 33 glaciers (Fig. 2) were sampled (Supplementary Table 1). Samples were collected in the Arctic (Greenland, Svalbard), the Subarctic (Alaska), Scandinavia (Norway, Sweden), the Alps (Austria, Italy, Switzerland), the Caucasus (Georgia), Siberia (Russia), Central Asia (Russia, China), Karakoram (Pakistan), Africa (Tanzania), South America (Tropical Andes, Central Andes, Patagonia), Maritime Antarctica (Anvers Island, King George Island), and Continental Antarctica (McMurdo Dry Valleys). Sampled glaciers differed in their characteristics: (i) geological settings, (ii) climate, (iii) type of glacier (e.g., tidewater, piedmont, valley, ice sheet), (iv) glacier thermal regime (i.e., polythermal, cold-based, temperate), (v) light availability (e.g., seasonal cycles in high latitudes of polar regions, daily cycles in lower latitudes), and (vi) elevation (e.g., marine terminating tidewater glaciers, ice caps and glaciers in high mountains up to 5895 m a.s.l.). Cryoconite from some glaciers was sampled during more than one sampling campaign over multiple years (e.g. Ebbabreen, Longyearbreen, Gulkana Glacier, Russell Glacier, Forni Glacier, Ecology Glacier, Canada Glacier), while other glaciers were sampled only once (e.g. Blåisen Glacier, Austerdalsbreen, Kersten Glacier, La Conojeras Glacier, Marr Glacier). Details of the sampled cryoconite on the investigated glaciers are provided in Supplementary Table 1.

Cryoconite was sampled either with independent sterile disposable Pasteur pipettes or by scoops sterilized before taking each sample. Samples were placed directly in vials, jars, or sterile Whirl-Pak® bags. Sediments from frozen holes in Antarctica were retrieved from a 10-cm diameter core and placed into sterile plastic bags. All sediment samples were either immediately frozen after fieldwork (a few hours), frozen after few days (samples from Baltoro Glacier) or preserved in 70% or 96% ethylic alcohol, then transported to home laboratories at the Adam Mickiewicz University in Poznań (Poland); Cardiff University (UK); Chiba University (Japan); University of Colorado Boulder (USA); or University of Milano-Bicocca (Italy).

2.2. Imaging

To evaluate cryoconite heterogeneity in size, form and tone of colour simultaneously, we used various approaches. A general overview of cryoconite forms (shape of particles) was performed using high resolution photography to allow comprehensive visual comparison. Images of cryoconite in a thin film of water with different focus depths were captured by SONY A7 Mark III camera with Laowa 25 mm f/2.8 2.5-5x ultra macro camera lens and later combined in Adobe Photoshop CC through focus stacking technique. Microscopic pictures have been taken using an OLYMPUS SZ camera and Quick PHOTO CAMERA 3.0 software. Pictures in the field were taken by SONY Cyber-shot, DSC-WX 300. Pictures of Eppendorf tubes were taken by Nikon D610 digital camera with Nikkor 50 mm f/1.8 lens, lit by 4x85 W 5500 K bulbs, white balance was controlled by using X-Rite Color Checker Passport in “mini” size (X-Rite, USA).

The tone and hue of colour was described only when the picture was taken in the field or in a professional photographic studio with a shadowless chamber. We extracted the colour tones of each sample by averaging 100×100 px square in the central field of the photographed material. Then, the mean colour values were transformed into an 8-bit gray-scale and sorted according to the value of the luminance histogram (in the range of 0–255). The median value of the samples in our scale ($N = 32$) was 68.5, with a minimum of 28 and a maximum of 121. Pictures taken under the stereomicroscope could not be used to present hues or tones due to different light luminosity, therefore we did not use them as a colour indicator. Abbreviations on images FC, WC and DC means cryoconite in the field, wet cryoconite and dry cryoconite respectively. Icons of the

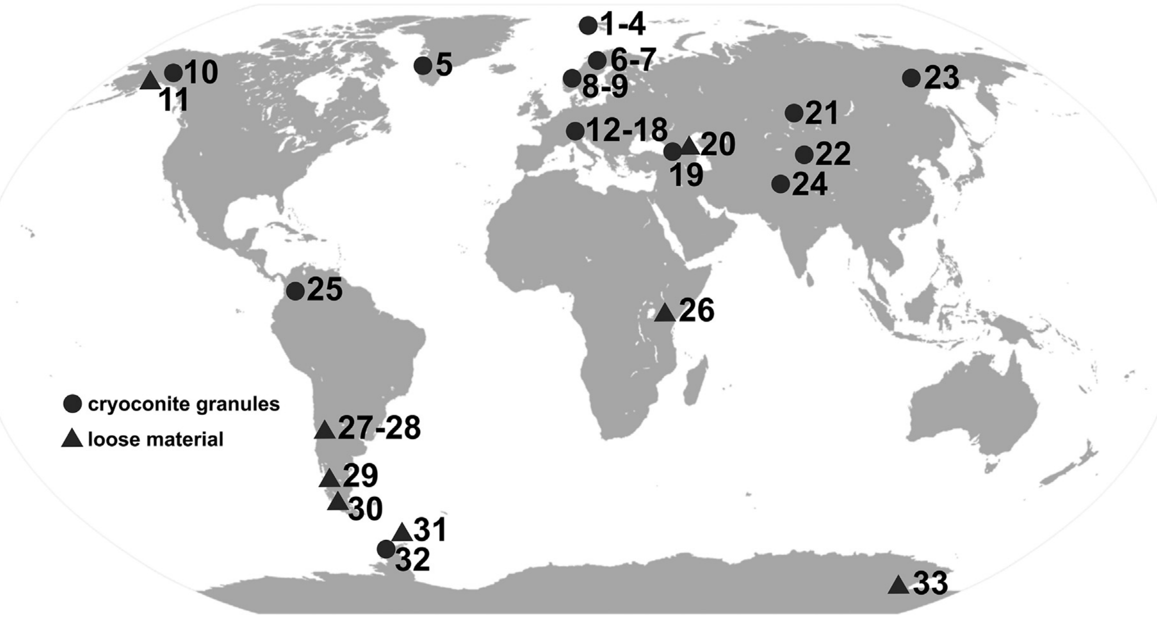

Fig. 2. Sampling sites. **Svalbard:** 1. Midtre Lovénbreen, 2. Ebbabreen, 3. Nordenskiöldbreen, 4. Longyearbreen; **Greenland:** 5. Russell Glacier; **Scandynavia:** 6. Steindalsbreen, 7. Storglaciären, 8. Austerdalsbreen, 9. Blåisen; **Alaska:** 10. Gulkana Glacier, 11. Harding Icefield; **the Alps:** 12. Mittelbergferner, 13. Rhonegletscher, 14. Oberaargletscher, 15. Aletschgletscher, 16. Glacier de Pièce, 17. Morteratschgletscher, 18. Forni Glacier; **the Caucasus:** 19. Adishi Glacier, 20. Gergeti Glacier; **Central Asia:** 21. Akkem Glacier, 22. Ürümqi No.1; **Siberia:** 23. Suntarhyata Glacier No.31; **Karakoram:** 24. Baltoro Glacier; **Equatorial America:** 25. La Conejeras Glacier; **Africa:** 26. Kersten Glacier; **the Andes:** 27. Iver Glacier, 28. El Morado Glacier, 29. Exploradores Glacier, 30. Tyndall Glacier; **Maritime Antarctica**: 31. Ecology Glacier, 32. Marr Glacier; **Continental Antarctica:** 33. Canada Glacier.

camera and microscope indicate instruments used for the preparation of pictures.

2.3. The cryoconite size measurements

The cryoconite and mineral grains were placed on a petri dish and measured under OLYMPUS SZ camera using Quick PHOTO CAMERA 3.0 software. Detailed information about number of measurements per glacier is provided in Table 1.

2.4. The cryoconite elemental composition

The concentrations of 56 elements (including major elements, trace elements, and rare earth elements (REE)) were determined for cryoconite samples from 23 glaciers (Supplementary Material: Geochemistry). Each sample was dried at 105 $\pm$ 5 °C in an electric oven (Thermocenter, Salvislab, Switzerland). Accurately weighted 0.200 $\pm$ 0.001 g of a dry sample was digested with concentrated nitric acid (65%; Sigma-Aldrich, USA) in 180 °C in closed Teflon containers in the microwave digestion system Mars 6 Xpress (Mars 6 Xpress, CEM USA). After cooling, the samples were filtered (Qualitative Filter Papers Whatman preliminary washed by water) to avoid blocking of sample introduction system and diluted to final volume of 15.0 mL by water (Direct-Q system, Millipore, Germany). Before analysis samples were diluted 25 times by water. The inductively coupled plasma mass spectrometer (ICP-MS) system PlasmaQuant MS Q (AnalytikJena, Germany) was used for elemental determination. The isobaric interferences were reduced using the integrated Collision Reaction Cell (iCRC) working sequentially in three modes: with hydrogen as reaction gas, helium as collision gas and without gases addition. The common conditions used for analysis were: nebulizer gas flow 1.05 L min^{-1}, auxiliary gas flow 1.5 L min^{-1}, plasma gas flow 9.0 L min^{-1}, Radio Frequency (RF) power 1.35 kW, signal was measured in 5 replicates (20 scans each). The uncertainty for the total analytical procedure (including sample preparation) was at the level of 20%. The detection limits were determined on the level of 0.00X mg/kg dry weight (DW) for all elements determined (as 3-sigma criteria of blank analysis ($n = 10$)). The detection limits for all determined elements were indicated in Supplementary Material: Geochemistry. The traceability was checked by analysis of the reference materials: CRM NCSDC (73349), CRM 2709, CRM S-1 – l, CRM 667, CRM 405, and the recovery (80–120%) was acceptable for most of the elements determined. For non-certified elements, the recovery in the standard addition method has been defined.

2.5. Organic matter measurements

The amount of organic matter (OM) in cryoconite was measured as a percentage weight loss through combustion at 550 °C for 3 h following drying at 50 °C for 24 h (Wang et al., 2011); method previously used in studies on organic matter content in cryoconite (Buda et al., 2020). Data on organic matter is presented for cryoconite from 29 glaciers (see Table 2).

2.6. Cyanobacteria and algae

Literature data about the algae and cyanobacteria in cryoconite on individual glaciers was identified using Scopus, Web of Science and Google Scholar. Additionally, cryoconite material from Nordenskiöldbreen, Longyearbreen, Steindalsbreen, Austerdalsbreen, Glacier de Pièce, Oberaargletscher, Rhonegletscher, Aletschgletscher, Mittelbergferner, Forni Glacier, and Russell Glacier, was preserved in alcohol and identified at the Wroclaw University of Live Sciences. The data on algae and cyanobacteria in cryoconite are presented for 23 glaciers (Fig. 10, Supplementary Table 3) including both original as well as literature data. For samples from 15 glaciers morphological microscopic analyses were made (including 11 with original data) while for 11 glaciers sequencing of environmental prokaryotes DNA was conducted (literature data). The methods of identification and calculation of bacterial and algae biomass are provided in the Supplementary Table 3.

2.7. Data analysis

To test for differences in the organic matter content between granules and loose cryoconite and between cryoconite classified as dark

Table 1
Cryoconite granules sizes for sampled glaciers (original data). Material has been measured under OLYMPUS SZ using Quick PHOTO CAMERA 3.2 software. For measurements of granules in other studies see data in Cook et al. (2015) and Uetake et al. (2019).

Glacier	Granule size average ± sd (mm)	Min–Max (mm)	Number of measurements	Region
Midtre Lovénbreen	0.67 ± 0.29	0.2–1.7	65	Arctic
Nordenskiöldbreen*	1 ± 0.36	0.4–1.8	70	
Longyearbreen*	1.7 ± 0.9	0.4–4.5	60	
Russell Glacier	0.52 ± 0.22	0.2–1.5	100	
Steindalsbreen	0.59 ± 0.35	0.2–2.3	65	Scandinavia
Storglaciären	0.52 ± 0.24	0.2–1.3	90	
Austerdalsbreen#	7.21 ± 3.11	3–12	9	
Blåisen	0.60 ± 0.31	0.2–1.5	80	
Gulkana Glacier	0.32 ± 0.12	0.1–0.7	80	Alaska
Mittelbergferner	0.44 ± 0.15	0.1–0.9	100	European Alps
Rhonegletscher	0.60 ± 0.24	0.1–1.3	201	
Oberaargletscher	0.57 ± 0.26	0.2–1.4	25	
Aletschgletscher	0.45 ± 0.23	0.1–1.4	55	
Glacier de Pièce	0.55 ± 0.15	0.2–0.9	75	
Morteratschgletscher	0.52 ± 0.34	0.2–2.1	100	
Forni Glacier	0.54 ± 0.20	0.2–1.3	120	
Adishi Glacier	0.58 ± 0.19	0.2–1.1	105	Caucasus
Suntarhyata Glacier No.31	0.54 ± 0.17	0.2–1.0	100	Siberia
Akkem Glacier	0.50 ± 0.19	0.2–1.1	80	Central Asia
Baltoro Glacier	0.85 ± 0.53	0.3–2.8	54	
Marr Glacier	1.06 ± 0.39	0.3–2.6	60	Maritime Antarctica

* In August 2021 the granules observed directly in the field reached about 1 cm in size.
\# Granules dominating only at the glacier terminus.

Table 2
List of glaciers with the average OM contents and cryoconite tone and form. Measurements of organic matter were conducted in this study or accessed from the literature. The cryoconite tone was assessed based on Fig. 7. G – Granules - oval forms/aggregates dominating in the samples. M – mixed - both granular and loose material were detected. L – loose - cryoconite was dominated by loose mineral material.

Glacier	OM	Cryoconite tone	G/L/M	Region
Midtre Lovénbreen	6.46%[2]	Bright	Granules	Arctic
Nordenskiöldbreen	6.25%[1]	Dark	Granules	
Longyearbreen	7.58%[1]	Bright	Granules	
Russell Glacier	16.18%[1]	Dark	Granules	
Steindalsbreen	15.84%[1]	Dark	Granules	Scandinavia
Storglaciären	19.01%[1]	Dark	Granules	
Austerdalsbreen	9.33%[1]	Dark	Mixed	
Blåisen	28.97%[1,*]	Dark	Granules	
Gulkana Glacier	8.2%[3]	Bright	Mixed	Alaska
Mittelbergferner	8.09%[1]	Dark	Granules	European Alps
Rhonegletscher	11.31%[1]	Dark	Granules	
Oberaargletscher	4.16%[1]	Dark	Mixed	
Aletschgletscher	11.03%[1]	Dark	Mixed	
Glacier de Pièce	8.56%[1]	Dark	Granules	
Morteratschgletscher	6.69%[4]	Bright	Mixed	
Forni Glacier	9.88%[1,#]	Dark	Granules	
Adishi Glacier	9.12%[5]	Dark	Granules	Caucasus
Gergeti Glacier	1.71%[1]	Bright	Loose	
Suntarhyata No. 31	12.41%[1]	Dark	Granules	Siberia
Ürümqi Glacier No. 1	9.7%[7]	Bright	Granules	Central Asia
Akkem Glacier	2.9%[6]	Dark	Granules	
Kersten Glacier	3.23%[1]	Dark	Loose	Africa
Iver Glacier	1.09%[1]	Bright	Loose	Andes
El Morado Glacier	1.70%[1]	Bright	Loose	
Exploradores Glacier	1.29%[1]	Bright	Loose	
Tyndall Glacier	1.8%[8]	Bright	Loose	
Ecology Glacier	6.74%[9]	Bright	Loose	Maritime Antarctica
Marr Glacier	11.63%[1]	Bright	Granules	
Canada Glacier	3%[10]	Bright	Loose	Continental Antarctica

1 Original, unpublished data.
2 Edwards et al. (2011).
3 Takeuchi (2002).
4 Baccolo et al. (2017).
5 Łokas et al. (2018).
6 Takeuchi et al. (2006).
7 Takeuchi and Li (2008).
8 Takeuchi (2002).
9 Buda et al. (2020).
10 Foreman et al. (2007).
* The highest concentration of OM in this study was detected on Blåisen where OM reached 38%.
\# The OM content varied between years, ranging from ca. 5% to more than 50% (authors observation, Zawierucha et al., 2019b).

and bright, the Wilcoxon rank-sum test was used. The descriptive statistics and correlations of chemical data were obtained using Excel.

3. Results

3.1. Categories of the cryoconite material

Based on morphology, cryoconite was classified into three general types:

1) Granular cryoconite: typically oval or roundish granules, often of large size (0.3–4.5 mm, sometimes reaching 1 cm – P. Rozwalak, K. Zawierucha personal observations, 2021) with smooth edges (Fig. 3(a), Fig. 4–3.2, 4–4.1).

2) Irregular cryoconite granules: similar to granular cryoconite but with irregular edges (Fig. 3(b), Fig. 4–7.1).

3) Loose material: loose mineral matter without typical bio-aggregations (Fig. 6–33.2). Loose material is highly variable in colour, size and particle types.

Irregular granules were more variable than granular cryoconite (Fig. 3, Fig. 5–17.1, 5–19.2). In turn, loose cryoconite was a simple mineral sediment with particles of a wide range of sizes (Table 1, Supplementary Table 2). Therefore, irregular granules and loose material can be further classified into subtypes. The irregular granules are divided into:

2a) granules overgrown by filamentous cyanobacteria (Fig. 3(c), Fig. 4–5.2),

2b) variable (chaotic) granules with a mixture of different shapes and sizes of granules (Fig. 3(d), Fig. 6–32.1).

Loose material can be divided into:

3a) fine-grained loose cryoconite with sand (<0.5 mm) (Fig. 6–31.1, 6–33.3).

3b) coarse-grained loose material mainly with coarse sand or gravel grains (0.5–64 mm) (Fig. 6–27.1, 6–28.1), which is not typical cryoconite.

Cryoconite varied between and within glaciers. For example, on Longyearbreen (Svalbard) granules might be disintegrated by strong rain and foehn winds to form loose, organic rich sediment (Zawierucha et al., 2019c). Otherwise, on Austerdalsbreen (Norway), granules were absent in the upper part of ablation zone but large, black granules were present at the terminus. However, according to our observations, mostly one morphological form (either granules or loose sediment) tends to dominate across samples and seasons on particular glaciers. For example, on Longyearbreen, Ebbabreen, Russell Glacier, Forni Glacier, and Ürümqi Glacier No. 1, granules were observed during multiple years, while on Ecology Glacier and Canada Glacier loose sediments dominated the samples.

3.2. Morphological differences of the cryoconite among glaciers

Granules were the most common cryoconite type in the Northern Hemisphere (23 out of 25 glaciers), whereas in the Southern Hemisphere this type was rare (found on one - Marr Glacier - out of the eight glaciers).

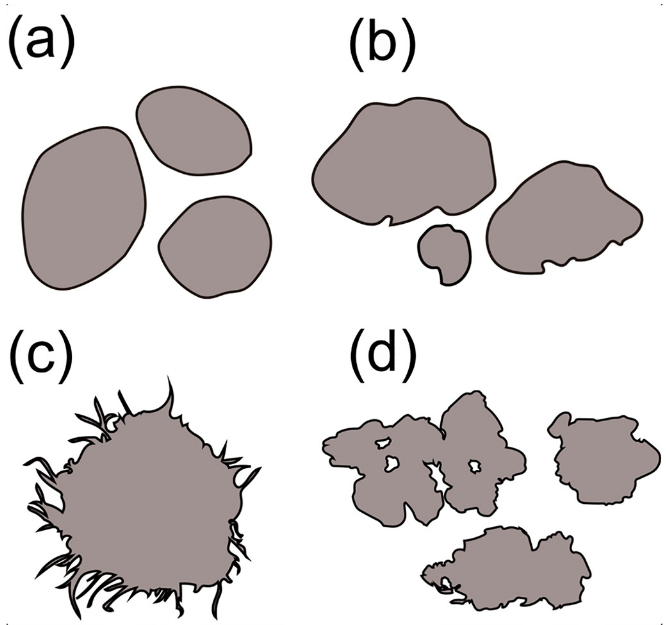

Fig. 3. Schemes present types of granules occurring or co-occuring on glacier surface and in cryoconite holes: **(a)** oval and smooth granules, **(b)** oval, smooth and with irregular edges, **(c)** granules overgrown by cyanobacteria, **(d)** very irregular granules.

Cryoconite granules differed in their shape and size, and varied from <1 mm to >1 cm (Table 1). The biggest granules were observed on Longyearbreen in Svalbard and Austredalsbreen in Norway. Cryoconite granules were mostly represented by irregular granules. Some of them were overgrown by cyanobacteria (e.g. Russell Glacier at the southwestern margin of the Greenland Ice Sheet, Figs. 4–5.1, 4–5.2, Suntarhyata Glacier No. 31 in Siberia, Fig. 6–23.2), covered by algal mats (e.g. Storglaciären in Sweden (Fig. 4–7.2)) or represented variable (not oval shaped) granules (e.g. Marr Glacier in maritime Antarctica; Fig. 6–32.1, 6–32.2). Others did not represent distinct surface features, and were heterogeneous in shape, such as those of Ebbabreen in Svalbard (Fig. 4-2.2), Steindalsbreen and Blåisen in Norway (Fig. 4-6.1, 4–9.1), Morteratschgletscher and Forni Glacier in the Alps (Fig. 5–17.1, 17.2; 5–18.1, 18.2), and other in the Caucasus (Adishi Glacier), Central Asia and Karakoram (e.g. and Baltoro Glacier) or tropics (La Conejeras Glacier in Colombia). Smooth granular cryoconite was only found on five glaciers: Midtre Lovénbreen, Nordenskiöldbreen and Longyearbreen (Fig. 4-4.1; 3.2, 4.1, 4.2, 4.3) in Svalbard, Austerdalsbreen in Norway (Fig. 4-8.1, 8.2) and Ürümqi Glacier No. 1 in Central Asia (Figs. 6–22.1, 22.2). These granules were relatively large-sized (those observed during fieldworks on Longyearbreen reached even 1 cm in size), light-coloured and sometimes symmetrical. Often, along with typical smooth and oval-shaped granules, also irregular granules were found.

Fine-grained loose cryoconite was found on five glaciers (Harding Ice Field in Alaska, Fig. 4–11.1; Gergeti Glacier in the Caucasus, Fig. 5–20.1, 5–20.2; Kersten Glacier in Tanzania, Figs. 6, 26.1–2; Tyndall Glacier in Chile, Fig. 6–30.1; Canada Glacier in Antarctica, Fig. 6–33.1, 33.2, 33.3). Other Chilean glaciers were characterised by coarse-grained loose material (Fig. 6). Ecology Glacier (Fig. 6–31.1) in the maritime Antarctic contained both fine-grained cryoconite and coarse-grained loose material. While, Ebbabreen in Svalbard and Gulkana Glacier in Alaska contained mixture of both loose and granular cryoconite.

3.3. The colouring of the cryoconite

Cryoconite represented various hue classes (Fig. 7, Table 2), ranging from very dark (e.g. Blåisen, Austerdalsbreen) to bright (e.g. Ecology Glacier, Canada Glacier), including brick red (Gergeti Glacier). All loose cryoconite was rather bright or brick coloured, except cryoconite from Kersten Glacier on Kilimanjaro (Figs. 7, 26). The darker tone of cryoconite was linked to organic matter content in sediments (Fig. 8). We observed that even very dark cryoconite after the combustion of organic matter at 550 °C became much lighter in colour (Supplementary Fig. 2). Other data for cryoconite from Ecology Glcaier, Longyearbreen, Morteratschgletscher, Ürümqi Glacier No. 1 are available in Buda et al. (2020), Langford et al. (2014), Baccolo et al. (2020) and Takeuchi et al. (2010) respectively.

3.4. Organic matter

Table 2 presents original as well as literature data on average OM content from glaciers worldwide. It varied from ca. 1% (Iver Glacier in South America) to 38% (Blåisen in Scandinavia). We found that granules have a higher organic matter content than loose sediment (Table 2, Fig. 8).

3.5. Chemical composition of the cryoconite

Despite geochemical heterogeneity between particular samples of cryoconite, some general patterns emerged when they are compared to other types of Earth surface materials (Supplementary Materials: Geochemistry and Supplementary Table 1). Concentrations of major and trace elements essential for life, were in similar ranges in most of the analysed samples (Fig. 9), except of samples from Ebbabreen in Svalbard and Kersten Glacier on Kilimanjaro where very high concentrations of Ca and Mg were found. The lowest values in respect to all the analysed elements were documented in samples from Caucasian Gergeti Glacier and Canada Glacier in Antarctic.

A comparison of the elements concentrations in major rock types (basalt, granite, shale, sandstone, carbonate) of the Earth's crust (Turekian and Wedepohl, 1961) with the cryoconite composition revealed that the geochemical composition of supraglacial sediments is a homogenous mix of elements without a clear link with a single potential source rocks in glacier catchment (Supplementary Materials: Geochemistry and Supplementary Table 1). Taking into account various potential endmember rock types, the cryoconite composition is the most similar to typical composition of sandstones (Supplementary Materials: Geochemistry, comparison examples). Locally, however, cryoconite may be enriched in some elements such as Ca, for instance in samples from Ebbabreen - draining carbonate rocks rich basin, and Fe, as in Forni Glacier with abundant Fe-rich rocks in the catchment. Large variability in amounts of heavy metals was documented (Fig. 9), which probably at least partially were derived from anthropogenic sources and then accumulated in cryoconite (Huang et al., 2019). Among the heavy metals, Pb and Hg were detected in particularly high concentrations on European glaciers. REE were generally depleted in cryoconite, with exception on Kersten Glacier in Kilimanjaro (the sum of the REE was 328.5 mg/kg) and Austerdalsbreen in Norway (274.2 mg/kg), where REE were significantly enriched in comparison to the average concentration of REE in the Earth's crust (130–240 mg/kg, Balaram, 2019).

3.6. Algae and cyanobacteria

Fig. 10 showed the most common photoautotrophic taxa on investigated glaciers. The most common families were Pseudanabaenaceae (*Leptolyngbya*, *Pseudanabaena*) and Phormidiaceae (*Phormidium*, *Phormidesmis*, *Wilmottia*, *Microcoleus*) among cyanobacteria, Mesotaeniaceae and Ulotrichaceae (*Klebsormidium*) among Chlorophyta and Naviculaceae (*Pinnularia, Navicula*) among Bacillariophyceae. The novel data, based on morphological identification with a

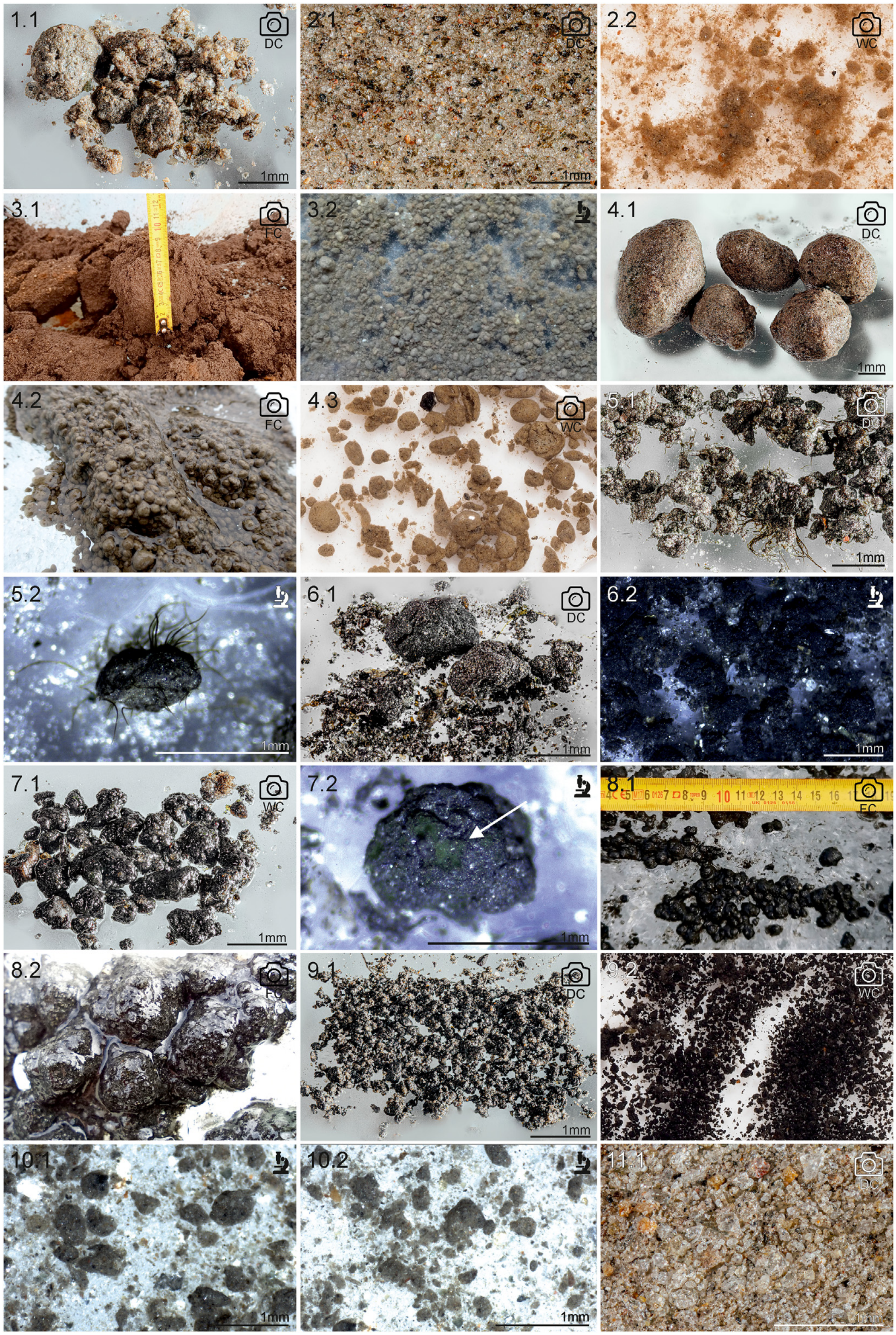

Fig. 4. Description of cryoconite: Midtre Lovénbreen: (1.1) Light-coloured granular cryoconite, granules were disaggregated into smaller pieces. **Ebbabreen: (2.1)** Light, brownish fine-grained loose cryoconite with silt and fine to medium-size quartz. **(2.2)** Loose mineral matter with some granular cryoconite. **Nordenskiöldbreen: (3.1)** tiny granules bound into smaller or larger aggregates. **(3.2)** Various sizes of smooth, oval granules. **Longyearbreen: (4.1)** Light-coloured large granular cryoconite with compact sand granules. **(4.2)** Macro photo of brownish aggregations of granules in the field. **(4.3)** Large, light – brown (ca. 2–4 mm in size), granular cryoconite, some granules were broken to reveal interior, with a mixture of organic and mineral compounds. **Russell Glacier: (5.1–5.2)** Irregular granules overgrown by thick and long cyanobacteria filaments (even longer than granule). **Steindalsbreen: (6.1–6.2)** Dark granules with irregular surface, and different size, some of them were destroyed during handling. **Storglaciären: (7.1)** Dark greyish/blackish, and greenish granules of various size and shape, with some large mineral particles. **(7.2)** Granules covered by the algal mats. **Austerdalsbreen: (8.1–8.2)** material bounded into large granules that disintegrate poorly, granules are often stuck together. Particles of quarts present on the dark surface. **Blåisen: (9.1)** Dark, irregular granules with some quartz grains visible. **(9.2)** Very dark/blackish irregular granules with sharp edges forming small pellets. **Gulkana Glacier: (10.1–10.2)** Irregular, dark granules and surrounded by loose cryoconite with quartz grains and organic matter, most probably originating from eroded granules. **Harding Ice Field: (11.1)** Quartz dominated, moderately and well sorted, sub-angular and rounded loose cryoconite. For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article. FC - cryoconite in the field, DC - dry cryoconite, WC - wet cryoconite.

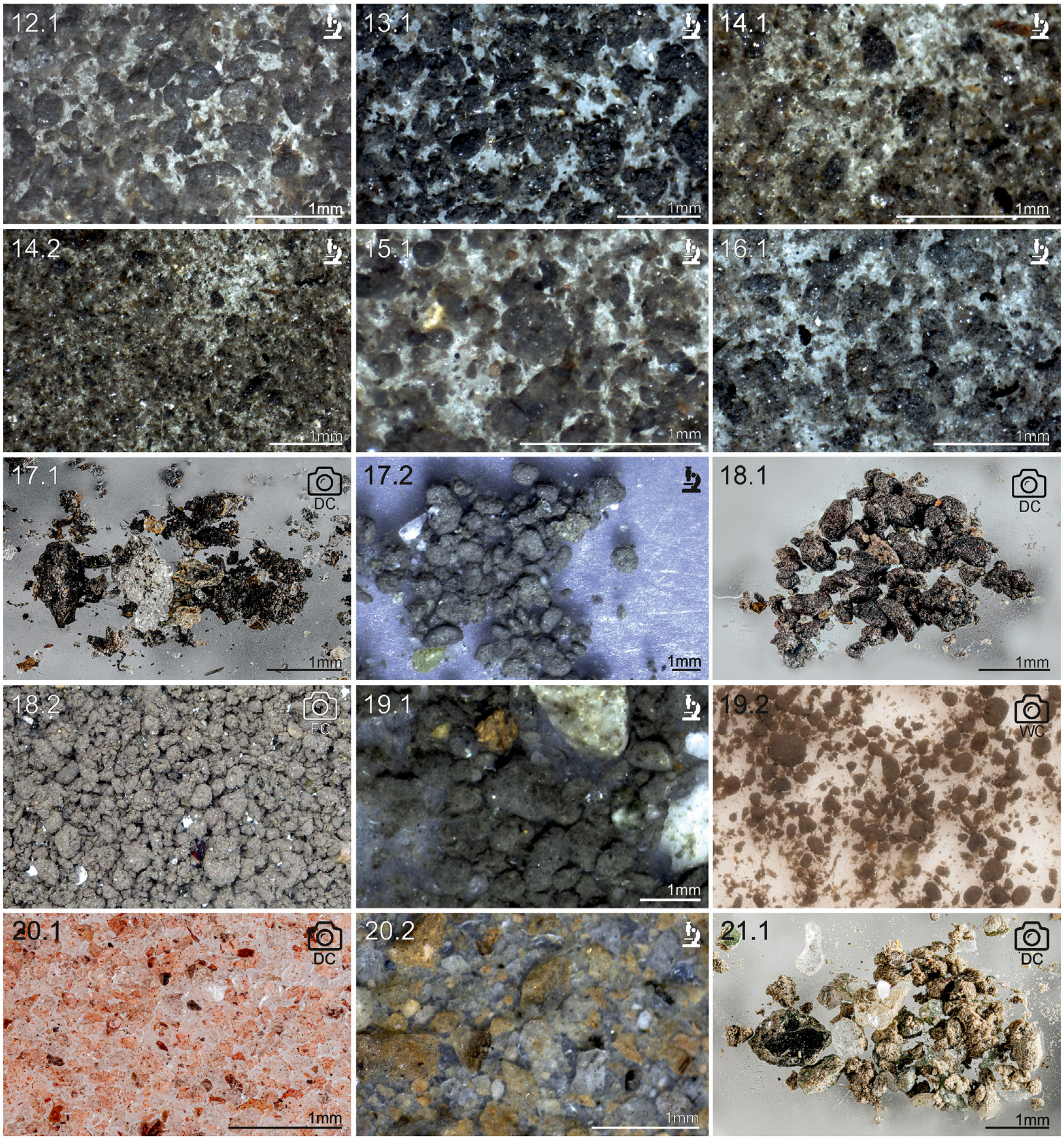

Fig. 5. Mittelbergferner: (12.1) Matter is bounded into mainly large dark grey granules of different shape. **Rhonegletscher: (13.1)** Dark, sometimes black granules of different size and shape. **Oberaargletscher: (14.1–14.2)** Part of the matter is in the form of loosely bounded aggregates and part in the form of sand; sometimes larger black granules are present. **Aletschgletscher (15.1)** Dark granules differing in size and shape (from oval to angular). **Glacier de Pièce: (16.1)** Granules of different colour (from grey to black) and size, part of the matter is in the form of sand, the remaining matter forms large loosely bounded granules. **Morteratschgletscher: (17.1–17.2)** Very irregular granules, mineral particles (mainly quartz) and organic particles visible. **Forni Glacier: (18.1)** Dark, oval as well as very irregular granules, organic matter and quartz grains sometimes visible. **(18.2)** Irregular cryoconite granules photographed in the field. **Adishi Glacier: (19.1–19.2)** Various dark, oval and roundish granules of different size and shape, accompanied with very large mineral particles. **Gergeti Glacier: (20.1)** Well sorted, sub-angular loose cryoconite. The picture depicts the real pinkish and reddish colour of the mineral material. **(20.2)** Moderately sorted, sub-angular loose cryoconite material. **Akkem Glacier: (21.1)** Irregular, bright granules with large mineral grains (quartz, biotite). FC - cryoconite in the field, DC - dry cryoconite, WC - wet cryoconite.

microscope, showed that cyanobacterial genera *Leptolyngbya* and *Pseudanabanea* were the most frequent ones in the cryoconite samples.

According to the DNA sequencing data (literature data) the most common cyanobacteria taxa on glaciers was *Phormidesmis* (Segawa et al., 2017; Uetake et al., 2019). The review of the literature and original identification conducted in this study revealed that the most common among algae were *Klebsormidium*, *Cylindrocystis*, *Chlamydomonas* and *Ancylonema*. However, the last two taxa are not typical for cryoconite environments (Hoham and Remias, 2020). Especially genus *Chlamydomonas* require careful revision (Procházková et al., 2019). The cyanobacterial and algal communities were the most diverse on Forni and Canada Glaciers, most likely driven by detailed long-term monitoring of these communities (Wharton et al., 1985; Darcy et al., 2018; Pittino et al., 2018, Sommers et al., 2018; Fig. 10, Supplementary Table 3). According to molecular studies the relative abundance of cyanobacterial sequences in total DNA from samples varied between regions, reaching the highest values on glaciers in the Northern Hemisphere: >70% on Gulkana Glacier (Segawa et al., 2017) and 40% on Forni Glacier (Pittino et al., 2018), as opposed to Andean glaciers with relative abundance of cyanobacterial sequences around 1% (Pittino et al., 2021).

4. Discussion

Even though cryoconite constitutes a crucial component in the functioning of supraglacial ecosystems, only a few descriptions of its morphology on a handful of glaciers were previously available (Takeuchi

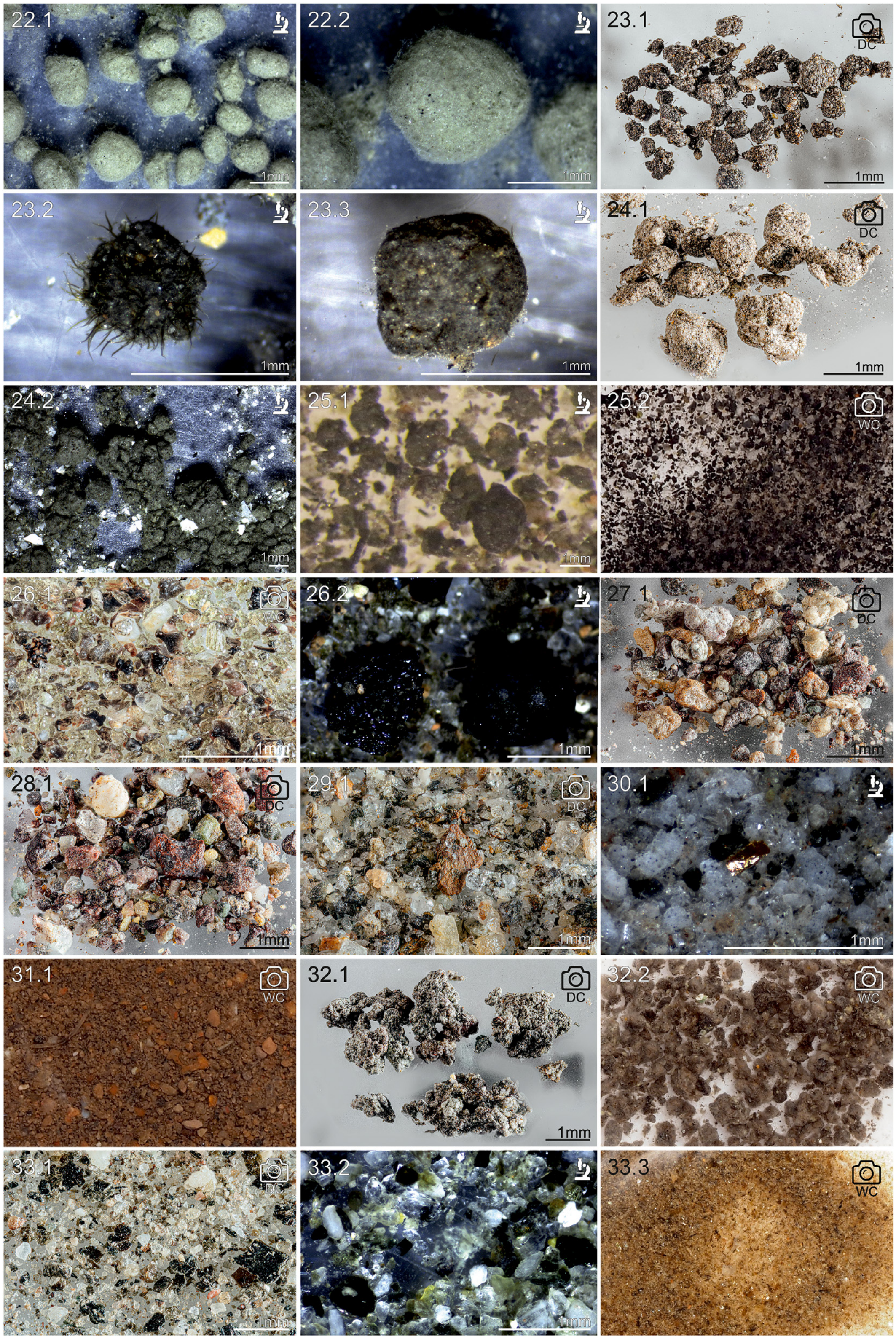

Fig. 6. Description of cryoconite: Ürümqi Glacier No.1: (22.1) Oval and roundish bright granules with scattered organic matter. **(22.2)** Smooth cryoconite granule covered by fine organic matter of filamentous shape. **Suntarhyata Glacier No.31: (23.1–23.2)** Irregular granules of different size and shape, overgrown by cyanobacterial filaments, with mineral particles visible. **(23.3)** Irregular cryoconite granule with very few to no filaments. Light mineral grains are entrapped in the granule. **Baltoro Glacier: (24.1–24.2)** Bright coloured, irregular granules of different size and shape, with mineral grains, mainly quartz entrapped. **La Conejeras Glacier: (25.1)** irregular grey granules of different size and shape. **(25.2)** Very dark/blackish granules resembling small pellets, well sorted, with angular edges and a large proportion of well sorted mineral grains **Kersten Glacier: (26.1)** Moderately sorted, sub-angular loose cryoconite, composed of volcanogenic minerals. **(26.2)** Porous volcanic glass in the foreground. **Iver Glacier: (27.1)** Poorly sorted, sub-rounded loose cryoconite, composed of diverse minerals and rock particles. **El Morado Glacier: (28.1)** Poorly sorted, sub-angular loose cryoconite, composed of diverse minerals and rock particles. **Exploradores Glacier: (29.1)** Poorly sorted, sub-angular loose cryoconite, composed of diverse minerals and rock particles. **Tyndall Glacier: (30.1)** Quartz dominated, well sorted, sub-rounded loose cryoconite with weathered biotite present (in the middle). **Ecology Glacier: (31.1)** Poorly sorted, sub-rounded loose cryoconite. **Marr Glacier: (32.1–32.2)** Greyish/brownish irregular granules of different shape and size, partly forming larger, irregular aggregates of multiple granules. **Canada Glacier (33.1):** Well sorted, sub-angular loose cryoconite with **(33.2)** numerous biotite and quartz minerals and **(33.3)** a brownish colour. DC - dry cryoconite, WC - wet cryoconite.

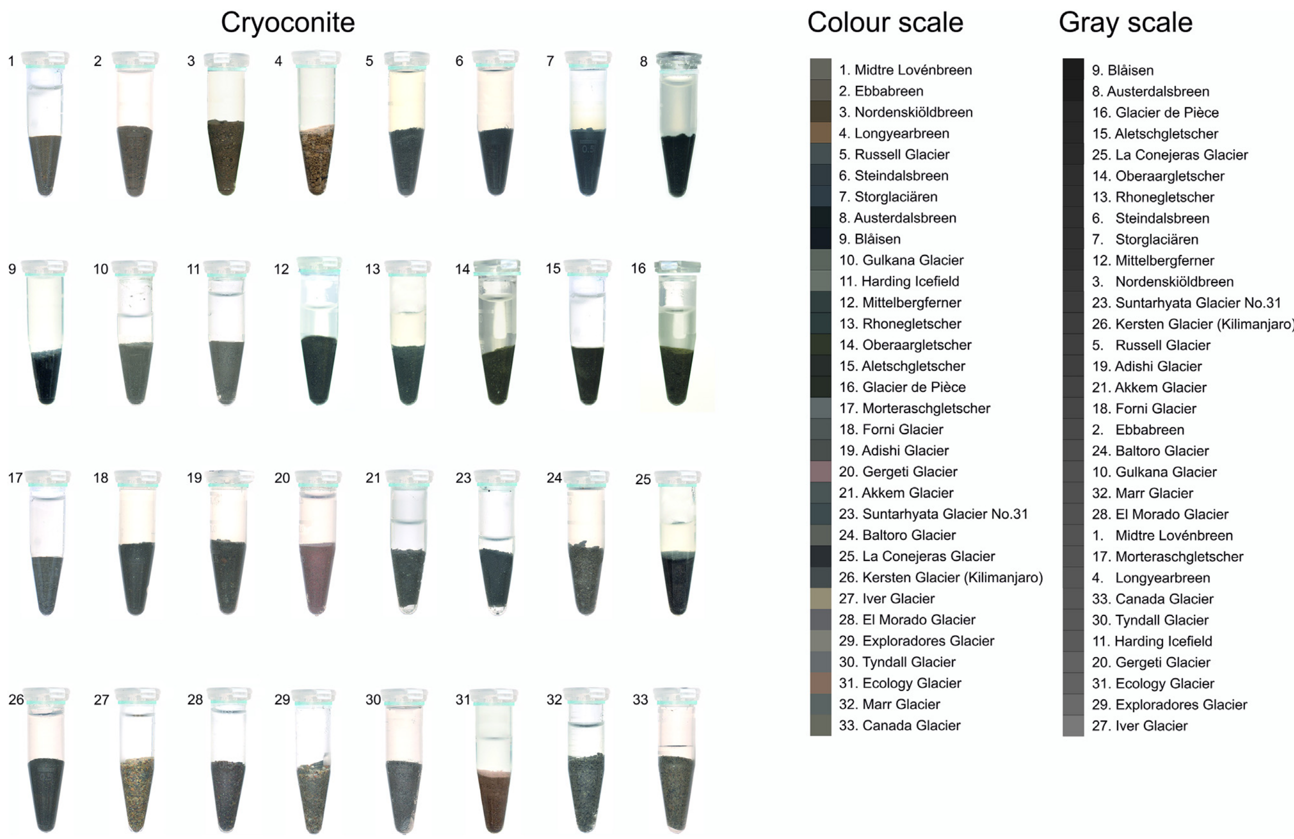

Fig. 7. Eppendorf tubes with cryoconite collected from around the world (except Ürümqi Glacier No. 1). Left panel presents names and colours of glaciers ordered from North to the South locations. Right panel presents gray scale.

et al., 2010; Irvine-Fynn et al., 2011; Langford et al., 2014; Zawierucha et al., 2019a). In this study, we described morphological forms of cryoconite from 33 glaciers worldwide using macro and microscopic photographs. We found that both loose cryoconite and granules strongly varied between regions. Granules ranged from very small (0.2 mm) and dark to relatively large (ca. 1 cm in Arctic and Scandinavia), with the larger granules being either light in colour or dark. Some glaciers generally lacked granules, whereas others had them continuously present.

Despite being called "cryoconite" all over the world, these supraglacial sediments exhibit diverse morphologies suggesting a more complex nature than previously anticipated. Granules themselves serve as distinct

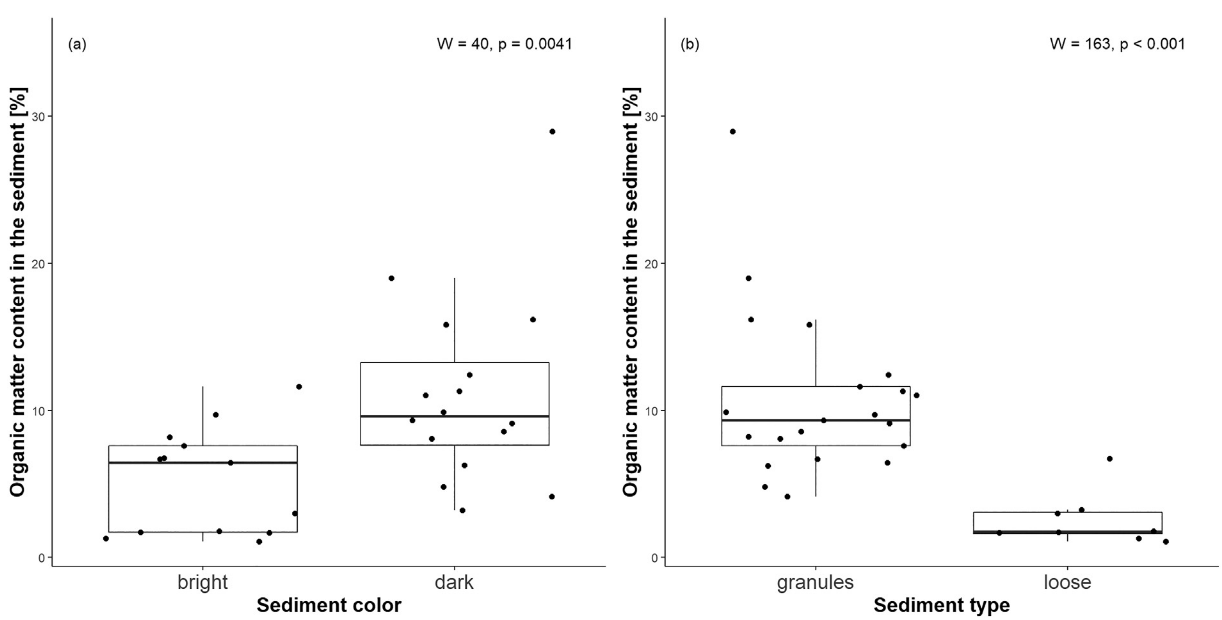

Fig. 8. Difference in the organic matter content between (a) sediment tones - cryoconite classified as bright or dark (for details see Table 2); (b) sediment type - cryoconite classified as granular or loose sediment. W-values refer to the statistic of the Wilcoxon rank-sum test. Boxes denote 25th, 50th, and 75th percentiles; whiskers represent the lowest and highest observation within the 1.5 interquartile ranges of the lower and upper quartiles. The horizontal distribution of dots is random.

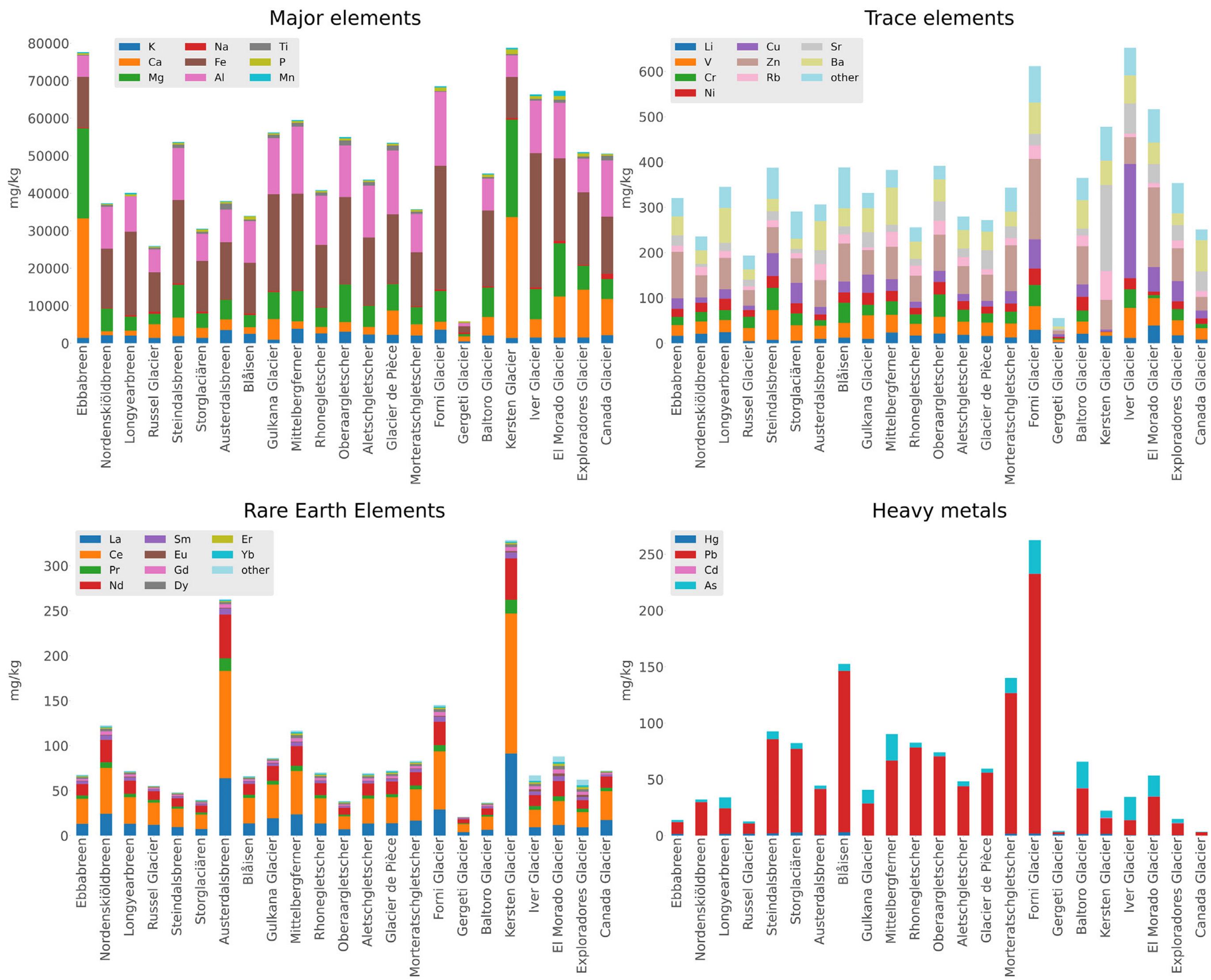

Fig. 9. Geochemical measurements of cryoconite from 23 glaciers around the world. Grouped by major, trace elements, rare earth elements (REE) and heavy metals.

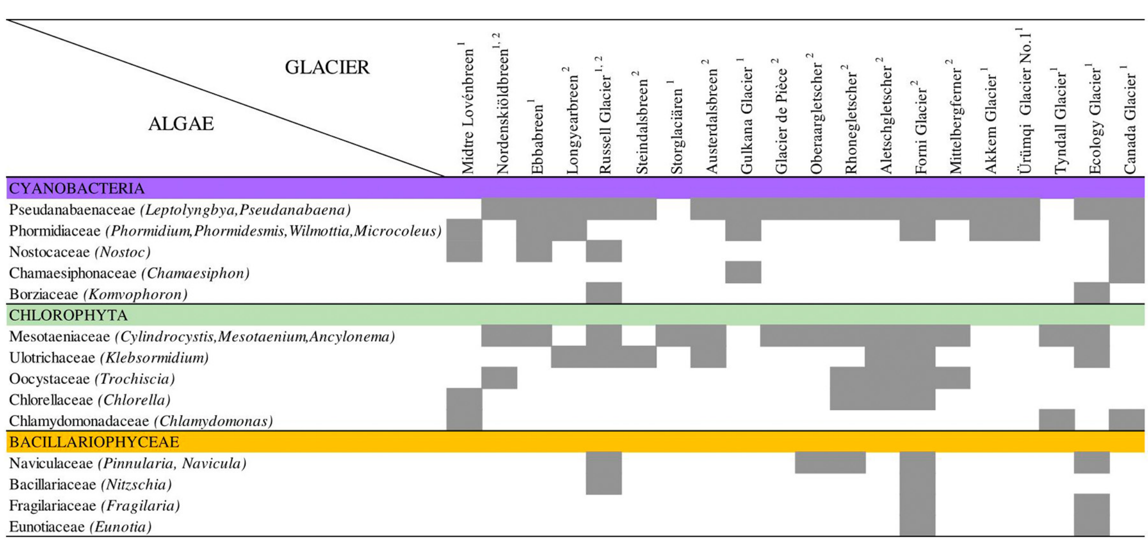

Fig. 10. Occurrence of the most common cyanobacteria and algae families on the investigated glaciers. The taxon is presented if it was detected on the glaciers more than once. 1 – literature data, 2 – novel data. For details see Supplementary Table 3.

ecological niches in cryoconite holes (Uetake et al., 2016; Poniecka et al., 2018; Segawa et al., 2020), but their role in glacial ecosystem productivity and biogeochemical cycles is still not fully understood at a global scale. For example, large granules can host both aerobic and anaerobic (in the innermost parts of granules) heterotrophs, but the surface is also a suitable substratum for photoautotrophs (Segawa et al., 2020), which in turn could serve as a food source for other trophic groups like grazing tardigrades (Zawierucha et al., 2019b). Thus, granular cryoconite can host a greater complexity of microbial functions (Segawa et al., 2020). In contrast, the cryoconite holes with only loose cryoconite or coarse grained material, most likely do not develop anaerobic conditions, especially if the sediment is poor in organic matter because it provides space between mineral grains for oxygen diffusion. The presence of loose versus granular cryoconite may thus suggest the presence of different biochemical functions on glaciers.

The reduction of ice surface albedo by cryoconite varies based on the size and colour of material deposited on glaciers (Takeuchi et al., 2001a; Takeuchi and Li, 2008; Takeuchi et al., 2014; Di Mauro et al., 2017). Therefore, incorporation of cryoconite forms as important factors in the so-called bio-albedo feedback concept (Cook et al., 2015; Di Mauro et al., 2020; Williamson et al., 2020), might be an important improvement in understanding and quantification of melting of glacier surfaces worldwide since granules and loose forms may differentially absorb solar radiation.

4.1. Potential factors in cryoconite granule formation

In general, the formation of granules (both regular and irregular) of some cryoconite is most likely due to the combined effects of the cohesive properties of clay minerals, which widely occur in cryoconite holes (Langford et al., 2010) and to active excretion of extracellular polymeric substances (EPS) by cyanobacteria (Langford et al., 2010, 2014). For example, benthic filamentous cyanobacteria can penetrate sediment substrates through gliding motility accompanied by the secretion of mucilaginous EPS (Hoiczyk, 2000). EPS supposedly act as a glue for organic and inorganic matter, hypothetically allowing the formation of regular or irregular spheres (Langford et al., 2010, 2014; Takeuchi et al., 2010; Uetake et al., 2016, 2019). Indeed, granules are sometimes completely covered by cyanobacteria filaments (e.g., Greenland Ice Sheet), although, based on the data presented in this paper, this type of granules seems to be rare. The most frequently detected cyanobacteria families on the glaciers studied here were Pseudanabanaceae and Phormidiaceae (Fig. 10). Those families include several genera that are known EPS producers (Vicente-García et al., 2004; Mugnai et al., 2018). However, other cyanobacteria like representatives of Nostocaceae (detected worldwide by DNA (Segawa et al., 2017)) might also be crucial in EPS production and cementing mineral grains on glaciers (Kanekiyo et al., 2005). For example, on a central Asian glacier the main drivers of granular forms are most likely oscillatorialean cyanobacteria (Takeuchi et al., 2010; Segawa et al., 2017). Extensive data on primary producers, that excrete EPS, in cryoconite on other glaciers than those investigated in our study are presented in Segawa et al. (2017) and Uetake et al. (2019).

The mere presence of potential EPS producers is not the only factor relevant for cryoconite granules formation, but their density would also matter to granule formation. For instance, cyanobacterial taxa occurring on Canada Glacier in Continental Antarctic have been found to produce EPS-like compounds (Kanekiyo et al., 2005; Singh et al., 2016), but distinctly cemented granules remained absent in the cryoconite on this glacier over multiple seasons of monitoring. The ratio of algae and cyanobacteria may also affect granule formation, particularly if the algae do not produce EPS and limit the growth of EPS-producing cyanobacteria. Even though cyanobacteria were present in cryoconite of some glaciers (e.g. on Ecology Glacier) their biomass was very low (Buda et al., 2020), which may suggest that when the biomass of EPS-producing cyanobacteria in cryoconite is low, the granule formation might be ineffective or long-lasting. Observations from marine environments suggests high activity of EPS consumers (Hoskins-Brown et al., 2003), if the same phenomenon is present in loose cryoconite, it may explain the lack of granules on some of the investigated glaciers. The differences in frequency of granular cryoconite between hemispheres could stem from biogeography of cryoconite microbial communities, especially cyanobacteria composition (Segawa et al., 2017), which in turn can be shaped by environmental and historical factors (Ribeiro et al., 2018), other than glacier type or local geology.

The production of EPS by cyanobacteria could be accelerated in some cases by cryoconite grazers. For example, Yang et al. (2008) demonstrated that common bloom-forming cyanobacterium *Microcystis aeruginosa* increases synthesis and secretion of EPS in the presence of flagellate grazer *Ochromonas* sp. EPS can contribute to resistance against grazers for the organisms that produce it, namely cyanobacteria but also microalgae (Liu and Buskey, 2000). Therefore, granule formation by cyanobacterial activity in cryoconite holes may be in part promoted by common cryoconite grazers such as tardigrades and rotifers (Zawierucha et al., 2021). Finally, although some cyanobacteria are known to form spherical structures (Brehm et al., 2003), the role of heterotrophic bacteria in the shaping of cryoconite forms cannot be ruled out, since they constitute a substantial proportion of cryoconite microbial communities worldwide (Darcy et al., 2018; Liu et al., 2017; Makowska et al., 2020). Clarifying the role of specific groups of organisms in granule formation will require a more systematic and comprehensive study of them than has been published to date.

Future work should also seek to more closely link the biological processes with physical and chemical processes in micro- and mesoscale, spatially and temporally, which may provide critical information on the conditions of granule formation (e.g., through differential freezing, length of ablation season or water circulation in cryoconite holes).

4.2. Geochemistry of cryoconite

The role of abiotic factors such as the chemical composition of ice and water, or minerals from distant and local sources, in the shaping of cryoconite forms is still not understood. Our study suggests that the chemical composition of cryoconite is not the major control on its morphology or colouring. Despite global representation of the sampling set, the investigated major and trace elements concentrations in cryoconite were relatively similar across almost all the samples with few exceptions (Fig. 9). All the investigated samples represented a mixed composition, when compared to chemical composition of the main rock types (e.g., basalt, granite, shale, sandstone, carbonate). Their elemental concentrations and ratios are the most similar to sedimentary rocks (see Supplementary Material: Geochemistry, comparison examples). Thus, in terms of cryoconite-related ecosystems, one may assume that glacial organisms have similar mineral nutrients source worldwide. Most likely both different microbial communities and regional physical factors influence differently weathering and realising of elements from mineral grains. Nevertheless, local geological settings and transport of natural and anthropogenic materials can influence the concentration of specific elements in cryoconite. For example, the high Pb content on the Forni Glacier is probably due to war activity on that glacier during World War I. Bullets and shrapnel artillery shells are regularly found on surface of Forni and they are the most likely source of Pb enrichment (230 mg kg^{-1}). Concentrations of Pb measured in cryoconite from other regions are usually several times lower, as in this study (Fig. 9) and in earlier work (Łokas et al., 2016, 2019; Singh et al., 2017). Similarly, high Hg concentrations documented in some cryoconite samples, mainly from glaciers close to industrialized areas, were most likely of anthropogenic origin as was also suggested by Huang et al. (2019).

Elements such as Ca and Na, by contrast, are highly mobile and are subjected to relatively fast chemical weathering from minerals, occurring on glacier surface (Baccolo et al., 2017; Zawierucha et al., 2019a).

In fact, these elements are generally depleted in cryoconite. For example, Longyearbreen occupies a catchment composed mainly of shales and sandstones with an average Na concentration in range of 7000–8500 mg/ kg^{-1} (Schlegel et al., 2013), while the Na concentration in the cryoconite on Longyearbreen is only 357 mg/kg^{-1}.

In summary, the cryoconite elemental composition does not result only from the local geological setting, but is also affected by contributions of organic matter and minerals from other sources (englacial origin, long-range transport). In some cases, the specific geological context or geographical isolation of a glacier may result in its cryoconite geochemistry having site-specific properties. A good example is the Kersten Glacier on Kilimanjaro, which has a very high abundance of REE, likely as a consequence of the common presence of volcanic glasses in the cryoconite samples (Dawson et al., 2008).

4.3. Biogeological links in cryoconite colour

We initially studied cryoconite colour as a function primarily of geological composition, but the geology alone failed to explain cryoconite colour. In order to determine the potential impact of geological settings on cryoconite colour, the main rock types of a glacial catchments were gathered from the literature and geological maps provided by geological surveys of the respective countries (Supplementary Table 1). However, it is important to note that most rock types consist of a mixture of lighter and darker minerals. In addition, there are numerous rock type variations, which are often generalized on the geological maps. Moreover weathering processes may change the colour of the sediments within cryoconite holes (e.g., due to oxidation). In most of the sites studied here, the rocks in the glacier catchments were composed of a mixture of generally lighter (e.g., sandstone, granite, gneiss, granodiorite) and darker rocks (e.g., gabbro, amphibolite, dacite) (Supplementary Table 1). The proportion of lighter and darker rock types vary, making it difficult to directly relate the colour of source rocks in the glacier's catchment to cryoconite colour. In the case of glaciers with one dominating colour-type of source rocks, the resulting cryoconite colour was found to be inconsistently related. For example, dark cryoconite (enriched in OM) from Russell Glacier (Greenland) and from Blåisen (Norway) were derived from relatively light-coloured rocks in the respective glacier catchments. On the contrary, the light cryoconite was documented on Gulkana Glacier, which is surrounded mainly by dark rocks (gabbro). In case of Svalbard glaciers, Midtre Lovénbreen and Longyearbreen, the light-coloured cryoconite reflected the relatively light colour-type of the rocks in their catchments, but the OM content was low on these glaciers. The colour of cryoconite may ultimately be a result of interacting effects of the source rock type, weathering processes, and OM content.

Our results suggest that the major driver of colouring of cryoconite is based not solely on rock source, but on the concentration of OM (most likely OM properties, Takeuchi (2002); Takeuchi et al., 2010; Langford et al. (2014); Figs. 7-8, Supplementary Fig. 2). Organic matter found in cryoconite is both produced in situ as well as delivered from ex situ sources like wind-blown organic particles (Stibal et al., 2010; Feng et al., 2016; Takeuchi et al., 2010; Zawierucha et al., 2019b). However, previous studies also highlight the important role of humic substances, which are dark-coloured organic matter derived from residues of bacterial decomposition, in cryoconite colouration (e.g. Takeuchi, 2002; Langford et al., 2014). The difference in humic substances along with differences in autochthonous and allochthonous sources of OM may interact with local geology to best explain geographical variation in the colour of our samples (Feng et al., 2016; Pautler et al., 2013; Takeuchi, 2002). Additionally, the presence of pigmented cyanobacterial "ecosystem engineers" along with other algae and fungi in cryoconite could also influence the colours of granules on various glaciers (Beutler et al., 2004; Williamson et al., 2020; Sajjad et al., 2020). Future work may be warranted to better understand the production of humic substances and concentrations of pigmented organisms in cryoconite.

4.4. Potential impact of other factors on cryoconite granules

We are still far from having a full understanding of cryoconite structure on different glaciers. Content of OM (and its components, see Takeuchi, 2002) affecting the colour of cryoconite may vary from year to year (personal observation of the authors on Forni Glacier). Moreover, OM produced in situ and delivered from ex situ sources (windblown) greatly differ between regions and depends on glacier location, topography, proximity of OM sources etc. (Feng et al., 2016; Pautler et al., 2013; Stibal et al., 2010; Takeuchi et al., 2010). Others uncertainties include the potential erosion of granules by streaming ablation water, the stability of cryoconite holes, and the regional diversity of glacial microbial assemblages (Segawa et al., 2017; Takeuchi et al., 2019; Stibal et al., 2015; Zawierucha et al., 2018, 2019b; Uetake et al., 2019). Cryoconite structure could also depend on local glaciological features (Baccolo et al., 2020). For example, Langford et al. (2014) have shown that the chemical and biological properties of granules change along the altitudinal and slope gradient of an Arctic glacier. Benthic cyanobacteria grow faster in stable environments, thus larger ice caps or glaciers characterised by relative stability, gentle slopes and limited surface water movement may favour cyanobacterial growth and the formation of granules. However, these conditions are not strictly required for the formation of granules since for example, Longyearbreen cryoconite holes are often subjected to intense ablation and collapsing depending on weather events (Zawierucha et al., 2019c) but granules are still present in these dynamic systems.

Our observation indicated that interannual changes does not affect the presence or absence of granules. For example, we observed granules on Longyearbreen (years: 2016, 2018, 2020, 2021) and Forni (years: 2012, 2016, 2018, 2019, 2020), while loose sediments on Ecology Glacier (years: 2017; 2018) and Canada Glacier (years: 2017, 2018, 2019) during more than one sampling campaign. Even though Pittino et al. (2018) found that microbial communities change on Forni over the course of a single year as well as over multiple years, granules were found in cryoconite holes over multiple years. The degree to which their micromorphological structures changed over that time remains an open question requiring future investigation.

5. Conclusions

In the first description of cryoconite morphology by Nordenskiöld (1883), the sediment was compared to "little balls" and indeed we found such granular structures on many glaciers. We analysed cryoconite from 33 glaciers in terms of its diversity of colours and forms. The cryoconite varied in form from loose material to compact granules covered by cyanobacteria. Granules differed in size and morphology, likely providing various ecological niches for glacial microbes hosting aerobic and anaerobic microbial communities. The morphology of cryoconite varied among regions, suggesting that local deterministic and stochastic processes may be responsible for cryoconite architecture. Further detailed studies on the evolution of cryoconite into granular forms during the ablation season and the erosion of granules by meltwater are needed to understand the biochemistry, ecology and bioalbedo feedbacks in supraglacial ecosystems. The light colour of the cryoconite on some glaciers situated in catchments dominated by dark mafic, bright felsic, or pyroclastic rocks cannot simply be explained solely by the mineralogy of the rocks. The geologic setting together with anthropogenic sources, however, can influence the concentration of specific elements concentrations within cryoconite. Our study illustrates the significant impact of organic matter in shaping colour of cryoconite on glaciers, showing that higher OM results in darker colour tones. Cryoconite granules dominated in samples from the Northern

Hemisphere while Southern Hemisphere glaciers were dominated by loose sediments. The biogeography of cyanobacteria producing EPS and local ratio of algae over cyanobacteria in cryoconite might explain this observation. Our work therefore provides further evidence that cryoconite is not simply a mass of mineral grains covering the glacier surfaces, but that it contains a complex bio-mineral structure and is important for the functioning of supraglacial ecosystems.

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Data availability statement

All data generated or analysed during this study are included in this published article (and its supplementary information files).

Ethical statement

The paper reflects the authors' own research and analyses in a truthful and complete manner. The paper properly credits the meaningful contributions of co-authors and co-researchers. The results are appropriately placed in the context of prior and existing research.

CRediT authorship contribution statement

Piotr Rozwalak: Data curation, Formal analysis, Methodology, Investigation, Writing - original draft. **Paweł Podkowa:** Methodology, Investigation, Writing - original draft. **Jakub Buda:** Investigation, Formal analysis, Writing – review & editing. **Przemysław Niedzielski:** Methodology, Investigation, Formal analysis, Writing - original draft. **Szymon Kawecki:** Investigation. **Roberto Ambrosini, Roberto S. Azzoni, Giovanni Baccolo, Jorge L. Ceballos, Joseph Cook, Biagio Di Mauro, Gentile Francesco Ficetola, Andrea Franzetti, Dariusz Ignatiuk, Piotr Klimaszyk, Edyta Łokas, Masato Ono, Ivan Parnikoza, Francesca Pittino, Ewa Poniecka, Dorota L. Porazinska, Steven K. Schmidt, Pacifica Sommers, Marek Stibal, Witold Szczuciński, Jun Uetake:** Investigation, Writing – review & editing. **Mirosława Pietryka, Dorota Richter:** Investigation, Formal analysis. **Juliana Souza-Kasprzyk:** Methodology, Investigation, Formal analysis. **Łukasz Wejnerowski:** Writing - original draft, Writing – review & editing. **Jacob Yde:** Logistical support, Writing – review & editing. **Nozomu Takeuchi:** Data curation, Formal analysis, Methodology, Investigation, Writing – review & editing. **Krzysztof Zawierucha:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Funding acquisition, Project administration, Supervision, Writing - original draft, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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