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Polar microbioerosion patterns exemplified in Arctic and Antarctic barnacles

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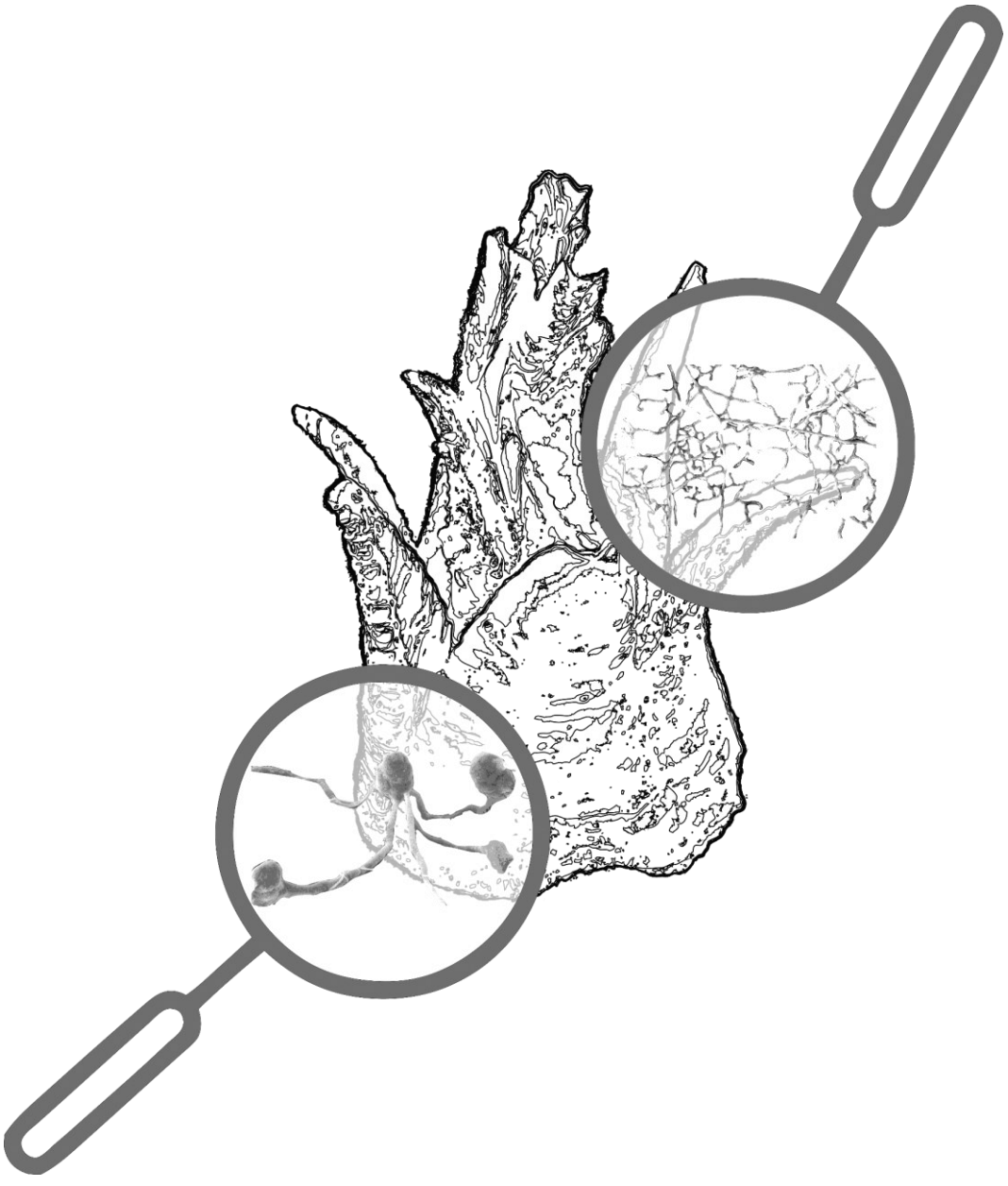

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Zusammenfassung

Bioerosion ist der Abbau harter Substrate durch lebende Organismen und findet vor allem in der marinen Umwelt statt. Sie ist eine wichtige Komponente des Kohlenstoff-Kreislaufes und wird den biosedimentären Prozessen zugeordnet. Zusätzlich erregt der Prozess vermehrt Aufmerksamkeit als das "andere Problem der Ozeanversauerung", da dieser als Folge des globalen Klimawandels beschleunigt wird. Durch die Bioerosion werden Spuren im Substrat hinterlassen, welche ein nützliches Mittel zur Untersuchung der Paläobathymetrie oder der Paläotemperatur sein können. Der Großteil der Bioerosionsstudien wurde bisher in niedrigen Breitengraden durchgeführt, wobei der Schwerpunkt auf dem Flachwasser lag. Es gab einige wenige Studien in den kaltgemäßigten Regionen, aber nahezu keine in den höchsten Breitengraden der Polarmeere. Dies bildet den Rahmen dieser Promotionsarbeit, die sich mit Bioerosions-Spuren in den Polargebieten befasst. Seepocken aus drei polaren Untersuchungsgebieten, die ein weites bathymetrisches Spektrum abdecken, wurden als Substrat verwendet, um die Spuren von Mikroorganismen in ihrem Panzer mittels Rasterelektronenmikroskopie von Epoxidharzabgüssen sichtbar zu machen. Die Proben aus dem arktischen Spitzbergen-Archipel stammten aus dem photischen Intertidal bis zu aphotischen Wassertiefen von 125 m; aus der Frobisher Bay in der ostkanadischen Arktis wurden Seepocken von 62 bis 94 m untersucht; und aus dem Rossmeer in der Antarktis stammten die Proben aus einer Wassertiefe von 37 m bis 1680 m. Jedes Gebiet wurde untersucht, indem die Ichnodiversität in Bezug auf einen bathymetrischen Trend und einen Breitengradienten semi-quantifiziert und statistisch ausgewertet wurde. In mehr als 200 Proben wurden insgesamt 29 verschiedene mikroendolithische Spuren erfasst, die von Cyanobakterien (4), Chlorophyta (2), Rhodophyta (1), Schwämmen (1), Pilzen (12), Foraminiferen (3), Bakterien (1), unbekannten Mikroorganismen (4) und Cirripedia (1, Makrobohrung) produziert wurden. Drei Spuren wurden an allen drei Lokationen beobachtet, acht Spuren wurden ausschließlich in Svalbard gefunden, eine nur in der Frobisher Bay, acht im Rossmeer und drei sind auf die Arktis beschränkt. Die angenommenen Spurenverursacher waren hauptsächlich organotroph und wurden erwartungsgemäß von Pilzen dominiert, da diese sehr robust sind und auch unter rauen Umweltbedingungen gedeihen. In den Polarregionen herrschen extreme Bedingungen, wie kalte Temperaturen, monatelange Meereisbedeckung und der Zyklus von Polartag und -nacht. Besonders letzteres spiegelt sich in einer allgemeinen Verarmung an phototrophen bioerodierenden Organismen wider, was in Spitzbergen statistisch signifikant bestätigt werden konnte. Das gleiche Probenmaterial ermöglichte zudem die Identifizierung

und Etablierung einer bisher unbekannten Bioerosionsspur, welche potenziell ein Indikator-Ichnotaxon für kühl- bis kalt-temperierte (Paläo-)Regionen ist. Durch Vergleiche mit Studien aus niedrigeren Breitengraden wurde der Schluss gezogen, dass die Ichnodiversität in aphotischen Wassertiefen über alle Breitengrade hinweg nahezu konstant ist. Ein paralleler Vergleich aller photischen Zonen konnte nicht durchgeführt werden, da es nur wenige geeignete Proben aus dem Flachwasser gab, was auf den Meereisabrieb von Seepocken und deren generell vergleichsweise begrenzte Vorkommen in flachen Wassertiefen in polaren Regionen zurückzuführen ist. Die drei umfassenden Mikrobioerosionsstudien sind ein wichtiger Schritt zu einem besseren Verständnis von polaren Mikrobioerosionsmustern und ermöglichen Vergleiche mit den niedrigeren Breiten und vorläufige Erkenntnisse in einem globalen Kontext. Fundierte Kenntnisse über die Bioerosion in polaren Umgebungen ist besonders wichtig, wenn man bedenkt, dass die Polarregionen besonders empfindlich auf den globalen Klimawandel reagieren.

Abstract

Bioerosion is the degradation of hard substrates by living organisms, primarily in marine environments. The process is an important component of the carbon cycle, it attributes to biosedimentary processes, and it gains attention as the “other ocean acidification problem” acknowledging the acceleration of bioerosion as a consequence of the global climate change. Bioerosion leaves traces in the substrate, which serve as a useful tool to investigate palaeobathymetry or -temperature. Most bioerosion studies were conducted at low latitudes, with a focus on shallow water depths. Few studies were performed in the cold-temperate regions, but almost none at the highest latitudes in the polar seas, thus setting the scene for this doctoral thesis exploring traces of microbial bioerosion in the polar realm. Acorn barnacles from three polar study sites, spanning a wide bathymetrical range, were used as a hard substrate to visualize the microbioerosion traces in their shells by means of scanning electron microscopy of epoxy resin casts. Samples from the Arctic Svalbard archipelago were from the photic intertidal to aphotic water depths of 125 m; from the Frobisher Bay, Canadian Arctic, barnacles from 62 to 94 m were examined; from the Ross Sea, Antarctica, samples originated from 37 m to 1680 m. Each study area was investigated by semi-quantifying and statistically evaluating the ichnodiversity regarding a bathymetric trend and latitudinal gradient. In total, 29 different microendolithic traces formed by cyanobacteria (4), chlorophytes (2), rhodophytes (1), sponges (1), fungi (12), foraminifera (3), bacteria (1), unknown microorganisms (4), and cirripeds (1, macroboring) were recorded in more than 200 samples. Three traces were identified at all three sites, eight traces were found exclusively in Svalbard, one in Frobisher Bay, eight in the Ross Sea, and three were restricted to the Arctic. The inferred trace-makers were mainly organotrophs and expectedly dominated by fungi, as they are very robust and thrive even under harsh environmental conditions. The polar regions are characterized by extreme conditions such as cold temperatures, months of sea ice cover and the cycle of polar day and night. Especially the latter is reflected in a general impoverishment in phototrophic bioeroders, as statistically confirmed in Svalbard. The Svalbard study material enabled the identification and establishment of a previously unknown bioerosion trace that is interpreted as a potential key ichnotaxon for cool- to cold-water (palaeo)environments. Comparisons with studies from lower latitudes led to the conclusion that the ichnodiversity in aphotic water depths is nearly constant across all latitudes. A parallel comparison of all photic zones could not be accomplished due to scarcity of suitable samples from shallow waters caused by the sea-ice abrasion of barnacles and their comparatively limited distribution in shallow water depths in polar environments. The three

comprehensive microbioerosion studies are an important step towards a better understanding of polar microbioerosion patterns and allow comparisons with lower latitudes and preliminary findings in a global context. Profound knowledge of bioerosion in polar environments is particularly important considering that the environment in the polar realm is responding to global climate change at an unprecedented pace.

Abbreviations

ANOSIM	ANalysis Of SIMilarities
C	Carbon
Ca^{2+}	Calcium ions
$CaCO_3$	Calcium carbonate
CET	Cast-Embedding Technique
CO_3^{2-}	Carbonate ion
CO_2	Carbon dioxide
HCO_3^-	Hydrogen carbonate
MA	Million years (numerical scale)
NMDS	Non-metric MultiDimensional Scaling
pCO_2	Partial pressure of carbon dioxide
PAR	Photosynthetically Active Radiation
SEM	Scanning Electron Microscopy
SIMPER	SIMilarity PERcentages

Content

Thesis outline and author contributions

This cumulative doctoral thesis includes nine chapters and begins with a general introduction to bioerosion and the scientific objectives in Chapter 1. Chapter 2 provides a general overview of polar environments and specifically of the three opposing study sites. Materials and methods are summarised in Chapter 3.

The scientific objectives are addressed with four manuscripts (Chapter 4 to 7) that are published (Chapter 4, Chapter 5), submitted (Chapter 6), or in preparation (Chapter 7) to international peer-review journals. The manuscripts are arranged in chronological order of submission.

Chapter 4: "*Saccomorpha guttulata*: a new marine fungal microbioerosion trace fossil from cool- to cold-water settings", Max Wisshak, Neele Meyer, Gudrun Radtke, Stjepko Golubic, published 2018 in PalZ, DOI: 10.1007/s12542-018-0407-7

- Content: Description of a new ichnotaxon, likely an indicator for cool- to cold-water settings; including material from Mosselbukta, Svalbard. The holotype is preserved in a belemnite from the Early Cretaceous.
- Contributions: M. Wisshak devised the study and collected the sample material, except for the Svalbard material, which was collected by M. Wisshak and N. Meyer. M. Wisshak primarily conducted the laboratory work (cast-embedding technique), SEM visualisation, and morphometric data measurements. N. Meyer applied the same methods to the Svalbard material. The manuscript was written by M. Wisshak with contributions and discussions by all co-authors. M. Wisshak created the figures and tables.

Chapter 5: "Ichnodiversity and bathymetric range of microbioerosion traces in polar barnacles of Svalbard", Neele Meyer, Max Wisshak, André Freiwald, published 2020 in Polar Research, DOI: 10.33265/polar.v39.3766

- Content: First comprehensive investigation of microbioerosion traces in polar balanids targeting a bathymetric transect at two sites in the Svalbard archipelago; including statistical analyses and a comparison to study sites from lower latitudes.
- Contributions: M. Wisshak was the applicant of the DFG project, primarily devised this study, and was the chief scientists during the MSM55 cruise, where the utilised samples were taken by N. Meyer, who also led the preparations of sample material on board. After a short briefing by M. Wisshak, samples were processed by means of the

cast-embedding technique by N. Meyer. The subsequent SEM visualisation, ichnodiversity analysis, semi-quantification, and statistical analyses (ANOSIM, SIMPROF, NMDS plots, diversity indices) were also performed by N. Meyer, in regular communication with M. Wisshak. Tables and figures were all prepared by N. Meyer, who wrote the first draft of the manuscript. M. Wisshak supervised, corrected and contributed to the improvement of the manuscript. A. Freiwald commented and contributed to the manuscript in a final round before submission.

Chapter 6: "Bioerosion ichnodiversity in barnacles from the Ross Sea, Antarctica", Neele Meyer, Max Wisshak, André Freiwald, submitted to Polar Biology (14 July 2020)

- Content: First comprehensive investigation of microbioerosion traces in barnacles from the Ross Sea, Antarctica, from a wide bathymetric transect; including statistical analyses and comparisons to Svalbard.
- Contributions: The study was devised by M. Wisshak through his role as project applicant of the DFG project. N. Meyer obtained most of the samples during a visit at the invertebrate collection at NIWA, New Zealand. M. Wisshak organised few additional samples from M. Taviani. The laboratory work was performed by means of the cast-embedding technique by N. Meyer (with support of a student assistant). N. Meyer performed the visualisation and took the pictures with the SEM. The semi-quantification and statistical analyses (ANOSIM, SIMPROF, NMDS plots, diversity indices) were carried out by N. Meyer. The first draft of the manuscript was written by N. Meyer, who also created all figures and tables. The co-authors helped to improve the manuscript with comments and fruitful discussions.

Chapter 7: "Microbioerosion traces in the Canadian Arctic and their assessment in a global context", Neele Meyer, Max Wisshak, André Freiwald, in prep., planned submission to Geobiodiversity

- Content: First comprehensive investigation of microbioerosion traces in barnacles from Frobisher Bay, East Canadian Arctic, from aphotic water depths; including comparisons with Svalbard and the Ross Sea, and integration in a global context.
- Contributions: The study was devised by N. Meyer, M. Wisshak, and A. Freiwald. Samples from Newfoundland were sent to Senckenberg am Meer, organised by N. Meyer. N. Meyer performed the laboratory work (cast-embedding technique), carried out the entire visualisation and semi-quantification by means of the SEM, and performed the statistical analysis. The first draft of the manuscript was written by N. Meyer with contributions and discussions by M. Wisshak and A. Freiwald.

The strong connection between the four manuscripts will be discussed in Chapter 8, followed by an outlook in Chapter 9. References can be found at the end of this thesis. Supplementary data is provided in the Appendix.

Chapter 1
Introduction

1.1 The concept of bioerosion

Bioerosion was originally described as "the removal of consolidated mineral or lithic substrate by the direct action of organisms" (Neumann 1966: p. 1). Bromley (1994: p. 1) redefined it as a "process by which animals, plants and microbes sculpt or penetrate surfaces of hard substrates". The process is thus at the interface between biology, geology, and chemistry and takes place in many environments, though mainly in marine settings. Calcareous substrates, like limestone or carbonate skeletons (e.g. corals or barnacles) are primarily affected, have been frequently studied, and are well understood (Daval et al. 2020). Bioerosion has also been reported in wood (e.g. Savrda 1991; Genise 2004; Shipway et al. 2019), silicates (Johnson et al. 2010; Daval et al. 2020), magmatic rocks (e.g. Allouc et al. 1996; McLoughlin et al. 2008; Santos et al. 2012), bone and teeth (reviews by Jans 2008; Turner-Walker 2019), and in anthropogenic artefacts and monuments from underwater or subaerial sites (e.g. Calcinai et al. 2019).

A variety of reasons demonstrate the great relevance of bioerosion. The process not only shapes landscapes by sculpting rocky shorelines (Davidson et al. 2018), it also produces calcareous sediment (Bromley 1994), while maintaining a dynamic balance between carbonate destruction and construction (Glynn & Manzello 2015).

Agents of bioerosion (Figure 1-1) contribute to biodiversity because the number of bioeroding biota is large (Wisshak et al. 2011) and because they often act as ecosystem engineers, by providing shelter in bioeroded substrates, locally increasing abundance of species assemblages (e.g. Pinn et al. 2008; Naylor et al. 2012; Bagur et al. 2019). The process is part of the global carbon cycle, more precisely of the exogenic cycle (Golubic et al. 1979; more details in Chapter 2.3), and acts as a sink for CO_2 (Gattuso et al. 1999). It gains more and more attention to understand biosedimentary processes, but also to acknowledge its role in current climate change debates. In consequence, it has been referred to as "the other ocean acidification problem" (Schönberg et al. 2017), as it is expected to increase with ongoing ocean acidification (for a review: Schönberg et al. 2017).

1.2 Development of bioerosion research

The earliest studies of bioerosion began at the start of the 19th century (Grant 1826; Osler 1826). While studies before the 1970s were rather descriptive, the mechanisms of bioerosion were better understood and the techniques improved in the 1980s. In the 1990s, research was sufficiently advanced to quantify bioerosion rates, budgets, etc. The interactions "between eroders and host organisms, the function of bioeroders as bioindicators and their role in interpreting climate change" (Schönberg & Tapanila 2006: p. 1) are currently the focus of research. During recent decades, bioerosion has been used "to highlight the impact of human activities on the health of the ecosystem" (Schönberg & Tapanila 2006: p. 1), with a large increase in publications and citations from two publications in 1981 to 92 in 2019 (as listed by Thomson ISI Web of Knowledge 2020).

Barnacles (e.g. Glaub et al. 2002; Meyer et al. 2020, submitted), bivalves (Casadío et al. 2001), rhodoliths (Botha et al. 2020), and other calcareous organisms haven often been used as substrates to study bioerosion. A growing number of experimental studies in the laboratory or in the field, for example with submerged experimental platforms, allowed detailed investigations and the calculation of bioerosion rates. Experiments in different carbonate environments helped to identify the variability of bioerosion (e.g. Kiene & Hutchings 1994; Vogel et al. 2000; Wisshak 2006; Tribollet et al. 2009; Wisshak et al. 2011; Färber et al. 2015).

In recent years, laboratory experiments have been promoted to analyse the effects of ocean acidification. Lowered pH and carbonate saturation will negatively affect calcification rates of marine organisms and will facilitate chemical bioerosion, as has already been shown (e.g. Tribollet et al. 2009; Wisshak et al. 2012; Reyes-Nivia et al. 2013; Enochs et al. 2015; Stubler et al. 2015; Schönberg et al. 2017). Ocean acidification and global warming are therefore a serious threat to calcifiers and the ecosystems they support, i.e. carbonate factories.

Although bioerosion takes place on a global scale in the marine, freshwater, and terrestrial environment, it is mainly the tropical marine environment at shallow-water depths that has been intensely studied (as reviewed by Wisshak 2006; Weinstein et al. 2019). Research in temperate regions has caught up to a certain extent, but studies remain rather descriptive (Figure 1-2). Therefore, there is a lack of comprehensive studies in cold to polar environments (after Wisshak 2006).

1.3 Bioeroding agents and their mechanisms

Bioeroding organisms are nearly ubiquitous in marine environments (Warme 1975) and mostly active at the sediment-water interface (Golubic et al. 1984; Glaub et al. 2007). They bioerode for reasons of nutrition (Golubic et al. 1975; Wisshak 2012; Perry & Harborne 2016) and to have shelter against predators, grazers (Schönberg & Wisshak 2012), and the

physical environment (de Gibert et al. 2012) – shelter for themselves or secondary organisms.

There is a great variety of different bioeroding taxa (Figure 1-1) with different metabolisms (Tribollet et al. 2011a) and ecological roles, "such as primary producers, decomposers, herbivores, predators, parasites, mutualists and ecosystem engineers" (Davidson et al. 2018: p. 1). Consequently, bioerosion takes place in different ways: mechanically, chemically, or by a combination of both, in that the chemical part is facilitated by prior mechanical bioerosion and vice versa.

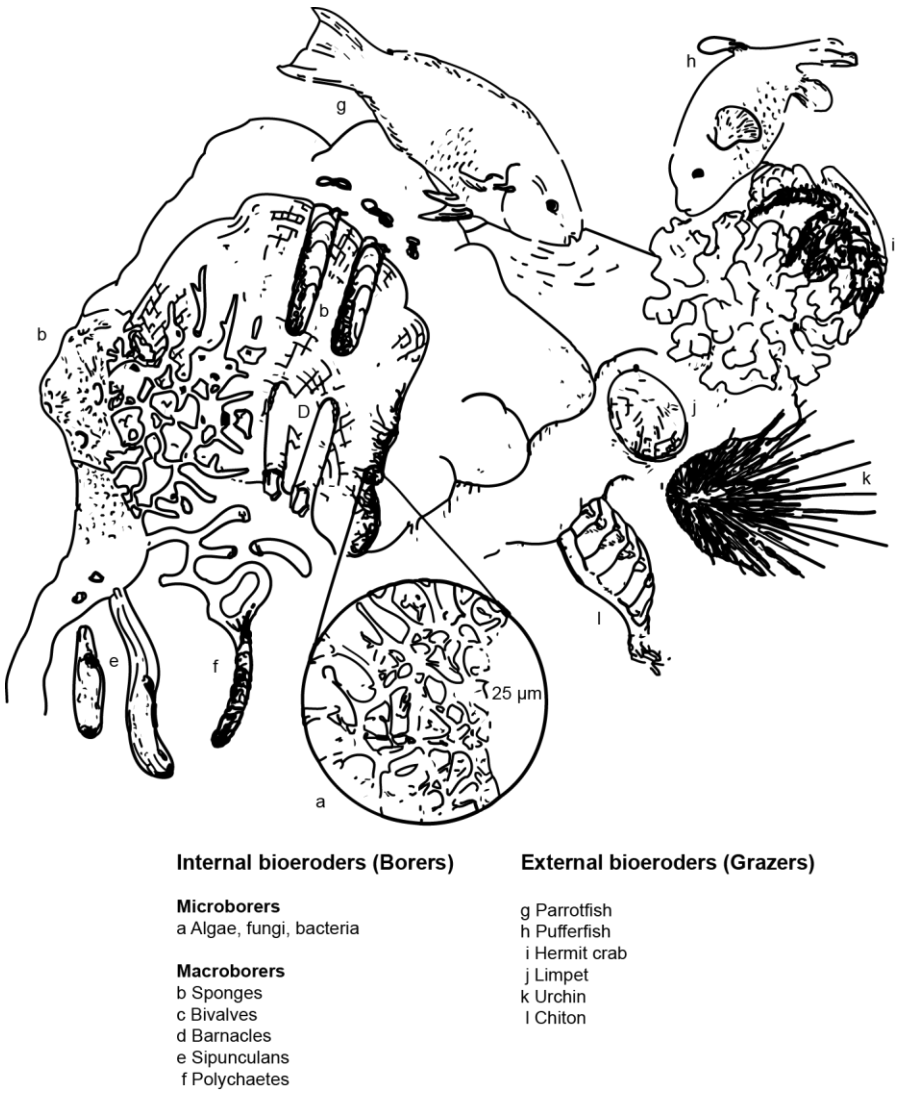

Figure 1-1 Overview of bioeroding organisms (modified after Glynn & Manzello 2015).

Bioeroding agents are divided into external and internal bioeroders (Figure 1-1). External bioeroders live outside the substrate (Tribollet & Golubic 2011) and are also known as grazers, represented by gastropods, echinoderms, crustaceans, and fish (e.g. Glynn & Manzello 2015; Schönberg et al. 2017). While feeding upon epiliths on the hard substrate (Tribollet & Golubic 2011), most of them bite, gnaw, bore, or otherwise mechanically remove parts of the hard substrate, thereby deconstructing it ('bioabrasion'; Figure 1-1).

Internal bioeroders (‘endoliths’, of which ‘euendoliths’ actively bore a cavity) excavate the substrate by chemically dissolving ('biocorrosion'; Golubic et al. 1981; Tribollet & Golubic 2011) or mechanically boring it. They are further subdivided into micro- and macroborers, dependent on the size of the trace they leave behind in a substrate. A trace larger than 1 mm with tunnel diameters usually wider than 100 µm (Wisshak 2012) is bioeroded by a macroborer, for instance by sponges, polychaetes, cirripeds, and bivalves (Figure 1-1). Many of them use a combination of chemical and mechanical means. In contrast, microborers utilize exclusively the chemical way and comprise endolithic cyanobacteria, rhodo- and chlorophytes, fungi, and bacteria (Chapter 1.3.2; Golubic et al. 1975; Tribollet 2008; Wisshak 2012). Their mechanisms of carbonate dissolution are still poorly understood (see Tribollet 2008 for a review).

1.3.1 Ichnotaxonomy

The multitude of bioeroders produces specific traces in all kind of shapes and size, on and inside substrates. Grazing traces or attachment scars are on the substrate and are mostly visible to the naked eye. Traces have a good preservation potential and are the subject of ichnology, the study of trace fossils and neoichnology, the study of modern traces.

Although most microborings match the outline of their producers (Radtke 1991), the trace-maker and the trace must strictly be treated separately. The traces are classified as ichnotaxa, following a uniform approach for the taxonomic treatment of traces (Bertling et al. 2006) and a taxonomic nomenclature governed by the International Code of Zoological Nomenclature (ICZN 1999; more details in Chapter 1.5), with currently more than 300 valid ichnospecies (Wisshak et al. 2019a).

1.3.2 Microbioerosion

Bioeroding biomes are represented in four of the six kingdoms (Rice et al. 2020), but the focus of this doctoral thesis is on microbioerosion traces, thus their producers are briefly described below.

As reviewed by Radtke & Golubic (2005), microbial endoliths may harm their hosts (e.g., Kaehler & McQuaid 1999; Bentis et al. 2000; Stefaniak et al. 2005), contribute to primary production (e.g., Schneider & Le Campion-Alsumard 1999; Larkum et al. 2003; Tribollet et al. 2006), produce large quantities of fine-grained sediments, and attract grazers (e.g., Schneider & Torunski 1983; Schneider & Le Campion-Alsumard 1999; Tribollet et al. 2002; Alvarado et al. 2017).

Microbioeroding organisms are tolerant to various environmental conditions and cope with all extremes from the poles to tropical reefs (Glaub et al. 2007). They are quite robust towards environmental fluctuations because they are buffered to some extent in the microenvironment of their borings (Wilkinson 1974; Vogel & Glaub 2004).

The major difference between microborers is whether they are phototroph, such as red or green algae, or organotroph, like fungi or bacteria. Phototrophs are dependent on light as an energy source, which is reflected in their distribution, as they are absent in aphotic water depths or deep inside a substrate. Organotrophs depend solely on the presence of organic matter and therefore occur in the entire water column (Tribollet et al. 2011a). Hence, nutrients and organic matter are important for the (bathymetric) distribution of microendoliths, although light is the most limiting factor (Glaub et al. 2007; Wisshak 2012).

Cyanobacteria (formerly known as "blue-green algae")

Cyanobacteria are the 'pioneer colonizers' and often pave the way for further bioerosion by macroborers and grazers (Schneider & Le Campion-Alsumard 1999). Their traces typically dominate in the euphotic zone, as they perform photosynthesis and are hence dependent on light. Borings show similarities to the actual body shape (Glaub et al. 2007) with cell structures, tunnels with variable branches, and filaments, which are mostly 1–15 µm and rarely 60 µm thick. They may reach a depth of 500 µm in the substrate (Schmidt 1992).

The most common ichnogenera are *Fascichnus*, *Planobola*, *Eurygonum*, and *Scolecia*.

Chlorophytes ("green algae")

Chlorophytes are phototrophs and the filaments of their traces are 2–150 µm wide and oriented parallel to the substrate surface (Schmidt 1992). The endoliths bioerode by chemical means (Schneider 1976; Garcia-Pichel 2006). Whilst some of them penetrate the carbonate substrate more than l cm deep, some are limited to the surface layer (Tribollet & Golubic 2011).

Ichnoreticulina, *Irhopalia*, and *Cavernula* are amongst the ichnogenera by chlorophytes.

Rhodophytes ("red algae")

Rhodophytes are phototropic, were observed less frequently, and are not yet well studied in the bioerosion context (Tribollet et al. 2018). Their complex heteromorphic life contains an endolithic stage (Campbell et al. 1979; Wisshak 2012; Radtke et al. 2016), resulting in an intricate boring system with filaments (1–7 µm), swellings (9 µm), and irregular tunnel diameters (5–20 µm) (Schmidt 1992).

Conchocelichnus seilacheri is the only established ichnotaxon by rhodophytes.

Foraminifera

Endolithic foraminifera often produce rosette-like bioerosion traces, regularly with a "fan-shaped plexus of branching and anastomosing galleries" (Wisshak 2017: p. 53). A good example is *Nododendrina europaea* with a maximum diameter of 0.7 mm (Bromley et al. 2007; Wisshak 2017). *Pyrodendrina* is probably another ichnogenus of foraminifera as trace-maker (Wisshak 2017), whereas *Kardopomorphos* isp. was confirmed as foraminiferal

trace (Beuck et al. 2008). The typical foraminiferal boring, however, is a hemispherical pit (Bromley et al. 2007 and references therein).

Fungi

Fungi are organotrophic microborers and colonise substrate in the whole water column, as they follow organic substrates for food rather than light (Golubic et al. 2005). The investigation of their traces is thus facilitated in samples taken from deep water depths, where the traces cannot be confused with those of algae. Both often show a convergent evolution of boring behaviour, which leads to a similar morphology (Golubic et al. 2016).

The fungal hyphae often produce tunnels with a constant diameter (up to 7 µm), which branch and appear in different ways. These tunnels commonly contain 'bag'-structures (up to 40 µm) that have formed during reproduction (sporangial cavities). The borings are most often close to the substrate surface and crisscross without a clear pattern.

Many ichnotaxa are assigned to fungal trace-makers, such as *Saccomorpha*, *Flagrichnus*, and an *Orthogonum* ichnospecies.

Sponges

According to Wisshak (2008), there are two ichnotaxa for microborings produced by sponges: two ichnospecies of 'dwarf' *Entobia*. The ichnotaxa are marked by "solitary or clustered, irregular cavities" (Wisshak 2008: p. 213) with a botryoidal surface texture and a maximum diameter of 756 µm (Wisshak 2008).

Macro-sponges utilise a chemical and mechanical way (e.g. Pomponi 1980; Schönberg 2008), but the way of the so-called micro-sponges is unknown.

Other organotrophs

Further microendolithic traces can be traced down to aphotic depths and are therefore likely bioeroded by organotrophs. Many of these traces are presumably of fungal origin but this cannot be confirmed yet (e.g. *Orthogonum lineare* or *Flagrichnus baiulus*).

Bacteria likely produce *Scolecia serrata* (Radtke 1991). Their borings have a typical morphology with spheres, ellipsoids, small rods or slices of 1–2 µm (Schmidt 1992). Bryozoans also produce microbioerosion traces (Pohowsky 1978).

1.4 Environmental impact on bioerosion

Bioerosion of micro- and macrobioeroders is controlled by various abiotic factors: temperature, nutrients, water chemistry, sedimentation, turbidity, substrate density and type, and availability (e.g. Hutchings et al. 1992; Tribollet & Golubic 2011; Schönberg et al. 2017). Biotic factors are succession, competition, and predation (as reviewed by Weinstein et al. 2019). Several studies emphasise that different environmental parameters interact (e.g. Tribollet et al. 2002).

In dead substrate, for example, there is always more colonization (Le Campion-Alsumard et al. 1995), whilst high turbidity and sedimentation have a negative impact, and higher temperature and higher pCO_2 levels a positive one (see table 3 in Schönberg et al. 2017 for a summary). However, light, and to a certain extent water depth, is the most important influence in that euendoliths with a phototrophic character decrease and organotrophs thrive (e.g. Dullo et al. 1995; Perry & Harborne 2016; Chapter 5).

Therefore, bioerosion rates can vary spatially within sites (Dullo et al. 1995; Perry & Harborne 2016). To provide an impression: In the Bahamas on experimental substrates, for instance, 0.001 kg $CaCO_3$/m²/year were removed by microbioeroders at 275 m and 0.52 kg $CaCO_3$/m²/year at 2 m (Vogel et al. 2000), whereas > 1.3 kg $CaCO_3$/m²/year were dissolved in 5–7 m in the Great Barrier Reef (Tribollet & Golubic 2005). In the cold waters around the Kosterfjord, Sweden, a maximum of 0.218 kg $CaCO_3$/m²/year were microbioeroded (Wisshak 2006). These quantities are small compared to the quantities caused by macrobioeroders. Sponges, for example, bioerode 0.0023 kg $CaCO_3$/m²/day (Zundelevich et al. 2007).

However, actual quantification is difficult because macro- and microborers often interact or successively. Microborers first weaken the substrate, thereby facilitating bioerosion by macroborers and by that enhancing the penetration of microborers into fresh substrate (Tribollet 2008).

1.5 Reconstruction of palaeoenvironments

Assemblages of traces form ichnocoenoses (Wisshak et al. 2011), which are groups of traces that occur in a specific area. Index ichnocoenoses were initially defined by Glaub (1994) and are implemented as a successful tool for the identification of recent and past temperature, salinity, and bathymetry (as has been applied by e.g. Vogel et al. 1995; Vogel et al. 1999; Glaub et al. 2001), as far back as for Silurian strata (Vogel et al. 1999).

1.5.1 Palaeobathymetry

An established index ichnocoenoses based on the co-occurrence of specific key ichnotaxa and general characteristics (Table 1-1) provides the potential to judge light availability in environmental settings (Wisshak 2012). Relative palaeobathymetry relies on the phototrophic character of many euendoliths and their dependence on light availability, which is influenced by turbidity, suspended material, or extremely illuminated settings.

The applied photic zonation distinguishes between an euphotic (the base is where light intensity has decreased to 1% of the surface illumination), dysphotic (base where the light intensity has decreased to ca. 0.01% of the surface illumination), and aphotic zone (Table 1-1; after Glaub 1994; Wisshak 2006).

The shallow euphotic to shallow subtidal zone is usually dominated by cyanobacteria (as they are resistant to variable environmental conditions), the deep euphotic to dysphotic zone

is greatly colonised by chlorophytes, and the aphotic zone is restricted to organotrophs. The trace assemblage in the supratidal is not yet defined (Table 1-1; as reviewed and revised by Wisshak 2012).

In this thesis, it is examined whether the index ichnocoenoses for relative bathymetry are also applicable in polar regions (Chapter 8).

Table 1-1 Index ichnocoenoses sorted by photic zones, including general characteristics of the microboring assemblage (as reviewed by Wisshak 2012).

Photic zonation		Index ichnocoenoses	General characteristics
euphotic zone (>1% surface illumination)	shallow I (supratidal)	not yet defined	dominance of cyanobacteria with sheath pigmentation
	shallow II (intertidal)	*Fascichnus acinosus* and *Fascichnus dactylus*	dominance of cyanobacteria, vertical orientation of borings
	shallow III (subtidal)	*Fascichnus dactylus* and *Irhopalia catenata* (replacing "*Palaeoconchocelis starmachii*")	cyanobacteria abundant and eukaryotes, change from vertical to horizontal orientation
	deep	*Irhopalia catenata* (replacing "*Palaeoconchocelis starmachii*") and *Ichnoreticulina elegans*	dominance of eukaryotes, mainly rhodophytes and chlorophytes, horizontal orientation, chemotrophs increasing, maximum diversity
dysphotic zone (0.01–1% surface illumination)		*Saccomorpha clava* and *Ichnoreticulina elegans*	dominance of chemotrophs, additionally *Ichnoreticulina elegans* and/or *Scolecia filosa*
aphotic zone (<0.01% surface illumination)		*Saccomorpha clava* and *Orthogonum lineare*	only chemotrophs

Irhopalia replaced *Rhopalia* (Wisshak et al. 2019a)

1.5.2 Palaeotemperature

Ichnotaxa may also have the potential to act as an indicator for paleotemperature (as already mentioned by Golubic et al. 1975), as some trace-makers are eurythermal and some are stenotherm, thus limited to a specific temperature range (Wisshak 2012), e.g. several endolithic algae (Lüning 1985; Wisshak 2006), cyanobacteria (Lukas & Golubic 1981), or fungi (Glaub et al. 2002). When trace-makers are limited, their traces are consequently missing. *Saccomorpha guttulata* Wisshak et al., 2018 (Chapter 4) and *Flagrichnus baiulus* Wisshak & Porter, 2006, for instance, were described as indicators for cold marine environments, and *Eurygonum nodosum* Schmidt, 1992 together with *Fascichnus grandis* (Radtke, 1991) for warm climates, whereas *Ichnoreticulina elegans* (Radtke, 1991) was described as a cosmopolitan ichnotaxon (Wisshak 2012).

The absence of ichnotaxa can also provide information about environmental conditions, although these must be regarded with caution since traces can be overlooked or simply do not

occur in a particular specimen. Additional obstacles are seasonal effects (summer vs. winter) and that the conditions in cold-water environments are similar to those at great water depths.

This thesis discusses if the proposed cold-water indicators are applicable to the polar regions and whether there are even more previously disregarded (or unknown) ichnotaxa (Chapter 8).

1.6 Latitudinal variability of bioerosion

As clearly demonstrated in Figure 1-2, the number of studies decreases significantly from the low to the high latitudes, thus bioerosion studies in polar environments are scarce (e.g. Aitken & Risk 1988; Casadío et al. 2001; Cerrano et al. 2001; Hanken et al. 2012; more details and references in Chapter 5 to 7 and Figure 1-2) and require further research. It would be interesting to investigate the impact of the extreme and harsh environmental parameters (more details in Chapter 2.2) on bioerosion. Environmental parameters are the biggest difference between the latitudes, such as temperature and light, the latter reaching low and high latitudes at different angles.

Due to the compressed photic zonation at high latitudes and the fact that many microendoliths are phototrophic and thus dependent on light, ichnodiversity and bioerosion rates were expected to decrease from lower to higher latitudes (Wisshak 2006; Wisshak et al. 2011). Besides, it was reported that species richness is generally decreasing from lower to higher latitudes (Gaston 2000). To test the hypotheses of reduced ichnodiversity and lower bioerosion rate at high latitudes, Wisshak (2006), Wisshak et al. (2011), and Wisshak (in prep.) conducted a series of experiments. Platforms with mounted, inter alia, limestone plates and bivalve shells were submerged for two years in the warm-temperate Azores (Wisshak et al. 2011), the cold-temperate Kosterfjord, Sweden (Wisshak 2006), and for 10 years in the polar Svalbard (in prep.) at similar water depths. A decrease in ichnodiversity and slowed bioerosion rate and pace from the Azores compared to Kosterfjord has already been confirmed (Wisshak et al. 2011). Preliminary results suggest that the ichnodiversity and bioerosion rate from all three study sites is lowest at Svalbard (pers. comm. with Max Wisshak).

This thesis provides considerable added value to the previous studies in that the substrates used within the series of paper were, on the one hand, living calcifiers (barnacles, Chapter 3), and, on the other hand, they cover a larger bathymetric transect – from the intertidal to aphotic water depths. In addition to the study site Svalbard (Chapter 5), two further research regions were evaluated: another location in the Arctic (Chapter 7) and one in the Antarctic (Chapter 6). The combined results of all three locations allow a picture of (micro)bioerosion in the polar regions. Since all three studies used the same substrate, a high degree of comparability was guaranteed.

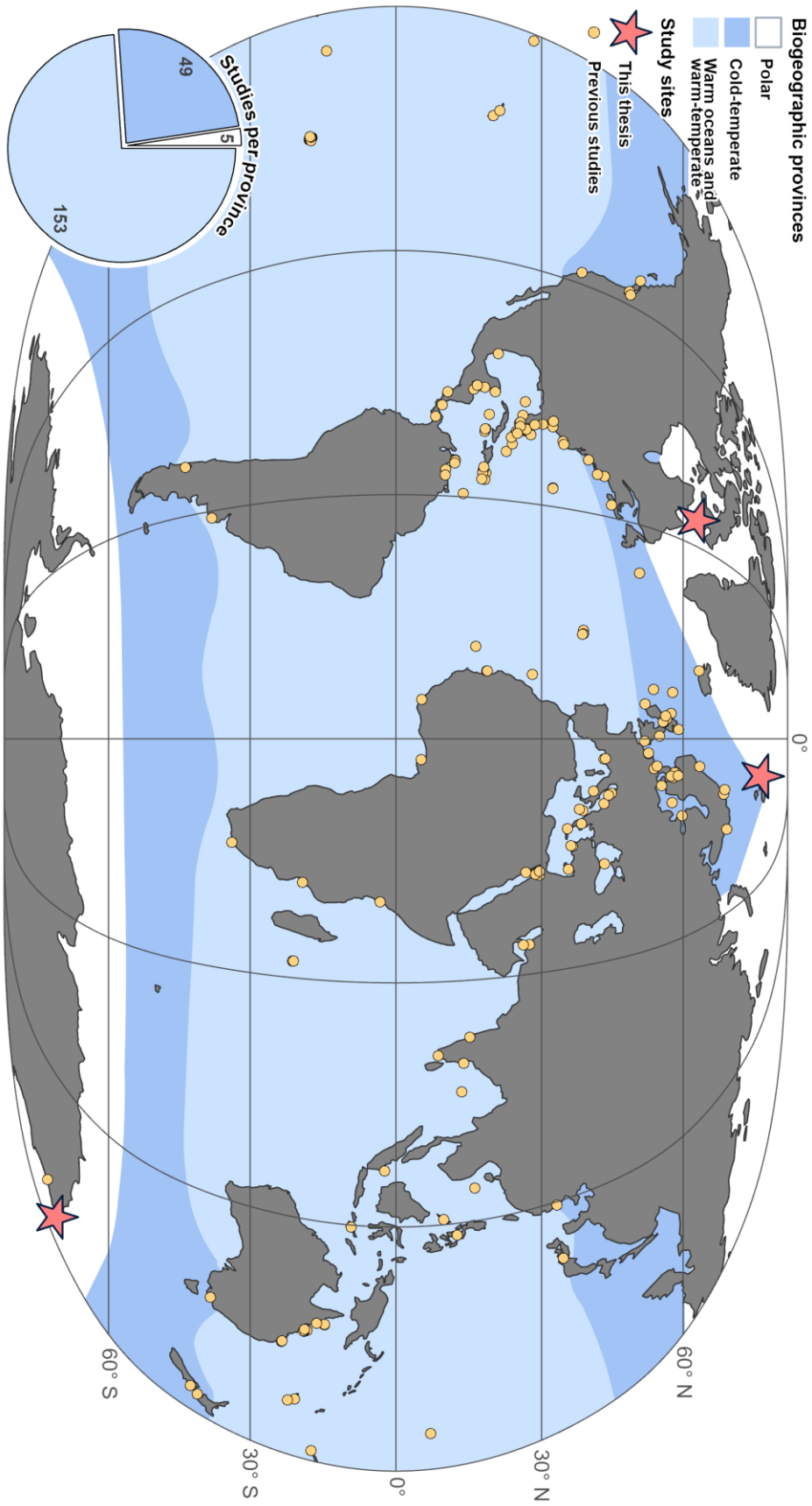

Figure 1-2 The marine biogeographic provinces (modified after Briggs & Bowen 2012) and illustration of previous study sites regarding microbioerosion and euendoliths. Studies are based on the bibliography by Radtke et al. (1997), Wisshak (2006), and a Thomson ISI Web of Knowledge (2020) search from 2006–2020 with the keywords 'microbioerosion' and 'microendoliths' (see the publication list in the Appendix).

1.7 Motivation and objectives

There is still a large demand for bioerosion research at higher latitudes (Figure 1-2, and as described below in Chapters 5–7). Fundamental research on the bioeroding agents or their traces as well as abundance, diversity, or rate is scarce, as is research targeting the effects of climate change on high latitude bioerosion.

This research backlog was the main motivation for this dissertation, which now provides an inventory of polar microbioerosion traces that will serve as an important data base for future studies. Based on a comprehensive microbioerosion trace record in barnacles from three different polar study sites (Figure 1-2), this dissertation concentrates on the following objectives:

I. Investigation of microbioerosion ichnodiversity in two Arctic locations (Chapter 5, Chapter 7)
II. Investigation of microbioerosion ichnodiversity in one Antarctic location (Chapter 6)
III. Investigation of the latitudinal distribution pattern (Chapter 4, Chapter 5, Chapter 6)
IV. Investigation of the bathymetric distribution pattern (Chapter 5, Chapter 6, Chapter 7)
V. Comparison of the above aspects (Chapter 7, Chapter 8)

These investigations enable the transfer of knowledge from a local to a more global scale and will promote the applicability of ichnotaxa as paleoenvironmental indicators.

Chapter 2
The polar environment

2.1 Polar environments

Life in the polar regions fascinated researchers for centuries. For a long time, they were considered the most unfavourable habitats for life. It was assumed that a small number of species and low productivity prevail, as polar habitats are characterised by extreme environmental conditions with sea ice cover, limited solar radiation, and low temperatures (Piepenburg 2005).

Polar environments are not only fascinating but are also important for the global climate system because they affect “large-scale processes that in turn shape the global climate” (as reviewed by Piepenburg 2005: p. 1). The origin of the ocean circulation lies, for example, in the polar regions and the polar oceans are thus considered the driving force for the global climate dynamics.

Polar ecosystems are probably the most sensitive to climate change, with the most severe and rapid changes (Smith 2015), and therefore receive increased attention. While the Arctic experienced rapid warming and melting of sea ice in the recent decades, the opposite has happened in the Antarctic with colder summer periods and larger sea ice extents (Marshall et al. 2014), though the latter now also loses sea ice (Sadai et al. 2020).

Besides, the impact of ocean acidification, where calcium carbonate becomes undersaturated, is assumed to become a significant problem for the polar water masses (Fabry et al. 2009). Cold seawater can also store more CO_2 (Barnes & Tarling 2017), so both subjects could promote bioerosion.

A variety of interactions between the atmosphere, land surfaces, ocean and sea ice lead to far-reaching consequences (Goosse et al. 2018), whose detailed description would go beyond the scope of this thesis.

2.2 Differences between the Arctic and the Antarctic

Although the Arctic and Antarctic are both, per definition, polar and alike in general physical and atmospheric conditions, they are dissimilar in size, age, oceanography, and several other aspects (Dunbar 1968; Smith 2015; Barnes & Tarling 2017).

The Earth's polar regions are influenced by comparatively extreme and harsh environmental parameters, which will be briefly introduced below, highlighting the

differences between the polar North and South. In contrast to the colder Antarctic at lower latitudes (south of 60°S), the Arctic (from about 67°N to the north) is not a continent and consists of ice sheets.

Geological evolution

Today's species diversity is the result of the palaeogeographic development. The northern and southern polar regions underwent different climatic conditions in the past due to different configurations of oceans and continents (Crame 1992; Brandt 2005), and variable ice sheets. "The variation in size and extent of the continental ice sheets, in response to Milankovitch climate variability" (Clarke & Crame 2010: p. 3662) forced marine fauna to migrate into different areas, e.g. down a continental slope and up again after melting (Clarke & Crame 2010). Additional global climate changes, faunal extinctions, and adaptions to all those factors (Brandt 2005) resulted in different diversities.

On geological time scales, the Arctic Sea is young compared to the Antarctic (Piepenburg 2005). The polar sea ice sheet in the northern hemisphere developed ca. 4 million years ago in the Pliocene and have cooled further since the beginning of the Pleistocene 1.8 million years ago, with intermittent glacial and interglacial periods (Piepenburg 2005; Michel et al. 2012; and references therein). The evolutionary origin of marine biota is dated back to 3.5 million years ago, when the Bering Strait opened. The biota became likely extinct several times during glaciation periods (Adey et al. 2008; Clarke & Crame 2010). As reviewed by Clarke & Crame (2010: p. 3659), "current marine fauna has thus only occupied the entire Arctic continental shelf for at most 13,000 years".

A significant cooling of the southerly polar region probably began 40 million years ago during the Eocene/Oligocene (Clarke & Crame 1989) and evolved in its present form as an isolated and cold-temperate Southern Ocean in the early Miocene (ca. 23 million years ago). At that time, the Drake Passage opened between South America and Antarctica and the Antarctic Convergence formed (Brandt 2005; Piepenburg 2005 and reference therein). The evolution of marine fauna is relatively complex (more details in Clarke & Crame 1989) and some taxa can be traced back to the Upper Cretaceous (after Clarke & Crame 2010). Meanwhile, it is known that the fauna originates from adjacent deep sea basins, spread in both directions along the Scottish arc from South America, and consists of relic autochthonous taxa (Clarke et al. 1992; Clarke & Crame 2010). Nowadays, Antarctica is described as a marine centre of origin with the world's most characteristic marine biota, from where the deep sea taxa spread out into all oceans (Briggs 2003).

Temperature

The most obvious environmental parameter in the polar regions is temperature, which is certainly cold and extreme, with constant water temperatures near or below freezing (Smith

2015). Temperature not only affects the stratification of the water column but is also crucial for biodiversity in the marine environment (Michel et al. 2012).

Ocean currents and water masses

The Arctic is surrounded by continental land masses and is connected to Atlantic and Pacific water masses by narrow and shallow gateways (Fahrbach et al. 2009; Michel et al. 2012; Smith 2015).

The Antarctic, in contrast, is more closely connected to other water masses, a continent surrounded by oceans and deep continental shelves (Fahrbach et al. 2009; Smith 2015). The absence of land barriers allows an eastward flow driven by westerly winds, which leads to a natural isolation of Antarctica and separates warm surface water in the north of the flow from cold water in the south (Gutt et al. 2010). The so-called Antarctic Circumpolar Current forms a physical barrier that connects all ocean basins and thus enables a global circulation. An over-turning cell allows the North Atlantic Deep Water to return to the surface. Thus, new ventilated and nutrient-enriched water masses are formed (Rintoul et al. 2001), which sink again and flow back to the north.

For more details, the reader is referred to Talley et al. (2011a) and Talley et al. (2011b).

Sea ice

Polar sea ice is another important environmental feature of the polar oceans and is one of the largest ecosystems on our planet, accounting for 3.9–4.9% of the total surface. More sea ice and greater seasonal fluctuations are found in the south compared to the north (Arrigo 2014). While Arctic sea ice is either always present or at least several years old (Talley et al. 2011a), almost all sea ice around Antarctica is renewed annually (Talley et al. 2011b).

After Gutt (2001), sea ice and glacier ice are the two main categories that are distinguished between. Whilst sea ice experiences seasonality and its age is decisive for its thickness (up to 40 m), with a up to 600 m, glacier ice can be thicker (Gutt 2001). Ice shelves sometimes reach the sea floor and scrape off local organisms, severely affecting biodiversity especially during glacial intervals (Clarke & Crame 1989; Piepenburg 2005).

By acting as a thermal insulator, sea ice influences the heat and momentum exchange between the atmosphere and the ocean (e.g. Gettelman & Rood 2016).

Additionally, sea ice affects biogeochemical cycling through its presence, formation, and melting (after Michel et al. 2012). Water column stratification of the polar seas is influenced locally by freezing and melting of sea ice, with prominent stratification in Arctic summer and less stratification in Antarctic summer (Barnes & Tarling 2017). Melting further influences the structure and function of the food web (Carmack & Wassmann 2006).

Finally, sea ice reduces the light incidence (Gutt 2001) and reflects most of the solar radiation due to the albedo effect (Hass 2009).

Light

The light regime is extreme and characterises the polar environment due to the low irradiation angle of the sun. There is constant light or none at all for months, which affects especially shallow water (Smith 2015; Figure 7-2). Light never reaches water depths of about 200 m and below due to the angle of incidence and the fact that light is absorbed and scattered with increasing water depth, depending on the wavelengths.

The polar regions receive, in total, less solar energy with low radiation in the winter months and extensive radiation in summer. In the global context, net energy is gained at the equator and lost in the polar regions (Dunbar 1968).

Light incidence is not only determined by the incoming solar radiation, but also by mixing in the water column and its stratification, clarity of the water column, and sea ice (see above).

Influence on organisms

The various Arctic regions differ in their species diversity and composition and are no less diverse than the Antarctic, which is a relic of over-generalization from the past. However, due to the oceanic isolation, the Antarctic flora and fauna is reduced and isolated, which has resulted in many endemic species. In contrast, the Arctic organisms are similar to those from the North Atlantic and North Pacific. Both regions appear to have an intermediate species richness (reviewed by Piepenburg 2005).

Above, only some environmental parameters from the polar regions were mentioned individually, but there are more that all interact with each other to a certain degree. There is, for example, also the seasonality in plankton blooms or the terrigenous sediment discharge, which are both largely controlled by (some of) the above-mentioned factors.

In summary, these extreme and seasonal parameters are the most important ones that have led to a different evolution of biodiversity in the northern and southern hemisphere, and the organisms found today must cope with the overall harsh conditions.

2.3 Cool-water carbonate factory

Bioerosion is the destruction of carbonate, but there is also the opposite: carbonate accretion, which happens in three different ways; (a) abiotic, (b) biotically induced, and (c) biotically controlled. After Schlager (2003: p. 1), these three precipitation types lead to three carbonate production systems:

1 “tropical shallow-water factory, dominated by biotically controlled (mainly photo-autotrophic) and abiotic precipitates
2 cool-water factory, dominated by biotically controlled (mainly heterotrophic) precipitates
3 mud-mound factory, dominated by biotically induced (mainly microbial) and abiotic precipitates”

The term “carbonate factory” was introduced by Schlager (2000) and describes the space and type of formation (Schlager 2003 and references therein). In the past, studies have focused primarily on shallow tropical seas, although production rates similar to those in the tropics have been observed in other regions (Schlager 2000 and references therein).

The cool-water system, which is mainly located in higher latitudes or deeper waters (Schlager 2003), is biotically controlled, meaning the (often organotrophic) organisms involved “determine the location, the onset and termination of the process, as well as the composition and texture of the precipitate” (Schlager 2000: p. 218).

A great example is Svalbard, where there are three main carbonate factories: (1) *Laminaria* kelp forests on the Spitsbergen Bank, (2) *Balanus balanus*-bryozoan-hydrozoan-soft coral-sponge build-ups on the Spitsbergen Bank (more details in Henrich et al. 1997), and (3) calcifying crustose coralline red algae that form rhodolith beds that form a belt in deep euphotic to dysphotic depths around Svalbard (more details in Wisshak et al. 2019b and references therein). In contrast to this, the Ross Sea, Antarctica, has multiple, discrete carbonate production sites instead of one all-encompassing factory, dominated by passive suspension feeders (more details in Frank et al. 2014).

Importance of carbonate

Carbonate is part of the global carbon cycle and therefore holds an important role. Carbon (C) can form various chemical bonds and is subject to a variety of transformations. C is distributed as carbon dioxide (CO_2) in the atmosphere and hydrosphere, and in the lithosphere mostly as calcium carbonate ($CaCO_3$). The spheres are carbon pools and linked with each other (see Golubic et al. 1979 for more details).

Bioerosion in the carbon(ate) cycle

The exogenic part of the carbon cycle in the atmosphere and hydrosphere includes amongst others weathering, sedimentation, carbonate accretion and dissolution, i.e. bioerosion (after Wisshak 2006). After repeated precipitation and bioerosion, carbonate enters the endogenic part of the cycle where it undergoes sedimentation and diagenesis (after Golubic et al. 1979).

Chemical bioerosion releases calcium ions (Ca^{2+}) and hydrogen carbonate (HCO_3^-) and leads to a decrease of pCO_2 in the hydrosphere. Carbonate accretion is the opposite and removes Ca^{2+} and HCO_3^- from the calcite-carbonate equilibrium and increases pCO_2.

In aqueous environments, respiration and photosynthesis influence the carbon cycle and the CO_2 removal in that respiration increases pCO_2 and carbonate ion CO_3^{2-} content, which in turn leads to a decreased pH and a higher solubility of $CaCO_3$, facilitating chemical bioerosion. In contrast, CO_2 and CO_3^{2-} is incorporated through photosynthesis, leading to an increase in pH and decrease of pCO_2, and to more carbonate precipitation (after Golubic et al. 1979; Wisshak 2006).

2.4 Study sites

Two study sites in the Arctic, Svalbard (Chapter 5) and Frobisher Bay (Chapter 7), and one in the Antarctic, Ross Sea (Chapter 6), are the focus of this doctoral thesis (Figure 1-2). Svalbard is north of the European mainland and is located mainly in the Arctic Ocean. The archipelago experiences higher temperatures than other areas on the same latitude, due to the nearby relatively warm North Atlantic Current. This irregularity is demonstrated by the second Arctic location: Frobisher Bay in the Labrador Sea, East Canadian Arctic, experiences a harsher polar climate, although it is located at lower latitudes. Therefore, Frobisher Bay, unlike Svalbard, does not experience a real polar night (Figure 7-2).

The Ross Sea in eastern Antarctica, south of New Zealand, has the most polar conditions of all three study sites with consistently low sea surface temperatures (below 0 °C), a long duration of sea ice coverage and real polar night (Figure 7-2).

The individual locations are described in detail in the corresponding chapter. Svalbard is outlined in Chapter 5, the Ross Sea in Chapter 6, and Frobisher Bay in Chapter 7. An overview map is provided with Figure 1-2.

Chapter 3
Materials and methods

3.1 Sample collection

In June 2016, cruise MSM55 with RV *Maria S. Merian* to Arctic Svalbard set out for a multi-disciplinary approach to characterise and compare two cold-water carbonate factories (see Wisshak et al. 2017 for the cruise report). The barnacles *Balanus balanus* (Linnaeus, 1758) and *Balanus crenatus* Bruguière, 1789 were collected with the research submersible JAGO, a rock dredge, a Shipek grab, and during shore excursions, where balanids were scratched from rocks in the intertidal (Figure 3-1, Figure 3-3). They were subsequently sorted on board. Prior to drying at ca. 30 °C, balanids were drained in fresh water to remove salt, then wrapped and shipped to Senckenberg am Meer, Wilhelmshaven, Germany. Details of their collection are outlined in Chapter 5; Table 5-1.

Figure 3-1 Sample collection during MSM55 in Svalbard with **a** the research submersible JAGO, **b** a dredge, **c** a Shipek grab, and **d** by hand during shore excursions (photo courtesy of JAGO team [a–c], Kerstin Nachtigall [d]).

Sample collection of Antarctic specimens of the barnacle species *Bathylasma corolliforme* (Hoek, 1883) (Figure 3-3b), was enabled in 2018 with the help of the National Institute of Water and Atmospheric Research (NIWA) in Wellington, New Zealand. From their extensive

invertebrate collection, Antarctic barnacles were chosen, which (a) originated from a roughly 100 m water depth interval, (b) were big enough, and (c) were sufficiently available. Specimens were stored in ethanol and evaporated under an exhaust hood overnight before they were wrapped up and transported to Wilhelmshaven (Figure 3-2). Details of their collection are outlined in Chapter 6, Table 6-1.

More samples from another Antarctic site would have been valuable for a more comprehensive understanding. Our target substrate (barnacles) is rare in the Antarctic, especially in shallow-water depths (Newman & Ross 1971; pers. comm. e.g. with Glenn Johnstone and Lloyd Peck), which hampered the quest for further samples, as confirmed by unsuccessful sample requests to more than nine institutes and collections.

Figure 3-2 Subsampling of Antarctic barnacles at NIWA, New Zealand. **a** Shelf full of barnacle samples, **b** jars of barnacles for closer examination, **c** close-up of the size range, **d** extracted barnacles to evaporate under the fume hood.

Specimens of the barnacle species *Balanus balanus* from the Eastern Canadian Arctic were kindly provided by the Memorial University of Newfoundland, Canada, and shipped to us in 2019. Details of their collection are outlined in Chapter 7, Table 7-1.

3.2 Barnacles as substrates

Fifteen different families belong to the sessile, so-called acorn, barnacles. All species from this study belong to the suborder Balanomorpha (Figure 3-3) and have several advantages (after Burgess et al. 2010) to study ichnodiversity and the bathymetric range of ichnotaxa:

1. They are sessile and ideally recovered in-situ to represent the real water depth when, for instance, growing on drop stones.
2. They are opportunistic in their choice of attachments.
3. They are abundant at all water depths (0–2500 m), from the intertidal to bathyal water depths.
4. They are ubiquitous at all latitudes and are therefore ideal substrates for comparisons.
5. They are perennial.

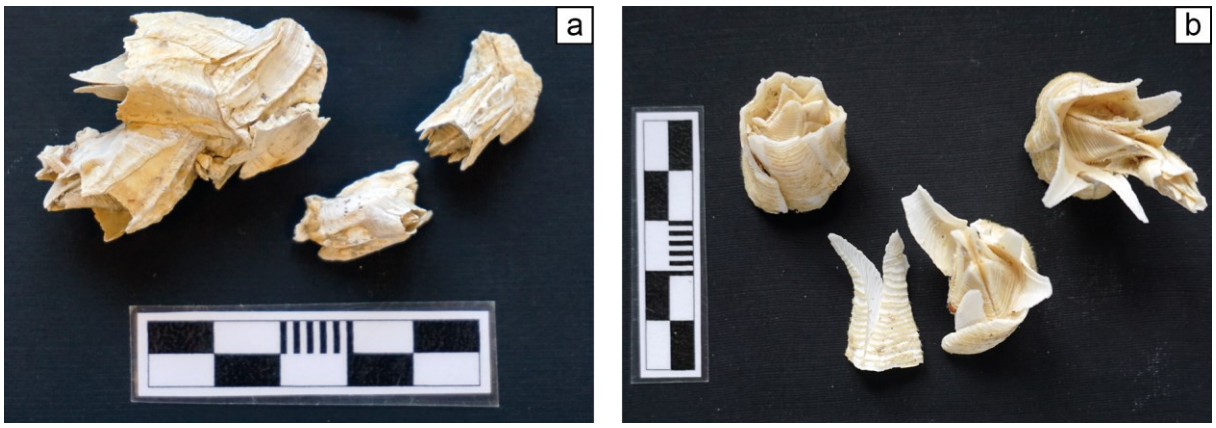

Figure 3-3 Barnacle species used in this thesis. **a** Example *Balanus balanus* from the Canadian Arctic (5g_G1) from 94 m water depth **b** Example *Bathylasma corolliforme* from the Antarctic (TAN0402_27719) from 538 m water depth. Scale bar in both ≙ 5 cm.

3.2.1 *Balanus balanus* and*Balanus crenatus*

During MSM55 (Wisshak et al. 2017), we primarily collected *Balanus balanus* Linnaeus, 1758 balanids, only a few from the intertidal stations were *Balanus crenatus* Bruguière, 1789 (Chapter 5). *B. balanus* was also the only available barnacle from the Eastern Canadian Arctic (Chapter 7).

Both species belong to the family Balanidae and have six wall plates. *B. balanus* (Figure 3-3a) is up to 30 mm large, and conically shaped with heavily ridged wall plates. *B. crenatus* is slightly smaller (up to 20 mm). In young individuals the wall plates are smooth and become more ribbed during growth. The cover plates are the main and most apparent distinguishing feature between both, which in *B. balanus* are pointy and formed like bird's beaks (Isaac & Moyse 1990).

They live associated with each other down to 60 m water depth, although *B. crenatus* settles primarily in the shallower water depths, whereas *B. balanus* predominantly occurs in deeper waters (Barnes & Powell 1953; Barnes & Barnes 1954; Luther 1987 described for balanids of German coastal waters; Isaac & Moyse 1990) from the subtidal to several hundred-metres depth (Barnes & Barnes 1954; Costello et al. 2001). Both species are limited as yet to the North Atlantic and North Pacific (Newman & Ross 1976; Kerckhof 2002).

3.2.2 *Bathylasma corolliforme*

Bathylasma corolliforme (Hoek, 1883) from the Ross Sea, Antarctica (Chapter 6) belongs to the family Bathylasmatidae and has six wall plates (Figure 3-3b). The shell has a distinct white colour and it is often covered with numerous hair-like chitinous bristles. The aperture is generally as large or larger than the base (Newman & Ross 1971).

The species was found alive between 37–1500 m (Burgess et al. 2010; Frank et al. 2014; Meyer et al. submitted) and is an endemic circumpolar species (Newman & Ross 1971; Dayton et al. 1982; Araya & Newman 2018).

3.2.3 Age determination of barnacles

For a more profound analysis (e.g. to potentially define the sequence of infestation) it would have been of additional value if an age determination of the barnacles had been feasible, which was impossible in the scope of this project for several reasons:

1. Measuring the various dimensions (as, for instance, conducted by Barnes & Powell 1953; Barnes & Barnes 1959) is inaccurate, as growth and in turn shapes of a single specimen is affected by different conditions: (a) temperature, light, and seasonality (Bourget & Crisp 1975b; Bourget 1980), (b) age (Crisp 1960), and (c) space availability regarding dominance and suppression of individuals also regarding colony formation (Wethey 1983; Crisp & Bourget 1985).
2. No analysis or counting of growth bands was performed, because there is no uniform technique. Studies measured differently, e.g. (a) by counting the growth rings on the immobile plates (Varfolomeeva et al. 2008) or (b) by the prior production of a replica of the outer surface (Bourget & Crisp 1975a).

   A general disadvantage of this technique is that growth patterns within shells are influenced by environmental parameters (reviewed by Bourget 1980; Crisp & Bourget 1985). Moreover, there seems to be no uniform terminology of e.g. growth bands, rings, lines, or even different growth ridges.

As the age determination was not as straightforward as hoped, and since neither bioerosion rates nor ichnotaxa successions were evaluated, this part was not followed up.

3.3 Visualisation and quantification of internal bioerosion

Internal bioerosion traces may be naturally filled with different kinds of precipitates or sediments, but they can also be artificially filled via the so-called cast-embedding technique (CET). The CET preserves the traces in situ and enables visualisation of the micrometre-sized borings.

3.3.1 Cast-embedding technique

The vacuum cast-embedding technique (CET) is the most frequently used and practical technique for the visualization of microboring traces (Wisshak 2006, 2012) and is a

modification of the acetone-series-based cast-embedding technique developed by Golubic et al. (1970).

In the course of the method (Figure 3-4), the boring tunnels inside the armour of the barnacle are first cleaned with sodium hypochlorite and deionised water and then filled with epoxy resin under vacuum conditions, enabling a complete infiltration. The cured resin is then sawn from all sides so that the calcareous barnacle armours are exposed until the shells are dissolved in hydrochloric acid. That causes the resin pieces to fall apart, only the 'positive' and filled casts remain. In order to improve the identification of traces, cross-sections were also produced. Those pieces were immersed in hydrochloric acid for only about 20 seconds.

Figure 3-4 Photo series of the cast-embedding technique **a** Initial *Balanus balanus* specimen from the Canadian Arctic (80 m water depth, scale bar ≙ 5 cm), **b** specimens in beaker glasses filled with sodium hypochlorite (customary cleaning agent) to clean the traces, **c** additional ultrasonic cleaning, **d** cleaned specimens dry at 30 °C in a drying cabinet, **e** barnacle fragments in cups prior to, **f** placement inside the vacuum chamber (CitoVac, Struers), the arrow points to the part where the epoxy resin is placed, **g** storage under a fume hood while the resin hardens, **h** hardened resin pieces, **i** sample pieces are sawn with a stone saw, **j** the resin pieces are sawn from all sides, **k** the positive epoxy resin casts were mounted on SEM stubs and then sputter coated with gold, and are then **l** ready for the SEM investigation.

A resin piece is finally sputtered with gold and can be visualized under a scanning electron microscope (SEM; Figure 3-4).

More details in the relevant chapters (Chapter 4–7) and Wisshak (2006; 2012).

3.3.2 Semi-quantification

A semi-quantification of traces encountered on the resin pieces has the major disadvantage that the analysis is subjective, but an actual quantification is unfeasible for our approach. The microbioerosion traces superimpose each other quite often and have a wide range of sizes. Induvial borings (e.g. *Nododendrina europaea*) could easily be counted, while for other traces, which form a network (e.g. *Conchocelichnus seilacheri*), this is impossible.

Therefore, each ichnotaxon was classified into one of five abundance classes to obtain ordinal data:

0 absent
1 very rare, only one or very few specimens
2 rare, few specimens
3 common, many specimens but not dominant
4 very common or dominant

However, it is always difficult to compare bio- and ichnodiversity, as they are always measured on different scales (in our case: the size of specimens, different barnacle species), in different habitats, and also because techniques have improved (Gray 2000, 2001), or new (ichno)species were discovered. This project worked with sample species richness, so “the species richness of a number of sampling units from a site of defined area” (after table 1 in Gray 2000), making the studies comparable.

3.2.2 Statistical analyses

The statistical analysis targeted potential differences between samples regarding the ichnodiversity and examined whether the bathymetry or study site had an influence. Besides, the concept of ichnodisparity (Buatois & Mángano 2013; Buatois et al. 2017) was statistically investigated for the first time(Chapter 5).

Statistical analyses were carried out with the statistical computing language R (R Core Team 2018, 2019) and PRIMER 6, version 6.1.16, software (Plymouth Marine Laboratory). Detailed descriptions are provided for each study individually in the corresponding chapters.

Chapter 4
Saccomorpha guttulata: a new marine fungal microbioerosion trace fossil from cool- to cold-water settings

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The format has been adapted to match the thesis.

Abstract

Euendolithic marine fungi are ubiquitous bioeroders of calcareous skeletal substrates, even under the extreme environmental conditions of the polar regions. The new bioerosion trace fossil *Saccomorpha guttulata* isp. nov. is presumably produced by a marine fungus that is interpreted to be well adapted to low temperatures, based on the provenance of the studied fossil and recent material. Its trace may thus serve as indicator for cool- to cold-water (palaeo) environments. The microboring is diagnosed by a radiating and ramifying system of club-shaped segments that gradually widen from a thin filament into a distal node. Below the initial point of entry, a stalked central cavity of slightly larger dimension and depth of penetration is developed, from which several segments emerge. The segments are interpreted to reflect a regular temporal sequence in the formation of hyphal filaments that widen into sporangial cavities. While all *Saccomorpha* ichnospecies share this composition of presumed sporangial cavities and hyphal filaments, with a varying degree of segmentation and gradation between these two elements, different strategies with regards to the temporal pattern in the formation of the different functional elements have evolved.

Keywords

Bioerosion · Microborings · Euendoliths · Marine fungi · Ichnotaxonomy · *Saccomorpha*

4.1 Introduction

Among the microbiota within the endolithic ecological niche, bioeroding fungi play an important role in marine waters from the intertidal down to abyssal depths (see Golubic et al. 2005 for a review). As a result from penetrating calcareous substrates, such as the mineralised skeletons of molluscs, corals, or other marine calcifiers, they leave specific boring structures that have a high fossilisation potential and can be described as trace fossils (Golubic et al. 2005). These microborings are often characterised by (presumably sporangial) cavities interconnected by thinner (presumably hyphal) filaments. Signature ichnogenus of such fungal microborings is *Saccomorpha*, established by Radtke (1991). This ichnogenus originally comprised three ichnospecies: *S. clava*, *S. sphaerula*, and *S. terminalis*. A fourth ichnospecies, *S. stereodiktyon,* was added by Golubic et al. (2014), together with a revision of *S. terminalis*. In the present account, this suite of *Saccomorpha* ichnospecies is augmented to a quintet by describing the new ichnospecies *S. guttulata* based on type material from the Early Cretaceous (icehouse phase) of the UK and supplemented by observations from various recent occurrences in cold-temperate to polar environments in both hemispheres.

4.2 Materials and methods

The new trace was encountered in calcareous skeletal substrates from a number of high-latitude (palaeo-) environments, as specified in Table 4-1. Fossil and recent shell material was subjected to the vacuum cast-embedding technique and subsequent scanning electron microscopy (SEM) of the three-dimensional display of polymer resin replicas (see Wisshak 2012 for a detailed review of this methodology).

The SEM images show the replicas of the bioerosion traces, but the diagnosis and description refer to the morphology of the hollow relief of the borings, observed directly or reconstructed based on the resin replicas. In addition, experimental substrates that were exposed for endolith colonisation for 10 years at aphotic 127 m water depth in Mosselbukta, Svalbard, were collected, fixed in > 90% ethanol immediately after recovery, and photographed with a Keyence VHX 2000 digital microscope in transmission light using extended focal imaging. Morphometrical measurements were performed on SEM images, using the measurement tools in the VEGA or ImageJ software. The employed morphological terms and the specific measurements are illustrated in Figure 4-1.

4.3 Systematic ichnology

This published work and the nomenclatural acts it contains have been registered in ZooBank: http://zoobank.org/references/A60338F6-9EDE-4F81-9ABE-0E399FA83AE7

Ichnogenus ***Saccomorpha*** Radtke, 1991

Original diagnosis. Sackartige Hohlraum-Formen unterschiedlicher Größe und Gestalt werden meist durch gleichmäßig dünne, fadenförmige Gänge miteinander verbunden. [Translation from German: Sac-shaped cavities different in size and shape interconnected by uniformly thin threadlike tunnels].

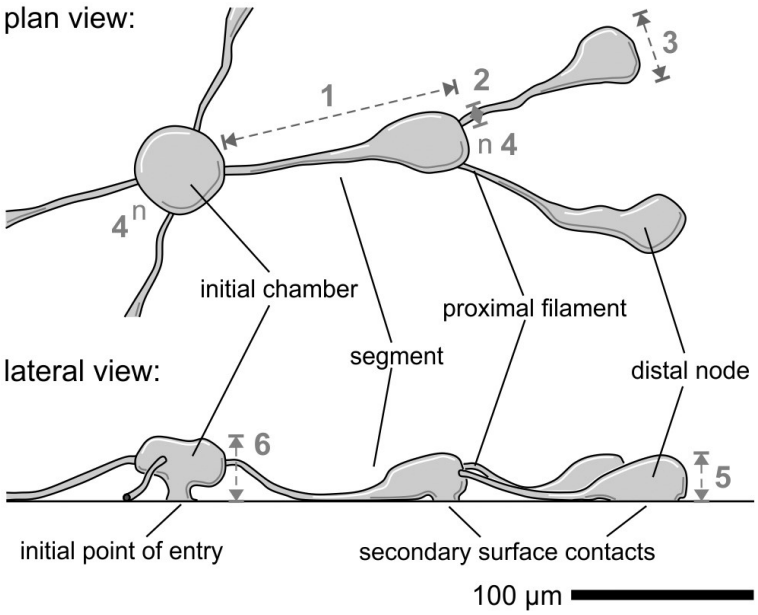

Figure 4-1 General morphological scheme of *Saccomorpha guttulata* isp. nov. as seen in plan and lateral views of epoxy resin casts. Numbers refer to the following specific morphometrical measurements taken: 1 = length of segment, 2 = width of proximal filament, 3 = width of distal node, 4 = number (*n*) of branches originating from distal node or initial chamber, 5 = penetration depth of distal node, 6 = penetration depth of initial chamber.

Emended diagnosis. Intertwined branching microboring systems in carbonate substrate, with sac-shaped cavities or club-shaped gallery segments interconnected by thin tunnels.

Remarks. The present translation and emendation of the original diagnosis was deemed necessary for better encompassing the morphological spectrum of the in total five ichnospecies established since the original description of the ichnogenus *Saccomorpha*, including the type ichnospecies *S. clava* Radtke, 1991.

Ichnospecies ***Saccomorpha guttulata*** isp. nov.

2013 *Rhopalia* isp. ?*R. catenata* Radtke, 1991—Taylor et al.: p. 233, fig. 10.

?2014 'consistent with *Entobia*'—Frank et al.: p. 9, fig. 9C.

Etymology. From *guttula* (Latin = droplet), referring to the drop-shaped morphology of the trace's segments.

Holotype. The holotype and numerous further specimens are preserved in a very slightly abraded belemnite guard split in two halves, one of which kept in its original preservation, the other one cast in epoxy for SEM analysis and selection of a suitable holotype; deposited in the trace fossil collection at the Senckenberg Institute in Frankfurt a. M., Germany, under the inventory numbers SMF XXX 888, and SMF XXX 889 (including the holotype), respectively.

Locality and horizon. Speeton Clay Formation, Ryazanian to Lower Albian, Early Cretaceous, sampled along the cliffs at Speeton, Yorkshire, UK (see Taylor et al. 2013 for further details).

Diagnosis. Radiating and ramifying system of club-shaped segments that gradually widen from a thin filament into a distal node. Below the initial point of entry into the substrate, a stalked central cavity of slightly larger dimension and depth of penetration is developed, from which several subsequent segments emerge.

Table 4-1 The investigated recent and fossil occurrences of *Saccomorpha guttulata* isp. nov.

Locality	Station(s) and sampling gear	Water depth [m] & photic zone(s)	Stratigraphy	Host substrate	References & remarks
Speeton, Yorkshire, UK		Aphotic	Speeton Clay Formation, Ryazanian to Lower Albian, Early Cretaceous	Belemnite	Taylor et al. (2013), type material, Figure 4-2
Stjernsund, Norway	R/V Johann Ruud, JR 115, box corer	275 m, aphotic	Recent	Bivalve *Delectopecten vitreus*	Freiwald et al. (1997), Figure 4-3
Straumsflaket, Jan Mayen, Norway	R/V Polarstern, ARK VII/1 (1990), 1868-1, box corer	78 m, dysphotic to aphotic	(Sub)recent	Bivalve *Chlamys islandica*	Thiede & Hempel (1991)
Mosselbukta, Svalbard, Norway	R/V M. S. Merian, MSM55-418, 443, 456, 468, 480, beam trawls	25, 50, 75, 100, 125 m, shallow euphotic to aphotic	Recent	Cirriped *Balanus balanus*	Wisshak et al. (2017), Figure 4-4a–c
Mosselbukta, Svalbard, Norway	R/V M. S. Merian, MSM55-430, settlement experiment	127 m, aphotic	Recent	Iceland spar and serpulid	Wisshak et al. (2017), Figure 4-4d–i
Mawson Bank, Ross Sea, Antarctica	R/V Italica, CARBONANT 34 and 39, dredge	385–389, 308–309 m, aphotic	(Sub)recent	Cirriped	Ramorino (2002), Figure 4-5

Description. The belemnite guard that contains the type material is very slightly abraded, so that the traces are clearly visible in SEM images taken from the surface as exposed (partly unroofed) galleries showing their tear-shaped, proximally widening segments in intermittent contact with the substrate surface (Figure 4-2a–c). Ramified and radiating traces of up to 2 mm in diameter can be recognised, even though lateral intercalation of the individual traces complicate recognition of trace delineation (but see fig. 10A in Taylor et al. 2013 for topotypic material with fine examples of more discrete traces).

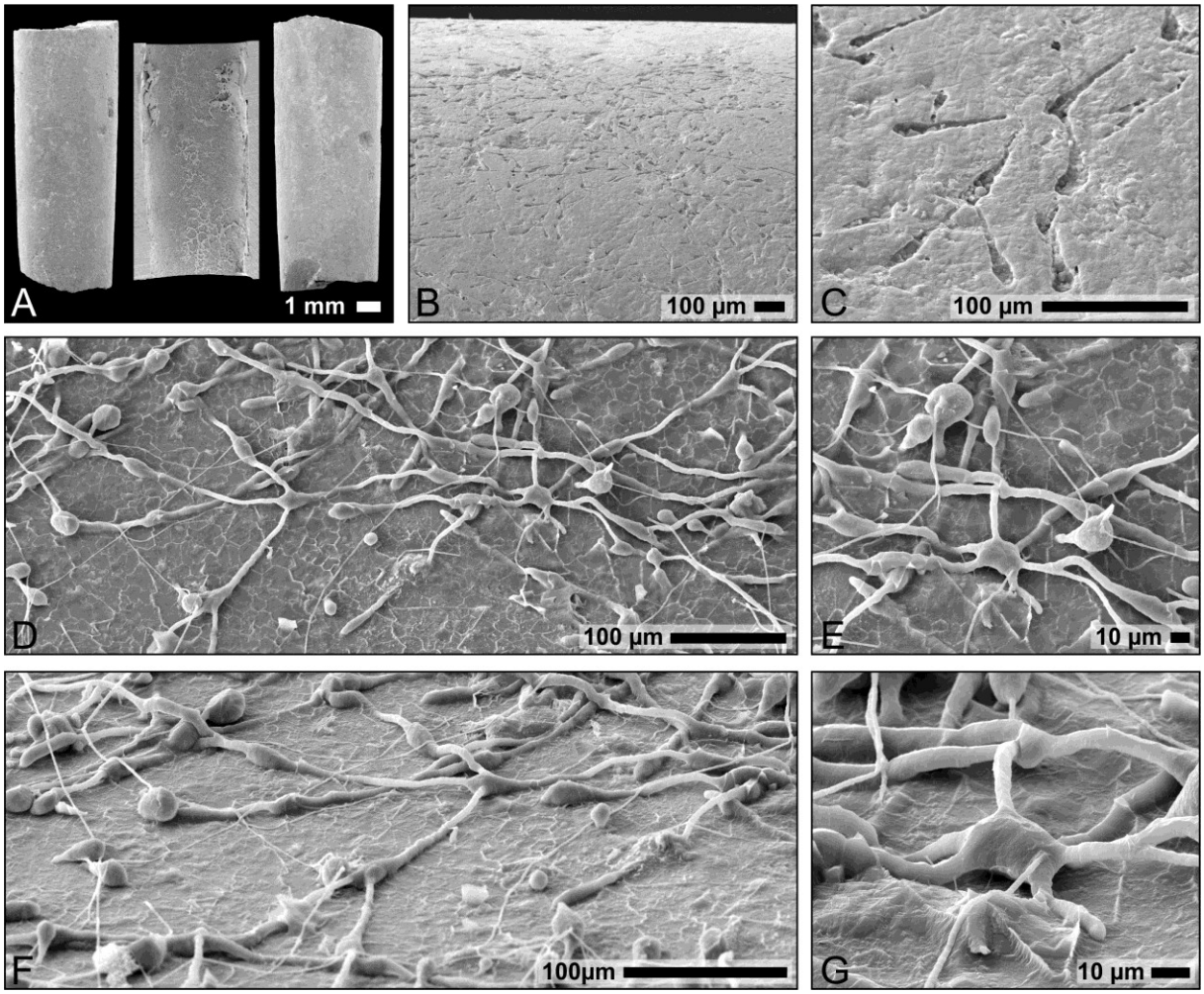

Figure 4-2 SEM images of a belemnite guard with numerous *Saccomorpha guttulata* isp. nov., including the holotype, from the Lower Cretaceous Speeton Clay Formation, Yorkshire, UK. **a** One half of the belemnite fragment before and after epoxy casting, and the retained second half of the belemnite (from left to right). **b**–**c** Overview and close-up of slightly abraded surface of the belemnite, featuring numerous unroofed *S. guttulata* with diagnostic distally widening segments. **d** Overview of the holotype trace of *S. guttulata* cast in epoxy resin, co-occurring with the type ichnospecies *S. clava* (sac-shaped cavities with slim neck and interconnecting very thin hyphal filaments). **e** Detail of **d**, showing the central cavity with six tunnels radiating from it. **f** Lateral view of the typical radiating and segmented tunnels of the holotype. **g** Lateral view of the central cavity.

In epoxy resin casts of the same belemnite specimen (Figure 4-2d–g), the individual club-shaped segments that gradually widen from a thin filament into a distal node become evident (see Figure 4-1 for a general morphological scheme). Subsequent segments emerge at the proximal end of each segment and roughly in the same direction, or they emerge as lateral branches from the widest point of the node, thereby most typically forming bi- or trifurcations at strongly varying angles (Figure 4-2d, f). Only the slightly larger and more deeply penetrating chamber below the initial point of entry differs from that pattern by giving way to a larger number of radiating segments (Figure 4-2e, g). The segmentation pattern structures the branches in relatively regular intervals (Table 4-2). Where branches of the same trace or of other traces meet, they avoid and surpass each other, thus, anastomoses do

not form. The segments emerge from the parent segment with some distance from the substrate surface and then run closely parallel to it, forming either an elongate lateral contact, or a single circular contact, or multiple contacts. This pattern becomes better evident in angular views of the resin casts of the investigated recent material, such as those observed in a *Delectopecten* shell from Stjernsund in Norway (Figure 4-3d, e, g–h). The general morphological similarity between the Lower Cretaceous type material and the various recent occurrences is striking (compare Figure 4-2 with Figure 4-3, Figure 4-4, and Figure 4-5), although there are some subtle differences when consulting the morphometrics (Table 4-2). In the Speeton belemnite traces the overall size of the trace, the length of the individual segments, the width of the proximal gallery, and the maximum number or segments originating from the initial cavity are well within the range of the recent occurrences. In contrast, the width and penetration-depth of the distal nodes and the depth of penetration of the initial cavity are lower. The weighted arithmetic means of all records and across all ichnogenetic stages are 672 µm in trace diameter, 121.9 µm segment length, 4.6 µm proximal segment width, 20.8 µm distal node width, 23.3 µm segment penetration depth, and 45.9 µm initial chamber penetration depth (see Table 4-2 for more detailed morphometrics).

Remarks. The new trace was first recognised from the type locality in a single belemnite guard by Taylor et al. (2013), who tentatively identified it as *Rhopalia catenata* Radtke, 1991. Upon recognition of significant similarity of these traces to the epoxy resin casts of the recent material studied herein, our sample request led to the recognition of a second belemnite specimen. This specimen is crowded with the new trace and was kindly provided by Paul Taylor for further analyses. It now serves as fossil type material for the new ichnospecies *S. guttulata*.

The new trace is clearly distinguished from *S. clava* Radtke, 1991, *S. sphaerula* Radtke, 1991, and *S. terminalis* Radtke, 1991 by the widening segmentation pattern rather than uniformly thin tunnels interconnecting discrete sac-shaped cavities (see Figure 4-2d–g and Figure 4-3a and b for a co-occurrence of both ichnotaxa that illustrate this marked morphological difference). Within the same ichnogenus, closest similarity is given to *S. stereodiktyon* Golubic et al., 2014 , which shares the segmented architecture and distal node of these segments, but differs by the presence of vertically and deeply penetrating tunnels and by occasionally forming discrete terminal swellings.

There is some similarity to the Conchocelis phase of bangialean rhodophytes, recently treated ichnotaxonomically as *Conchocelichnus seilacheri* Radtke, Campbell and Golubic, 2016. *S. seilacheri* is also segmented, but exhibits a more complex architecture with segments strongly varying in shape and size within a single trace, and occasionally being connected to a bush of upright (conchosporangial) filaments. The given similarity in segmentation is another example of convergence in microborings of widely differing trace

maker groups (Golubic et al. 2016), in this case organotrophic marine fungi versus phototrophic rhodophytes. Further similarity is seen to a fungal microboring only informally described as 'Dendroid from 1' in Wisshak et al. (2011: fig. 7J) and also illustrated by Golubic et al. (2016: fig. 2b) as another example of morphological convergence, in that case to the chlorophyte microboring *Rhopalia catenata* Radtke, 1991. However, in contrast to *S. guttulata* isp. nov., the 'Dendroid form 1' does not form the sac-shaped initial cavity and is not segmented but shows an irregular array of swellings along more randomly branching tunnels that are connected to the substrate surface via densely spaced apertures about every 10 µm along the tunnel (Wisshak et al. 2011). The same holds true for some morphotypes of *Orthogonum tubulare*, as described by Radtke (1991). The final morphological similarity of *S. guttulata* isp. nov. was found in larger microborings produced by ctenostomate bryozoans,

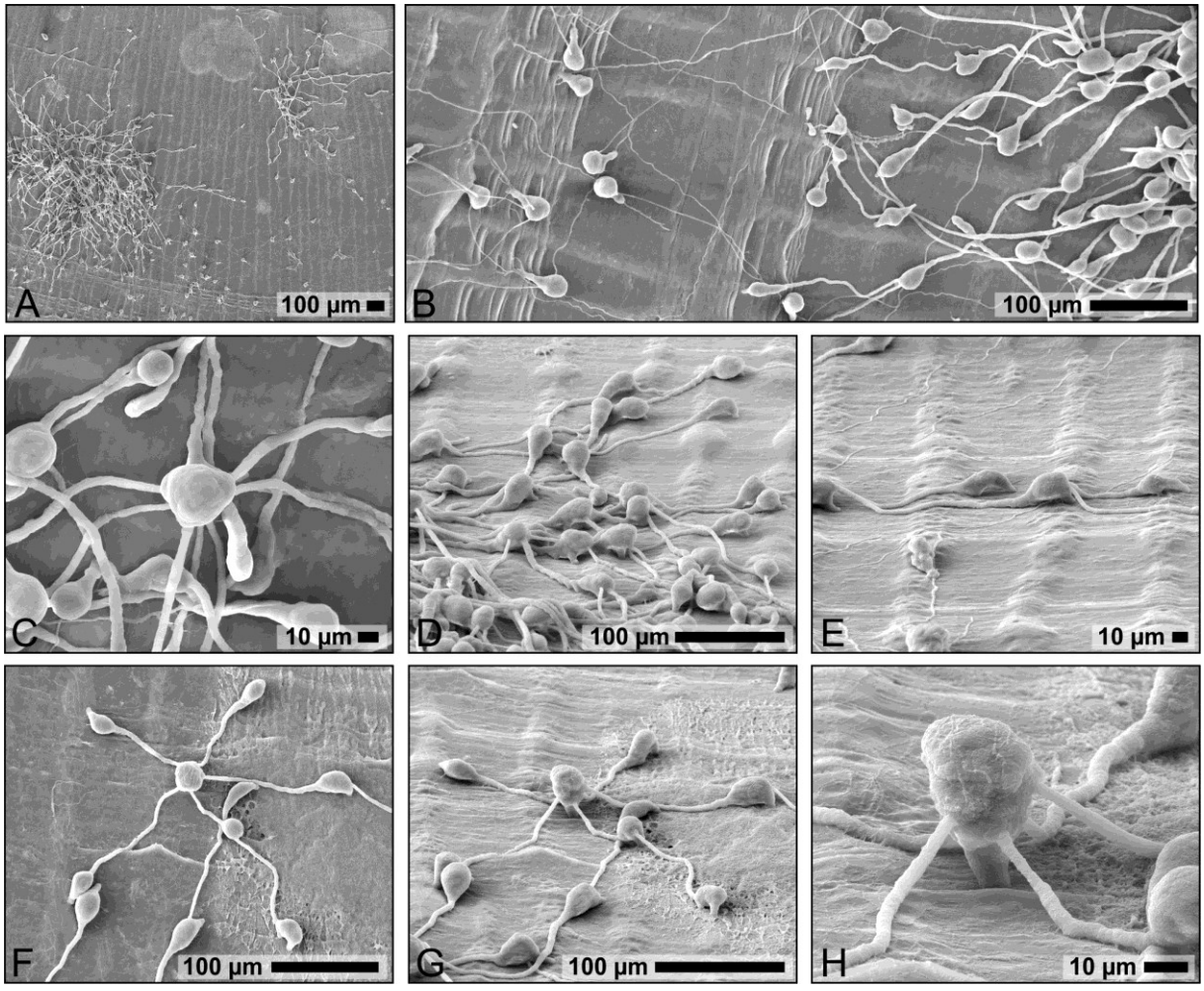

Figure 4-3 SEM images of epoxy resin casts taken from modern *Delectopecten vitreus* bivalve shell from a cold-water coral reef in Stjernsund, northern Norway, featuring several traces of *Saccomorpha guttulata* isp. nov. **a** Traces in a late, an intermediate, and a very early ichnogenetic stage (from lower left to upper right). **b** Close-up of peripheral part of the largest trace (right), illustrating the marked difference to the co-occurring *Saccomorpha clava* (left). **c** Central cavity of that same trace, with several segments radiating from it. **d–e** Angular views of the same trace, showing the diagnostic segments widening from a thin filament to a club-shaped cavity that is connected to the substrate surface. **f–g** Planar and angular views of an early ichnogenetic trace (upper right corner in a). **h** Close-up of central cavity (in **g**) with a stalked connection to the surface and with five radiating segments.

such as the (ichno?) genera *Rhopalonaria* and *Orbignyopora* (for good illustrations, see Pohowsky 1978). This applies particularly to the appearance of *S. guttulata* isp. nov. as seen on the surface of slightly abraded substrates (e.g., Figure 4-2b and c), whereas epoxy casting reveals the marked differences in the morphology of the ctenostomates' zooidal chambers and stolon network compared to the segments of *S. guttulata* isp. nov.

Table 4-2 Morphometric data for *Saccomorpha guttulata* isp. nov. (mean ± SD, min. to max., n; all values given in µm).

Locality, stratigraphy, substrate	Diameter of colony	Length of segments	Diameter of proximal filaments	Diameter of distal node	Number of branches	Depth of node	Depth of initial chamber
Stjernsund, Norway, Recent, bivalve	1251±605 418–1885 *n* = 5	144.8±47.1 48.9–293.4 *n* = 67	3.6±0.6 2.4–5.6 *n* = 97	21.7±5.4 10.6–37.8 *n* = 106	1–7	23.3±5.7 11.7–36.9 *n* = 34	38.7±1.6 37.0–40.2 *n* = 3
Jan Mayen, Norway, Recent, bivalve	1924 *n* = 1	158.2±54.3 56.3–353.1 *n* = 25	5.3±1.0 3.5–8.7 *n* = 27	23.8±5.3 14.1–34.3 *n* = 25	1–6	32.6±6.6 27.4–44.2 *n* = 9	57.6±11.5 49.5–65.7 *n* = 2
Mosselbukta, Spitsbergen, Norway, cirriped	489±143 253–713 *n* = 15	134.4±49.2 59.9–283.0 *n* = 89	4.4±1.0 2.4–8.1 *n* = 210	23.8±5.5 9.9–34.2 *n* = 116	1–9	38.9±10.5 20.5–63.0 *n* = 34	54.7±14.3 33.8 to 85.2 *n* = 17
Mawson Bank, Ross Sea, Antarctica, cirriped	447±116 240–641 *n* = 14	102.3±34.9 41.8–208.8 *n* = 107	5.5±1.1 3.7–9.8 *n* = 124	21.4±5.5 8.8–43.5 *n* = 131	1–7	22.4±4.8 11.6–33.7 *n* = 63	38.0±9.4 25.6–54.0 *n* = 7
Speeton, UK, Lower Cretaceous, belemnite	1105±239 855–1341 *n* = 4	109.4±32.3 34.5–217.0 *n* = 117	4.8±0.9 3.0–7.9 *n* = 138	16.5±3.5 10.4–29.9 *n* = 141	1–7	16.2±2.7 10.0–23.8 *n* = 80	26.7±8.3 19.0–38.7 *n* = 5
Weighted mean:	672 µm	121.9 µm	4.6 µm	20.8 µm		23.3 µm	45.9 µm
Overall min:	240 µm	34.5 µm	2.4 µm	8.8 µm	1	10.0 µm	19.0 µm
Overall max:	1924 µm	353.1 µm	9.8 µm	43.5 µm	9	63.0 µm	85.2 µm
Total *n*:	39	405	596	519		220	34

See Figure 4-1 for an illustration of morphological terms and morphometrical measurements

4.4 Discussion

Even though its exact biological identity remains undetermined, the dimensions and morphology of the microbioerosion trace under study as well as the aphotic (palaeo-) environments of the studied material strongly suggest a fungal trace maker. The transmission light micrographs of experimental substrates from a settlement experiment carried out in Arctic Svalbard (Figure 4-4d–i) shows dark aggregates forming a node in each individual segment of the trace. These aggregates could represent the sporangia of the unidentified fungal trace maker.

The complexity of fungal and other microborings composed of morphologically and functionally different parts has been recognized (e.g. Radtke 1991; Radtke & Golubic 2005; Golubic & Radtke 2008; Golubic et al. 2014) and is partly reflected in the nomenclature of these trace fossils. For example, the conspicuous sporangial swellings in *Saccomorpha*

provided the ichnogenus name for the trace, whereas the thin hyphal tunnels between them became part of its description. In turn, the wide tunnels with conspicuous perpendicular orientation of branches gave way to the name of the microboring ichnogenus *Orthogonum*, while swellings and other changes in diameter became part of the description. These distinctions are inconsistent and intuitive, but do not disturb the nomenclature as long as there are clear distinctions between different morphological elements.

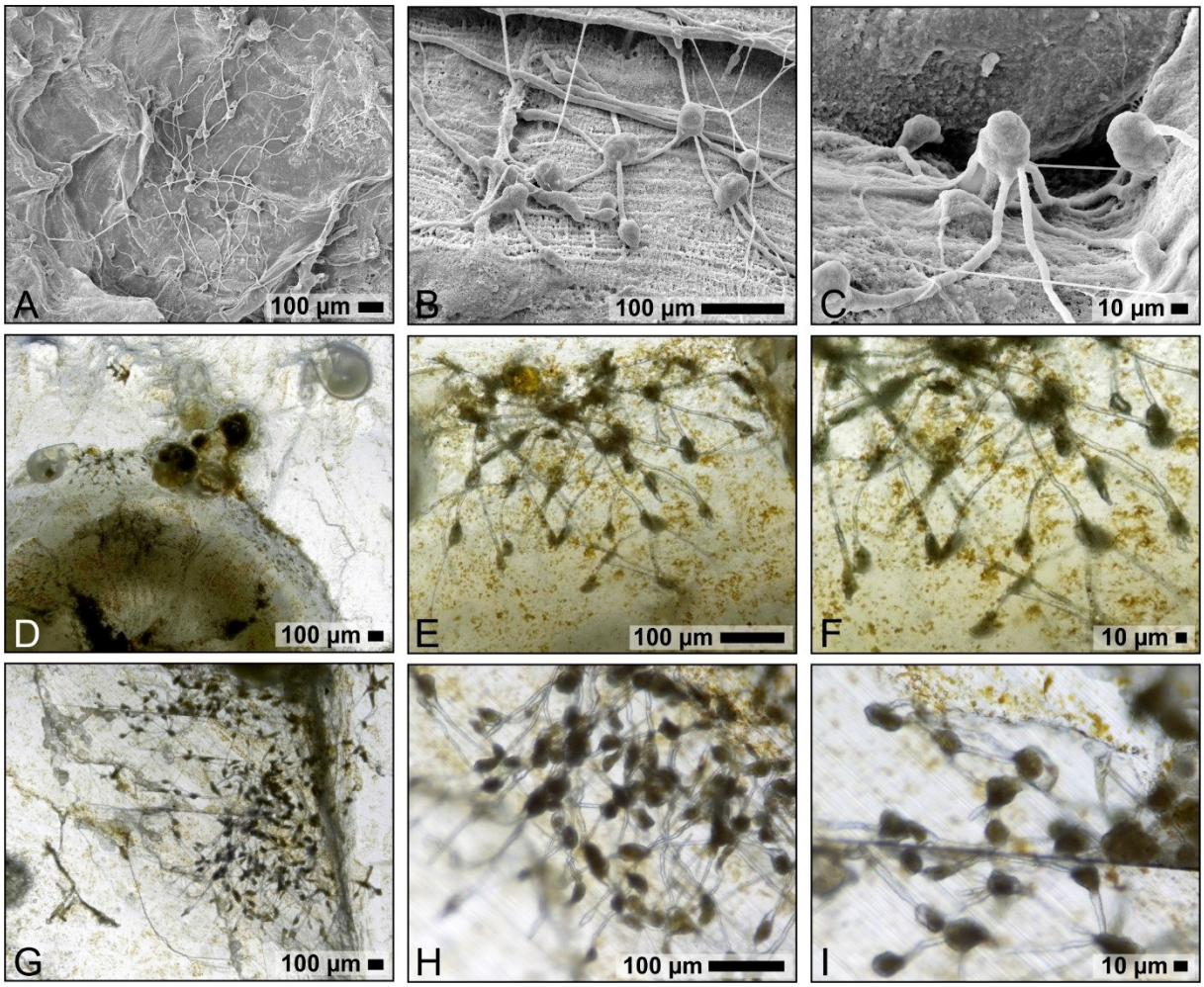

Figure 4-4 SEM images of epoxy resin casts taken from *Balanus balanus* skeletons sampled at station MSM55-456 **a**–**c** and transmission light micrographs of experimental substrates that were deployed for 10 years in 127 m water depth at Mosselbukta, northern Spitsbergen, Svalbard **d**–**i** featuring several traces of *Saccomorpha guttulata* isp. nov. and its presumed trace-making fungus. **a** Plan view of a midsized trace. **b** Angular view of the initial chamber (upper right) and a number of segments with weakly to strongly swollen nodes emerging from it. **c** Angular close-up of a stalked initial chamber and radiating segments. **d**–**f** Overview and two close-ups of a colony bioeroded in a serpulid worm. **g**–**i** Overview and two close-ups of another colony, bioeroded in a calcite spar crystal; note the dark aggregates in the nodes, possibly representing sporangial content of the unknown fungal trace maker.

We deal here with complex substrate-penetrating systems, composed of functionally different elements. These systems are morphologically similar in some properties and distinct in others. The problem appears in intermediate cases, where there are transitions which connect two morphologically different elements. The new *Saccomorpha* ichnospecies

described here represents such a case, where interconnecting tubes gradually widen into bags. As always, when dealing with organisms, the function may support the distinction. The borings of *S. guttulata* isp. nov. start penetrating from the substrate surface and expand into the interior forming an initial cavity from which tunnels emerge. *S. guttulata* develops a network composed of segments, each starting with a narrow tunnel that gradually expands distally into a drop-shaped swelling. The next segment starts again as a tunnel at the distal end of the swelling, which often carries additional side branches originating at its widest distal end. Hence, the ramifications and swellings form along the tunnels as the organism's need for expansion and reproduction is triggered, and in that temporal alternation. The resulting relatively regular segmentation and branching pattern is very similar to that of *S. stereodiktyon*. But sporangial cavities in *S. stereodiktyon* do not develop as gradual expansion of the segments, but instead are formed as terminal and discrete sac-shaped cavities abruptly connected to the segmented tunnel system (Golubic et al. 2014). These cavities are formed at a later stage during ichnogeny (sensu Belaústegui et al. 2016), as indicated by large traces of *S. stereodiktyon* devoid of any sporangial cavities, and in such they do not form in a repetitive temporal sequence, but rather as a separate reproductive phase late during the trace's development. This feature of terminal sporangial cavities is shared by *S. terminalis* (Golubic et al. 2014). In contrast, *S. clava* and *S. sphaerula* also form discrete sporangial cavities, but they are intercalated and not terminal. These cavities are interconnected by short stretches of uniformly thin (narrower than those of *S. guttulata* isp. nov.) hyphal filaments throughout ichnogeny (Radtke 1991; Wisshak et al. 2005). The filaments, which originate from the interiors of *S. clava* swellings (e.g. Radtke 1991: pl. 13, fig. 4), are interpreted as new, resulting from spores germinating while still inside the sporangium. Hence, just as in the new *S. guttulata*, a temporal sequence in the formation of sporangial cavities and hyphal filaments is developed. In summary, all *Saccomorpha* ichnospecies share the architecture composed of cavities and tubular connections between them, but show varying degree of segmentation, and differ in size and diameter consistency of tubular connections. Their trace-makers evolved different strategies regarding the temporal pattern in the formation of the different morphological and functional elements.

All recent occurrences known to date (Table 4-1) and the tentative record in Frank et al. (2014) are from polar waters of the Arctic and the Southern Ocean marine biogeographic realms, except for Stjernsund in northern Norway, located near the boundary between the Arctic and the temperate Northern Atlantic realms (bioregionalisation after Spalding et al. 2007). At the depth and year of sampling in Stjernsund, at 275 m in 1992, respectively, the temperatures were stable throughout the year around 6 °C (fig. 4 in Freiwald et al. 1997). While the present biogeographic distribution pattern could be a sampling artefact, it is considered likely that the unknown marine fungus that produces *S. guttulata* isp. nov.

favours low (palaeo-) temperatures, which are either encountered in polar regions or in deep-water settings of lower latitudes.

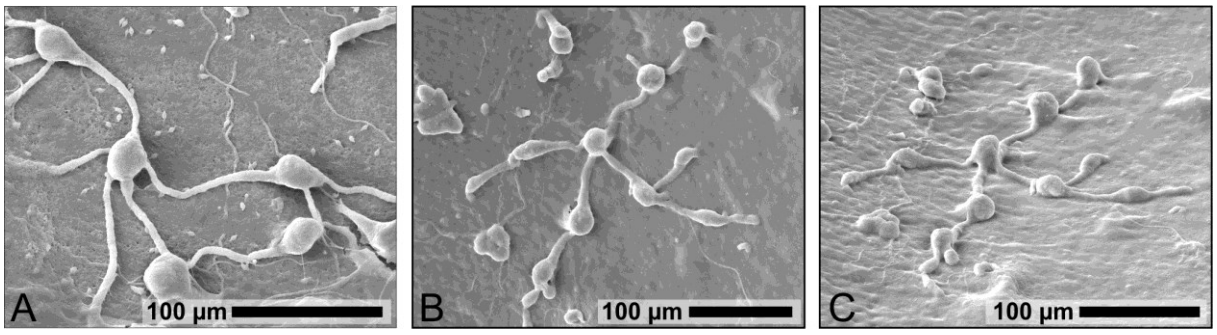

Figure 4-5 SEM images of epoxy resin casts taken from a balanid from Mawson Bank, Ross Sea, Antarctica, featuring several traces of *Saccomorpha guttulata* isp. nov. **a** Detail showing characteristic segmented pattern. **b** and **c** Planar and angular views of an early ichnogenetic trace, with comparatively thick distal diameter, but nevertheless clearly recognisable segmentation pattern.

During the mild Icehouse phase of the Early Cretaceous, the site of deposition of the Speeton Clay, i.e. the type stratum for *S. guttulata* isp. nov., was located at only about 42° northern latitude, according to Ronald Blakey's palaeogeography maps for the Early Cretaceous at 125 Ma (Blakey 2017). However, this phase (Ryazanian to Albian) was characterized by a series of borealisation events that, according to Mitchell (1992), are marked by the appearance of the presumed cold-water belemnite species *Acroteuthis rawsoni* and *Praeoxyteuthis danfordi* migrating from the Arctic Ocean. The exact stratigraphic position of the sampled specimens within the Speeton Clay, unfortunately, remains uncertain; thus, a more precise link to palaeotemperature reconstructions cannot be drawn. Nevertheless, a cool- to cold-water palaeoenvironment is indicated by the depth of deposition, most probably on a deeper shelf setting in aphotic waters, as indicated by the complete lack of bioerosion traces that could be unequivocally attributed to phototrophic euendoliths (Taylor et al. 2013; therein the trace *Rhopalia* being a tentative identification of *S. guttulata* isp. nov. traces only). Hence, a relatively cold palaeoenvironment for the type specimen is likely, but this cannot be specified more precisely due to the stratigraphic uncertainty.

In conclusion, even though the present record of *S. guttulata* isp. nov. is still limited in (geological) time and (geographical) space, there is a fair degree of indication that this ichnotaxon may serve as a suitable cool- to cold-water indicator, since the observed material draws the picture of a fungal microboring that shows a strong preference for cold-water settings. This is best exemplified by the Spitsbergen record from the polar waters at close to 80° northern latitude, where *S. guttulata* isp. nov. almost completely replaces *S. clava* in microboring trace assemblages, the former indicating cold waters by its presence and abundance, the latter trace by its scarcity.

Acknowledgements

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4.5 References

References are listed at the end of this thesis.

Chapter 5
Ichnodiversity and bathymetric range of microbioerosion traces in polar barnacles of Svalbard

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The format has been adapted to match the thesis.

Abstract

This first comprehensive investigation of microbioerosion traces in polar barnacles addresses two bathymetrical transects from the intertidal down to subtidal water depths in two different carbonate factories in the Svalbard Archipelago: the bay Mosselbukta and the ocean bank Bjørnøy-Banken. Scanning electron microscopy of epoxy resin casts of barnacle shells yielded 20 different microendolithic bioerosion traces, probably produced by cyanobacteria (three), chlorophytes (two), rhodophytes (one), sponges (one), foraminifera (three), fungi (nine) and bacteria (one). The lowest ichnodiversity in both locations was observed in the shallow euphotic zone and is likely a result of strong temperature fluctuations, extreme seasonality of light levels and episodic sea-ice cover. At 25–150 m water depth, the ichnodiversity remains relatively constant (9–13 ichnospecies), albeit with differing ichnospecies composition, generally dominated by borings from chlorophytes and fungi. Ichnotaxa at Mosselbukta and Bjørnøy-Banken were similar in numbers but differed in abundance and slightly also in ichnospecies composition. Statistical tests indicate that water depth (affecting the availability of light) is the most significant driver for the development of different microbioerosion trace assemblages across the bathymetrical transects. In contrast, no significant differences in ichnodisparity were found, indicating a comparable suite of architectural designs of the microborings throughout bathymetry and location. The comparison of our results with literature data confirms a decrease in ichnodiversity from lower to higher latitudes, although targeted bioerosion analyses from other polar

environments are needed to gain a more complete picture of the role of bioerosion in polar carbonate factories.

Keywords

Bioerosion · Ichnotaxonomy · Ichnodisparity · Arctic · Mosselbukta · Bjørnøy-Banken

Abbreviations

ANOSIM	analysis of similarities
NMDS	non-metric multidimensional scaling
PAR	photosynthetically active radiation
SIMPROF	similarity profile analysis
SEM	scanning electron microscopy

5.1 Introduction

Bioerosion is the degradation of hard substrates by biological means (Neumann 1966) and plays an important ecological and biosedimentological role from low to high latitudes. The process is divided into internal and external bioerosion (Bromley 2004). Internal bioeroders excavate the substrate for shelter, whilst external ones bioerode by means of grazing or fixation (Bromley 2004; Tribollet et al. 2011b). Internal bioerosion is further subdivided into micro- (e.g., by cyanobacteria, chlorophytes, fungi) and macrobioerosion (e.g., by polychaetes, bivalves, sponges), distinguished by the trace dimensions (smaller or larger than 1 mm) they leave behind in the substrate (Wisshak 2012). These bioerosion traces and trace fossils are taxonomically treated as ichnotaxa. They are commonly analysed via SEM of epoxy casts, prepared by applying the vacuum cast-embedding technique (Wisshak 2006, 2012).

Although bioerosion is a key process on a global scale, bioerosion research has so far mainly focussed on subtropical and tropical environments, there particularly on coral reefs, and therefore considering primarily the photic zone. High latitudes have received much less attention (for a review, see Wisshak 2006), and the North Atlantic is represented, inter alia, by studies off the Scottish coast (Akpan & Farrow 1985; Glaub et al. 2002), Norway (Bromley & Hanken 1981; Schmidt & Freiwald 1993; Glaub et al. 2002) and Sweden (Wisshak et al. 2005). Spitsbergen was, for instance, studied with a focus on polychaete bioerosion (Hanken et al. 2012) and the Canadian Arctic with a focus on macroborings (Aitken & Risk 1988). A comprehensive investigation of bioerosion traces, considering a broader bathymetrical range and including the different types of bioerosion traces, is lacking for polar environments and would help to better understand the role of bioerosion in polar carbonate factories.

Therefore, this study establishes a comprehensive catalogue of microbioerosion traces in two high-latitude carbonate depositional environments in the Svalbard Archipelago at 74° and 80° northern latitude. Barnacles were the chosen substrate because they are sessile calcifiers that are most likely to bear bioerosion traces from the corresponding water depth

when sampled alive. They occur from the intertidal down to aphotic water depths in Svalbard, allowing an establishment of bathymetric transects extending from the shore to 125 m water depth at Mosselbukta (northern Spitsbergen) and east of the island of Bjørnøya (southernmost Svalbard). We provide a statistical ichnodiversity analysis to compare these two locations. This approach allows us to evaluate the ichnodiversity variability of bioerosion within the Arctic environment and at different water depths. In addition, we apply the ichnodisparity concept to determine the diversity of architectural designs in bioerosion traces and, therefore, the established behavioural patterns of microbioeroders (Buatois et al. 2017). Finally, we assess our observations in the context of a low to high latitudinal gradient.

5.2 Methods

5.2.1 Study sites

Svalbard (Figure 5-1a) is in an Arctic environment on the north-western margin of the Barents Shelf, approximately 650 km north of the Norwegian mainland. In 2016, Mosselbukta, our first study site, near the northern tip of Spitsbergen (Figure 5-1b), was covered by drift ice for 14 days, whereas Bjørnøy-Banken, the second study site in the south (Figure 5-1c), was covered by very open to open drift ice at the end of March for about a week (Figure 5-2; Norwegian Meteorological Institute 2019).

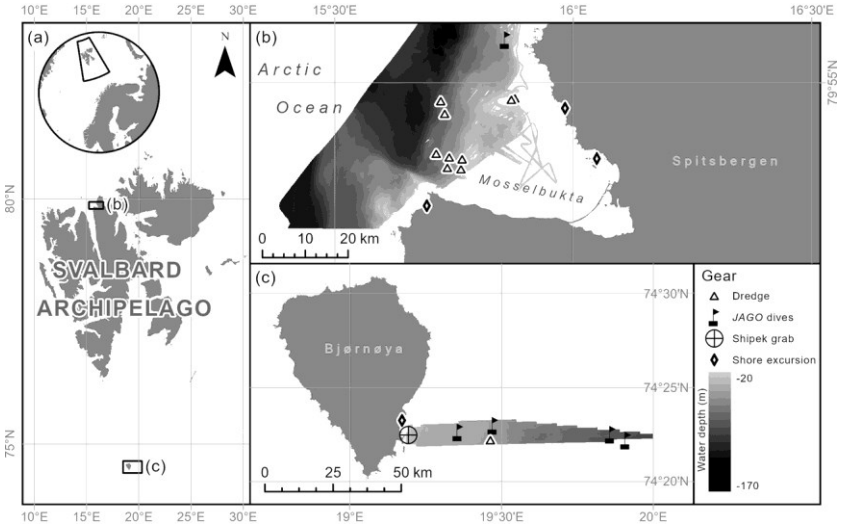

Figure 5-1 Map of the **a** Svalbard Archipelago and bathymetry for **b** Mosselbukta and **c** Bjørnøy-Banken (east of Bjørnøya), including stations for sample collection and applied gear of recovery (station metadata are listed in Table 5-1).

Mosselbukta is influenced by 123 days of polar night (data for 2016 obtained from NOAA Global Monitoring Laboratory 2020; Figure 5-2). The local carbonate factory is characterized by rhodoliths beds, which cover up to 100% of the seafloor in some areas (Teichert et al. 2014). Bjørnøy-Banken is a shallow (20–150 m) shelf platform to the east of Bjørnøya (Bear Island), where extensive biogenic carbonate sediments accumulate in a strong hydrodynamic regime (Henrich et al. 1997; Wisshak et al. 2017; Wisshak et al. 2019b), and experiences

88 days of polar night (data for 2016 obtained from NOAA Global Monitoring Laboratory 2020). The temperature in 2006 in Mosselbukta at 46 m water depth ranged from -2 °C to 6.3 °C, whereas salinity remained relatively constant from 33.2 to 35.4 (Wisshak et al. 2019b). The boundary between the euphotic and dysphotic zones in summer was between 20 and 25 m water depth at Mosselbukta, whilst the base of the dysphotic zone was located at ca. 64 m (Teichert et al. 2014). Neither annual temperature or salinity data nor PAR-measurements for the determination of photic zones are available for Bjørnøy-Banken. However, PAR measurements via lander deployments at Mosselbukta and Bjørnøy-Banken in the summer of 2016 showed higher (tidal) current-induced turbidity and lower light levels at Bjørnøy-Banken (Wisshak et al. 2019b), suggesting that the photic zonation is a bit more condensed compared with Mosselbukta. A detailed environmental characterization for the two study sites is provided by Wisshak et al. (2019b).

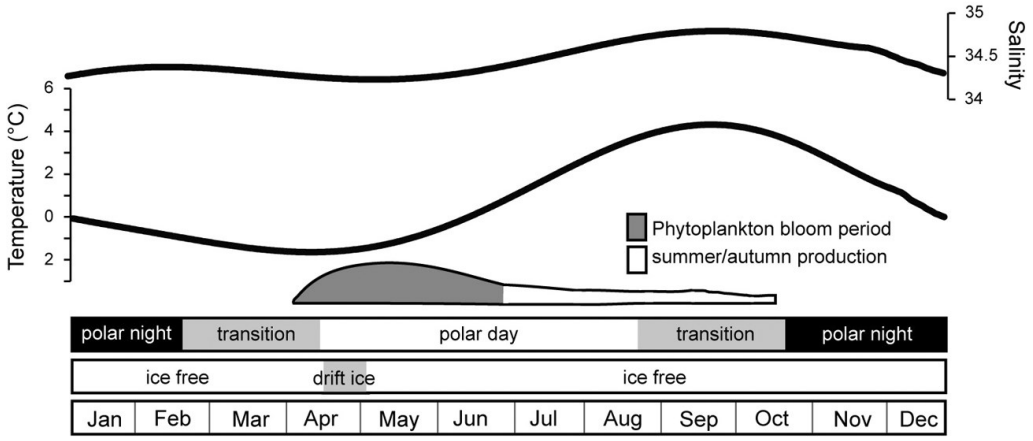

Figure 5-2 Schematic overview of the seasonality at Mosselbukta. (Salinity and temperature data for 2006 simplified after Wisshak et al. (2019b). Phytoplankton bloom and subsequent summer/autumn production based on Zenkevitch (1963). Polar night and day data retrieved from the NOAA Global Monitoring Laboratory (2020). Ice data for 2016 obtained via the ice chart archive of the Norwegian Meteorological Institute (2019).)

5.2.2 Sample collection

During the MSM55 cruise with the RV *Maria S. Merian* in the summer of 2016 (Wisshak et al. 2017), we collected live balanids (barnacles) of the species *Balanus balanus* (Linnaeus, 1758) with a rock dredge, a Shipek grab and the research submersible *JAGO* along bathymetrical transects, growing on boulders or *Chlamys islandica* (Müller, 1776). The collection was complemented by a few *Balanus crenatus* Bruguière, 1789 sampled in the intertidal zone during shore excursions. Both species live in association down to 60 m water depth, although *B. crenatus* is primarily a sublittoral species, whereas *B. balanus* prefers deeper waters (e.g., Barnes & Powell 1953; Barnes & Barnes 1954; Luther 1987). In accordance with the approach by Barnes & Barnes (1954), our analysed specimens of *B. balanus* were perennial and at least four to six years old, as some of the detached balanids had a rostro-carinal diameter of 30–40 mm (consistent with observations of *Balanus balanoides* in Spitsbergen by Feyling-Hanssen, 1953, and Luther, 1987). *Balanus crenatus*

specimens were likely younger, as they were analysed to have a lifespan of one to two years (Barnes & Powell 1953).

Balanids are suitable substrates for bioerosion studies (e.g., Glaub et al. 2002; Feussner et al. 2004) and are abundant in polar waters around Svalbard at all water depths (Figure 5-3). Balanids were collected in roughly 25 m depth intervals, spanning the intertidal to 95 and 125 m water depth at Bjørnøy-Banken and Mosselbukta, respectively (Table 5-1, Figure 5-1b, c).

Table 5-1 List of analysed samples, including water depth, station number, coordinates, gear and number of samples obtained during the MSM55 cruise. For the JAGO and the rock dredge, the coordinates indicate the location of the vessel at the start of the survey. Station locations are shown in Figure 5-1.

Depth (m)	Station	Location		Gear	No. of samples
Mosselbukta					
0	MSM55 437-1	79°54.44′ N	15°58.95′ E	Shore excursion	4
0	MSM55 437-2	79°53.33′ N	16°02.95′ E	Shore excursion	5
0	MSM55 451-1	79°52.29′ N	15°41.57′ E	Shore excursion	7
0–20	MSM55 447-1	79°55.94′ N	15°51.47′ E	*JAGO* dives	10
0–20	MSM55 437-1	79°54.44′ N	15°58.95′ E	Shore excursion	9
25	MSM55 468-1	79°54.78′ N	15°52.65′ E	Dredge	4
25	MSM55 468-2	79°54.75′ N	15°52.21′ E	Dredge	4
50	MSM55 443-1	79°53.22′ N	15° 45.88′ E	Dredge	4
50	MSM55 443-2	79°53.44′ N	15°46.02′ E	Dredge	4
75	MSM55 456-1	79°53.25′ N	15°44.17′ E	Dredge	4
75	MSM55 456-2	79°53.48′ N	15°44.40′ E	Dredge	4
100	MSM55 418-1	79°53.56′ N	15°42.76′ E	Dredge	4
125	MSM55 480-1	79°54.72′ N	15°43.33′ E	Dredge	4
125	MSM55 480-2	79°54.44′ N	15°43.83′ E	Dredge	4
Bjørnøy-Banken					
0–20	MSM55 507-2	74°23.25′ N	19°10.33′ E	Shore excursion	8
21	MSM55 501-1	74°22.48′ N	19°11.57′ E	Shipek grab	6
38	MSM55 489-1	74°22.62′ N	19°21.42′ E	*JAGO* dives	8
50	MSM55 484-1	74°22.98′ N	19°28.35′ E	*JAGO* dives	4
50	MSM55 488-3	74°22.50′ N	19°27.80′ E	Dredge	4
76	MSM55 516-1	74°22.50′ N	19°51.55′ E	*JAGO* dives	8
95	MSM55 522-1	74°22.19′ N	19°54.55′ E	*JAGO* dives	8

5.2.3 Sample preparation and analysis

Immediately after the recovery, balanids were soaked in freshwater to remove the salt and then dried at 50 °C. Prior to the vacuum cast-embedding technique (Wisshak 2006, 2012), organic material was removed with sodium hypochlorite (customary cleaning agent); afterwards, the specimens were rinsed with deionized water and dried at 30 °C for 12 hrs. To enhance the impregnation with R&G “water clear” epoxy resin, the balanids were placed in a CitoVac (Struers) vacuum chamber. Once the resin cured, the embedded samples were cut with a rock saw and treated with ca. 5% hydrochloric acid to remove the carbonate. One hundred seventeen casts were glued onto stubs and sputter-coated with gold (Cressington sputter coater 108) for SEM investigation using a Tescan VEGA3 xmu scanning electron microscope, using the secondary electron detector at 20 kV.

Bioerosion traces were identified at ichnospecies level where applicable and otherwise treated in open nomenclature or addressed by informal names. A semi-quantitative analysis

of the identified bioerosion traces was performed because actual quantification is unfeasible for bioerosion traces. There is a wide range of sizes, traces may superimpose each other, and whilst individual borings can be easily recognized in some of the ichnotaxa, this is impossible for larger and intergrown networks. We classified each ichnotaxon per sample into one of four abundance classes: absent (0); very rare, only one or very few specimens (1); rare, few specimens (2); common, many specimens but not dominant (3); very common or dominant (4). These were then averaged by the number of investigated samples per water depth (after Wisshak et al. 2011).

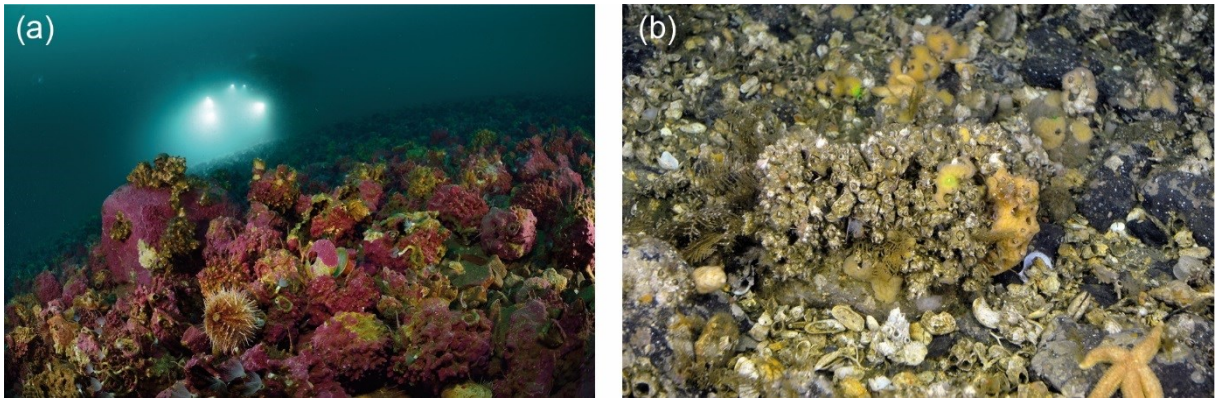

Figure 5-3 The seafloor in Svalbard carbonate factories, illustrating the abundance of balanids at **a** the rhodolith beds in Mosselbukta (ca. 45 m water depth; submersible *JAGO* in the background; photo courtesy of Solvin Zankl) and at **b** the carbonate platform at Bjørnøy-Banken (ca. 100 m water depth).

5.2.4 Statistical ichnodiversity analyses

To evaluate the ichnodiversity, we used the R version 3.5.2 software (R Core Team 2018) to perform multivariate normality tests (Mardia and Royston) using the mvn package (Korkmaz et al. 2014). Prior to the following tests, we computed a Bray–Curtis dissimilarity matrix using the vegan R package (Oksanen et al. 2018) from the untransformed ordinal data, which is a common practice for an ANOSIM (Hammer & Harper 2008; Greenacre & Primicerio 2013) and can be used for relative abundance data (Greenacre & Primicerio 2013). For the non-parametric ANOSIM test, we used vegan (999 permutations) to statistically test that there was no significant difference between two or more groups (null hypothesis). The output is the p value and an R value between −1 and 1; a number close to 0 means that there is no difference between sites. The vegan package was also utilized for the NMDS plots to visualize similarities in two dimensions (Hammer & Harper 2008). The clustsig package (Whitaker & Christman 2014) with the cluster method “average” was used for the cluster analyses with SIMPROF to determine and visualize the number of significant clusters. The biodiversity indices Margalef’s richness index d, Simpson index of dominance λ and diversity $1-\lambda$, Shannon index $H'(\log_e)$ and Pielou’s evenness J' were calculated using PRIMER 6, version 6.1.16, software (Plymouth Marine Laboratory). Whilst these indices are usually based on counts of specimens (Hammer & Harper 2008), we used our ordinal data and transformed the abundance classes in different orders of magnitude (4 was transformed

to 1000; 3 to 100; 2 to 10; 1 kept as 1) to obtain relative abundances, following the approach introduced by Wisshak et al. (2011).

5.3 Results

5.3.1 Ichnodiversity of microborings

A total of 20 different microbioerosion traces were detected: 18 ichnotaxa in 71 samples from Mosselbukta and 16 traces in 46 samples from Bjørnøy-Banken. Four traces were unique to Mosselbukta and two to Bjørnøy-Banken. All ichnotaxa are dwelling traces in the ethological class "domichnia" (after Vallon et al. 2016). Traces were grouped in accordance with the inferred or assumed type of microendolithic trace-makers (Table 5-2); these include cyanobacteria (three traces), chlorophytes (two), rhodophytes (one), sponges (one), foraminifera (three), fungi (nine) and bacteria (one).

Table 5-2 List of ichnotaxa recorded from Mosselbukta and Bjørnøy-Banken, the inferred or assumed (in parentheses) microendoliths based on the original interpretation of the ichnotaxon authority and the relevant figure number.

Microendolith	Ichnotaxa	Mossel-bukta	Bjørnøy-Banken	Fig.
(Cyanobacteria)	"*Fascichnus* isp. I"	X		5-4a
(Cyanobacteria)	"*Fascichnus* isp. II"	X		5-4b
(Cyanobacteria)	*Planobola* cf. *microgota* Schmidt, 1992	X	X	5-4c
Chlorophytes	*Cavernula pediculata* Radtke, 1991	X		5-4d
Chlorophytes	*Ichnoreticulina elegans* (Radtke, 1991)	X	X	5-4e–g
Rhodophytes	*Conchocelichnus seilacheri* Radtke et al., 2016	X	X	5-4g–i
(Sponges)	*Entobia mikra* Wisshak, 2008	X	X	5-4j
Foraminifera	*Nododendrina europaea* (Fischer, 1875)	X	X	5-4k, l
(Foraminifera)	*Pyrodendrina arctica* Wisshak, 2017	X	X	5-6e, f
(Foraminifera)	*Pyrodendrina villosa* Wisshak, 2017	X	X	5-6g
(Fungi)	*Flagrichnus baiulus* Wisshak & Porter, 2006	X	X	5-5a, b
(Fungi)	*Flagrichnus* cf. *baiulus* Wisshak & Porter, 2006	X	X	5-5c, d
(Fungi)	*Flagrichnus* cf. *profundus* Wisshak & Porter, 2006	X	X	5-5e, f
(Fungi)	*Orthogonum*-form 1 *sensu* Wisshak et al., 2005	X		5-6a
(Fungi)	*Orthogonum lineare* Glaub, 1994	X	X	5-6b
(Fungi)	*Orthogonum tubulare* Radtke, 1991	X	X	5-6c
(Fungi)	*Orthogonum giganteum* Glaub, 1994	X		5-6d
Fungi	*Saccomorpha clava* Radtke, 1991	X		5-5g
(Fungi)	*Saccomorpha guttulata* Wisshak et al., 2018	X	X	5-5h, i
Bacteria	*Scolecia serrata* Radtke, 1991	X	X	5-6h, i

Composition of ichnotaxa varied slightly between location and water depth and in abundance (Table 5-3). In the shallow euphotic zone, mainly microborings by cyanobacteria (*Fascichnus* ichnospecies), chlorophytes (e.g., *Cavernula pediculata*) and rhodophytes (*Conchocelichnus seilacheri*) were recorded. Traces of unknown organotrophic producers such as foraminifera or fungi (e.g., *Pyrodendrina arctica* or *Flagrichnus* ichnospecies) were rare. The deep euphotic to dysphotic zone was densely colonized and had the highest ichnodiversity, with *Ichnoreticulina elegans* as the dominant ichnotaxon, followed by *Flagrichnus* isp. and *C. seilacheri*. The aphotic zone was characterized by a high abundance

of inferred or assumed fungal microborings (e.g., *Saccomorpha guttulata*) and a high ichnodiversity (Table 5-3).

5.3.2 Description of some microborings

In the following, we elaborate on the morphological characters of microborings whose morphology differs from the original diagnoses of the respective ichnotaxa. A few traces are described here in informal names, indicated by quotation marks. Abundance and quantification of all observed microborings are outlined in Table 5-3.

Table 5-3 Results of semi-quantitative analysis of microbioerosion traces at Mosselbukta and Bjørnøy-Banken. Abundances are categorized as very common (++), common (+), rare (-) and very rare (--).

	Depth (m)													
	Mosselbukta							Bjørnøy-Banken						Total
Ichnotaxon	0[a]	0–20[a]	25[b]	50[b]	75[b]	100[c]	125[c]	0–20[a]	20[a]	38[b]	50[b]	75[b]	100[c]	range (m)
'*F.* isp. I'	--													0
F. isp. II'										--				38
P. cf. *microgota* Schmidt, 1992	--	--								--				0–38
C. pediculata Radtke, 1991	--													0
I. elegans (Radtke, 1991)		++	++	++	--			+	--	--	-	-		0–75
C. seilacheri Radtke et al., 2016		-	+	-				+	+	-	-			0–50
E. mikra Wisshak, 2008				--	+	+	-						--	50–125
N. europaea (Fischer, 1875)		--	--	-	-	-	-	--		--	-	-	+	0–125
P. arctica Wisshak, 2017			--	--	-	-	--	--				-	-	25–125
P.villosa Wisshak, 2017		--		--	-	-	--	--	--	-	--	-	-	0–125
F.baiulus Wisshak & Porter, 2006	--	--	--	--	-	+	+	--	--	-	--	+	+	0–125
F. cf. *baiulus* Wisshak & Porter, 2006	-	--						--		--	--	--	--	0–100
F. cf. *profundus* Wisshak & Porter, 2006		--	--		--	--		--	-	-	--	--	-	0–100
O.-form I *sensu* Wisshak, 2005										--	--	--	--	38–100
O. lineare Glaub, 1994				-	-	-	-			-	--	--	--	38–125
O. tubulare Radtke, 1991			--	--	+	+	-			--	--	--	--	25–125
O.giganteum Glaub, 1994		--				--	--							0–125
S.guttulata Wisshak et al., 2018			--	--	-	+	-				--	--	-	25–125
S. clava Radtke, 1991						--								100
S. serrata Radtke, 1991	--	--	--	-	+	-	-			--	-	--		0–125
Number of traces	6	10	9	11	11	12	10	8	5	13	12	12	11	

	Svalbard							
	0	0–20	25	38	50	75	100	125
Number of traces	6	11	9	13	14	13	14	10

[a]Euphotic conditions. [b]Dysphotic conditions. [c]Aphotic conditions.

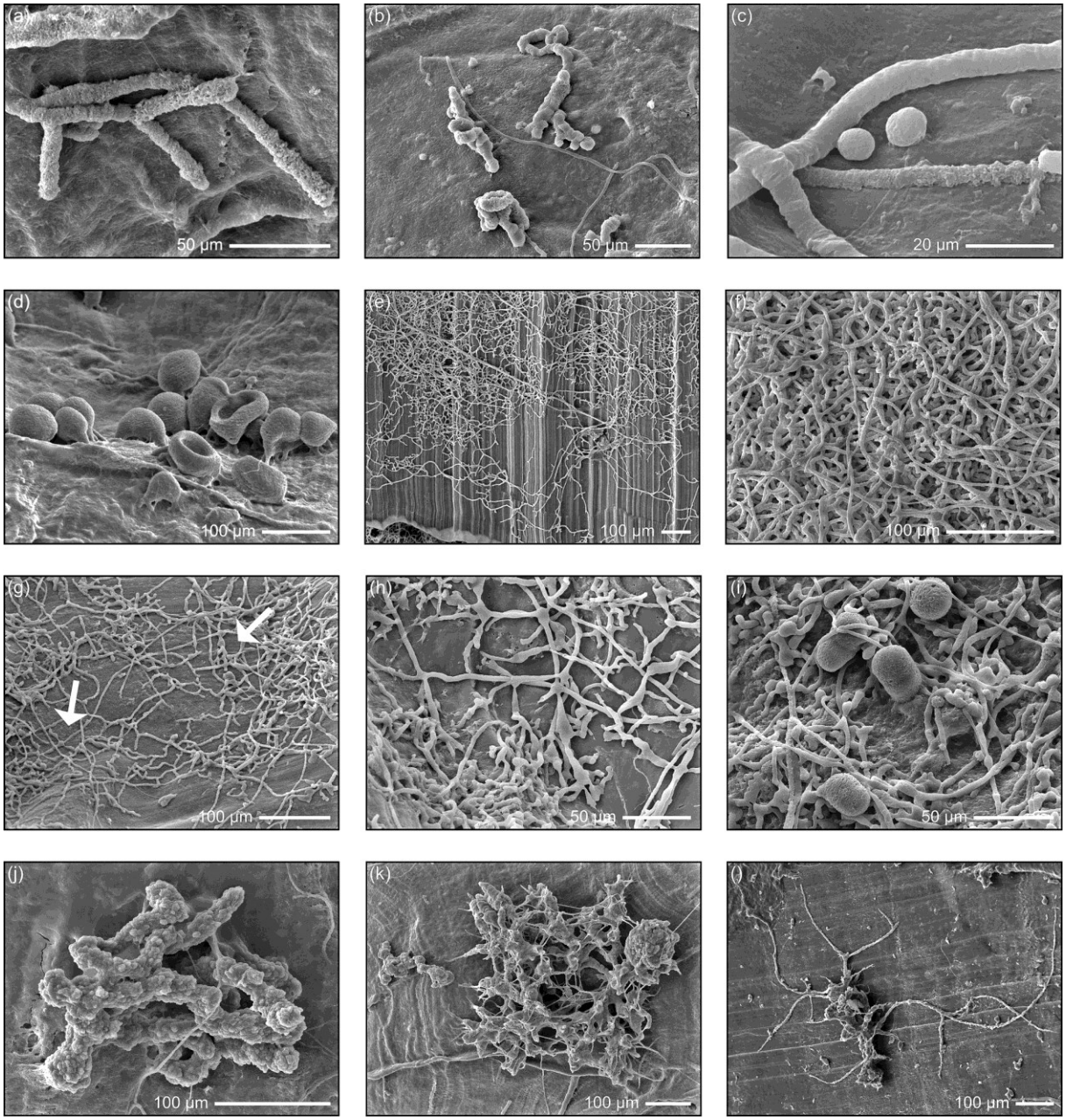

Figure 5-4 Microborings inferred or assumed produced by **a**–**c** cyanobacteria, **d**–**g** chlorophytes, **g**–**i** rhodophytes, **j** sponges and **k**–**l** foraminiferans. **a** "*Fascichnus* isp. I" from the intertidal at Mosselbukta. **b** "*Fascichnus* isp. II" from 38 m water depth at Bjørnøy-Banken. **c** *Planobola* cf. *microgota* from 0 to 20 m water depth at Mosselbukta. **d** *Cavernula pediculata* from the intertidal at Mosselbukta. **e** Overview and **f** close-up of *Ichnoreticulina elegans* from 50 m water depth at Mosselbukta. **g** *Ichnoreticulina elegans* associated with *Conchocelichnus seilacheri* (white arrows) from 50 m water depth at Bjørnøy-Banken. **h** *Conchocelichnus seilacheri* from 0 to 20 m water depth at Mosselbukta. **i** *Conchocelichnus seilacheri* from 50 m water depth at Bjørnøy-Banken with prominent swellings. **j** *Entobia mikra* from 75 m water depth at Mosselbukta. **k** *Nododendrina europaea* from 100 m water depth at Mosselbukta and a small *Entobia mikra* to the left. **l** *Nododendrina europaea* from 95 m water depth at Bjørnøy-Banken with prominent long whips.

"*Fascichnus* isp. I"

It has 100-µm-long, uniformly thick tunnels with a diameter of 10–12 µm, occasionally bifurcating with a 90° angle. The trace shows a somewhat radiating appearance of the tunnels

collapsed to the surface of the cast. Although the boring was too rare to provide a lot of details, we assumed a cyanobacterium as producer (Figure 5-4a).

"*Fascichnus* isp. II"

This trace grows from swelling with a 10 µm diameter into a segmented and rarely twisted string with a maximum length of 75 µm (Figure 5-4b).

Planobola cf. *microgota* Schmidt, 1992

This spheroid to bulbous boring has similarities in size to *P. microgota* but lacks a latitudinal contact to the substrate surface via vertical tubules. Because further lack of characteristics prevented an assignment to a specific ichnospecies, we listed this ichnotaxon as *P.* cf. *microgota* (Figure 5-4c).

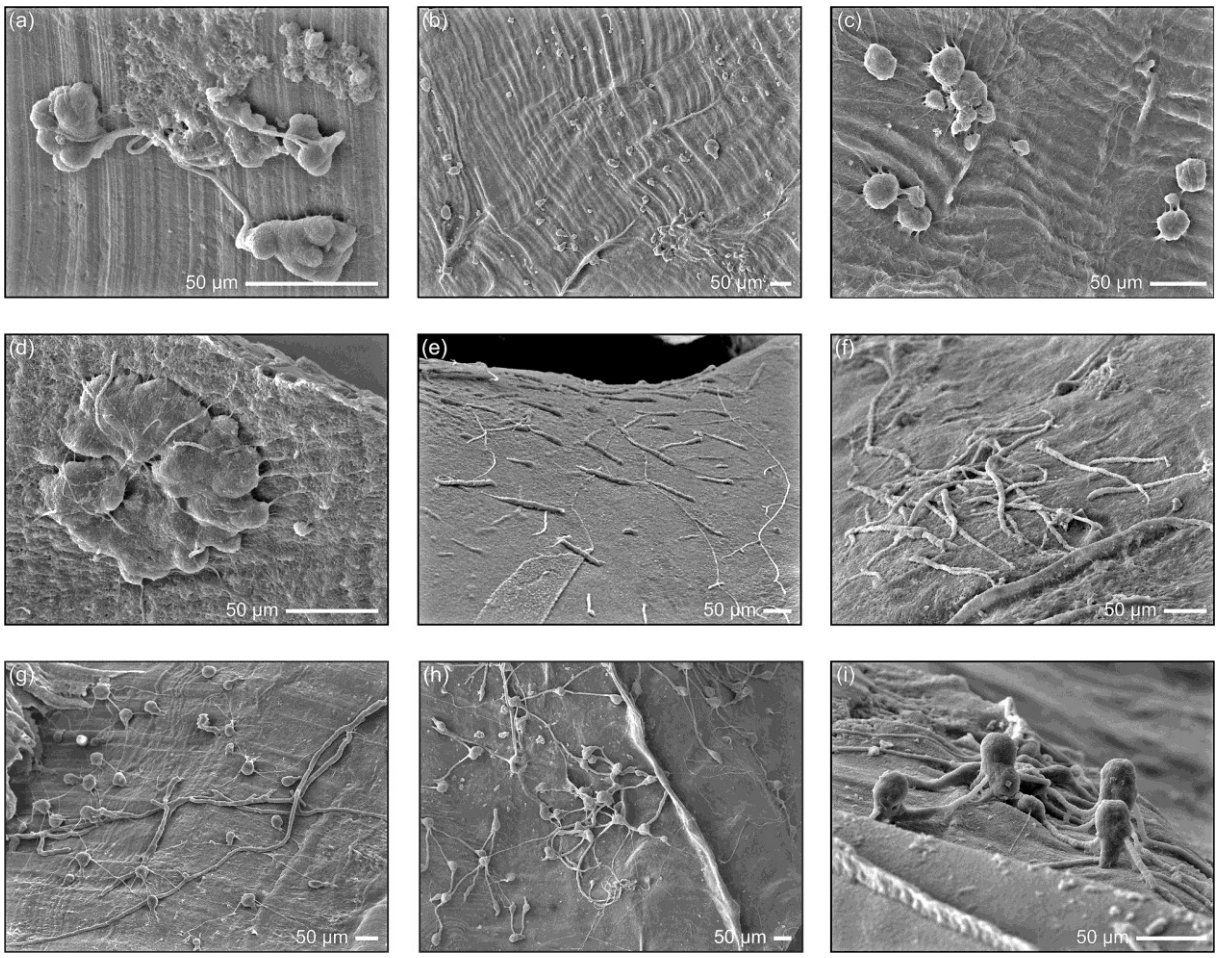

Figure 5-5 Microborings inferred or assumed by fungi. **a** Close-up of *Flagrichnus baiulus* from 75 m water depth at Bjørnøy-Banken. **b** Initial *Flagrichnus baiulus* from the intertidal at Mosselbukta. **c** *Flagrichnus* cf. *baiulus* from the intertidal at Mosselbukta and **d** forming a rosette as observed in the intertidal at Bjørnøy-Banken. **e** *Flagrichnus* cf. *profundus* from 50 m water depth at Bjørnøy-Banken and from **f** 100 m water depth at Mosselbukta. **g** *Saccomorpha clava* from 100 m water depth at Mosselbukta. **h** Overview of *Saccomorpha guttulata* from 95 m water depth at Bjørnøy-Banken. **i** *Saccomorpha guttulata* from 75 m water depth at Bjørnøy-Banken.

Conchocelichnus seilacheri Radtke et al., 2016

Conchocelichnus seilacheri has a high morphological variability. Branchings are either wide, irregular and pancake-like with a diameter of 3–14 µm or marked with almost perfectly shaped spherical swellings of up to 16 µm. The upright filament bushes of *C. seilacheri* have similarities to *Fascichnus frutex* (Radtke, 1991; Figure 5-4g–i), complicating distinction of the two ichnospecies.

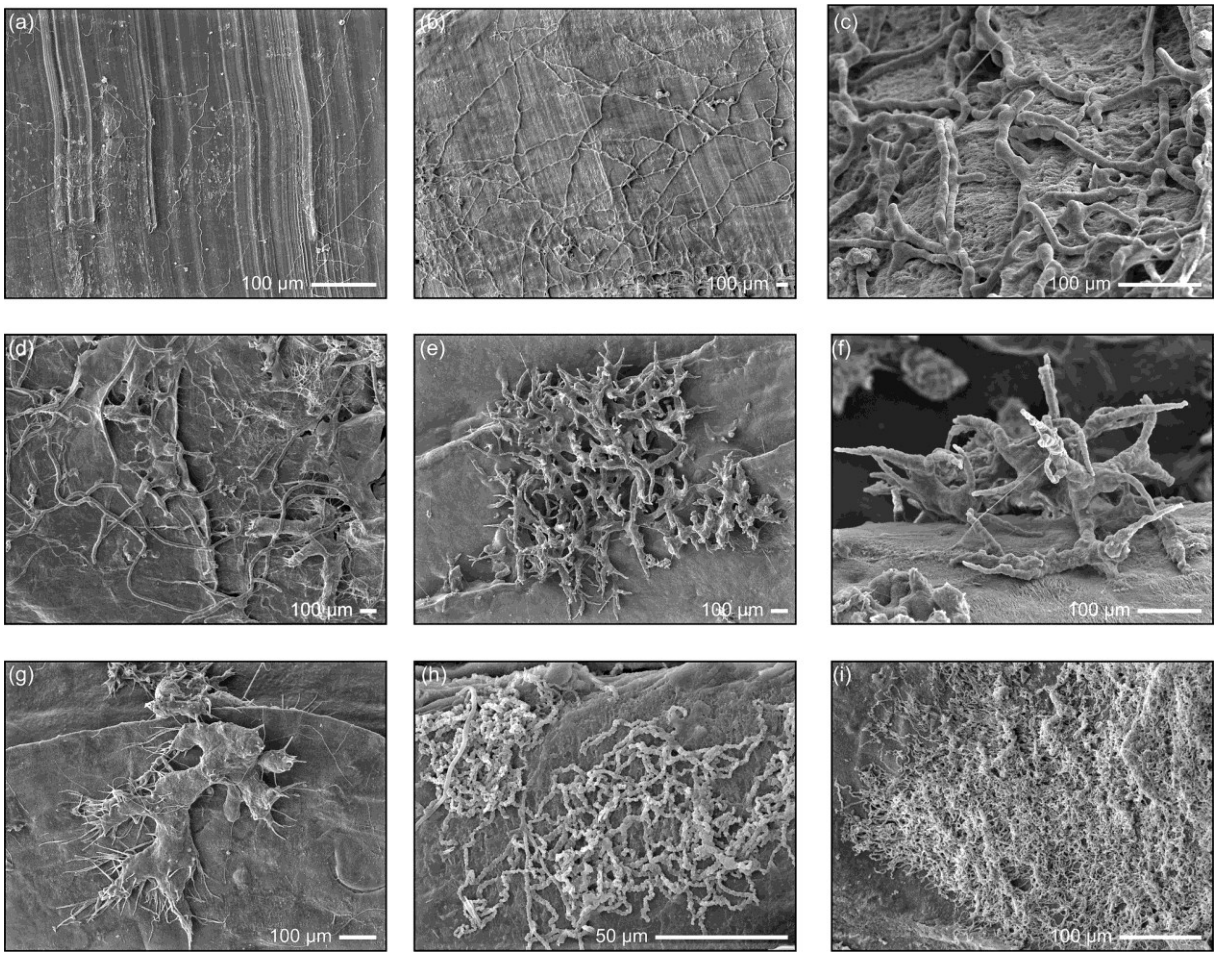

Figure 5-6 Microborings produced by yet unknown organotrophic producers. **a** "*Orthogonum*-form 1" from 95 m water depth at Bjørnøy-Banken. **b** *Orthogonum lineare* from 100 m water depth at Mosselbukta. **c** *Orthogonum tubulare* from 100 m water depth at Mosselbukta. **d** *Orthogonum giganteum* from 100 m water depth at Mosselbukta. **e** A large *Pyrodendrina arctica* from 95 m water depth at Bjørnøy-Banken and **f** in angular view from 95 m water depth at Bjørnøy-Banken. **g** *Pyrodendrina villosa* from 95 m water depth at Bjørnøy-Banken. **h** Close-up of *Scolecia serrata* from 75 m water depth at Mosselbukta and **i** an overview from 50 m water depth at Bjørnøy-Banken.

Nododendrina europaea (Fischer, 1875)

Nododendrina europaea has occasionally thick galleries of up to 100 µm in diameter and merging of single branches to a large plexus. At the Bjørnøy-Banken, striking long whips, originating from and around the single main chamber, were rarely observed (Figure 5-4k, l).

Flagrichnus cf. *baiulus* Wisshak & Porter, 2006

Flagrichnus cf. *baiulus* appears to lack the diagnostic long, thin, filamentous tube. Instead, the boring features thin filaments in the circumference. Typical sack-shaped cavities were occasionally connected with tunnels about 10 µm in length. In a few Bjørnøy-Banken samples, some of the traces show a rosette similar to the Cretaceous ichnogenus *Dendrina* Quenstedt, 1849, but they are much smaller in dimension (Figure 5-5d). The unknown trace-maker may be identified based on Tribollet et al. (2011b): their figure 4b shows a fungus, whose morphology is similar to *F.* cf. *baiulus* (Figure 5-5c, d).

Flagrichnus cf. *profundus* Wisshak & Porter, 2006

This trace gradually tapers towards the end instead of a diagnosed basal-swelling leading to a deeply penetrating gallery, as described for *F. profundus*. The microsculpture is uneven and it does not penetrate as deep (Figure 5-5e, f).

"*Orthogonum*-form 1" *sensu* Wisshak et al, 2005

This form comprises galleries 3–5 µm in diameter that run closely parallel to the substrate in a wavy manner for a few millimetres (Figure 5-6a).

5.3.3 Statistics of ichnodiversity and ichnodisparity

Table 5-4 Ichnogenera categorized into nine different ichnodisparity groups, according to Buatois et al. (2017).

Architectural designs	Ichnogenera	No. of ichno-species
59—Cylindrical vertical to oblique borings	*Flagrichnus*	3
64—Globular to spherical borings	*Planobola*	1
66—Clavate-shaped borings	*Cavernula*	1
68—Branched tubular borings	*Ichnoreticulina*, *Scolecia, Conchocelichnus*	3
69—Non-camerate network borings	*Orthogonum*	4
70—Camerate network borings	*Saccomorpha*	2
71—Non-camerate boxwork borings	*Entobia*	1
74—Radial borings	*Fascichnus*	2
75—Dendritic and rosetted borings	*Nododendrina*, *Pyrodendrina*	3

Mardia's and Royston's Multivariate Normality Tests resulted in $p < 0.05$ for ichnodiversity and multivariate normality was therefore rejected. An ANOSIM to test for significant differences between locations resulted in $R = 0.10$ and a significance level of 0.15% (not significant). A second ANOSIM to test the factor "water depth" (the light regime being the principal underlying factor) resulted in $R = 0.80$ and a significance level of 0.002% (significant). An NMDS plot based on the Bray–Curtis similarity measure with the factor "location" showed that the microbioerosion trace assemblages in greater water depths cluster and were therefore similar to one another, whilst the shallow euphotic samples were outliers, reflecting dissimilarity (Figure 5-7a). A cluster analysis with SIMPROF was computed to determine the number of significant clusters, which are four (Figure 5-7c).

For the ichnodisparity analysis, each of the documented ichnogenera was assigned to one out of nine different groups (Table 5-4), following the categories of architectural designs in trace fossils established by Buatois et al. (2017).

For the ichnodisparity analysis, Mardia's and Royston's Multivariate Normality Tests resulted in $p < 0.05$, so multivariate normality was rejected. An ANOSIM with the factor "location" computed $R = 0.09$ and a significance level of 0.18% (not significant), whilst the factor "water depth" resulted in $R = -0.09$ and a significance level of 0.62% (not significant).

An NMDS plot based on the Bray–Curtis similarity measure (Figure 5-7b) indicated that architectural designs are similar in greater water depths, whereas the shallowest stations are dissimilar. The SIMPROF cluster analysis (Figure 5-7d) resulted in two to three main clusters: Mo_0 was fairly excluded from the rest, whereas the other two clusters split into several smaller ones (roughly corresponding to the photic zones), including a mix of samples from the different water depths and sites (Figure 5-7d).

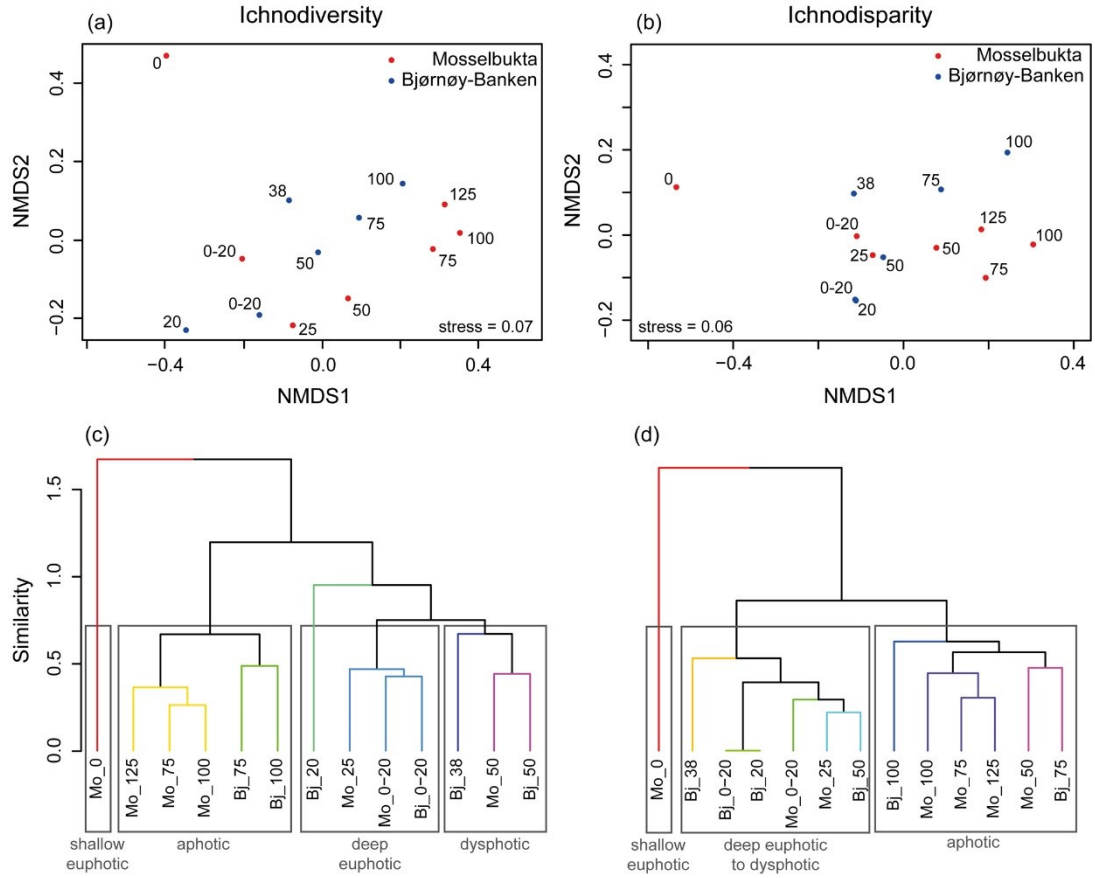

Figure 5-7 Non-metric multidimensional scaling plots for the **a** ichnodiversity and **b** ichnodisparity at both study sites (data transformed with square root) and respective results of the cluster analyses with **c** and **d** similarity profile. For **c** ichnodiversity, the clustering correlates to four photic zones, shallow and deep euphotic, dysphotic, and aphotic, whereas **d** ichnodisparity, in contrast, shows a slightly less conclusive clustering in three photic zones.

5.3.4 Indices of ichnodiversity and ichnodisparity

According to the ichnodiversity indices, samples from deep euphotic water depths were dominated by single ichnotaxa (λ close to 1, *I. elegans*) and have therefore a low diversity

(*1-λ′* and *H′(log$_e$)* close to 0) and a general unevenness (*J′* close to 0). Samples from dysphotic water depths had almost equally common ichnotaxa (*λ* close to 0), with high diversity (*1-λ′* and *H′(log$_e$)* close to 1 and higher, respectively) and high evenness (*J′* close to 1). This pattern is more pronounced in Mosselbukta (Table 5-5, Figure 5-8a, b, d, e).

Ichnodiversity indices for the ichnodisparity concept demonstrate that Svalbard samples from the deep euphotic stations were marked by a single dominant group of architectural designs (*λ* close to 1, branched tubular borings), as were the samples from 100 m water depth at Bjørnøy-Banken (dendritic and rosetted borings). Those sites had also a low diversity (*1-λ′* close to 0) and unevenness (*J′* close to 0). The 0-m site at Mosselbukta and 20 m at Bjørnøy-Banken showed contrasting results; Mosselbukta samples showed that ichnotaxa were equally common (*λ* close to 0) with a high diversity (*1-λ′* = 1), although *H′(log$_e$)* demonstrated that several architectural designs were found. Ichnodisparity indices were generally even (*J′* closer to 1 than to 0) and marked by several groups, except for the deep euphotic stations at Mosselbukta (Table 5-5, Figure 5-8d–f).

Table 5-5 Diversity indices for ichnodiversity and ichnodisparity of microborings at Mosselbukta and Bjørnøy-Banken, comprising ichnospecies richness *S*, Margalef's richness index *d*, Simpson index of dominance *λ* and diversity *1-λ′*, Shannon index *H′(log$_e$)* and Pielou's evenness *J′*.

Sample	Ichnospecies richness *S*	Margalef's richness index *d*	Simpson index of dominance *λ*	Simpson index of diversity *1-λ′*	Shannon index *H′(log$_e$)*	Pielou's evenness *J′*
Ichnodiversity						
Mo_0	6	1.85	0.47	0.57	1.17	0.65
Mo_0-20	10	1.30	0.97	0.03	0.12	0.05
Mo_25	9	1.14	0.82	0.18	0.35	0.16
Mo_50	11	1.44	0.93	0.07	0.22	0.09
Mo_75	11	1.70	0.23	0.77	1.69	0.71
Mo_100	12	1.80	0.20	0.80	1.80	0.72
Mo_125	10	1.79	0.44	0.56	1.30	0.56
Bj_0-20	8	1.31	0.47	0.53	0.86	0.41
Bj_20	5	0.85	0.79	0.21	0.45	0.28
Bj_38	13	3.08	0.17	0.85	2.01	0.78
Bj_50	12	2.84	0.18	0.84	1.95	0.79
Bj_75	12	2.20	0.48	0.52	1.23	0.50
Bj_100	11	1.82	0.34	0.66	1.37	0.57
Ichnodisparity						
Mo_0	5	2.49	0.20	1.00	1.61	1.00
Mo_0-20	6	1.07	0.91	0.09	0.27	0.15
Mo_25	5	0.85	0.79	0.21	0.45	0.28
Mo_50	6	1.06	0.78	0.22	0.49	0.28
Mo_75	6	1.02	0.59	0.41	0.87	0.49
Mo_100	6	1.01	0.52	0.48	1.03	0.57
Mo_125	6	1.57	0.35	0.67	1.26	0.70
Bj_0-20	4	1.17	0.61	0.42	0.79	0.57
Bj_20	4	1.17	0.61	0.42	0.79	0.57
Bj_38	7	1.86	0.32	0.7	1.34	0.70
Bj_50	5	1.52	0.53	0.51	0.99	0.62
Bj_75	5	1.28	0.38	0.64	1.13	0.70
Bj_100	5	0.85	0.79	0.21	0.45	0.28

5.4 Discussion

5.4.1 Bathymetric distribution

Our inventory of microbioerosion traces obtained from polar balanids conforms to the general bathymetrical zonation pattern of microendolithic borings (e.g., Golubic et al. 1975; Schmidt 1992; Glaub 1994; Vogel et al. 2000; Glaub et al. 2002; Wisshak 2012), in which cyanobacterial borings were only identified in the deep euphotic zone, chloro- and rhodophyte borings dominated from the euphotic down to the dysphotic zone and traces by fungi occurred primarily in the aphotic zone. For practical reasons, we refer to photic zones, although during the polar night, they become largely irrelevant due to "aphotic" conditions throughout the water column. However, ichnodiversity was found to be surprisingly low in

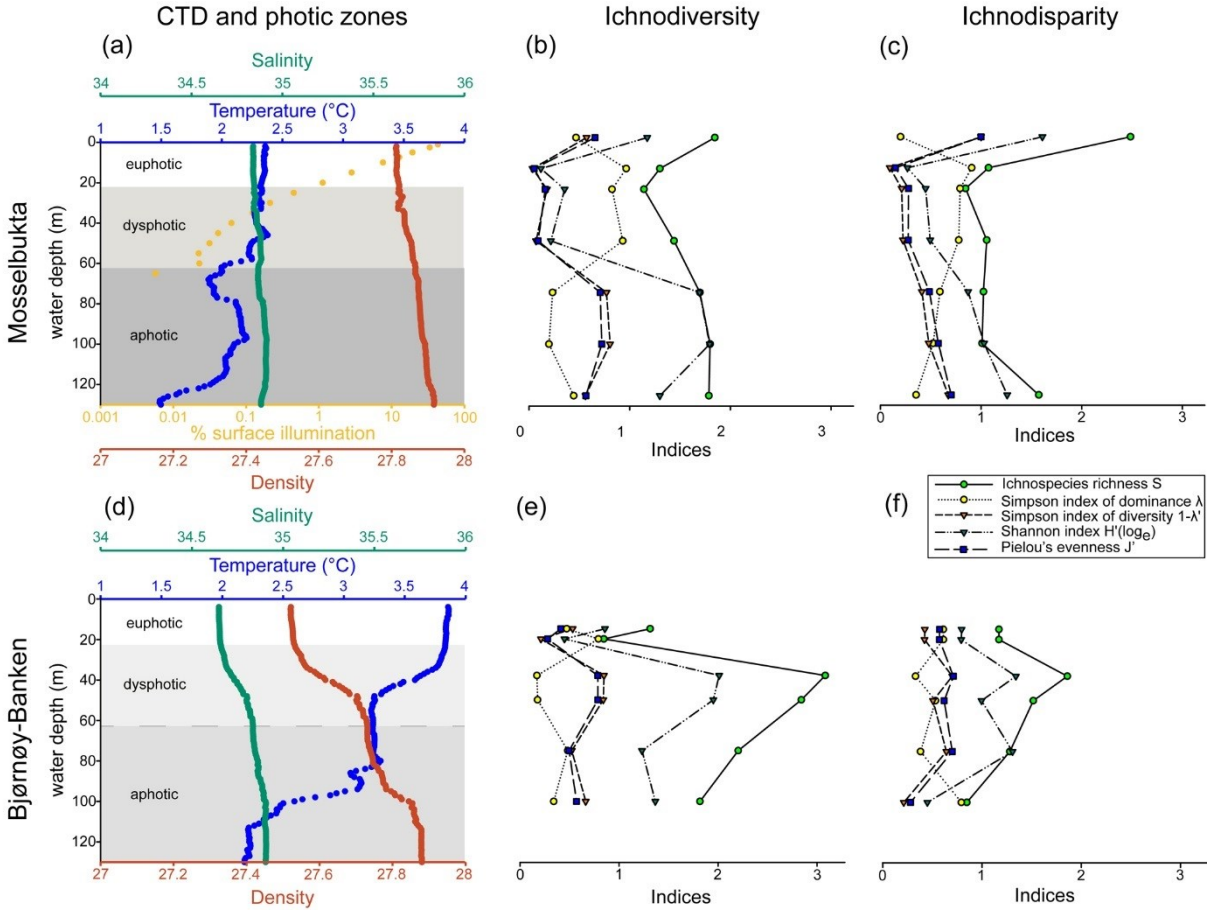

Figure 5-8 Assessment of diversity indices for **b** and **e** ichnodiversity and **c** and **f** ichnodisparity across the bathymetrical transect **a**–**c** at Mosselbukta and **d**–**f** at Bjørnøy-Banken. Salinity, temperature and density data (Wisshak et al. 2017) were plotted with light intensities expressed as percent of the surface illumination in the logarithmic plots shown in **a** and **d** (light intensity data from Teichert et al. 2014). As no light intensity data were available for **d** Bjørnøy-Banken, the photic zonation in Mosselbukta is used as an approximation.

the euphotic zone, where we would have expected a high diversity in borings produced by phototrophic microendoliths. As a result, an almost uniform total number of ichnotaxa was observed along the bathymetrical transect, with more traces of organotrophic microendoliths gradually compensating for the decrease of traces produced by phototrophic microphytes

towards deeper waters (Table 5-3). Hence, whilst the ichnodiversity remains nearly constant, the composition changes with water depth. This finding contrasts the general trend that the highest variety of microbioerosion traces is usually observed in the euphotic zone, with a gradual decrease towards deeper waters (Wisshak 2012). We explain this discrepancy with strong environmental fluctuations in the intertidal zone and upper water column (Figure 5-8a, d; Glaub et al. 2007; Golubic et al. 2016). The upper part of polar oceans is influenced by extreme seasonal variations, primarily in light levels and temperature, periods of sea ice cover and consequential meltwater influx (Figure 5-2, Figure 5-8; Wiencke et al. 2006). Furthermore, we assume that drift ice piling up along the shore during winter/spring prohibits balanids from growing old and becoming intensely bioeroded before the ice abrades them, which results in colonization and bioerosion only by opportunistic microendoliths and allowing the establishment of only immature, low-diversity microboring trace assemblages. In deeper water, light levels are low throughout the year and variations of temperature and salinity are less extreme (Figure 5-8a, d), providing stable environmental conditions for organotrophic microendoliths in the dysphotic and aphotic zones. This interpretation is supported by the NMDS plots, cluster analyses (Figure 5-7) and ichnodiversity indices (Figure 5-8): the shallow euphotic zone, in particular the intertidal zone, is dissimilar to the deeper euphotic zone and beyond. Deeper samples can be subdivided into distinct clusters, representing deeper euphotic, dysphotic and aphotic conditions.

The observed bathymetrical distribution pattern and ANOSIM results indicate that water depth, affecting the light regime, is the major factor for the establishment of bioerosion trace assemblages in balanids of the polar waters of Svalbard. In contrast, the site factor was much less relevant, with Mosselbukta and Bjørnøy-Banken yielding almost the same suite of ichnotaxa at equivalent depth stations (Table 5-3).

5.4.2 Intensity of microbioerosion

Comparatively greater abundances of various microborings in Mosselbukta possibly reflect more favourable environmental conditions. These are also reflected in the presence of rhodoliths beds at intermediate water depths, which have been demonstrated to increase benthic diversity and abundance, owing to an increase in habitat diversity provided by the bio-engineering crustose rhodophyte *Lithothamnion glaciale* Kjellman, 1883 (Teichert 2014; Wisshak et al. 2017; Schoenrock et al. 2018; Wisshak et al. 2019b). Mosselbukta is better protected from currents, whilst a strong hydrodynamic regime and the nearby Polar Front with colder surface temperatures persist at Bjørnøy-Banken (Henrich et al. 1997; Wisshak et al. 2017; Wisshak et al. 2019b). Water masses at Mosselbukta and around Bjørnøy-Banken also differ in turbidity, with the strong tidal currents at Bjørnøy-Banken leading to resuspension of sediment and food particles following every flood tide. This also results in less light reaching the seafloor, as evident from PAR data logged during two lander deployments at Mosselbukta and Bjørnøy-Banken (Wisshak et al. 2019b). These factors

appear to promote more intense bioerosion in Mosselbukta compared with Bjørnøy-Banken, resulting in a greater abundance of microborings in Mosselbukta but not a significant variation in ichnodiversity (Table 5-2, Table 5-3).

5.4.3 Ichnodiversity versus ichnodisparity

Whilst ichnodiversity reflects the number of species (ichnotaxonomic richness), ichnodisparity is "a measure of the variability of morphologic plans" (Buatois et al. 2017: p. 104) and is based on a classification into categories of architectural designs. Within each of these architectural groups present in our data set, there may be different ichnospecies (Table 5-4). A high ichnodiversity does not necessarily mean that the ichnodisparity is also high (see figure 80 in Buatois et al. 2017); likewise, the same degree of ichnodisparity does not mean that the same architectural designs are present. The application of the ichnodisparity concept as a complementing approach did not yield clear differences between the two sites or between the various water depths (low *R* values and significance levels). The ichnodisparity indices (Figure 5-8c, f) and the NMDS plot (Figure 5-7b) draw a similar picture, with only the intertidal station in Mosselbukta showing a different signature that is most likely a result of the low ichnodiversity in the initial microboring trace assemblage (see discussion above). The cluster analysis (Figure 5-7c, d) for ichnodiversity and ichnodisparity, however, differed in that the ichnodiversity showed four distinct clusters related to the different photic zones, whereas the architectural groups showed three distinct clusters, which are related to "shallow euphotic", "deep euphotic to dysphotic" and "aphotic" conditions. The diversity in the architectural designs and, therefore, boring behaviour by microendoliths differs to some degree throughout the bathymetric transect, but not between the different sites (Figure 5-7d). The clustering is statistically not significant, however, probably reflecting a combination of microborings by phototrophs and organotrophs within the different groups. Categories including ichnotaxa by phototrophs occurred primarily in the photic zone (e.g., "globular to spherical borings", "radial borings"), but as the bacterial ichnogenus *Scolecia* belongs together with *Ichnoreticulina* and *Conchocelichnus* to "branched tubular borings", the design persists throughout the bathymetric transect.

5.4.4 Comparison with lower latitudes

Putting our catalogue of the Svalbard microborings in the context of global distribution patterns, we compared our findings primarily with two studies with a comparable bathymetrical transect from lower latitudes in the North Atlantic: the cold-temperate Kosterfjord in Sweden and the warm-temperate Azores Archipelago (further results of ichnodiversity studies in various settings were summarized by Wisshak et al. (2011), Table 5-3). This comparison indicates that the Svalbard ichnotaxa record complies with the overall bathymetrical decrease of microboring ichnodiversity towards higher latitudes (Wisshak 2006; Wisshak et al. 2011). Although we here compare natural substrates with two-year

experimental exposures and despite Arctic balanids being mostly older than the analysed platforms, by far the highest ichnodiversity was detected in the Azores, a warm-temperate setting with apparently more favourable environmental conditions for microbioerosion (Wisshak et al. 2011). At the cold-temperate Kosterfjord site, temperatures are colder than in the Azores and have a stronger seasonal fluctuation. Moreover, the water is more turbid and the photic zonation is considerably condensed, which results in a reduced ichnodiversity (Wisshak 2006). Svalbard has the lowest temperatures and most strongly limited light regime, combined with the strongest seasonal fluctuations, and this is reflected in the lowest ichnodiversity among the three sites.

As far as the spectrum of inferred or assumed microendolithic trace-makers is concerned, 20 microbioerosion traces were documented in Svalbard waters. In contrast, nearly twice as many (37) were encountered on experimental settlement platforms in the Azores, including 11 cyanobacterial microborings, seven traces by chlorophytes, eight of fungal origin and 11 other organotrophic microborings (Wisshak et al. 2011). In the Kosterfjord, Sweden, an intermediate ichnodiversity of 26 different traces on three different substrate types was recorded. On the experimental substrates, seven of the investigated traces were produced by cyanobacteria, four by chlorophytes, six by fungi and four by unidentified organisms (Wisshak 2006). Seven microborings at the Svalbard sites were attributed to phototrophic microendoliths (three cyanobacteria, two chlorophytes, one rhodophyte trace-maker). This comparison indicates that it is chiefly the depletion in microalgae and cyanobacteria that is reflected in the low ichnodiversity.

The polar night, in combination with a condensed photic zonation during the polar day and transitional months, imposes significant limitations for these phototrophic organisms. In consequence, traces produced by low-light specialists were found most abundant in the phototrophic borer spectrum, specifically *I. elegans* (produced by the chlorophyte *Ostreobium quekettii* Bornet & Flahault, 1889) and *C. seilacheri* (produced by bangialean rhodophytes). Apart from the seasonal availability of light for photosynthesis (e.g., Schmidt & Freiwald 1993; Zacher et al. 2009), the distribution of microphytes is commonly limited by low temperatures, with only a few specialists coping well with the harsh Arctic conditions. Few studies of marine Arctic microalgae (Wulff et al. 2009) have been undertaken, but they all show that abundance and diversity are generally poor (Garbary 2001), with only a few endemic species in the Arctic (Wulff et al. 2009). Polar species have different metabolic strategies to adapt to low light availability and low temperatures, such as red algae that accumulate floridean starch grains from food remnants during the polar day to adapt to the polar night (e.g., Woelkerling 1990; Freiwald & Henrich 1994; Viola et al. 2001). The different strategies allow perennial algae to survive throughout the polar night (Lüning 1985; Heimdal 1989; Gómez et al. 2009; McMinn & Martin 2013). The question of how specific microborers adapt to the polar environment has received little attention and is beyond the

scope of the present study. However, euendoliths are generally relatively robust with respect to environmental fluctuations as they are buffered in the microenvironment of their borings (Vogel & Glaub 2004) and could therefore also be expected to survive the polar night.

Light availability is irrelevant for organotrophs, and as the temperature becomes more stable towards greater water depths, the conditions are less extreme. Organotrophs thrive in cold environments at all water depths and dominate in the aphotic zone. Those circumstances influence not only the abundance and diversity of microborings but also the dominant ichnospecies in the various biogeographic realms.

Samples from the deep euphotic zone were dominantly bored by phototrophic microendoliths. In Svalbard, mainly *C. seilacheri* or *I. elegans* occurred, whilst the intertidal at Kosterfjord was primarily colonized by *Cavernula pediculata* and *Fascichnus* ichnospecies. There, the shallow euphotic zone was characterized by *C. pediculata*, *Eurygonum nodosum*, *Fascichnus dactylus* and *Orthogonum fusiferum* (Wisshak 2006). The most common ichnotaxa at the Azores at shallow water depths were *E. nodosum* and *Scolecia filosa*, both produced by cyanobacteria (Wisshak et al. 2011).

The dysphotic zone in Svalbard was densely colonized and had the highest ichnodiversity, with *I. elegans* as the most dominant ichnotaxon. In the Kosterfjord dysphotic zone, *Flagrichnus* ichnospecies, *Saccomorpha clava* and *Orthogonum lineare* were prominent ichnotaxa, with the same trend in aphotic depths (Wisshak 2006). The aphotic zone in Svalbard was dominated by fungal microborings, e.g., *Orthogonum tubulare* or *S. guttulata*. *Nododendrina europaea* and other borings by unknown producers, such as the *Pyrodendrina* ichnospecies, resulted in a comparatively high ichnodiversity (Table 5-3). *Ichnoreticulina elegans* was dominant in deep euphotic to dysphotic water samples from the Azores, whereas *S. clava* and *N. europaea* were common at dysphotic to aphotic depths of the Azorean water column (Wisshak et al. 2011).

This work shows that in spite of the similarity between deep-water conditions at low latitudes and conditions at high latitudes, some ichnotaxa common in warm- and cold-temperate realms—such as the cyanobacterial ichnotaxa *E. nodosum* and *S. filosa* and the chlorophyte microborings in the ichnogenus *Rhopalia*—were not observed in the polar region under investigation. Ichnotaxa so far exclusive to the cold-temperate and polar realm are *F. baiulus*, *Entobia mikra*, *N. europaea* and *S. guttulata* (Wisshak & Porter 2006, , respectively; Bromley et al. 2007; Wisshak 2008; Wisshak et al. 2018); all of them assumingly bored by fungi, foraminifera and sponges. *Orthogonum*-form 1 was until now also only described from the Kosterfjord and is therefore also restricted to cold-temperate and polar regions (Wisshak 2006). *Saccomorpha clava* is usually a ubiquitous fungal ichnotaxon (e.g., Wisshak 2006; Wisshak et al. 2011; Färber et al. 2015), but only one single colony was observed in Mosselbukta, whilst we commonly found *S. guttulata* as a substitute of this trace. *Fascichnus* isp. I, II or *Flagrichnus* cf. *baiulus* are informally described and referred to as “cf.” in the

present study, because they show “undescribed” features or an adapted boring behaviour and are thus different to the original diagnosis. Those “adaptations” may be effects of the limiting environmental parameters.

5.5 Conclusions

We address the lack of comprehensive Arctic (micro)bioerosion research by presenting a catalogue of 20 different ichnotaxa that we have recorded in more than 100 balanid samples from euphotic to aphotic depths from two polar carbonate factories in Svalbard waters. A remarkably low ichnodiversity was observed in shallow euphotic waters, which is herein explained by limitations in the availability of multiannual balanids as substrate and by the harsh environmental conditions characterized by a lack of PAR during the polar night, low and fluctuating temperatures and the influence of sea ice. Light availability is the most significant factor for the establishment of different microbioerosion trace assemblages in different water depths. The extreme light regime and low temperatures led to a depletion of particularly the phototrophic microborer spectrum that lacks several of the “usual suspects” among the ichnotaxa commonly encountered in lower latitudes. Overall, this results in a comparatively low ichnodiversity that accords with a general decrease in ichnodiversity towards higher latitudes. More studies, considering different types of substrate, further polar sites in both hemispheres and studies of the bioerosion rate, are needed to gain a more complete picture of the role of bioerosion in polar carbonate factories.

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Disclosure statement

The authors report no conflict of interest.

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5.6 References

References are listed at the end of this thesis.

Chapter 6
Bioerosion ichnodiversity in barnacles from the Ross Sea, Antarctica

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Abstract

Breakdown of skeletal and lithic hard substrates by organisms, known as bioerosion, is part of the global carbon cycle and gets more and more attention, but little is known about the process of bioerosion in polar environments. Here, we study bioerosion traces (addressed as ichnotaxa) recorded in the barnacle *Bathylasma corolliforme* from the Ross Sea, Antarctica. Traces were visualized via scanning electron microscopy of epoxy casts prepared with the vacuum cast-embedding technique. In 50 samples from shallow 37 m to bathyal 1680 m water depths, 16 different bioerosion traces were found, classified into microborings presumably produced by cyanobacteria (1), chlorophytes (1), fungi (9), foraminifera (1), unknown organotrophs (5), and macroborings produced by cirripeds (1). Statistical ichnodiversity analysis resulted in a significant (p = 0.001) ANOSIM with moderate differences (R = 0.5) between microbioerosion trace assemblages at different water depths and revealed two main clusters (NMDS, SIMPROF) equivalent to the photic and aphotic stations. A comparison between this study and a corresponding study from the Svalbard archipelago, Arctic Ocean, shows that the ichnodiversity in calcareous barnacle skeletons is similar in polar waters of both hemispheres. This includes several ichnotaxa that are indicative for cool- to cold-water environments, such as *Flagrichnus baiulus* and *Saccomorpha guttulata*. Thereby, nine of the investigated ichnotaxa occur in both polar regions and seven ichnotaxa show a bathymetrical range down to the deep sea at bathyal 1680 m water depth.

Keywords

Ichnology · Microborings · Ross Sea · Antarctica · trace fossil assemblage · *Bathylasma corolliforme*

6.1 Introduction

Bioerosion is the degradation of hard substrates by organisms (Neumann 1966) and thus a process that is part of the global carbon and carbonate cycles with a great impact on the preservation of calcareous substrates in the sedimentary record (e.g. Warme 1975; Hutchings 1986; Tribollet 2008). The various bioeroding organisms utilise a wide range of strategies to bioerode by chemical (biocorrosion) and/or mechanical (bioabrasion) means and are categorised primarily into grazers (e.g. echinoids, gastropods), macroborers (e.g. sponges, worms) and microborers (e.g. fungi, bacteria, algae). The two latter categories are divided by the traces that are left behind in calcareous, siliceous, osteic, and xylic hard substrates, as microbioerosion traces are < 1 mm with a common diameter of tunnels < 100 µm (Wisshak 2012). The traces have a high fossilization potential and are addressed as trace fossil ichnotaxa, with more than 300 valid ichnospecies established so far (Wisshak et al. 2019a).

Bioerosion is a process on a global scale and there are comprehensive studies for trace fossil assemblages for tropical environments (e.g. Kiene & Hutchings 1994; Chazottes et al. 1995; Vogel et al. 2000; Tribollet & Golubic 2005), and warm-temperate regions, such as the Azores (Wisshak et al. 2011) and the Mediterranean Sea (Färber et al. 2015). Besides few studies in the North Atlantic (e.g. Akpan & Farrow 1985; Schmidt & Freiwald 1993; Glaub et al. 2002; Beuck & Freiwald 2005; Wisshak 2006) and North Pacific (e.g. Young & Nelson 1988), the cold-temperate regions are poorly studied and the polar regions even less. There is a bioerosion study from the Canadian Arctic (Aitken & Risk 1988), while the Svalbard archipelago in the far North was subject of a study with a focus on polychaete bioerosion (Hanken et al. 2012) and a more comprehensive microbioerosion study (Meyer et al. 2020). Bioerosion research in cooler environments predominantly concentrated on the Northern Hemisphere, whereas the Southern Hemisphere was disregarded for a long time. Few studies were conducted in the cold-temperate region Patagonia (e.g. Malumián et al. 2006; Richiano et al. 2017; Aguirre et al. 2019) and in the polar region Antarctica. A bioeroded bryozoan trace was observed on Seymour Island, Antarctica (Casadío et al. 2001), and bioerosive activities were recorded in the Ross Sea in a scallop and mollusc (Cerrano et al. 2001), and skeletal material (Frank et al. 2014; Frank et al. 2020). We are not aware of further bioerosion studies in the Antarctic, although knowledge of bioerosion patterns in the Southern Hemisphere will allow a direct comparison between both polar regions and determine tolerance limits for key bioerosion traces. Both aspects will help to understand the role of bioerosion in polar environments and therefore foster the knowledge of bioerosion from a local to a global scale.

We have visualised bioerosion traces by means of the cast-embedding technique under a scanning electron microscope to: (I) compile an extensive list of bioerosion traces preserved in barnacles from the Ross Sea, Antarctica; (II) provide data on the bathymetrical range of

these ichnotaxa down to bathyal water depths; (III) statistically analyse the ichnodiversity along this bathymetrical transect (37–1680 m); and (IV) compare our findings with those of a similar study from the Arctic Svalbard archipelago.

6.2 Materials and methods

6.2.1 Study site

Our samples were recovered in the Ross Sea sub-division of the Southern Ocean, between Marie Byrd Land and Victoria Land, towards the Pacific part of the Southern Ocean, south of New Zealand (Figure 6-1). Although it is one of Antarctica's most intensively studied regions (Smith Jr. et al. 2007), it is an area with a very low human impact (Halpern et al. 2008).

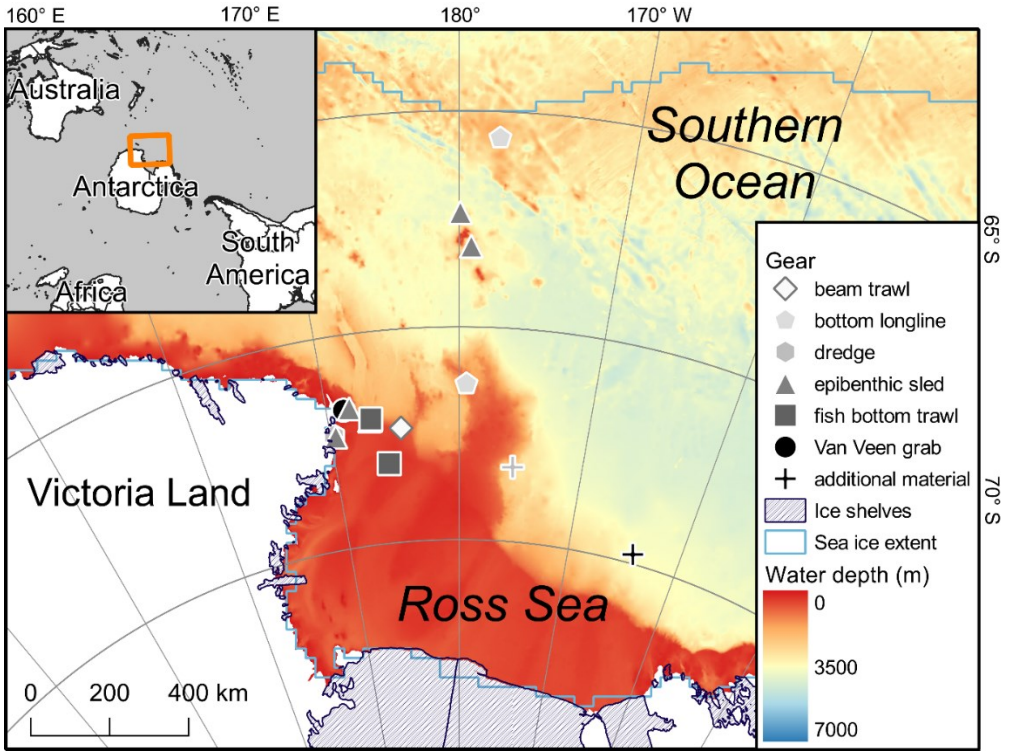

Figure 6-1 Map of sample locations in the Ross Sea, Antarctica, including stations for sample collection and applied gear of recovery (more details in Table 6-1). Locations of additional material, not utilised for the statistical analyses, are indicated with crosses. Bathymetric data was retrieved from Arndt et al. (2013), ice shelves data for 2017 from Mouginot et al. (2017), and the sea ice extent for July 2019 from Fetterer et al. (2017).

The Ross Sea covers a broad continental shelf and water depth is shallower in the West than in the East (Figure 6-1). The oceanography is governed by two clockwise rotating gyres over the continental shelves, which are synchronized with the bigger nearby Ross Sea Gyre. The gyre is driven by the westerly winds of the Antarctic Circumpolar Current (as reviewed by Smith Jr. et al. 2012).

Water temperatures range from -1.9 to +3.2 °C and salinity ranges from 34.0 to 34.9 (Smith Jr. et al. 2007; Smith Jr. et al. 2012). The base of the euphotic zone, where light intensity declines to 1% of the surface illumination, is at a mean of 34 ± 13 m in spring, at ca. 26 ± 9 m in summer (Smith Jr. et al. 2013), and at 14–66 m in winter (Fabiano et al.

1993), depending on seasonal variations (inter alia due to turbidity and nutrient availability, hence plankton blooms) and exact location within the Ross Sea (El-Sayed et al. 1983). The aphotic zone, below a transitional dysphotic zone, is below ca. 100 m water depth (according to Azzaro et al. 2006).

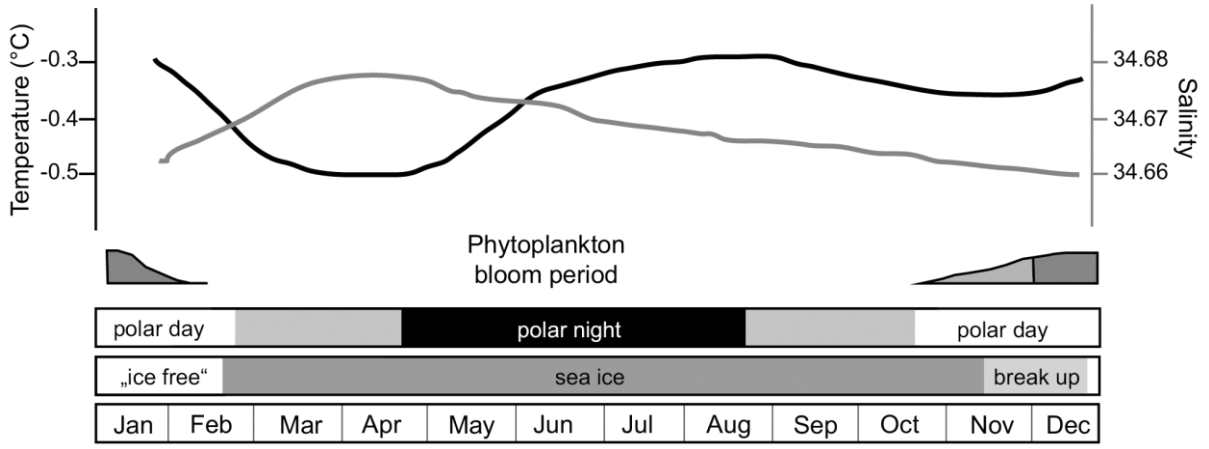

Figure 6-2 Schematic overview of key environmental parameters in the Ross Sea, Antarctica. Fig. 2 in Gordon et al. (2015) was traced for temperature and salinity data (from 500 m water depth); phytoplankton bloom is based on Asper & Smith Jr. (1999) with the highest peak in mid-December to much lower levels in January to February; polar night and day data for 2004 retrieved from Thorsen (1995–2020); sea ice data for 2004 obtained via Fetterer et al. (2017) – in January, there was still some sea ice left, but the Ross Sea was mostly ice-free.

The Ross Sea is Antarctica's biologically most productive region and has the greatest phytoplankton biomass (Smith Jr. et al. 2000; Smith Jr. et al. 2014). Besides polar day and night, important seasonal and extreme features in the Ross Sea are sea ice (Figure 6-2) and polynyas, known as unfrozen regions in an ice pack. Sea ice impedes the exchange of heat and works as an insulator between ocean and atmosphere, as well as affecting life in polar environments (Parkinson 2004). During winter, the sea ice extent reaches up to 60°S (Smith Jr. et al. 2007; Frank et al. 2014; Figure 6-1) and except for the most eastern parts, the Ross Sea is almost completely free of sea ice in January and February (Figure 6-2; Parkinson 2004; excluding the Ross Ice Shelf).

6.2.2 Sample material

Our chosen substrates were barnacles, as several studies showed that they are well suitable for bioerosion analyses (e.g. Glaub et al. 2002; Feussner et al. 2004; Meyer et al. 2020). Specimens were kindly provided by the Invertebrate Collection at the National Institute of Water and Atmospheric Research (NIWA) in Wellington, New Zealand. Barnacles were sampled from different water depths with different gear and during various cruises between 1965 and 2008 (Table 6-1, Figure 6-1). Barnacles were (mostly) recovered alive and thus record the trace fossil assemblages from the actual water depth of sampling. Samples from the collection were stored in ethanol and evaporated prior to shipping. Additional material kindly provided by Marco Taviani comprised broken barnacle shells from sediments that

might have experienced considerable transport (Figure 6-1, Table 6-1) and, therefore, were excluded from the statistical analysis.

Table 6-1 List of analysed *Bathylasma corolliforme*, including water depth during recovery, station ID, date of collection, coordinates (at start of deployment), and gear. The latter two entries list data for the additional sample material, not utilised for the statistical analyses.

Depth (m)	Station ID	Collection Date	Latitude	Longitude	Gear	No. of samples
37	E182	19/01/1965	-72.305	170.271	dredge, cone mesh with bag	4
154	TAN0402/52	12/02/2004	-72.337	170.394	epibenthic sled	4
277	TAN0402/30	09/02/2004	-71.746	171.291	Van Veen grab	4
321	TAN0802/17	09/02/2008	-73.125	174.321	fish bottom trawl	4
466	TAN0402/15	05/02/2004	-71.728	171.735	epibenthic sled	4
538	TAN0402/74	14/02/2004	-72.073	173.136	epibenthic sled	4
620	TAN0402/72	13/02/2004	-72.061	173.245	epibenthic sled	4
770	TAN0402/85	14/02/2004	-72.037	173.249	fish bottom trawl	4
879	TAN0802/206	03/03/2008	-68.121	-179.248	epibenthic sled	3
980	TAN0802/129	21/02/2008	-72.317	175.489	beam trawl	3
1130	TAN0802/256	08/03/2008	-67.340	-179.932	epibenthic sled	4
1310	TRIP2731/49	13/01/2009	-71.332	-179.475	bottom longline	4
1680	TRIP2730/9	09/12/2008	-65.603	-177.710	bottom longline	4
214	CARBONAT_Carb10	16/01/2002	-74.783	-164.170	Van Veen grab	4
389	CARBONAT_Carb34	16/01/2002	-73.243	-175.639	dredge	4

We concentrated on the acorn barnacle species *Bathylasma corolliforme* (Hoek, 1883) as substrate, attached to i.e. rocks or sponges. *B. corolliforme* is relatively large (up to10 cm) with a long lifespan (Burgess et al. 2010; Frank et al. 2014), although no results on growth rates and longevity are available. The biology of *B. corolliforme* is poorly understood (Burgess et al. 2010), but calcification likely slows down or stops in winter due to lowered food availability. *B. corolliforme* is the predominant barnacle species in the Ross Sea (Dayton et al. 1982; Taviani et al. 1993), and an endemic circumpolar species from south of the Antarctic convergence (Newman & Ross 1971; Dayton et al. 1982). Barnacles are relatively rare in Antarctica, especially in shallow water depths (Newman & Ross 1971). While earlier studies have stated that *B. corolliforme* does not live in depths of less than 100 m (Newman & Ross 1971; Dayton et al. 1982), more recent studies and our sample material (Table 6-1) demonstrate that they are found at least as shallow as 37 m (Burgess et al. 2010; Frank et al. 2014). Current velocities, and thus nutrient availability, are likely decisive for their vertical distribution (Dayton et al. 1982). However, also iceberg scouring is an important disturbance in shallower water depths. Up to 70% of the sea floor from 20 to 25 m in McMurdo Sound are affected, though the Terra Nova Bay shows nearly no disturbances (as reviewed by Smith Jr. et al. 2007). The maximum keel depth at the floating margins (hence potential icebergs) of the Ross Ice Shelf was recorded as 255 ± 52 m thick (Dowdeswell & Bamber 2007).

6.2.3 Cast-embedding technique

The cast-embedding technique is a common method to visualise bioerosion traces (Golubic et al. 1970; Wisshak 2006, 2012). The barnacles were soaked for 24 hours in sodium hypochlorite (customary cleaning agent) to remove organic material and afterwards rinsed several times with deionised water. The cleaned skeletal elements were dried at 30 °C in a drying cabinet. The bioeroded tunnels inside the barnacle armour were subsequently filled with R&G "water clear" epoxy resin in a CitoVac (Struers) vacuum chamber. The samples cured for 4–5 days before dissection with a rock saw. During treatment with ca. 5% hydrochloric acid, the calcareous barnacles shell dissolved, and the pieces fell apart. Fifty samples were sputter-coated with gold (Cressington sputter coater 108) and analysed under a scanning electron microscope (SEM, Tescan VEGA3 xmu) using the secondary electron detector at 20 kV acceleration voltage.

6.2.4 Identification, quantification and statistical analyses

Bioerosion traces were identified on ichnospecies level and morphological forms yet untreated in ichnotaxonomy were assigned to informal names. We conducted a semi-quantitative analysis, because an actual quantification is unfeasible for bioerosion traces (due to a wide range of sizes, colonies vs. single borings, etc.), and gathered ordinal data in that each ichnotaxon/form recorded in each sample were categorised into one of five abundance classes (absent = 0; very rare, only one or very few specimens = 1; rare, few specimens = 2; common, many specimens but not dominant = 3; very common or dominant = 4), following the approach of assessing ichnodiversity outlined by Wisshak et al. (2011) and Meyer et al. (2020).

To analyse our data as a multivariate data set, we used each sample individually. We utilised R version 3.6.2 (R Core Team 2019) and the package "MVN" (Korkmaz et al. 2014) to perform both Mardia and Royston multivariate normality tests. Data was not transformed, because they are on an ordinal scale, and transformation is not required for the following non-parametric tests. The package "vegan" (Oksanen et al. 2018) was used for ANOSIM (ANalysis Of SIMilarities; with 999 permutations) and for the NMDS (Non-metric Multi-Dimensional Scaling) plots, whilst the package "clustsig" (Whitaker & Christman 2014) was used for the cluster analyses with SIMPROF (SIMilarity PROFile; with the cluster method 'average'). Prior to the tests, we computed a Bray-Curtis dissimilarity matrix with "vegan", which is common practice for an ANOSIM (Hammer & Harper 2008; Greenacre & Primicerio 2013). The biodiversity indices (i.e. ichnodiversity indices) Margalef's richness index *d*, Simpson index of dominance λ and diversity $1\text{-}\lambda$, Shannon index $H'(\log_e)$, and Pielou's evenness *J'* were also calculated with R. We computed the indices based on ranked semi-quantitative abundance data by transforming the abundance classes as follows (based on Wisshak et al. 2011): '4' to 1000; '3' to 100; '2' to 10, and '1' as 1 per sample. Subsequently,

we calculated means per water depth and a grand mean. As indices are usually based on counts of specimens (Hammer & Harper 2008), this approach allows an evaluation of relative abundance.

6.3 Results

6.3.1 List of bioerosion traces

Table 6-2 List of ichnotaxa recorded from the Ross Sea, together with the inferred or assumed (in brackets) trace-makers, based on the original interpretation of the ichnotaxon authority, and some descriptive remarks with respect to differences in morphology compared to the original diagnoses. The last two ichnotaxa in the list were noted in additional sample material and are listed for completeness, but not included in the statistical analysis.

Trace-maker	Ichnotaxon	Remarks	Figure
Cyanobacteria *Hyella gigas*	*Fascichnus frutex* (Radtke, 1991)	-	6-3a
Chlorophyte *Ostreobium quekettii*	*Ichnoreticulina elegans* (Radtke, 1991)	the surface was rarely a bit fuzzy	6-3b
(Fungi)	*Flagrichnus baiulus* Wisshak & Porter, 2006	highly diverse, occasionally "dendritic" form, rarely with undescribed elongated chambers	6-4a–c
(Fungi)	*Flagrichnus* cf. *baiulus*	see text	6-4d
(Fungi)	*Flagrichnus*-form I	see text	6-4e
Fungi *Dodgella priscus*	*Saccomorpha clava* Radtke, 1991	sometimes a pronounced collar around the base	6-4f
(Fungi)	*Saccomorpha guttulata* Wisshak et al., 2018	occasionally similarities to young stage of *Polyactina araneola*	6-4g
(Fungi)	*Orthogonum*-form I *sensu* Wisshak et al., 2005	see text	6-4h
(Fungi)	*Orthogonum lineare* Glaub, 1994	-	6-4i
(Fungi)	*Orthogonum giganteum* Glaub, 1994	-	6-4j
Fungi *Conchyliastrum merritti*	*Polyactina araneola* Radtke, 1991	highly diverse, occurred at different stages	6-4k–l
(Foraminifera)	*Pyrodendrina villosa* Wisshak, 2017	-	6-3c
Unknown	Finger-form	see text	6-3e–f
Unknown	Nidus-form	see text	6-3g–h
Unknown	Proturbero-form	see text	6-3i
Acrothoracid barnacles	*Rogerella* isp. de Saint-Seine, 1951	macroboring	6-3d
(Bacteria)	*Scolecia serrata* Radtke, 1991	observed in additional sample material	6-3j
Unknown	Clavate-form	observed in additional sample material, see text	6-3k–l

We recorded sixteen different bioerosion traces (respectively ichnotaxa) in our samples, one of them was presumably produced by cyanobacteria, one by chlorophytes, nine by fungi, one by foraminifera, one by barnacles, and three unknown forms were produced by unidentified organotrophs and listed with informal names (Table 6-2).

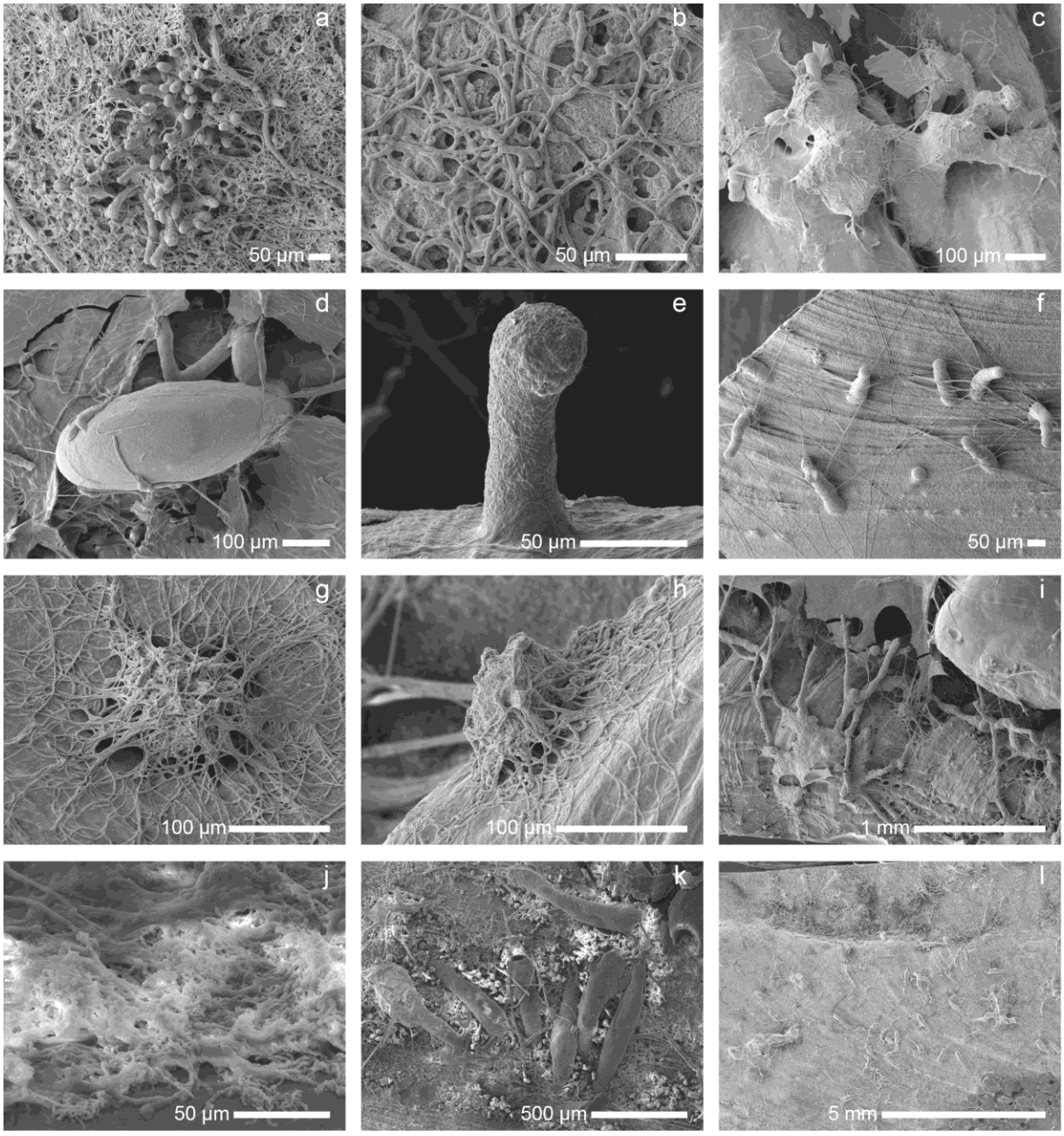

Figure 6-3 Microborings produced (inferred or assumed) by cyanobacteria, chlorophytes, barnacles, bacteria, or unknown organotrophs **a** *Fascichnus frutex* from 37 m water depth **b** *Ichnoreticulina elegans* from 37 m water depth **c** *Pyrodendrina villosa* from 466 m water depth **d** *Rogerella* isp. from 466 m water depth **e** Finger-form from 879 m water depth **f** Finger-form from 277 m water depth **g** Nidus-form from 620 m water depth **h** Lateral view of Nidus-form from 620 m water depth **i** Proturbero-form from 466 m water depth **j** *Scolecia serrata* from additional sample material **k** close-up of Clavate-form from 214 m water depth **l** Clavate-form from 214 m water depth.

Detailed results of the semi-quantitative analysis of the bioerosion traces are provided in Table 6-3. The ichnocoenoses and ichnodiversity varied between water depths, with the highest ichnospecies richness at 466 m (12 different traces), the second largest ichnospecies richness at 277 m (seven traces), and the lowest diversity at 980 m (two traces). Whilst ichnotaxa presumably produced by photosynthesising bioeroders at shallow water depths (*Fascichnus frutex*, *Ichnoreticulina elegans*) were very rare, those by organotrophic fungi

were the dominant microborings, e.g. *Flagrichnus baiulus* and *Saccomorpha guttulata*, both almost consistently occurring in the whole water column (Table 6-3). *Flagrichnus baiulus*, *Flagrichnus* cf. *baiulus*, *Saccomorpha clava*, and Finger-form were recorded at the deepest water depth.

Table 6-3 Results of semi-quantitative analysis of bioerosion traces in the Ross Sea. Abundances are categorised as '++' = very common, '+' = common, '-' = rare, and '--' = very rare, excluding data from the additional sample material.

Ichnotaxon/form	Water depth (m)												
	37	154	277	321	466	538	620	770	879	980	1130	1310	1680
Fascichnus frutex (Radtke, 1991)	--												
Ichnoreticulina elegans (Radtke, 1991)	++												
Flagrichnus baiulus Wisshak & Porter, 2006		+	-	-	--	-	-	--	--	--	-	+	-
Flagrichnus cf. *baiulus*		--	--	--	--	-	--				--	--	-
Flagrichnus-form I			--		--	--		--					
Saccomorpha clava Radtke, 1991						--			--		--	++	--
Saccomorpha guttulata Wisshak et al., 2018		-	--	--	++	-	--	--	-	--	-	++	
Orthogonum-form I *sensu* Wisshak et al., 2005					--		--	--					
Orthogonum lineare Glaub, 1994					--				--		--	--	
Orthogonum giganteum Glaub, 1994	--		--		--								
Polyactina araneola Radtke, 1991					-			--	-		-	-	
Pyrodendrina villosa Wisshak, 2017	--	--	--		-								
Finger-form	--	--	--		--				--				--
Nidus-form	--						--						
Proturbero-form					--								
Rogerella isp. de Saint-Seine, 1951					-								
Number of ichnotaxa/forms		5	7	3	12	5	5	5	6	2	6	6	4

The following bioerosion traces did not match established ichnotaxa diagnoses and are briefly described in open nomenclature (e.g. cf.) or under informal names in the following account. Potential comments regarding differences in morphology to the known and diagnosed ichnotaxa are provided in Table 6-2.

Flagrichnus cf. *baiulus*

The diagnostic long, thin, filamentous tube of *Flagrichnus baiulus* that usually extends deep into the substrate lacks in this trace, but as the typical sac-shaped cavities are still the main morphologic feature, this microboring is referred to as *Flagrichnus* cf. *baiulus*. An

additional characteristic are thin filaments in the circumference, which are more fanned out than described in the original diagnosis (Figure 6-4d; Meyer et al. 2020).

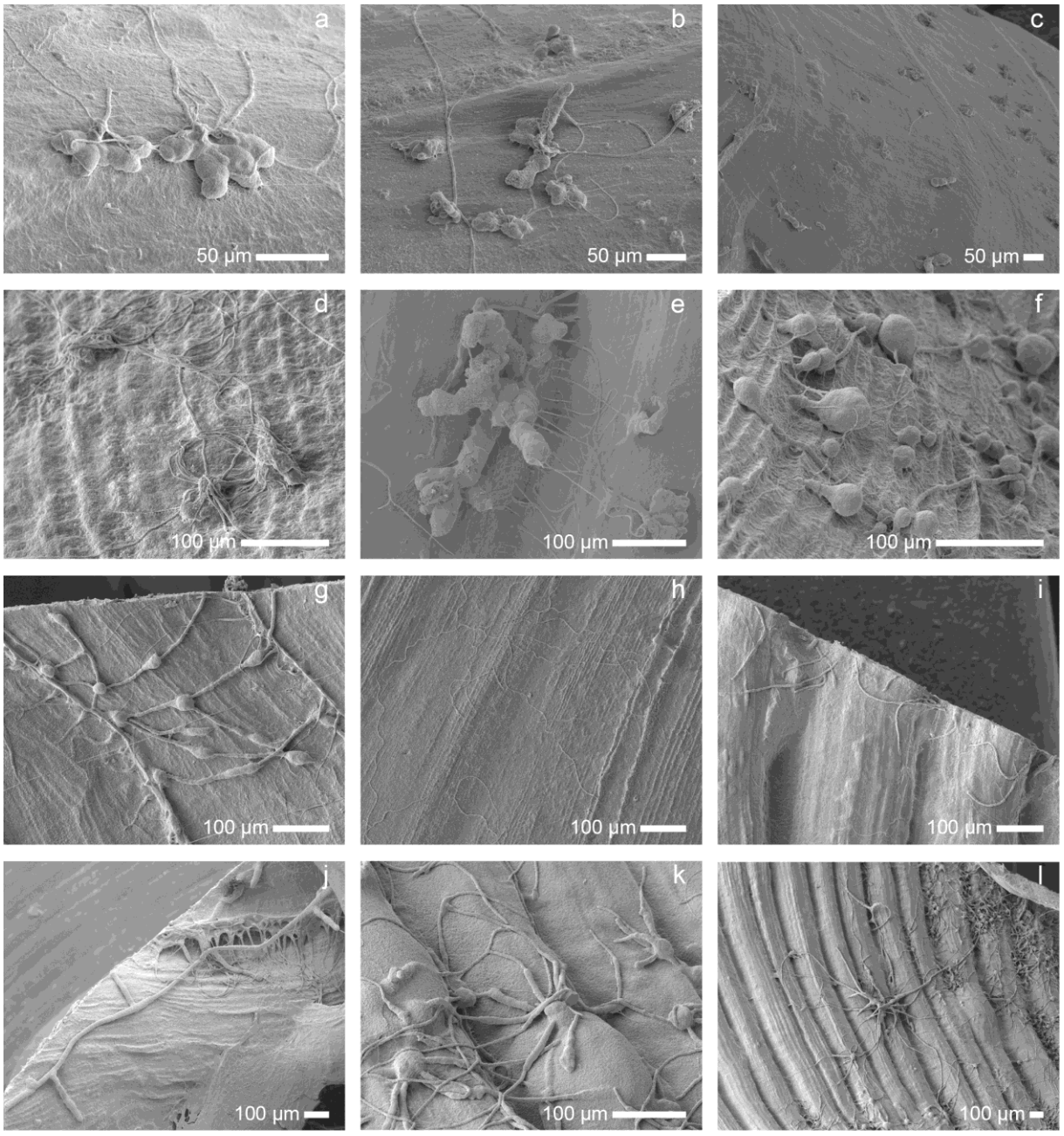

Figure 6-4 Microborings of inferred or assumed fungal origin **a** *Flagrichnus baiulus* from 154 m water depth **b** *Flagrichnus baiulus* from 1130 m water depth with atypical elongated chambers **c** *Flagrichnus baiulus* from 1130 m water depth **d** *Flagrichnus* cf. *baiulus* from 1130 m water depth **e** *Flagrichnus*-form I from 466 m water depth **f** *Saccomorpha clava* from 1310 m water depth **g** *Saccomorpha guttulata* from 980 m water depth **h** *Orthogonum*-form I from 620 m water depth **i** *Orthogonum lineare* from 879 m water depth **j** *Orthogonum giganteum* from 277 m water depth **k** juvenile stage of four *Polyactina araneola* from 879 m water depth **l** adult stage of *Polyactina araneola* from 879 m water depth.

Flagrichnus-form I

Flagrichnus-form I is another microboring with affinity to the ichnogenus *Flagrichnus*. It has similar characteristics, but bigger (> 15 µm) sac-shaped cavities (Wisshak & Porter 2006), which merge to a greater extent. The trace is up to 150 µm in diameter (Figure 6-4e).

Orthogonum-form I *sensu* Wisshak et al., 2005

Orthogonum-form I runs wavy and closely parallel to the substrate, with a tunnel diameter of 3–5 µm. This microboring was also recognised by Wisshak et al. (2005) and Meyer et al. (2020)(Figure 6-4h).

Finger-form

This single-tunnel-trace has the morphology of fingers and occasionally occurs in a cluster of up to 10. It penetrates straight and deep into the substrate (up to 200 µm) and is up to 50 µm wide at the base, slightly thinning towards the convex ends (Figure 6-3f).

Nidus-form

Nidus-form has a certain resemblance to a nest (lat. "nidus"). The trace is a pit-shaped boring > 175 µm in diameter, almost completely covered by thin filaments (tunnel width: 1–3 µm), which form a bundle on top of the pit, before they run closely parallel to the substrate for several mm (Figure 6-3g–h).

Proturbero-form

The Proturbero-form (lat. "stand out") is comparatively large. The tunnel-system with widths of up to 75 µm is irregular with bulbous swellings in the course. Bifurcations are often rectangular, but sometimes the tunnels split randomly into two to four. The beginning of the tunnels is usually wider and gets thinner towards the bifurcations (Figure 6-3i).

Additional sample material

We also investigated few additional samples from the Ross Sea (Figure 6-1, Table 6-1). However, therein observed ichnotaxa were excluded from the semi-quantitative and subsequent statistical analysis, because the samples were isolated barnacle skeletal elements from sediment samples that do not necessarily record the actual water depth of the living animal. We recorded two further microborings, which were not noticed in the other material, and added them to the ichnotaxa list from the Ross Sea. We found *Scolecia serrata* Radtke, 1991 by (inferred) bacteria, and an unknown bioerosion trace:

Clavate-form

This bioerosion trace has planar and slightly clavate tunnels with convex ends, which are wider than 100 µm (> 160 µm), with a length of up to 830 µm. They run either parallel or are collapsed to the substrate surface. In the single sample, they occur irregularly in clusters, occasionally parallel or crossing each other. In two cases, several tunnels emerged from a deformed central point of entry (Figure 6-3k–l).

6.3.2 Statistical ichnodiversity analyses

As the Mardia and Royston normality tests both resulted in $p < 0.001$, normality was rejected, and we performed the non-parametric, multivariate ANOSIM to statistically test

differences between groups (= water depths). ANOSIM resulted in R = 0.5022 with a significance = 0.001 (significant). The possible and actual permutations were 35.

Table 6-4 Calculated means of ichnodiversity indices of ichnotaxa in the Ross Sea per water depth, with a grand mean and a mean without the shallow water samples.

Water depth (m)	Ichnospecies richness *S*	Margalef's richness index *d*	Simpson index of dominance *λ*	Simpson index of diversity *1-λ*	Shannon index *H'(log$_e$)*	Pielou's evenness *J'*
37	3.00	0.29	0.99	0.01	0.04	0.03
154	3.50	0.84	0.76	0.24	0.41	0.42
277	3.25	1.35	0.47	0.54	0.90	0.82
321	1.25	0.48	0.88	0.13	0.17	1.00
466	6.25	0.94	0.72	0.28	0.55	0.34
538	3.50	1.20	0.50	0.50	0.89	0.73
620	2.25	0.76	0.72	0.28	0.49	0.65
770	2.50	1.81	0.52	0.48	0.80	1.00
879	3.00	0.54	0.67	0.33	0.55	0.50
980	1.67	1.44	0.67	0.33	0.46	1.00
1130	3.75	0.90	0.57	0.43	0.76	0.66
1310	4.75	0.55	0.60	0.41	0.72	0.47
1680	2.25	1.31	0.57	0.43	0.66	0.93
Grand mean	3.15	0.96	0.66	0.34	0.60	0.66
w/o 37 m	3.16	1.01	0.64	0.36	0.61	0.71

The NMDS result (Figure 6-5a) together with the cluster analysis with SIMPROF (Figure 6-5b) show a clear distinction in two clusters, a small one for the few samples from the photic zone and a more widely scattered one for all aphotic stations. In the SIMPROF (Figure 6-5b) analysis, the two respective main branches diverge at height 3.48. There is sub-clustering below height 2.5 within the branch that contains all the aphotic stations that appear independent of the water depth without any other obvious difference.

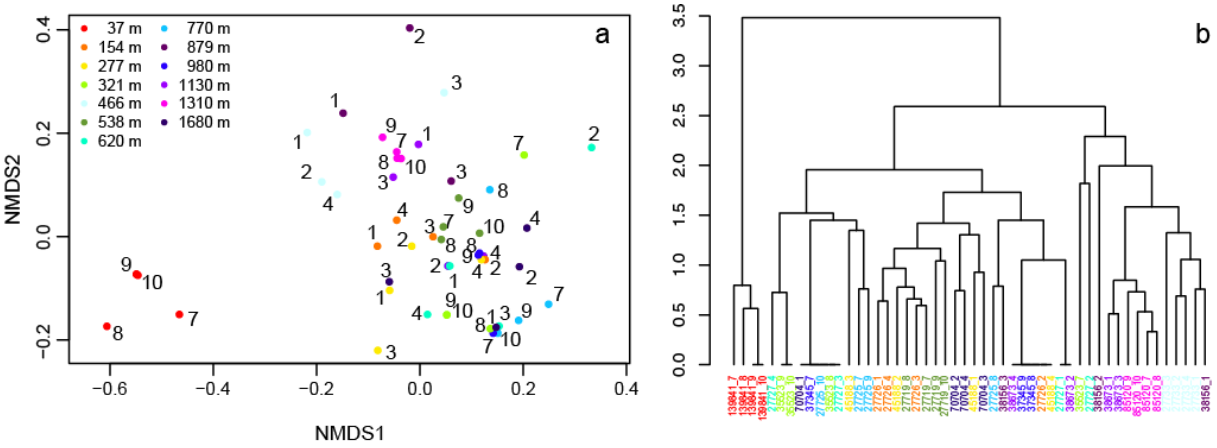

Figure 6-5 NMDS plots for the **a** ichnodiversity at Ross Sea and respective results of the cluster analyses with **b** SIMPROF, with two principal clusters represented by all stations from the photic zone versus those from the aphotic zone. Several clusters of points were drawn apart for the purpose of presentation, as some of the dots were on top of each other.

Besides samples from 466 m with high species richness, the (ichno)diversity indices yielded similar values along the bathymetric transect, though varying within the same water depth (not shown herein). The Shannon index $H'(\log_e)$ and Pielou's evenness J' vary a little more than the Simpson indices (details in Table 6-4). However, there is an overall trend of a decreasing Simpson index of dominance λ and a general increase of the Shannon index $H'(\log_e)$ from the photic to greater water depths. Thus, the shallowest station has a high dominance of one single dominant taxon (λ close to 1; *Ichnoreticulina elegans*) and low diversity ($1-\lambda$ close to 0; $H'(\log_e)$ close to 0).

6.4 Discussion

6.4.1 Ichnotaxa from the Ross Sea

The wide continental shelf of the Ross Sea is in an extreme environment regarding the seasonal formation of sea ice and the variable light regime including polar night and day. It is one of the most comprehensively studied regions of the Southern Ocean and has a comparatively high species richness (Clarke et al. 2007). However, the process of bioerosion and the ichnodiversity of bioerosion traces have received very little attention, a fact that applies for entire Antarctica.

Sixteen different microbioerosion traces were observed in barnacles from the Ross Sea. One of the traces was bioeroded by chlorophytes, one by cyanobacteria, nine by fungi, one by foraminifera, one by barnacles, and three traces are yet of unknown affinity. Two further microborings were noticed in additional sample material – one by bacteria and one of unknown origin (Table 6-2, Figure 6-3, Figure 6-4). Finger-, Nidus-, and Proturbero-form are unspecified yet and have no similarity to the morphology of any known ichnotaxa. *Fascichnus frutex* and *Ichnoreticulina elegans* are ichnotaxa bioeroded by phototrophic cyanobacteria and chlorophyte algae, respectively, and account for the smallest share of the ichnospecies richness (Table 6-2), whereas fungal microborings constitute the largest share.

We do not entirely agree with the few identifications of (micro)bioerosion traces in previous studies from the Ross Sea, which listed *Trypanites*, *Scolecia serrata*, *Flagrichnus baiulus*, and microborings by sponges (Frank et al. 2014; Frank et al. 2020). The investigated two-dimensional thin sections bear limitations in addressing three-dimensional bioerosion traces. In particular, we doubt the identification of sponge borings (fig. 9c in Frank et al. 2014; fig. 7a and b in Frank et al. 2020) and suggest that those "forms of branching galleries" (Frank et al. 2020) are in fact internal canals of stylasterid coral such as those visualised in Wisshak et al. (2009; fig. 5) with the cast-embedding technique. In our opinion, fig. 9b in Frank et al. (2014) and fig. 7a in Frank et al. (2020) do not allow a clear assignment to *Trypanites*. Furthermore, we would tentatively identify the trace assigned to *F. baiulus* in fig. 7c in Frank et al. (2020) as *Saccomorpha guttulata* (Wisshak et al. 2018; Chapter 4). The identification of *Scolecia serrata* in fig. 7d in Frank et al. (2020) appears reasonable, but it is

an ichnotaxon and not its producer. The bioerosion traces illustrated in fig. 1 by Cerrano et al. (2001) are difficult to address but likely show *Ichnoreticulina elegans*, a very common trace produced by the chlorophyte alga *Ostreobium quekettii*. Hence, there are no reports of ichnotaxa from Antarctica in the literature that would complement the microbioerosion trace diversity we have recorded from the Ross Sea.

6.4.2 Bathymetric distribution of ichnotaxa

The bathymetric distribution of ichnotaxa in our study is similar to the usual bathymetric zonation pattern of microendolithic borings, which comprises typically a dominance of cyanobacterial borings from the supratidal down to the deep euphotic zone, complemented by chloro- and rhodophyte borings in the euphotic down to the dysphotic zone, and the exclusive occurrence of traces formed by fungi and other organotrophs in the aphotic zone (e.g. Golubic et al. 1975; Schmidt 1992; Glaub 1994; Vogel et al. 2000; Glaub et al. 2002; Wisshak 2012).

Fascichnus frutex and *Ichnoreticulina elegans* are the only ichnotaxa by photosynthesising organisms and were exclusively recorded in the upper water column (photic zone). Their trace-makers, the cyanobacterium *Hyella gigas* Lukas & Golubic, 1983 and the chlorophyte alga *Ostreobium quekettii* Bornet & Flahault, 1889, respectively, appear to cope well with the polar night and its almost complete absence of photosynthetic active radiation (Figure 6-2). The photic zonation at such a high latitude is strongly condensed, so that only our 37 m station was within the photic zone. Barnacles are rare in that zone of the Ross Sea (Newman & Ross 1971), because of sea ice abrasion (Smith Jr. et al. 2007) and strong currents (Dayton et al. 1982). More samples from shallower depths would probably have led to the recognition of further microborings of phototrophic euendoliths, thus our present inventory has a shortcoming for the shallow euphotic zone.

The vast majority of microborings in aphotic waters with known trace-makers are produced by organotrophic organisms (e.g. Golubic et al. 1975; Schmidt 1992; Glaub et al. 2002; Beuck & Freiwald 2005), such as fungi. They thrive in all environments and are very stable towards varying environmental conditions, which is confirmed by the often cosmopolitan distribution of their traces (Table 6-3; Golubic et al. 2005; Wisshak 2012). Fungi are independent of light, but dependent on substrates with organic content to feed on (as reviewed by Golubic et al. 2005). Trace-makers are not yet known for all recorded ichnotaxa assigned to a fungal producer (Table 6-2), although an organotrophic producer is inferred from the trace morphology and occurrence down to bathyal water depths. For the Finger-, Nidus-, and Proturbero-form, we likewise assume an organotrophic trace-maker due to their distribution in the aphotic zone.

We provide first observations of several ichnotaxa (e.g. *Flagrichnus baiulus*, *Saccomorpha clava*) for the deep sea down to water depths of 1680 m. *Saccomorpha clava* and *Saccomorpha guttulata* are very abundant at 1310 m, co-existing with *Polyactina araneola*,

Orthogonum lineare, and *Flagrichnus baiulus* and *Flagrichnus* cf. *baiulus* (Table 6-3), all bioeroded by organotrophic trace-makers (likely fungi). *Flagrichnus baiulus* is so far the only ichnotaxon found at deeper water depths (3266 m; Hook & Golubic 1993). Previous microbioerosion studies that have identified microbioerosion traces were conducted in shallower water depths in, for instance, the Bahamas (210 to 1450 m; Zeff & Perkins 1979), Puerto Rico (down to 500 m; Budd & Perkins 1980), the western North Atlantic Ocean (down to 871 m; Hook et al. 1984), the Porcupine Seabight (northeastern Atlantic Ocean, down to 650 m; Beuck & Freiwald 2005), and the Azores (down to 500 m; Wisshak et al. 2011). Although these studies were not conducted in high latitudes or in the Southern Hemisphere, the same microborings (as *Saccomorpha clava* in Zeff and Perkins, 1979 or *Flagrichnus baiulus* in Hook and Golubic, 1993) were detected, because the deep sea has similar environmental parameters at all latitudes as far as cold temperatures and an aphotic light regime is concerned.

It is a widespread conception that biodiversity decreases with water depth. However, for benthic invertebrates in the Southern Ocean, it has been shown that bivalves, gastropods, and polychaetes have a roughly constant species richness from between 1000 and 6000 m water depth (Brandt et al. 2009). Our results suggest that this applies also for the ichnodiversity of microbioerosion traces between 154 and 1680 m water depth in the Ross Sea (Table 6-3).

6.4.3 Statistical evaluation of the bioerosion ichnodiversity

As an aim of this study is a comparison between the high latitudes in the North and the South, we applied the same statistical outline as Meyer et al. (2020), and tested whether bathymetry (i.e. a reflection of the availability of light) has a significant impact on the ichnodiversity.

The number of ichnotaxa, their abundance, and the ichnodiversity varies with water depth (Table 6-3). Bioerosion traces by phototrophic organisms were detected, as expected, exclusively in the shallow water samples, whilst borings by organotrophic organisms dominate the deeper water samples. The significant ANOSIM demonstrates moderate differences (R-value = 0.5022) between sampling depths, as our bathymetric transect covers mainly the aphotic zone, with roughly the same ichnotaxa occurring at all depth stations (Table 6-3). The observation is confirmed by the NMDS and cluster analysis, that both show a separation into two main clusters, represented by our photic and aphotic stations (Figure 6-5).

The statistical analysis might be affected to some degree by a sampling bias: specimens from 466 m, for instance, were up to 6 cm long and showed the highest ichnodiversity, whereas specimens from 980 m were only 0.8 cm long and had the lowest number of traces, implying that the age of the host organism might be a controlling factor on the observed ichnotaxa assemblages, as microendoliths infest the substrate and bioerode at different rates

(e.g reviewed by Wisshak 2006), leading to a succession of bioerosion stages (e.g. Beuck & Freiwald 2005). However, we observed no evident correlation between sample size and the number of traces. An additional potential sampling bias might be that cover plates (barnacles from 879 m) and the armour (or shell pieces from 37 m) were analysed, but not both at every depth station.

The mean ichnodiversity indices varied little along the bathymetric (mainly aphotic) transect, although a general trend of a decreasing dominance and increasing evenness is noticeable due to the switch from the photic to the aphotic zone. The shallowest station is marked with a high dominance of one ichnotaxon by a phototrophic bioeroder (Simpson λ very close to 1), confirmed with a low Shannon diversity *H'* and evenness *J'*. According to the grand mean, the assemblages have a moderate dominance of ichnotaxa, and they are rather equally common than very different. The results are similar with or without the shallow water samples (Table 6-4), reducing the impact of the shallow water samples.

6.4.4 Ichnotaxa in the polar North and South

To put the ichnodiversity of the Antarctic Ross Sea in a wider context, we here compare our findings to our previous study of microbioerosion traces in Arctic barnacles (*Balanus balanus* and *Balanus crenatus*) from the Svalbard archipelago (Meyer et al. 2020), as both studies follow the same statistical approach and are based on the same type of substrate.

Svalbard and the Ross Sea are both in a polar environment with seasonally ceasing light levels, sea ice formation and ice-scouring, overall low temperatures, and strong fluctuations of environmental variables in the upper water column (Zacher et al. 2009). The environmental conditions in the Ross Sea are more extreme than in Svalbard, which is still in the far reach of the warm Gulf Stream. In consequence, the Mosselbukta, Svalbard, is roughly 11 months mostly ice-free (after fig. 2 in Meyer et al. 2020), whilst the Ross Sea is roughly two months ice-free (Figure 6-2). Antarctica is more isolated and completely surrounded by the Southern Ocean and the Antarctic Circumpolar Current, whereas the Arctic is surrounded by continental land masses (e.g. Dayton et al. 1982; Zacher et al. 2009). The areas have experienced different paleogeographic, palaeoceanographic, and palaeoclimatic evolutions that had an impact on the present (ichno)diversity (e.g. Clarke et al. 1992; Crame 1992; Brandt 2005; Zacher et al. 2009).

In the Ross Sea, we found eighteen different ichnotaxa and in Svalbard twenty (table 3 in Meyer et al. 2020), thus portraying a very similar ichnodiversity. The abundance of bored traces at both polar study sites was similar, with few ichnotaxa being dominant at certain stations (see Table 6-3 and table 3 in Meyer et al. 2020).

Six traces by phototrophic borers were observed in the Svalbard archipelago and two in the Ross Sea, which are *Fascichnus frutex* (by cyanobacteria) and *Ichnoreticulina elegans* (by chlorophytes). *F. frutex* was only recognised in the Ross Sea, but not off Svalbard, where we have recorded two other *Fascichnus* forms, which were not seen in the Ross Sea.

Conchocelichnus seilacheri (by rhodophytes) was occasionally dominant in Svalbard (table 3 in Meyer et al. 2020) but did not occur in the Ross Sea. Those contrasts are likely due to the varying number of samples from the euphotic to dysphotic zone: 65 samples from Svalbard were from the euphotic and 16 from the dysphotic zone (table 1 in Meyer et al. 2020), whereas only four samples from the Ross Sea were from the deep euphotic to dysphotic zone (Table 6-1). As expected, microbioerosion traces by phototrophs are rare in the Arctic and Antarctic. Cyanobacteria and chlorophytes are almost completely absent in the Ross Sea (Smith Jr. et al. 2012), as well as their traces. According to our findings, rhodophyte traces are also rare in the Ross Sea and thus likely also their producers.

The number of fungal bioerosion traces is the same at both locations, though the distribution differs. Two *Flagrichnus* cf. species were described from Svalbard, and an additional *Flagrichnus* cf. species was recorded in the Ross Sea. So far, we have no explanation why a only single colony of *Saccomorpha clava* was found off Svalbard, whilst the ichnotaxon was dominant in the Ross Sea, although the environmental conditions in Svalbard would be more favourable and the ichnotaxon is very common in the adjacent cold-temperate waters of the Norwegian shelf. Our observation appears to rule out temperature and sea ice coverage as a limiting factor for its producer *Dodgella priscus* Zebrowski, 1936.

The more extreme environment in the Antarctic additionally influences bioeroding foraminifera and bacteria, as *Nododendrina europaea* (produced by endolithic foraminifera), a very common trace in Svalbard waters, was not observed and the inferred bacterial trace *Scolecia serrata*, another microboring of high abundance in Svalbard, was found exclusively in the additional sample material. Both ichnotaxa were occasionally dominant and occurred almost in the entire water column off Svalbard. The ‘dwarf entobian’ *Entobia mikra* has so far primarily been recorded in cool to cold-water (palaeo)environments (Wisshak & Porter 2006; Wisshak 2008), but their unknown producers seem to be limited by the harsh conditions in the studied polar environments, especially in the more extreme Ross Sea.

Four yet undiagnosed microborings (*Flagrichnus*-form I, Finger-form, Nidus-form, Proturbero-form) were investigated in the Ross Sea. All of them are most likely the work of marine fungi, as these traces occur primarily in aphotic water depths, and are so far only found in the Antarctic. It is possible that the specific trace-makers are endemic species in Antarctica, as this biogeographic region is characterised by a high degree of endemism (as reviewed by Brandt 2005; Zacher et al. 2009).

Only a single macrobioerosion trace, *Rogerella* isp., a very common ichnogenus for traces produced by acrothoracid barnacles, was detected in the Ross Sea and none in Svalbard, although more samples were analysed there. As macroborers usually are not among the first to colonise substrates and commonly take a few years to establish (as described, e.g. by Farrow & Fyfe 1988; Kiene & Hutchings 1992; Wisshak 2006; Färber et al. 2016), this lack could again be due to the size and thus age of the investigated specimens, or it could reflect a

general scarcity of macroborers in polar environments, as demonstrated by few reports on macrobioerosion traces (e.g. Aitken & Risk 1988; Hanken et al. 2012).

Ichnotaxa occurring in polar waters at both hemispheres, such as *Ichnoreticulina elegans*, *Saccomorpha guttulata*, *Orthogonum* ispp., *Flagrichnus* ispp., and *Pyrodendrina villosa*, are usually among the first bioeroded traces (e.g. Wisshak et al. 2005; Wisshak et al. 2011). Thereof, *Flagrichnus baiulus*, *Saccomorpha guttulata*, and *Orthogonum*-form I have previously been suggested as indicators for cold-water environments in high latitudes and the deep ocean (Wisshak 2006; Wisshak & Porter 2006; Wisshak et al. 2018), a view that is supported by the present findings in the Ross Sea. *Entobia mikra* and *Nododendrina europaea* were also primarily reported from cold environments (Wisshak 2008), including Svalbard (Meyer et al. 2020), but were not detected in the Ross Sea. Therefore, we assume that their producers are either somewhat less well adapted to polar environmental conditions or that their biogeographic range does not extend that far south. *Saccomorpha terminalis* and *Saccomorpha stereodiktyon* are further microborings commonly associated with cold water environments (Wisshak 2006), but were found neither in our Svalbard study, nor in the present study, suggesting that their producers are limited by polar environmental conditions.

For both study sites, the performed statistical tests indicate that depth (i.e., availability of light) is a significant driver for the development of different microbioerosion trace assemblages across the bathymetric range. While this observation was very clear in Svalbard (ANOSIM R = 0.80; Meyer et al. 2020), the statistical difference was less significant for the Ross Sea (ANOSIM R = 0.50), because most samples were from the aphotic zone. We aimed for a profound comparison, but due to the lower number of samples from the shallower water depths and the overall varying number of samples, this approach was inconclusive.

6.5 Conclusions

This study provides a first comprehensive ichnotaxa list from the Ross Sea, Antarctica, where eighteen different bioerosion traces were recorded in barnacles. These traces are produced by cyanobacteria (1), chlorophytes (1), fungi (9), foraminifera (1), barnacles (1), bacteria (1), and unknown organotrophs (4), most of them were also recorded for the first time in deep waters down to bathyal 1680 m water depth. Together with our corresponding study from the Arctic Svalbard archipelago (Meyer et al. 2020), these data help constraining the ecophysiological limits of the producers of certain key ichnotaxa several of which are considered indicative for cool to cold-water environments (foremost *Flagrichnus baiulus* and *Saccomorpha guttulata*). Statistical tests indicated only minor differences between groups from different water depths, as the samples came mainly from the aphotic zone. The ichnospecies richness was only slightly lower than what has been recorded in the Svalbard study (18 vs. 20 ichnotaxa). This finding can be attributed to a sampling bias, as the barnacles are scarce in shallow waters of the Antarctic region, which made it difficult to draw

conclusions about intertidal ichnodiversity. Hence, also other substrates should be considered in future studies to obtain a better picture of euphotic shallow-water and intertidal bioerosion in Antarctica. More studies of bioerosion patterns from the Arctic and Southern Oceans are needed to develop a database that allows more general conclusions on the biogeographic distribution of bioerosion traces and their producers for the overall aim of a better understanding of the bioerosion process in polar environments.

Acknowledgements

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6.6 References

References are listed at the end of this thesis.

Chapter 7
Ichnodiversity in the Eastern Canadian Arctic in the context of polar microbioerosion patterns

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Abstract

Studies on marine microbioerosion in polar environments are scarce and led us to investigate bioerosion traces preserved in sessile balanid skeletons from the Arctic Svalbard archipelago and the Antarctic Ross Sea. Here, we present results from a third study site, Frobisher Bay in the Eastern Canadian Arctic, and synthesise the present knowledge on polar bioerosion in both hemispheres. Barnacles from 62 to 94 m water depth from Frobisher Bay were treated with the cast-embedding technique to enable visualisation of microboring traces under a scanning electron microscope. In total, six microboring traces by organotrophic bioeroders were found, without a significant difference between samples from different water depths. All recorded ichnotaxa were present in Svalbard (20 ichnotaxa) and most of them in the Ross Sea (18 ichnotaxa). In comparison, Frobisher Bay had a low ichnodiversity, which may contribute to the small number of samples and a high sedimentation rate. Together, the three studies allow us to make provisional considerations on the biogeographic distribution of polar microbioerosion traces based on possible migration pathways and ecophysiological limits or adaptations to the harsh environmental conditions. Additional samples of potential migration routes between the poles are required in order to prove and further investigate these explanation attempts.

Keywords

Ichnotaxa · Ichnodiversity · Microfossil trace assemblage · Polar environment · Arctic · Antarctic

7.1 Introduction

Bioerosion is after Bromley (1994: p. 1) “the process by which animals, plants and microbes sculpt or penetrate surfaces of hard substrates”, and was first defined by Neumann

(1966). The process is an important mechanism of calcium carbonate recycling (see review by Schönberg et al. 2017) and affects primarily calcareous material from the marine environment. Bioerosion is referred to as "the other ocean acidification problem" because its chemical part is assumed to increase significantly with ongoing ocean acidification, leading to an imbalance (as reviewed by Schönberg et al. 2017).

Bioeroding agents are categorized into grazers, macro- and microborers (Wisshak 2012). Typical microboring organisms are cyanobacteria, chlorophytes, fungi, and bacteria (Golubic et al. 1975; Wisshak 2012), while macrobioeroders are, for instance, sponges or polychaetes (Glynn & Manzello 2015). Bioerosion is performed either chemically (biogenic dissolution) or mechanically (e.g. rasping or biting of substrate), or by an interlinked technique. Microborers, however, exclusively use the chemical way (Schönberg et al. 2017).

During bioerosion, characteristic traces are produced, which often allow conclusions to be drawn about the trace-maker. Traces by bioeroding microendoliths often conform to the outline of their producer and are less than 100 µm in size (Wisshak 2012). Officially diagnosed traces are addressed as ichnotaxa, with more than 300 valid ichnospecies (Wisshak et al. 2019a).

Although bioerosion takes place on a global scale, research in the cool to cold regions is scarce, as most studies were conducted in the tropical to warm-temperate environments (few example microbioerosion studies: Kiene & Hutchings 1992; Chazottes et al. 1995; Kiene et al. 1995; Le Campion-Alsumard et al. 1995; Vogel et al. 2000; Tribollet & Golubic 2005; Alvarado et al. 2017), focussing on a variety of topics, such as different bioerosion agents in and on various substrates, their traces, bioerosion pace and rate, as well as expected changes with climate change.

Currently, there are very few comprehensive studies from the cold-temperate regions of the northern hemisphere, as for instance in the North Atlantic (e.g., Akpan & Farrow 1985; Schmidt & Freiwald 1993; Glaub et al. 2002; Beuck & Freiwald 2005; Wisshak 2006) and North Pacific (e.g., Young & Nelson 1988). The cold-temperate regions of the southern hemisphere are, to our knowledge, represented by research in the Patagonia area (e.g., Malumián et al. 2006; Richiano et al. 2017; Aguirre et al. 2019), of which the most recent substrate dates from the Quaternary period.

The polar regions of both hemispheres were the least frequent locations of bioerosion studies, with the Arctic (Aitken & Risk 1988; Hanken et al. 2012) being studied more intensively than the Antarctic (Casadío et al. 2001; Cerrano et al. 2001; Casadío et al. 2007). So far there are only two comprehensive studies that have published a list of microbioerosion traces and their bathymetric trend for the Arctic Svalbard (Meyer et al. 2020) and the Antarctic Ross Sea (Meyer et al. submitted).

Following up this series of papers, we conducted this third study in the East Canadian Arctic to further develop our understanding of polar microbioerosion and to evaluate the

results in a global context. Svalbard is not considered very polar, so the results from the Canadian Arctic are important for an improved insight into microbioerosion traces from the Arctic and polar environments in general.

We (a) visualise, analyse, and list microbioerosion traces in barnacles from different water depths by implementing the commonly applied cast-embedding technique, and (b) evaluate their occurrence and (c) potential migration processes in a polar north-south comparison.

7.2 Materials and methods

7.2.1 Sample material

To ensure the best possible comparability with our previous studies (Meyer et al. 2020, submitted) and as they have proven to be highly suitable (e.g. Glaub et al. 2002; Feussner et al. 2004), we concentrated on barnacles, namely the species *Balanus balanus* (Linnaeus 1758), which were kindly provided by Evan Edinger and Erin Herder, Memorial University of Newfoundland. Details about their collection in Table 7-1.

Table 7-1 Details of barnacle sample collection. Latitude, longitude, and water depth were recorded at the start of the deployment.

Water depth (m)	Sample-ID	Date	Latitude	Longitude	Gear	Number of samples
62	FB2-2_G3	16/07/2016	63.67522	-68.43048	Box Core	3
63	FB2-2_G1	16/07/2016	63.67523	-68.43035	Box Core	4
74	5c_G4	10.11.2016	63.66102	-68.42195	Van Veen	4
80	FB2-1_G1	16/07/2016	63.66358	-68.42238	Box Core	4
81	FB2-1_G3	16/07/2016	63.66350	-68.42167	Box Core	4
86	5g_G3	10/11/2016	63.66272	-68.41404	Van Veen	4
90	5f_G6	10/11/2016	63.66395	-68.41961	Van Veen	4
90	5f_G8	10/11/2016	63.66424	-68.41944	Van Veen	4
91	5g_G4	10/11/2016	63.66222	-68.41398	Van Veen	4
93	5g_G2	10/11/2016	63.66209	-68.41443	Van Veen	4
94	5g_G1	10/11/2016	63.66209	-68.41443	Van Veen	4

7.2.2 Study site

Barnacles were sampled in the Inner Frobisher Bay, Baffin Island, East Canadian Arctic, close to the northern tip of the bay and the east shore, from 62 to 94 m water depth (Figure 7-1, Table 7-1).

Frobisher Bay is a partially enclosed embayment, ca. 250 km long, ca. 65 km wide at the widest point towards the entry of the Hudson Strait, and ca. 20 km wide in the inner area. The outer bay is up to 800 m deep, while the inner bay is shallower with one third deeper than 100 m. Both parts are separated by the mid-bay islands.

The Frobisher Bay is in the Arctic biogeographic realm (Spalding et al. 2007) at ca. 63.60°N and 68.40°W without true polar night, but long day lengths from June to July (Figure 7-2). Sea ice is stable by December, with the maximum sea ice thickness in late May/early June (Figure 7-2; Fetterer et al. 2017), without multi-year sea ice (Grainger et al.

1985). Sea ice scouring was observed in water depths shallower than 50 m (Deering et al. 2018), and extensive iceberg scouring down to 80 m (Todd et al. 2016).

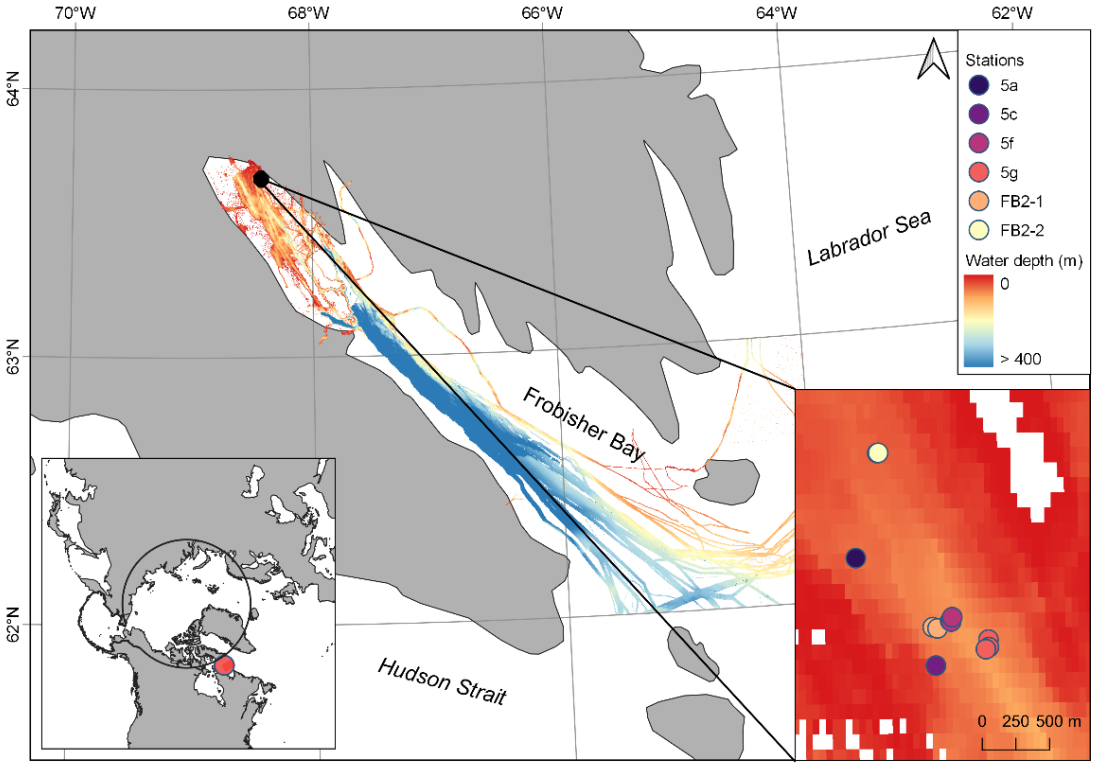

Figure 7-1 Map of the Eastern Canadian Arctic and details of sample origin in Frobisher Bay. Bathymetric data was retrieved from Canadian Hydrographic Service (2018) and the boundary of the Arctic was provided by the US Arctic Research Commission (2009).

The inner bay experiences extreme tides up to 12.6 m (McCann & Dale 1986; Deering et al. 2018), which is the maximum tidal amplitude in the Canadian Arctic (Collins et al. 2011). The high tidal amplitudes with great amounts of suspended sediment occlude the sea floor, which reduces the amount of light reaching the sea floor. Sediment movement from the land to the sea depends on the season, due to snow melting (Andrews 1987). The highest sedimentation rate (Andrews 1987; Atkinson & Wacasey 1987) and primary productivity peak (Grainger 1979) is from June to July, together with the phytoplankton bloom right after the sea ice breakup (Hsiao 1992).

The lower part of the euphotic zone is below 25 m (Hsiao 1985). As no PAR (Photosynthetically Active Radiation) data was available for Frobisher Bay, we used data from the Labrador Sea (Latitude: 61.52, Longitude: -56.00) to determine the photic zones. There the euphotic zone (1% surface illumination marks the lower boundary) reaches ca. 45 m and the base of the dysphotic zone (0.01% surface illumination) is at ca. 104 m water depth (station TARA_210, measured on 27 October 2013 with a rosette vertical sampling system; Picheral et al. 2014). Concludingly, it can be assumed that all stations were located in the dysphotic zone (Table 7-1).

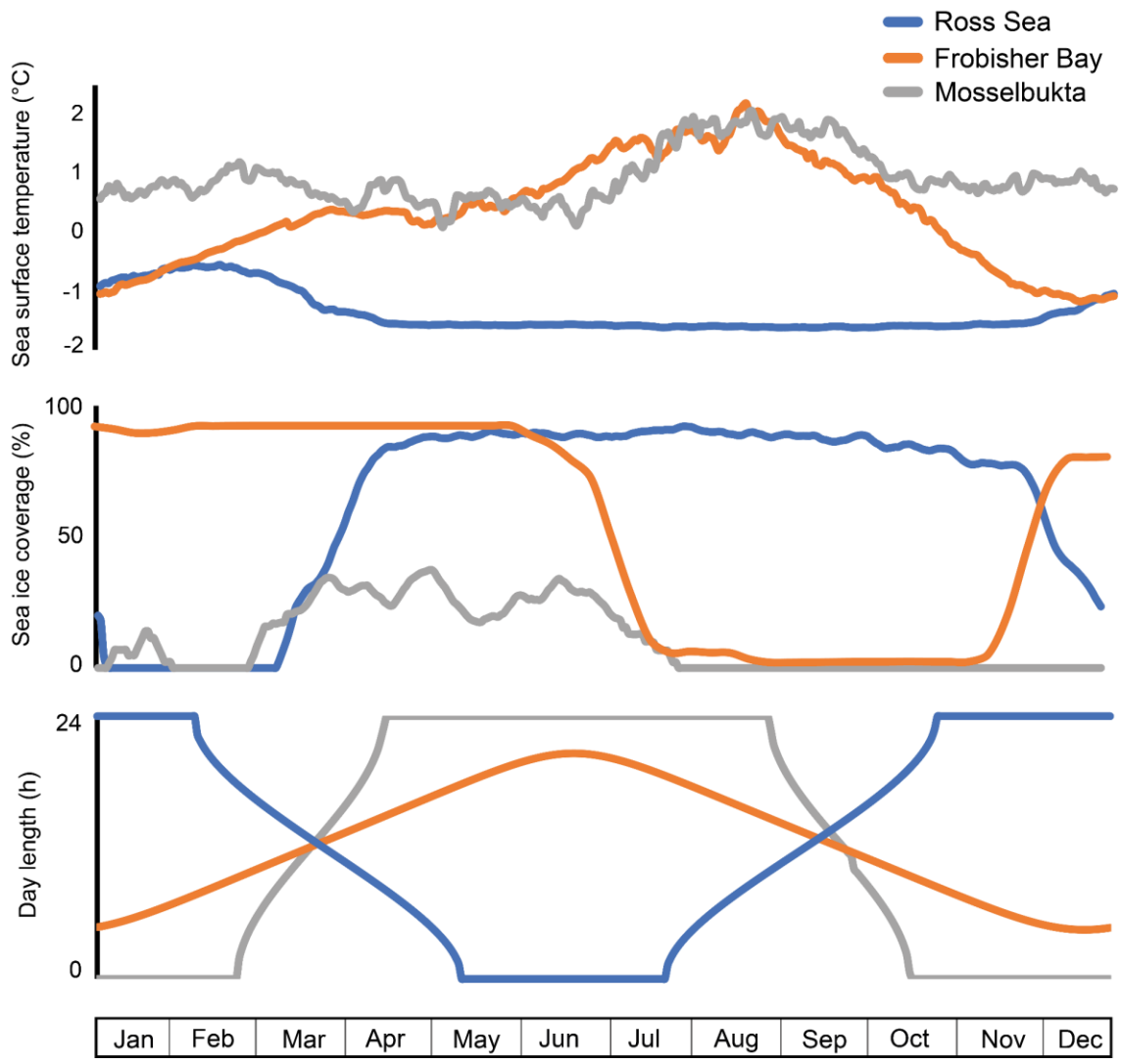

Figure 7-2 Schematic overview of the seasonality at the three study sites. Day length data for 2016 was obtained via Time and Date AS (2020), sea ice coverage for the Ross Sea and Mosselbukta was retrieved as daily mean from 2004–2016 via Fetterer et al. (2017) and for Frobisher Bay as a weekly mean from 2007–2016 via Canadian Ice Service (2009), sea surface temperature is the daily mean from 2004–2016 via Physical Science Laboratory (2020).

The geological setting comprises Paleoproterozoic marble in the north, Ordovician carbonate rocks to the northwest and likely towards the outer bay, and Paleoproterozoic metamorphic and igneous rocks along the shore (Deering et al. 2018). The bay has hardgrounds along the sidewalls and bedrock outcrops in the fjord (Dale et al. 1989), with a highly variable seabed (Mate et al. 2014), characterized by ridges, plateaus, and troughs (Deering et al. 2018). Seabed instability and geological hazards were suspected by Mate et al. (2014).

7.2.3 Cast-embedding technique

To visualise the microbioerosion traces inside the calcareous barnacle armour, we treated them with the commonly applied cast-embedding technique (Wisshak 2006, 2012). First, we

removed organic material by immersing the barnacles in sodium hypochlorite (customary cleaning agent) for 24–48 hours. The barnacles were then several times rinsed with deionised water before they dried at 30 °C for 12 hours. By means of a vacuum chamber on the CitoVac (Struers), the cleaned tunnels inside the barnacle armour were filled with R&G "water clear" epoxy resin. The hardened resin pieces were sawn on all sides with a stone saw and then placed in ca. 5% hydrochloric acid until the exposed carbonate was dissolved. In total, we have glued 43 samples on stubs. Prior to scanning electron analysis (Tescan VEGA3 xmu, with the secondary electron detector at 20 kV), the stubs were sputter-coated with gold (Cressington sputter coater 108).

Whenever applicable, bioerosion traces were identified at ichnospecies level and otherwise given informal names. As an accurate quantification is not feasible for several reasons (traces differ in size; they may superimpose each other; some are networks, whilst other ones are individual borings), we have carried out a semi-quantitative analysis by gathering ordinal data and categorising each trace into one of five abundance classes: absent (0); very rare, only one or very few specimens (1); rare, few specimens (2); common, many specimens but not dominant (3); very common or dominant (4), as first performed by Wisshak et al. (2011).

7.2.4 Statistical analysis

To test whether the individual samples vary in ichnodiversity, we utilised R version 3.6.2 (R Core Team 2019) to test Mardia and Royston multivariate normality with the package "MVN" (Korkmaz et al. 2014). The package "vegan" (Oksanen et al. 2018) was utilised for ANOSIM (ANalysis Of SIMilarities; with 999 permutations) with the untransformed ordinal data (more details in Meyer et al. 2020, submitted).

7.3 Results

7.3.1 Ichnodiversity

Six different microbioerosion traces were rarely to very rarely recorded in acorn barnacles from the Canadian Arctic, except for *Nododendrina europaea* common at 91 m water depth. Four of the ichnotaxa were probably bioeroded by fungi, one by foraminifera, and one by bacteria, thus all were produced by organotrophic trace-makers (Table 7-2).

Scolecia serrata was exclusively found at 62 m water depth, *Flagrichnus* cf. *profundus* appeared from a water depth of 86 m on, while the other traces occurred almost in the entire bathymetric transect (Table 7-2).

We occasionally noticed small deviations to the originally described morphology of some ichnotaxa. *Flagrichnus baiulus* (Figure 7-3b) and *Nododendrina europaea* (Figure 7-3h), for instance, showed a great variety of forms and sizes (e.g. pancake-form in *Flagrichnus baiulus*).

Table 7-2 List of ichnotaxa recorded in barnacles from the Canadian Arctic and their assumed trace-makers (based on the original interpretation of the ichnotaxon authority) and results of the semi-quantitative analysis. Abundances are categorised as '++' = very common, '+' = common, '-' = rare, and '--' = very rare.

Ichnotaxon	Trace-maker	Figure	Water depth (m)										
			62	63	74	80	81	86	90.1	90.2	91	93	94
Flagrichnus baiulus Wisshak & Porter, 2006	Fungi	7-3a–b	--	--		--	--		--	--		-	
Large tongue-form	Fungi	7-3c–d			--	-	--		-		--		--
Flagrichnus cf. *profundus* Wisshak & Porter, 2006	Fungi	7-3e						--		--	--		--
Saccomorpha guttulata Wisshak et al., 2018	Fungi	7-3f	--	--	--	--		--	--			--	--
Nododendrina europaea (Fischer, 1875)	Foraminifera	7-3g–h	+	--	--	-	--	--	--	--	+	-	--
Scolecia serrata Radtke, 1991	Bacteria	7-3i	--										

The Large tongue-form (Figure 7-3c–d) is not officially established and is therefore briefly described in terms of morphology: The trace consists of an initial point of entry into the substrate (exemplary measured on four traces: 2–5.5 µm wide, 4.3–10.6 µm long), with a gradual transition to a central spherical cavity above it (maximum diameter: 6.2–12.5 µm), which sometimes looks flattened and slightly bent, like a tongue. We noticed a resemblance to the ichnogenus *Saccomorpha*, but this form is strikingly larger.

The multivariate data set is not normally distributed, as Mardia's and Royston's multivariate normality test both resulted in $p < 0.001$. The result of the ANOSIM is $R = 0.18$ (significance = 0.008).

7.4 Discussion

7.4.1 Ichnodiversity in the Canadian Arctic

Six different ichnotaxa were recorded in 43 samples from 62 to 94 m water depth. Four of them were bioeroded by fungi, one probably by foraminifera, and one by bacteria. All observed traces are already known from previous studies. The Large tongue-form is not yet ichnotaxonomically established but was also reported from Svalbard (publication in prep. by MW).

The ichnotaxonomic inventory was limited to traces of light-independent organotrophs. Regarding the not very deep water depths, we would have expected to find the ichnotaxon *Ichnoreticulina elegans*, which is usually a cosmopolitan and then very common ichnotaxon by the low-light extremist (observed by Lukas 1978 at 370 m water depth; Wisshak 2012) and phototrophic euendolith *Ostreobium quekettii* Bornet & Flahault, 1889. Therefore, we

assume that we did not have samples from the dysphotic zone, as stated in the introduction, but instead from the aphotic zone caused by the strong turbidity of the water and high sedimentation rate. Sedimentation impedes bioerosion (Perry & Harborne 2016; as reviewed by Weinstein et al. 2019), as terrigenous input covers the carbonate-bearing substrate, hampering the colonization of microorganisms, or obscures the seafloor, thus decelerating bioerosion (Risk & Edinger 2011; Tribollet et al. 2011a; Perry & Harborne 2016).

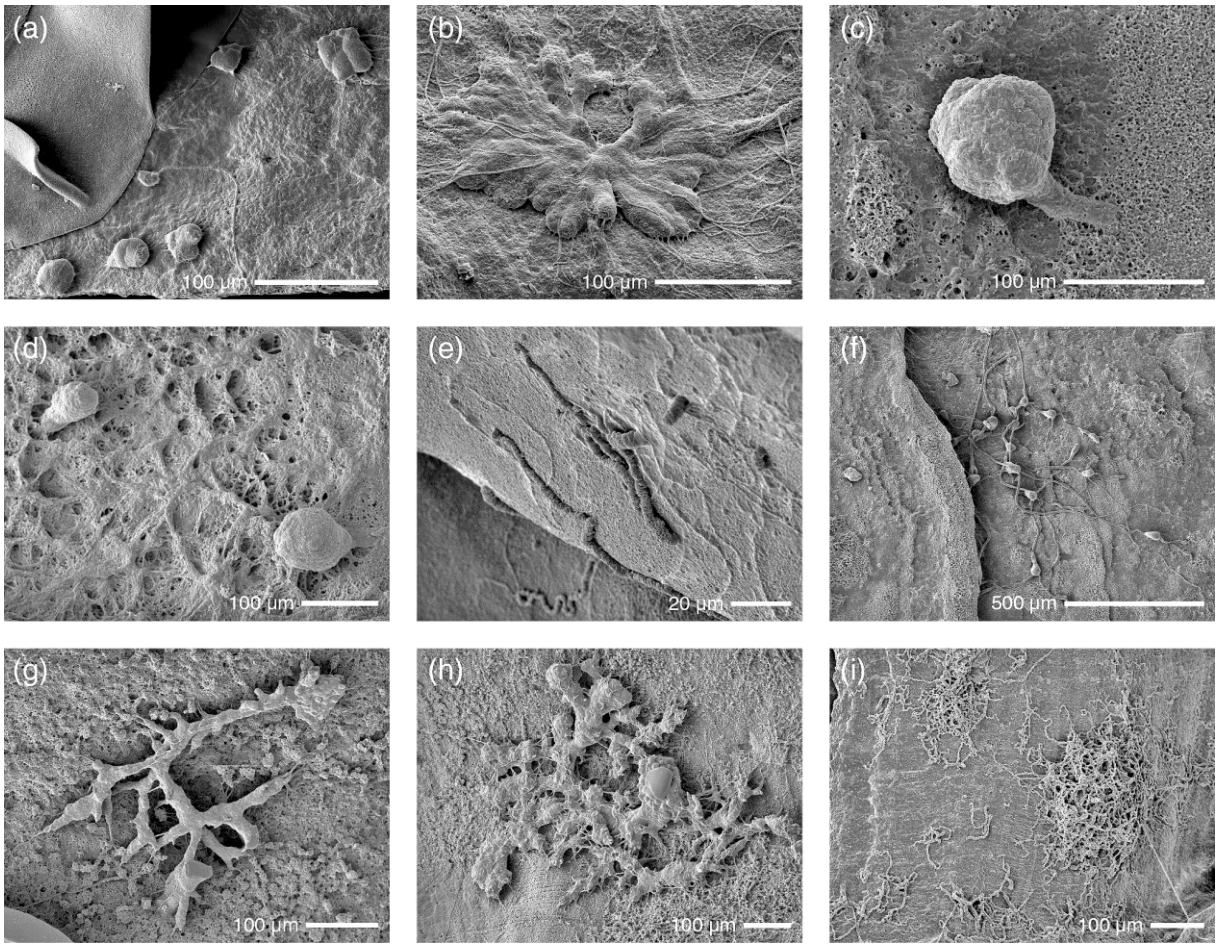

Figure 7-3 Observed microborings from Frobisher Bay. **a** *Flagrichnus baiulus* from 93 m. **b** Unusual *Flagrichnus baiulus* ('pancake-form') from 63 m. **c** Large tongue-form from 74 m and **d** from 90 m. **e** *Flagrichnus* cf. *baiulus* from 91 m. **f** *Saccomorpha guttulata* from 74 m. **g** *Nododendrina europaea* from 91 m and **h** two larger forms from 91 m. **i** *Scolecia serrata* from 62 m.

The ANOSIM was significant ($p < 0.05$) without strong differences between the samples ($R = 0.18$). This result indicates that the different water depths were less decisive in this study, as all samples probably originated from the aphotic zone. It is more likely that the barnacles were of individual age and size, causing different assemblages.

The ichnodiversity (and abundance of bioerosion, Table 7-2) is comparatively very low (compared e.g. with Wisshak 2006 [cold-temperate, 26 microborings]; Wisshak et al. 2011 [warm-temperate, 37 microborings]), which we relate to three factors: (1) the seasonal light conditions are extreme (Figure 7-2) and diminish ichnotaxa by phototrophs, (2) extreme tides and turbidity prevail in Frobisher Bay and an agitated water setting causes lower

bioerosion (Scoffin et al. 1980), and (3) Frobisher Bay yielded a low number of samples covering a narrow bathymetric range. With more samples from different water depths, we probably could have found more and other ichnospecies.

7.4.2 Comparison with previous studies of polar microbioerosion ichnodiversity

Characteristic polar environmental parameters, such as cold temperatures, compressed photic zonation, and sea ice affect the formation of trace assemblages (Wisshak 2006; Meyer et al. 2020, submitted). To acquire a broader understanding of polar microbioerosion, we have compared our small-scale results with two related polar microbioerosion studies from Svalbard (Meyer et al. 2020) and the Ross Sea, Antarctica (Meyer et al. submitted; Figure 7-4). We exclude that variations in ichnospecies composition between the three studies are the result of different approaches since the same substrate and the same method was applied.

The Arctic vs. the Arctic

Both regions were covered by ice sheets during the Last Glacial Maximum, Frobisher Bay by the Laurentian Ice Sheet (Andrews 1987; Deering et al. 2018) and Svalbard by the Barents Ice Sheet (Landvik et al. 1998), restricting the settlement of substrate, i.e. barnacles, and the general evolution of species. Despite this, the Canadian Arctic showed a much lower ichnodiversity than Svalbard (6 vs. 20 in barnacles from the *Balanus* genus), but all recorded ichnotaxa have also been observed in Svalbard (Large tongue-form was not reported in Meyer et al. (2020) but by MW, pers. comm.). This large gap is explained by the availability of more samples from Svalbard, covering a wider range of water depths, i.e. the euphotic to aphotic zones. More samples from different water depths would probably have resulted in a greater ichnodiversity, although traces of the phototrophic organisms could still be scarce due to turbidity (see above).

If only samples from the aphotic are considered, Svalbard had 14 traces and Frobisher Bay six. The remaining large difference is likely due to the same reasons as mentioned above (fewer samples, high sediment input, etc.) or because we have been unable to find signs of a polar carbonate factory in Frobisher Bay, and are only aware of carbonate-bearing rocks (Deering et al. 2018). Therefore, it is possible that the evolution of ichnodiversity was constrained in Frobisher Bay by a lack of suitable substrate, whereas the polar carbonate factories (see Wisshak et al. 2019b for more details) in Svalbard were an excellent habitat for the colonisation of the bioeroding agents. Another factor that could have hindered the establishment of bioeroders and the traces they produce are the widespread marine geohazards (Mate et al. 2014; Todd et al. 2016; Deering et al. 2018), which prevent the settlement of barnacles and thus leave little substrate for the bioeroding agents.

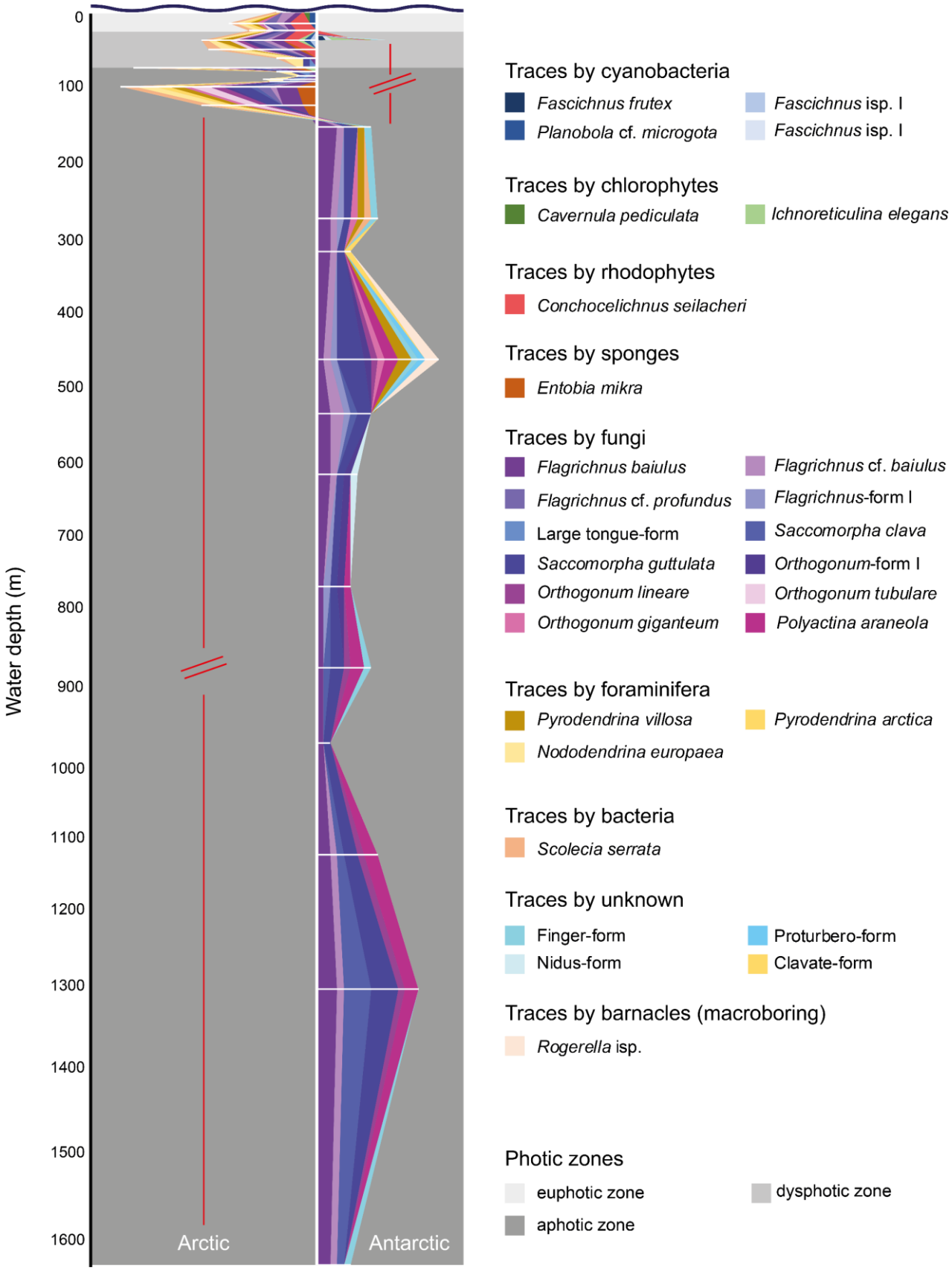

Figure 7-4 Stacked area chart including ichnodiversity and abundance data from this study and Meyer et al. (2020, submitted) in the Arctic and Antarctic. The white horizontal lines denote the actual water depth of the samples, areas in between are interpolated. The red vertical lines indicate that no samples were available from these water depths and not that no ichnodiversity was observed.

Polar north vs. polar south

There are a total of 21 microbioerosion traces in the Arctic (six ichnotaxa in Frobisher Bay, 20 in Svalbard) and 18 in the Antarctic (Meyer et al. submitted). Figure 7-4 clearly illustrates that overall, especially fungal traces (in light pink to blue shades) dominate the assemblages. At first, this result could be explained by the least extreme polar conditions at Svalbard, which are demonstrated by longer lasting sea ice cover in Antarctica and Frobisher Bay (Figure 7-2). However, this attempted explanation is yet too simple.

Traces of phototrophic organisms often account for the largest proportion (Wisshak 2012) and owing to the extreme light conditions at high latitudes, their quantity is reduced (see discussion in Meyer et al. 2020). While this could be proven for Svalbard, we can only assume this to hold true for the Ross Sea and Frobisher Bay given the small number of samples from the euphotic zone.

Based on available data we would discuss the dysphotic to aphotic zone in more detail, but since the determination of the dysphotic zone is mostly based on PAR data of one day or potentially impacted by high turbidity, we concentrate instead on results from 60 m downwards. This strategy translates into 46 considered samples from the Antarctic and 79 from the Arctic (Svalbard = 36, Frobisher Bay = 43). The approach shows a slightly different outcome with a similar number of ichnotaxa (Figure 7-4): in Frobisher Bay, there are still six traces, in Svalbard 15, and in Antarctica the most with 16 traces. Three traces remain restricted to Svalbard (*Entobia mikra*, *Orthogonum tubulare*, *Pyrodendrina arctica*), and seven to the Ross Sea (*Flagrichnus*-form I, *Polyactina araneola*, Finger-form, Nidus-form, Proturbero-form, Clavate-form, *Rogerella* isp.). Three traces occur exclusively in both Arctic regions (*Flagrichnus* cf. *profundus*, *Nododendrina europaea*, Large tongue-form); regardless of the occurrence at lower latitudes. The highest number of new (and thus endemic?) species was recorded in the Ross Sea. In summary, the number and abundance of ichnotaxa are almost identical in barnacle samples from both hemispheres, despite the differing number of samples.

Ichnotaxa existence in a polar north-south comparison

The questions remain how ichnotaxa can occur in both polar regions and why some were already known from other latitudes. Even if this question cannot be finally resolved in the context of this study, considerations on possible migration processes of the ichnotaxa producers are discussed here, nevertheless. It is to be noted that patterns for certain fauna groups are often generalized to an overall picture, although this cannot be confirmed, because data is still missing for many species (Clarke & Crame 2010). Several reviews for benthic organisms (e.g. Dunton 1992; Clarke & Johnston 2003; Brandt 2005; Clarke et al. 2007; Clarke & Crame 2010; Griffiths 2010; Gutt et al. 2010; Michel et al. 2012) make clear that the general understanding of the origin, evolution, and dispersal of species in both polar regions is not yet fully understood. Both areas were severely affected by glacial periods, which

possibly led to the extinction of species and/or pressure to migrate down the slopes and back up after melting (Clarke & Crame 2010).

The evolution of macrobioerosion traces is quite well understood (for reviews: Wilson & Palmer 2006; Tapanila 2008; Tribollet & Golubic 2011), whereas the understanding of microborings through time needs more investigation (Tapanila 2008; see Wisshak et al. 2008 for a preliminary review of the state of knowledge on the evolution of microendoliths).

An extreme increase in global ichnodiversity and potential modes of life, specifically bioerosion (Tribollet & Golubic 2011; Buatois et al. 2020), began in the Terreneuvian, an epoch of the Cambrian, 540-520 Ma (million years, numerical scale), and intensified during the so-called Great Ordovician biodiversification event (ca. 485 Ma). Ichnotaxa such as *Ichnoreticulina elegans*, *Conchocelichnus seilacheri*, *Saccomorpha clava*, or *Polyactina araneola* (all observed in our series of papers) were traced back to the Ordovician or Silurian (Paleozoic; Vogel & Glaub 2004). This fact affirms the longevity of microendoliths (Wisshak et al. 2008), although it cannot be determined whether individual types of borings were bioeroded by the same trace-makers through time (Vogel & Glaub 2004), as unrelated organisms may produce similar traces (Golubic et al. 2016).

This makes some (trace-makers of the) ichnotaxa older than the Arctic and Antarctic with their present polar environmental conditions. The Arctic in its polar setting developed ca. 1.8 million years ago in the Pleistocene and is therefore relatively young compared to the Antarctic, which developed in its present isolated form ca. 23 million years ago in the Miocene. The Antarctic was formerly part of the supercontinent Gondwana, before its breakup in the Jurassic (Mesozoic), followed by successive isolation and cooling during the Late Cretaceous (Crame 1992; Brandt 2005). It is therefore possible that the trace-makers have either adapted in situ to the polar environment or migrated afterwards (see discussion in Clarke & Crame 1989).

The Ross Sea has the highest number of previously unknown ichnotaxa, which are possibly endemic, given that the Antarctic has repeatedly been identified as being characterized by a large number of endemic species (as reviewed by Crame 1997; Gray 2001; Brandt 2005; Piepenburg 2005), as it is quite isolated due to its geological history and ocean currents (Rintoul et al. 2001; Smith 2015).

It is puzzling that there may be several endemic (ichno)species in the Antarctic because especially fungi can easily be dispersed over long distances (Gladfelter et al. 2019; Hassett et al. 2020) and given that the Antarctic is far from being as isolated as thought through the deep water masses (Brandt 2005; Brandt et al. 2007; Brandt et al. 2009). Moreover, studies stated that some microorganisms have a worldwide distribution (Finlay 2002; Hassett et al. 2020). Despite all this, these studies have not examined polar regions and therefore may have underestimated the Antarctic Polar Front, which is a strong natural barrier to dispersal

because of the intense currents and prominent thermocline (Flaviani et al. 2018). Especially the large temperature difference allows only a few species to survive on both sides of the front (Gutt et al. 2010).

In contrast to this is the Arctic with ichnotaxa, almost all of which are also known from locations in lower latitudes (e.g. found in Vogel et al. 2000; Glaub 2004; Wisshak et al. 2011; Tribollet et al. 2018), corresponding to the close relation of Arctic marine fauna to the North Atlantic and Pacific (Dunton 1992; Clarke & Crame 2010; Bodil et al. 2011), because of its deep water connection to, for instance, the Fram Strait (Bodil et al. 2011).

To conclude, it is not yet possible to fully understand the influences on the evolution and dispersal of the trace-makers, but it seems that the existence of ichnotaxa in polar regions is a mixture of migration processes and evolutionary adaptations in situ (consistent with e.g. Clarke & Crame 1989, 2010). Arguments in favour of migration are that many ichnotaxa were observed in different environmental settings (e.g. the cosmopolitan *Ichnoreticulina elegans*) and that microorganisms can generally easily disperse since biogeographic restrictions are less restrictive for them (Finlay 2002). These findings further support that some producers are very robust because they can thrive in various environments. Since there are also endemic species or species that have only been observed in the polar regions, e.g. *Saccomorpha guttulata* (Wisshak et al. 2018) and Large tongue-form, or *Nododendrina europaea* being restricted to the Northern Hemisphere, some of the producers likely evolved in situ.

7.5 Conclusions

In the context of polar microbioerosion studies, barnacles from the dysphotic zone of Frobisher Bay, Eastern Canadian Arctic, were investigated regarding their ichnodiversity utilizing the cast-embedding technique. The assemblage consists of six traces, four bioeroded by fungi, one by foraminifera, and one by bacteria, and is thus impoverished in ichnotaxa by phototrophic euendoliths, which is explained on the one hand by the lacking samples from the euphotic zone and on the other hand by the high turbidity. Compared to two corresponding studies from the Arctic (Svalbard, 20 traces) and Antarctic (Ross Sea, 18 traces), the ichnodiversity is lowest mainly due to the small number of samples. We compared all three studies and realised that the ichnodiversity in the aphotic zone is almost equal though differed in composition. Additionally, we observed that some ichnotaxa are present in all three regions. From our research we conclude that some of the trace-makers must have migrated after the Last Glacial Maximum whereas others might have evolved in situ (endemism), indicating a promising avenue for further research, including more polar sample sites, samples from potential migration pathways, and suitable substrates from intertidal and shallow-subtidal water depths.

Acknowledgements

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7.6 References

References are listed at the end of this thesis.

Chapter 8
Synthesis

The studies that constitute this thesis not only address the five objectives (as listed in Chapter 1.7) but also provide first insights into (micro)bioerosion patterns at the highest latitudes. For this purpose, detailed inventories of microbioerosion traces at three different locations in the polar realm (Chapter 4–7) were carried out by means of the cast-embedding technique (Chapter 3.3.1). Additionally, a new key ichnotaxon for the polar realm was established (Chapter 4). The distribution patterns were evaluated regarding a bathymetric and latitudinal gradient (Chapter 5–7).

8.1 Microbioerosion ichnodiversity at high latitudes

In order to adequately address all hypotheses, a core element of this work was the evaluation of microbioerosion ichnodiversity at high latitudes. In total, 29 different traces were found of which all are characterized as dwelling traces in the ethological class 'domichnia' (after Vallon et al. 2016). Trace-makers comprise cyanobacteria (4), chlorophytes (2), rhodophytes (1), sponges (1), fungi (12), foraminifera (3), bacteria (1), unknown microbiota (4), and cirripeds (1, macroboring). Three traces occurred at both poles, eight traces were exclusive to Svalbard (Chapter 5), one trace to Frobisher Bay (Chapter 7), and eight to the Ross Sea (Chapter 6). Three traces were observed at both Arctic sites, but not in the Antarctic (see Figure 7-4 in Chapter 7 and the complete overview in the Appendix). This doctoral thesis extends the biogeographic distribution for all observed species towards higher latitudes (Chapters 4–7) and for some to bathyal water depths (Chapter 6).

As expected, particularly bioerosion traces by phototrophic euendoliths were rare. This observation is not only because of the small number of samples from the euphotic zone but also on account of the seasonal light distribution, which governs the composition of microboring trace assemblages (as demonstrated in Chapter 5). Nevertheless, there are a few traces whose producers must be very robust against environmental conditions, such as *Hyella gigas* Lukas & Golubic, 1983 (trace: *Fascichnus frutex*) and *Ostreobium quekettii* Bornet & Flahault, 1889 (trace: *Ichnoreticulina elegans*). The high proportion of traces by organotrophic producers, especially fungi, were also expected, due to their light-independence and their ability to thrive at all water depths (see Chapter 1.3.2, Figure 7-4).

Saccomorpha guttulata is a new bioerosion trace, which was found in the scope of the Svalbard studies and is now officially established (Chapter 4; Wisshak et al. 2018).

Additionally, there are some forms, which are unknown to date and are possibly limited to polar regions. These are either new to science (e.g. Finger-form or Nidus-form; Chapter 6) or show slightly different morphologies from the original descriptions (e.g. *Flagrichnus* cf. *baiulus* or *Flagrichnus* cf. *profundus;* e.g. in Chapter 5) and thus may show adaptations to the harder conditions.

Considering only the dysphotic to aphotic zone (as performed in Chapter 7), the diversity and abundance of ichnotaxa (most of them were rare to very rare, the fewest were very common, see the Appendix) is similar at all three sites, with slightly different compositions, although the sample size is quite different. Details of the factors causing the varying compositions are provided in the corresponding chapters and in the concluding Chapter 7.

How do the bioerosion agents survive?

This issue is beyond the scope of this work, but the reader is reminded here that euendoliths are quite robust towards environmental conditions by being buffered in the microenvironment of their borings to a certain degree (Wilkinson 1974; Vogel & Glaub 2004). Surprisingly many species can survive at temperatures from a few to about zero degrees (Gray 2001).

For coping strategies and mechanisms of microalgae in high latitudes, the reader is referred to the review by Young & Schmidt (2020), in which it is stated that algae are well adapted to the low light conditions, possibly because many algae remain in a vegetative state for the dark period. A large part of the already fixed carbon remains as detritus in the water column in this period (Barnes & Tarling 2017).

Reflection on macrobioerosion

It is highly interesting that except for a single trace in the Antarctic (*Rogerella* isp.; Chapter 6), no other macrobioerosion trace was been recorded. The same trace was also likely found by Newman & Ross (1971) in fossil material from ca.73°S and 68°W, Antarctic Peninsula.

Bioeroding sponges are among the most destructive macrobioeroders worldwide in tropical and temperate environments (Schönberg et al. 2017) and yet there were none in our material – except for the 'dwarf' entobians (*Entobia mikra*) in Svalbard (Chapter 5). Although in some earlier studies from polar environments, there were several indications of alleged sponge borings (e.g. Hoskin & Nelson Jr. 1971; Newman & Ross 1971; James 1997).

Macroborings appear to play only a very marginal role, restricting their biogeographic distribution to warmer environments as cold as in the Kosterfjord, where all principal macrobioeroders were present (Wisshak 2006).

A shortcoming for the evaluation can be the young substrate because macroborers are usually not the first colonizers and it may take several years before they appear in the trace assemblages, but then increased with exposure time. Therefore, they may become more

important when assessing long-term bioerosion (Kiene & Hutchings 1994; Wisshak et al. 2011; Patterson et al. 2020), but even in experimental substrates that were deployed for 10 years in Svalbard waters, macroborers had not established (Max Wisshak, pers. comm.), suggesting that macroborers indeed are a rare phenomenon in polar waters.

8.2 Latitudinal gradient of microbioerosion

While the geographical scope of our studies is not sufficient to determine detailed biogeographic distribution patterns, an initial approximation is possible to deal with hypotheses III and IV.

Comparing the results of this doctoral thesis with reported ichnodiversity in the literature is complicated due to different approaches/methodologies and bathymetric transects, and the fact that microbioerosion ichnotaxonomy is still a relatively young discipline. To put this result into a global context, two detailed microbioerosion studies with a similar approach are used for comparison: one from the warm-temperate Azores (ca. 38.3°N; table 1 in Wisshak et al. 2011; see table 3 therein for a summary of additional ichnodiversity studies) and one from the cold-temperate Kosterfjord, Sweden (58.5°N; fig. 10 in Wisshak 2006).

Because of the same obstacles described in Chapter 7 (as a reminder: PAR data, the definition of a photic zonation, samples from incomparable water depths), the considered samples are brought to a comparable level. The base of the euphotic zone in the Azores is at ca. 70 m; in euphotic 60 m water depth there were 21 microbioerosion traces, eight of them from phototrophic euendoliths. Down to 150 m the light conditions are dysphotic with 13 different traces. This number was reduced to ten at 500 m (aphotic). Experimental platforms from aphotic 85 m in the Kosterfjord comprised seven traces.

From this perspective, the ichnodiversity in great water depths is highest in the polar seas, lowest in the Kosterfjord, and moderate in the Azores, although the Azores are generally characterized by high biodiversity (Wisshak et al. 2010) and yielded the highest total number of ichnotaxa (Wisshak et al. 2011). While it has often been said that species diversity decreases from low to high latitudes (e.g. Crame 1997; Gray 2001; Clarke & Crame 2010), this does not hold true for ichnotaxa at aphotic depths. Reasons for this distribution pattern cannot be made conclusive within this doctoral thesis, but possible explanations are given below.

The number of different ichnotaxa in aphotic water depths is similar in the Azores (13) and the Arctic and the Antarctic (15 and 16, respectively, see Chapter 7 and the Appendix). While the minor difference is presumably related to the prevailing small-scale environmental differences (currents, sediment input, etc.), the great resemblance is explained by similar and stable conditions at deep water depths at all latitudes.

Why Kosterfjord stands out is not quite clear, but it could have been decisive that not only was the sample size highest in the polar regions, but also that the barnacles were on average older than the exposure duration, so that the bioerosion agents in the polar regions had the longest time to bioerode.

It has been shown that bioerosion is slowed down at higher latitudes (Wisshak 2006; Wisshak et al. 2011). The abundance of bioerosion traces and rates at 85 m in the Kosterfjord were remarkably low after two years, which was a reason to run the same experiment in Svalbard for 10 years (pers. comm. with Max Wisshak). If the platforms in the Kosterfjord had been exposed longer, the microbioerosion trace assemblages would probably have been more diverse. Samples of the cold-water coral *Lophelia pertusa* from the same study were older than the duration of exposure and demonstrated with 12 microbioerosion traces in fact a higher ichnodiversity (Wisshak 2006). Moreover, this study was conducted 14 years ago, and a greater diversity would probably be recognized today (pers. comm. with Max Wisshak).

In the Azores, bioerosion is due to the favourable environmental conditions naturally faster (Wisshak et al. 2011), which led to a similar ichnodiversity as in the Arctic and Antarctic.

Perhaps the glaciation events also had an impact, since taxa found shelter in deeper water depths during glaciation events, leading to a broader bathymetric distribution, eurybathic taxa (as reviewed for isopoda by Brandt 2005) and a greater species richness.

It is also worth mentioning that the Azores have such a high level of ichnodiversity even though the islands are in the middle of the North Atlantic Ocean and relatively isolated from the continental shelf (Wisshak et al. 2011). The Kosterfjord, Frobisher Bay, the two Svalbard study sites, and the Ross Sea are much closer to continents or ice shelves.

The occurring ichnotaxa at all considered latitudes are similar and expectedly dominated by fungal traces. Many of the ichnotaxa from the Azores and the majority of the Kosterfjord inventory are also present in the polar regions. Nevertheless, some are missing in the Arctic and Antarctic, as discussed below.

No comparisons regarding bioerosion rates are given here since this cannot be answered with the conducted research. Nonetheless, bioerosion rates are higher at the Azores than in the Kosterfjord (Wisshak et al. 2011) and according to preliminary results lowest in Svalbard (pers. comm. with Max Wisshak). Furthermore, all results taken together seem to indicate that the abundance is highest in the Azores and decreases with higher latitudes.

This discussion confirmed that a generalization of decreasing ichnodiversity from low to high latitudes is too simple. The pace and rate of bioerosion may be greatly diminished (Wisshak 2006), but this cannot generally be related to ichnodiversity. While a lower diversity is still assumed for shallow waters (owing to the greatly impaired phototrophic bioeroders), this does not hold true for aphotic depths, where a comparable ichnodiversity exists.

8.3 Temperature limits of microbioeroders as a tool

As described in Chapter 1.5.2, ichnotaxa have the potential to act as an indicator for paleotemperature, based on the temperature limits of the trace-makers. Some key ichnotaxa for polar environments were already discussed in Chapter 5. At that point, however, only the results of the first study from Svalbard were available. After the series of publications is completed, possible key ichnotaxa are reviewed again to address hypothesis III. Right at the beginning, it is stressed that there is an analogy between deep water conditions at low latitudes and conditions at high latitudes, which should be kept in mind during the following discussion. Moreover, seasonal fluctuations also influence the formation of trace assemblages, as demonstrated by *Flagrichnus baiulus*. The trace was initially only known from cold-temperate regions and was then abundantly found in the Mediterranean Sea during the winter months (Färber et al. 2015).

For Svalbard, *Flagrichnus baiulus*, *Entobia mikra*, *Nododendrina europaea*, *Saccomorpha guttulata,* and *Orthogonum*-form 1 (Chapter 5 and as originally suggested in Wisshak et al. 2005; Wisshak & Porter 2006; Bromley et al. 2007; Wisshak 2008; Wisshak et al. 2018) were confirmed as ichnotaxa which are exclusive to cold-temperate and polar regions (all presumably bioeroded by organotrophic organisms). Some of them (e.g. *Entobia mikra*, *Nododendrina europaea*), however, can only be confirmed to a limited extent, as they did not occur at all study sites. *Flagrichnus baiulus* and *Saccomorpha guttulata* (Chapter 4, Figure 7-4) were present (and dominating) at all three regions and may therefore act most likely as key ichnotaxa to cold-temperate regions. *Scolecia serrata* also appeared throughout the studies, though not exclusive to polar regions (e.g. Wisshak et al. 2011). *Saccomorpha terminalis* (or *S. stereodiktyon* as described in Golubic et al. 2014) and *Flagrichnus profundus* were also suggested as key ichnotaxa (Wisshak 2006), but both were absent at all three locations, so the assumption is rejected.

Few ichno-'forms' (e.g. *Fascichnus* isp. I and II, *Flagrichnus*-form I, Finger-form, Nidus-form) have been described for the first time, but this does not mean that they are limited (or endemic) to high latitudes. With time, other methods, deeper bathymetric transects, and more samples there are frequently new traces (Wisshak et al. 2011; Wisshak et al. 2019a); some may have been overlooked before. Besides, some ichnotaxa have a slightly different morphology than described in the original diagnosis. These variations may also be due to the necessity to adapt to the harsher conditions (see Chapter 5–7 for descriptions).

While *Nododendrina europaea* is common in both Arctic studies, the trace was not observed in the Antarctic and may, therefore, be limited to the Northern Hemisphere. Although the name would suggest this, *Pyrodendrina arctica* was not encountered in the Canadian Arctic, but only in Svalbard.

The absence of usually common ichnotaxa can also act as indicator for cold regions, although statements based on negative evidence are not sufficient evidence. For instance,

some of the most common ichnotaxa are *Eurygonum nodosum* (latitudinal limited up to Kosterfjord until now; Wisshak 2006), *Irhopalia* (e.g. *I. catenata* latitudinal limited up to Tromsø until now; Glaub et al. 2002), few *Saccomorpha* (e.g. *S. stereodiktyon* latitudinal limited up to Kosterfjord until now; Wisshak 2006) ichnospecies, *Orthogonum fusiferum*, or *Scolecia filosa* (both latitudinal limited up to Kosterfjord until now; Wisshak 2006) – none of which were observed in the polar regions. Therefore, if they are missing, it may mean that a sample originates from polar regions.

The general assumption that the ichnotaxon *Saccomorpha clava* is cosmopolitan, is contradicted here. While it dominated at an aphotic zone station in the Ross Sea (Chapter 6), it was very rare in Svalbard (Chapter 5) and lacked in Frobisher Bay (Chapter 7). The same applies to *Cavernula pediculata* and *Planobola* ispp., which were found only rarely in Svalbard. *Ichnoreticulina elegans* was also assumed to be a ubiquitous trace (as reviewed by Wisshak 2006) and since it was found in Svalbard and the Ross Sea, this assumption is still valid.

8.4 Polar bathymetric distribution patterns as a tool

Macrobioerosion trace assemblages are good tools to recognise rocky-coasts or as evidence of sea level changes, as certain borings occur only up to a certain water depth. Provided the outcrop has good conditions, traces can be correlated at different localities, which can facilitate paleogeographic reconstruction (e.g. de Gibert et al. 1998; for several examples see de Gibert et al. 2012).

A similar approach is also feasible with the microbioerosion traces (Chapter 1.5.1). Light was repeatedly identified as the main factor for the establishment of microbioerosion trace assemblages (e.g. Glaub 1994; Vogel et al. 1995; Glaub et al. 2002; Meyer et al. 2020, submitted). However, this could only be sufficiently investigated in Svalbard, where light was statistically confirmed as the main factor. The two different study sites with different conditions (e.g. higher turbidity and stronger currents at Bjørnøy-Banken) were not decisive, which again confirms light as the main factor (Chapter 5).

Based on the light dependence of many phototrophic euendoliths and their specific low-light tolerance limit, a set of index ichnocoenoses was established. A vertical zonation pattern allows to assess light availability and thus relative bathymetry (Chapter 1.5.1, Table 1-1; e.g. Glaub 1994; Vogel et al. 1995; Glaub et al. 2002; Wisshak 2012).

Ichnocoenoses were developed in fossil material and have been successfully applied (e.g. Vogel et al. 1995; Vogel et al. 1999; Glaub et al. 2001; Vogel & Brett 2009). In the tropical to warm-temperate environments, the assemblages match well with the established ichnocoenoses (e.g. Budd & Perkins 1980; Perry & Macdonald 2002; Glaub 2004; Radtke & Golubic 2005), and also for the Mediterranean Sea the applicability of the ichnocoenoses was

judged as "good" (Färber 2016). The single study regarding ichnocoenoses in the cold temperate environments also showed a close approximation (Wisshak 2006).

The applicability of the index ichnocoenoses for the assessment of relative bathymetry in polar settings is more difficult, especially for the euphotic zone. This limitation is partly due to the lack of samples from the intertidal and partly to the extreme seasonality, resulting in a reduced number of phototrophic euendoliths. The condensed photic zonation with higher latitudes (because of less sunlight and seasonal eutrophication; after Wisshak 2006) leads to a less pronounced boundary of the euphotic subzones and dysphotic zones, reflected in a less clear and characteristic ichnocoenoses. There are three additional obstacles: Firstly, a general problem is that only three ichnotaxa occurred at all three sites (Chapter 7). Secondly, the supratidal to subtidal euphotic zones cannot be adequately assessed due to the few samples (Wisshak (2006) suggested *Cavernula pediculata* as substitute for the *Fascichnus acinosus*, which seems possible given its occurrence in Svalbard.). Thirdly, it is challenging to choose a specific ichnotaxon as a part of the index ichnocoenoses, because most ichnotaxa do not exclusively dominate in a specific zone but are found uniformly in the whole water column. Besides, the boundary between the dysphotic and aphotic zone is blurred and was only precisely defined in Mosselbukta, Svalbard (Chapter 5). Consequently, the following explanations are based primarily on the results from Svalbard (supported by findings from the two other study sites, if applicable) but can nevertheless address hypothesis IV.

Photic zone	Proposed index ichnocoenoses	General characteristics
deep euphotic	*Conchocelichnus seilacheri* *Ichnoreticulina elegans*	co-existing with other traces by phototrophic euendoliths
dysphotic	*Conchocelichnus seilacheri* *Ichnoreticulina elegans*	no other traces by phototrophic euendoliths
aphotic	*Saccomorpha guttulata* *Flagrichnus baiulus*	only traces by organotrophic euendoliths

Initially, the body fossil *Paleoconchocelis starmachii* was part of the index ichnocoenoses for the shallow III to deep euphotic zone, which was later replaced by *Irhopalia catenata* (Wisshak 2012; *Irhopalia* replaced *Rhopalia* in Wisshak et al. 2019a). Meanwhile, the microbioerosion trace of *Paleoconchocelis starmachii* was officially established as *Conchocelichnus seilacheri* (Radtke et al. 2016). Since *Conchocelichnus seilacheri* was commonly observed in that zone in Svalbard, this ichnotaxon might be an option together with the very common *Ichnoreticulina elegans* for the index ichnocoenoses of the deep euphotic zone.

According to Wisshak (2012), the dysphotic zone is characterised by *Ichnoreticulina elegans* and *Saccomorpha clava*, but the last-mentioned ichnotaxon was too rare and is hence rejected. Instead, *Conchocelichnus seilacheri* is suggested together with *Ichnoreticulina elegans*.

These suggestions would mean that the same ichnotaxa indicate two different photic zones. For this reason, the general characteristics must be used additionally: a co-existence with other traces of phototrophic agents indicates the deep euphotic zone and an absence of these traces indicates the dysphotic zone.

The aphotic zone does not correspond well to the proposed ichnotaxa assemblage, as *Saccomorpha clava* was too rare and *Orthogonum lineare* was exclusively observed in Svalbard. Instead, *Saccomorpha guttulata* is a strong index ichnotaxon, together with *Flagrichnus baiulus*. Both occur also in the whole water column, but in aphotic zones, there would be no traces by phototrophic organisms.

8.5 Evaluation of methodology

Regarding the substrate used, barnacles are strongly recommended for further ichnodiversity studies. They were, as expected (see Chapter 3.2), excellent for the comparisons and were a very suitable substrate to display the embedded traces. The fact that barnacles are removed in winter in the intertidal (Hoskin & Nelson Jr. 1971) is, without doubt, a problem, as it limits sample availability. To incorporate more samples from the intertidal/euphotic zone, solutions must be sought in the future.

The CET (Chapter 3.3.1) is a straightforward and uncomplicated method, but it has the major disadvantage that the substrate is completely dissolved and therefore no subsequent investigations can be carried out. Therefore, it might be useful to use the double-embedding procedure (as outlined in Golubic et al. 2019) to visualise the bioerosion traces in situ without having to completely dissolve the substrate. In this way, the trace-makers could finally be determined more precisely, which is another restrictive issue. Even if the traces are treated strictly by their makers, findings of the producers could provide more information.

Wisshak et al. (2011) were the first to conduct statistical biodiversity analyses in a bioerosion ichnodiversity study. The same methodology (ANOSIM, NMDS, ichnodiversity indices) was successfully applied in this doctoral thesis, providing and proving significant findings, especially for the Svalbard study (Chapter 5). Therefore, similar approaches are highly recommended for future ichnology studies.

The same case study was used to successfully apply the methodology for the ichnodisparity concept for the first time (Chapter 5). The same concept was tested for the second study (Chapter 6), but since the majority of the samples were taken from the aphotic zone, the information was of limited value and results were therefore not published. As the bathymetric transect from the Canadian Arctic (Chapter 7) yielded exclusively samples from the dysphotic zone, the method was not applied from the start. Ichnodisparity itself is a great tool “to assess the variability of morphologic plans in biogenic structures” (Buatois et al. 2017: p. 1) and to interpret the behaviour of trace-makers (Buatois et al. 2017) that deserves more attention in future studies.

Chapter 9
Outlook

This doctoral thesis was the first approach towards a broad understanding of polar microbioerosion patterns and will be a basis for future bioerosion studies at the highest latitudes. It has taken the first important step towards an understanding of polar bioerosion patterns, although further work is undoubtedly needed. Additional questions and topics remain unanswered that deserve more attention and have either not yet been mentioned in the context of this work or should be highlighted again.

Probably the biggest difficulty of this series of papers was the small number of samples from the intertidal and euphotic zone. Such samples, however, would be of great importance to investigate cosmopolitan ichnotaxa or some which are exclusive to the Arctic and Antarctic. Regarding the fact that ichnotaxa by phototrophic euendoliths account usually for the largest part of ichnodiversity composition, it would be exciting to see which ones are robust against the harsh environmental conditions. Therefore, future studies should focus on covering these areas. For a better polar microbioerosion overview, additional samples from the Antarctic, such as the Weddell Sea, should be included, which would also allow improved conclusions about the Antarctic distribution of ichnotaxa.

An evaluation of Max Wisshak's experimental study from Svalbard is currently in progress (pers. comm.), which will allow the calculation of bioerosion rates and will enhance latitudinal comparison, but this only covers the North Atlantic from the Azores across Kosterfjord to Svalbard. A similar approach in the Pacific and/or experimental platforms at least in the Antarctic is necessary.

As previously mentioned, it is about time to identify producers of aphotic microbioerosion traces (possibly by means of a genetic methodology, which has only recently started according to Golubic et al. 2019) – many ichnotaxa are known for more than 30 years and yet it is not with absolute certainty known from which kingdom the trace-makers originate. Although this is a different field, a combination of both research areas could result in a better understanding and would help to interpret processes.

Fungi and rhodophytes are not yet well studied as bioerosion agents and especially the fungi deserve to be in the focus of future studies due to their general abundance and dominance at aphotic depths.

Macrobioerosion needs better investigation in the polar regions in the future. Such research can be achieved, for instance, with *Clathromorphum compactum*, a coralline alga, in which traces can already be seen with the naked eye. Given their importance in warmer regions, it is necessary to understand the role of macrobioeroders in the polar realm for further investigations.

Chemical bioerosion, especially microbioerosion, will accelerate with ocean acidification (see introduction and discussion in Chapter 1) in combination with other abiotic factors (Tribollet & Golubic 2011). Since carbonate saturation in polar seas can have a negative influence in addition to ocean acidification due to naturally low temperatures, one issue that should be addressed in the future is the impact of climate change and ocean acidification on polar bioerosion. While the Arctic is the region with the quickest change due to climate change (see Chapter 2), the "Ross Sea plays a significant role in the Southern Ocean carbon cycle as a major regional anthropogenic CO_2 sink" (Smith Jr. et al. 2014: p. 473). Hence, bioerosion at high latitudes needs to be studied in more detail regarding climate change. In order to enable this, however, additional fundamental research similar to this doctoral thesis is necessary.

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Appendix

13.1 Publication list for the summary of microbioerosion studies

Authors	Year	Title	DOI
Acton	1916	On a new penetrating algae	
Akpan	1986	Depth distribution of endolithic algae from the Firth of Clyde: Implications for delineation and subdivision of the photic zone	10.1017/S0025315400042910
Akpan	1990	Bioerosion of oyster shells in brackish modern mangrove swamps, Nigeria	10.1080/10420949009386341
Akpan, Farrow	1984	Shell-boring algae on the Scottish continental shelf: Identification, distribution, bathymetric zonation	10.1017/S0263593300009743
Akpan, Farrow	1985	Shell bioerosion in high-latitude low-energy environments: Firths of Clyde and Lorne, Scotland	10.1016/0025-3227(85)90152-5
Alderman, Jones	1967	Shell disease of *Ostrea edulis* L.	10.1038/216797a0
Alexandersson	1974	Carbonate cementation in coralline algal nodules in the Skagerrak, North Sea; biochemical precipitation in undersaturated waters	10.1306/74D72964-2B21-11D7-8648000102C1865D
Alexandersson	1975	Marks of unknown carbonate-decomposing organelles in cyanophyte borings	10.1038/254212b0
Alexandersson	1976	Actual and anticipated petrographic effects of carbonate undersaturation in shallow seawater	10.1038/262653a0
Allouc, Le Campion-Alsumard, Leung Tack	1996	La bioérosion des substrats magmatiquesen milieu littoral: L'exemple de la presqu'ile du Cap Vert (Sénégal Occidental)	10.1016/S0016-6995(96)80007-6
Al-Thukair, Golubic	1991	New endolithic cyanobacteria from the Arabian Gulf	10.1111/j.0022-3646.1991.00766.x
Amor, López Armengol, Iñiguez Rodriguez et al.	1991	Intertidal endolithic fauna and it's relationship to the mineralogical, physical and chemical characteristics of the substrate	10.1007/BF01319709
Anagnostidis, Pantazidou	1985	*Cyanosaccus aegaeus* n. sp., a new marine endolithic cyanophyte from the Aegean Sea, Hellas (Greece)	
Anagnostidis, Pantazidou	1988	*Hyella kalligrammos* sp. nov., *Hyella maxima* (Geitl.) comb. nov., and other freshwater morphotypes of the genus *Hyella* Born. et Flah. (Chroococcales, Cyanophyceae)	
Bak, Laane	1987	Annual black bands in skeletons of reef corals (Scleractinia)	10.3354/meps038169
Bathurst	1966	Boring algae, micrite envelopes and lithification of molluscan biosparites	10.1002/gj.3350050104
Beuck, Freiwald	2005	Bioerosion patterns in a deep-water *Lophelia pertusa* (Scleractinia) thicket (Propeller Mound, northern Porcupine Seabight)	10.1007/3-540-27673-4_47
Boekschoten	1966	Shell borings of sessile epibiontic organisms as palaeoecological guides (with examples from the dutch coast)	10.1016/0031-0182(66)90023-X

Boerboom, Smith, Risk	1998	Bioerosion and micritization in the deep sea coral *desmophyllum cristagalli*	10.1080/08912969809386572
Bromley, Hanken	1981	Shallow marine bioerosion at Vardø, arctic Norway	
Bromley, Hanken, Asgaard	1990	Shallow marine bioerosion: Preliminary results of an experimental study	
Budd, Perkins	1980	Bathymetric zonation and paleoecological significance of microborings in Puerto Rican shelf and slope sediments	
Charó, Cavallotto, Acenolaza	2017	Macrobioerosion and microbioerosion in marine molluscan shells from Holocene and modern beaches (39°-40°S, South of Buenos Aires Province, Argentina)	10.1111/1755-6724.13356
Carreiro-Silva, McClanahan, Kiene	2009	Effects of inorganic nutrients and organic matter on microbial euendolithic community composition and microbioerosion rates	10.3354/MEPS08251
Carreiro-Silva, Kiene, Golubic et al.	2012	Phosphorus and nitrogen effects on microbial euendolithic communities and their bioerosion rates	10.1016/j.marpolbul.2011.12.013
Cavaliere, Alberte	1970	Fungi in animal shell fragments	
Cerrano, Bavestrello, Calcinai et al.	2001	Bioerosive processes in Antarctic seas	10.1007/s003000100294
Chazottes	1996	Etude expérimentale de la bioérosion et de la sédimentogenèse en milieu récifal : effets de l'eutrophisation (Ile de la Réunion, Océan indien occidental)	
Chazottes, Le Campion-Alsumard, Peyrot-Clausade	1995	Bioerosion rates on coral reefs: Interactions between macroborers, microborers and grazers (Moorea, French Polynesia)	10.1016/0031-0182(95)00043-L
Chazottes, Le Campion-Alsumard, Peyrot-Clausade et al.	2002	The effects of eutrophication-related alterations to coral reef communities on agents and rates of bioerosion (Réunion Island, Indian Ocean)	10.1007/s00338-002-0259-0
Chazottes, Hutchings, Osorno	2017	Impact of an experimental eutrophication on the processes of bioerosion on the reef: One Tree Island, Great Barrier Reef, Australia	10.1016/j.marpolbul.2017.02.047
Chu, Hua	1982	A new species of *Hyella* (*H. simplex*) from the Xisha Islands, Quangdong	
Chu, Wu	1984	Studies on the lime-boring algae of China	10.1007/978-94-009-6560-7_40
Clokie, Boney	1980	*Cochocelis* distribution on the Firth of Clyde: Estimates of the lower limits of the photic zone	10.1016/0022-0981(80)90096-9
Clokie, Scoffin, Boney	1981	Depth naxima of *Conchocelis* and *Phymatolithon rugulosum* on the N. W. Shelf and Rockall Plateau	
Coombes, La Marca, Naylor et al.	2015	The influence of light attenuation on the biogeomorphology of a marine karst cave: A case study of Puerto Princesa Underground River, Palawan, the Philippines	10.1016/j.geomorph.2014.10.007
Curry	1983	Microborings in Recent brachiopods and the functions of caeca	10.1111/j.1502-3931.1983.tb01707.x
Curin, Peharda, Calcinai et al.	2014	Incidence of damaging endolith infestation of the edible mytilid bivalve *Modiolus barbatus*	10.1080/17451000.2013.814793
Dalongeville, Le Campion, Fontaine	1994	Bilan bioconstruction - biodestruction dans les roches carbonatées en mer Méditerranée: étude expérimentale et implications géomorphologiques	10.1127/zfg/38/1994/457
Davies, Hutchings	1983	Initial colonization, erosion and accretion on coral substrate	10.1007/BF00304729
Delvoye	1992	Endolithic algae in living stony corals: Algal concentrations under influence of depth-dependent light conditions and coral tissue fluorescence in *Agaricia agaricites* (L.) and *Meandrina meandrites* (L.)	

		(Scleractinia, Anthozoa)	
Dharmaraj, Chellam, Velayudhan	1987	Biofouling, boring and predation of pearl oyster	
Donn, Boardman	1988	Bioerosion of rocky carbonate coastlines on Andros Island, Bahamas	
Duerden	1902	Boring algae as agents in the disintegration of corals	
Edwards, Perkins	1974	Distribution of microborings within continental margin sediments of the southeastern United States	10.1306/212F6C53-2B24-11D7-8648000102C1865D
Färber, Wisshak, Pyko et al.	2015	Effects of water depth, seasonal exposure, and substrate orientation on microbial bioerosion in the Ionian Sea (Eastern Mediterranean)	10.1371/journal.pone.0126495
Farrow, Allen, Akpan	1984	Bioclastic carbonate sedimentation on a high-latitude, tide-dominated shelf; Northeast Orkney Islands, Scotland	10.1306/212F8422-2B24-11D7-8648000102C1865D
Folk, Roberts, Moore	1973	Black phytokarst from hell, Cayman Islands, British West Indies	10.1130/0016-7606(1973)84<2351:BPFHCI>2.0.CO;2
Fork, Larkum	1989	Light harvesting in the green alga *Ostreobium* sp., a coral symbiont adapted to extreme shade	10.1007/BF00397273
Försterra, Beuck, Häussermann et al.	2005	Shallow-water *Desmophyllum dianthus* (Scleractinia) from Chile: Characteristics of the biocoenoses, the bioeroding community, heterotrophic interactions and (paleo)-bathymetric implications	10.1007/3-540-27673-4_48
Freiwald	1995	Bacteria-induced carbonate degradation: A taphonomic case study of *Cibicides lobatulus* from a high-boreal carbonate setting	10.2307/3515159
Freiwald	1998	Microbial maceration and carbonate dissolution on cold-temperate shelves	10.1080/08912969809386570
Freiwald, Wilson	1998	Taphonomy of modern deep, cold-temperate water coral reefs	10.1080/08912969809386571
Gaspard	1989	Quelques aspects de la biodegradation des coquilles de brachiopodes; consequences sur leur fossilisation	10.2113/gssgfbull.V.6.1207
Gehman, Harley	2019	Symbiotic endolithic microbes alter host morphology and reduce host vulnerability to high environmental temperatures	10.1002/ecs2.2683
Gektidis	1999	Development of microbial euendolithic communities: The influence of light and time	
Gektidis, Golubic	1996	A new endolithic cyanophyte/cyanobacterium: *Hyella vacans* sp. nov. from Lee Stocking Island, Bahamas	
Gektidis, Dubinsky, Goffredo	2017	Microendoliths of the shallow euphotic zone in open and shaded habitats at 30°N – Eilat, Israel – paleoecological implications	10.1007/s10347-006-0091-z
Glaub	2004	Recent and sub-recent microborings from the upwelling area off Mauritania (West Africa) and their implications for palaeoecology	10.1144/GSL.SP.2004.228.01.04
Glaub, Gektidis, Vogel	2002	Microborings from different North Atlantic shelf areas-variability of the euphotic zone extension and implications for paleodepth reconstructions	
Golubic	1960	Über die Blaualgenvegetation in den nordadriatischen Hafen Jugoslawiens	
Golubic	1969	Distribution, taxonomy, and boring patterns of marine endolithic algae	10.1093/icb/9.3.747
Golubić, Al-Thukair, Gektidis	1996	New euendolithic cyanobacteria from the Arabian Gulf and the Bahama Bank: *Solentia sanguine*a sp. nova	10.1127/algol_stud/83/1996/291
Golubic, Radtke, Campbell et al.	2014	The complex fungal microboring trace *Saccomorpha stereodiktyon* isp. nov. reveals growth strategy of its maker	10.1080/10420940.2014.888301
Grange, Rybarczyk,	2015	The three steps of the carbonate biogenic dissolution process by microborers in coral reefs (New Caledonia)	10.1007/s11356-014-4069-z

Tribollet			
Gutiérrez-Isaza, Espinoza-Avalos, León-Tejera et al.	2015	Endolithic community composition of *Orbicella faveolata* (Scleractinia) underneath the interface between coral tissue and turf algae	10.1007/s00338-015-1276-0
Günther	1990	Distribution and bathymetric zonation of shell-boring endoliths in recent reef and shelf environments: Cozumel, Yucatan (Mexico)	10.1007/BF02536953
Hartmann, Carilli, Norris, Charles, Deheyn	2010	Stable isotopic records of bleaching and endolithic algae blooms in the skeleton of the boulder forming coral *Montastraea faveolata*	10.1007/s00338-010-0667-5
Henderson, Styan	1982	Description and ecology of Recent endolithic biota from the Gulf Islands and banks in the Strait of Juan de Fuca, British Columbia	10.1139/e82-120
Highsmith	1981	Lime-boring algae in hermatypic coral skeletons	10.1016/0022-0981(81)90117-9
Hoek	1958	The algal microvegetation in and on barnacle-shells, collected along the Dutch and French coasts	
Hoffmann	1985	Distribution patterns of recent microbial endoliths in the intertidal and supratidal zones Bermuda	
Höhnk	1969	Über den pilzlichen Befall kalkiger Hartteile von Meerestieren	10.2312/berichte_dwkfm_20_129-140
Höhnk	1955	Niedere Pilze vom Watt und Meeresgrund (Chytridiales und Thraustochytriaceae)	10.1007/BF00589670
Hook, Golubic	1988	Mussel *Periostracum* from deep-sea redox communities as a microbial habitat: 2. The pit borers	10.1111/j.1439-0485.1990.tb00242.x
Hook, Golubic, Millman	1984	Micritic cement in microborings is not necessarily a shallow-water indicator	10.1306/212F8431-2B24-11D7-8648000102C1865D
Hoskin, Reed, Mook	1986	Production and off-bank transport of carbonate sediment, Black Rock, southwest Little Bahama Bank	10.1016/0025-3227(86)90115-5
Jeffrey	1968	Pigment composition of Siphonales algae in the brain coral *Favia*	10.2307/1539621
Johnston, Anderson	1962	A fungus in *Anomia* simplex shell	
Kiene	1985	Biological destruction of experimental coral substrates at Lizard island, Great Barrier Reef, Australia	
Kiene	1988	A model of bioerosion on the Great Barrier Reef	
Kiene	1997	Enriched nutrients and their impact on bioerosion: Results from ENCORE	
Kiene, Hutchings	1994	Experimental investigations on patterns in the rates of bioerosion at Lizard Island, Great Barrier Reef	
Kiene, Hutchings	1994	Long-term bioerosion of experimental coral substrates from Lizard Island, Great Barrier Reef	
Kiene, Radtke, Gektidis et al.	1995	Factors controlling the distribution of microborers in Bahamian reef environments	doi.org/10.1007/BF02536867
Kloos	1982	Destruction of tests of the foraminifer *Sorites orbiculus* by endolithic microorganisms in a lagoon on Curaçao (Netherlands Antilles)	
Kobluk, Risk	1977	Calcification of exposed filaments of endolithic algae, micrite envelope formation and sediment production	10.1306/212F71C6-2B24-11D7-8648000102C1865D
Kobluk, Risk	1977	Rate and nature of infestation of a carbonate substratum by a boring alga	10.1016/0022-0981(77)90131-9
Kohlmeyer	1967	Intertidal and phycophilous fungi from Tenerife (Canary Islands)	10.1016/S0007-1536(67)80070-6
Kohlmeyer	1968	Marine fungi from the Tropics	10.1080/00275514.1968.12018567
Kohlmeyer	1969	Deterioration of wood by marine fungi in the deep sea	10.1520/STP32012S

Kohlmeyer	1969	Marine fungi of Hawaii including the new genus *Helicascus*	10.1139/b69-210
Kornmann	1962	Zur Kenntnis der Porphyra-Arten von Helgoland	10.1007/BF01609954
Kornmann	1962	Die Entwicklung von *Monostroma grevillei*	10.1007/BF01609436
Kylin	1935	Über einige kalkbohrende Chlorophyceen	
Lazar, Loya	1991	Bioerosion of coral reefs-A chemical approach	10.4319/lo.1991.36.2.0377
Le Bris, Le Campion-Alsumard, Romano	1998	Characteristics of epilithic and endolithic algal turf exposed to different levels of bioerosion in French Polynesian coral reefs	10.1016/S0399-1784(99)80025-5
Le Campion-Alsumard	1966	Contribution à l'étude des Cyanophycées lithophytes des étages supralittoral et medio-littoral (Région de Marseille)	
Le Campion-Alsumard	1970	Cyanophycées marines endolithes colonisant les surfaces rocheuses dénudées (étages supralittoral et médiolittoral de la région de Marseille)	10.1007/BF02502569
Le Campion-Alsumard	1975	Etude expérimentale de la colonisation d'éclats de calcite par les cyanophycées endolithes marines	
Le Campion-Alsumard	1991	Three *Hyella* taxa (endolithic cyanophytes) from tropical environments (Lizard Island, Great Barrier Reef)	
Le Campion-Alsumard, Campbell, Golubic et al.	1982	Endoliths and the depth of the photic zone; discussion and reply	10.1306/212F8134-2B24-11D7-8648000102C1865D
Le Campion-Alsumard, Golubic, Hutchings	1995	Microbial endoliths in skeletons of live and dead corals: *Porites lobata* (Moorea, French Polynesia)	
Le Campion-Alsumard, Golubic, Priess	1995	Fungi in corals: symbiosis or disease? Interaction between polyps and fungi causes pearl-like skeleton biomineralization	
Le Campion-Alsumard, Romano, Peyrot-Clausade et al.	1993	Influence of some coral reef communities on the calcium carbonate budget of Tiahura reef (Moorea, French Polynesia)	10.1007/BF00349377
Liljedahl	1986	Endolithic micro-organisms silicification of a bivalve fauna from the Silurian of Gotland	10.1111/j.1502-3931.1986.tb00740.x
Lukas	1969	An investigation of the filamentous, endolithic algae in shallow-water corals from Bermuda	
Lukas	1978	Depth distribution and form among common microboring algae from the Florida continental shelf	
Lukas, Golubic	1981	New endolithic cyanophytes from the North Atlantic Ocean. II. *Hyella gigas* Lukas & Golubic sp. nov. from the Florida continental margin	10.1111/j.0022-3646.1983.00129.x
Mallela, Perry	2007	Calcium carbonate budgets for two coral reefs affected by different terrestrial runoff regimes, Rio Bueno, Jamaica	0.1007/s00338-006-0169-7
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Margolis, Rex	1971	Endolithic algae and micrite envelope formation in Bahamian Oölites as revealed by Scanning Electron Microscopy	10.1130/0016-7606(1971)82[843:EAAMEF]2.0.CO;2
Martinez	1990	The Conchocelis-phase of Porphyra (Rhodophyta) in the intertidal of San Juan Island, Washington, USA	10.2216/i0031-8884-29-4-391.1
Marquet, Nicastro, Gektidis et al.	2013	Comparison of phototrophic shell-degrading endoliths in invasive and native populations of the intertidal mussel *Mytilus galloprovincialis*	10.1007/s10530-012-0363-1
May, MacIntyre,	1982	Distribution of microborers within planted substrates along	

Perkins		a barrier reef transect, Carrie Bow Cay, Belize	
May, Perkins	1979	Endolithic infestation of carbonate substrates below the sediment-water interface	10.1306/212F7748-2B24-11D7-8648000102C1865D
Peyrot-Clausade, Le Campion-Alsumard, Harmelin-Vivien et al.	1995	La bioerosion dans le cycle des carbonates; essais de quantification des processus en Polynesie francaise	
Morse, Morse, Duncan	1981	Algal tumors in the Caribbean Octocorallian, *Gorgonia Ventalina*: II. Biochemical characterization of the algae, and first epidemiological observations	
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Nadson	1927	Les algues perforantes de la Mer Noire	
Naylor, Viles	2002	A new technique for evaluating short-term rates of coastal bioerosion and bioprotection	10.1016/S0169-555X(02)00139-3
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Nielsen	1972	A study of the shell-boring marine algae around the Danish island Laeso	
Nielsen	1987	Marine algae within calcareous shells from New Zealand	10.1080/0028825X.1987.10413359
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Perry, Macdonald	2002	Impacts of light penetration on the bathymetry of reef microboring communities: Implications for the development of microendolithic trace assemblages	10.1016/S0031-0182(02)00446-7
Perkins, Tsentas	1973	Microbial destruction of carbonate substrates “planted” on the North Eastern St. Croix shelf	
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Peyrot-Clausade, Chazottes, Pari	1999	Bioerosion in the carbonate budget of two Indo-Pacific reefs: La Réunion (Indian Ocean) and Mooréa (Pacific Ocean)	
Porter, Lingle	1992	Endolithic Thraustochytrid marine fungi from planted shell fragments	10.1080/00275514.1992.12026142

Potts	1980	Blue-green algae (Cyanophyta) in marine coastal environments of the Sinai Peninsula; distribution, zonation, stratification and taxonomic diversity	10.2216/i0031-8884-19-1-60.1
Purdy, Kornicker	1958	Algal disintegration of Bahamian limestone coasts	
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Radtke	1993	The distribution of microborings in molluscan shells from recent reef environments at Lee Stocking Island, Bahamas	10.1007/BF02536921
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Ramos-Flores	1983	Lower marine fungus associated with black line disease in star corals (*Montastrea annularis*, E. & S.)	10.2307/1541208
Reyes-Nivia, Diaz-Pulido, Kline et al.	2013	Ocean acidification and warming scenarios increase microbioerosion of coral skeletons	10.1111/gcb.12158
Risk, Pagani, Elias	1987	Another internal clock; preliminary estimates of growth rates based on cycles of algal boring activity	10.2307/3514757
Rooney, Perkins	1972	Distribution and geologic significance of microboring organisms within sediments of the Arlington Reef Complex, Australia	10.1130/0016-7606(1972)83[1139:DAGSOM]2.0.CO;2
Roth, Orpurt, Ahearn	1964	Occurrence and distribution of fungi in a subtropical marine environment	10.1139/b64-037
Roush, Garcia-Pichel	2020	Succession and colonization dynamics of endolithic phototrophs within intertidal carbonates	10.3390/microorganisms8020214
Schmidt, Freiwald	1993	Rezente gesteinsbohrende Kleinorganismen des norwegischen Schelfs	
Schroeder	1972	Calcified filaments of an endolithic alga in recent Bermuda reefs	
Scoffin, Alexandersson, Bowes et al.	1980	Recent, temperate, sub-photic, carbonate sedimentation; Rockall Bank, Northeast Atlantic	10.1306/212F7A04-2B24-11D7-8648000102C1865D
Shashar, Stambler	1992	Endolithic algae within corals - life in an extreme environment	10.1016/0022-0981(92)90055-F
Silbiger, Donahue, Brainaird	2017	Environmental drivers of coral reef carbonate production and bioerosion: A multi-scale analysis	10.1002/ecy.1946
Stubler, Peterson	2016	Ocean acidification accelerates net calcium carbonate loss in a coral rubble community	10.1007/s00338-016-1436-x
Sparrow	1936	Biological observations on the marine fungi of woods hole water	10.2307/1537470
Sparrow	1937	The occurrence of saprophytic fungi in marine muds	10.2307/1537586.
Taylor	1983	The black band disease of Atlantic reef corals	10.1111/j.1439-0485.1983.tb00116.x
Thomas, Fujita, Iryu, Bard et al.	2012	Assessing subsidence rates and paleo water-depths for Tahiti reefs using U-Th chronology of altered corals	10.1016/j.margeo.2011.12.006
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Tribollet, Atkinson, Langdon	2006	Effects of elevated pCO_2 on epilithic and endolithic metabolism of reef carbonates	10.1111/j.1365-2486.2006.01249.x
Tribollet, Langdon, Golubic et al.	2006	Endolithic microflora are major primary producers in dead carbonate substrates of Hawaiian coral reefs	10.1111/j.1529-8817.2006.00198.x
Tribollet, Godinot, Atkinson et al.	2009	Effects of elevated pCO_2 on dissolution of coral carbonates by microbial euendoliths	10.1029/2008GB003286
Tribollet, Grange, Parra et al.	2018	Limited carbonate dissolution by boring microflora at two volcanically acidified temperate sites: Ischia (Italy, Mediterranean Sea) and Faial (Azores, NE Atlantic Ocean)	10.1002/2016GB005575
Tribollet, Pica, Puce et al.	2018	Euendolithic *Conchocelis* stage (Bangiales, Rhodophyta) in the skeletons of live stylasterid reef corals	10.1007/s12526-017-0684-5
Tudhope, Risk	1985	Rate of dissolution of carbonate sediments by microboring organisms, Davies Reef, Australia	10.1306/212F86F7-2B24-11D7-8648000102C1865D
Urish	1976	Microfloral borers in recent Caribbean Scleractinian corals	
Vénec-Peyré	1987	Boring forminifera in French Polynesian coral reefs	10.1007/BF00300966
Vogel, Kiene, Gektidis et al.	1996	Scientific results from investigation of microbial borers and bioerosion in reef environments	
Vogel, Gektidis, Golubic et al.	2000	Experimental studies on microbial bioerosion at Lee Stocking Island, Bahamas and One Tree Island, Great Barrier Reef, Australia: Implications for paleoecological reconstructions	10.1080/00241160025100053
Wilkinson, Burrows	1972	The distribution of marine shell-boring green algae	10.1017/S0025315400018579
Wisshak	2006	Temperate bioerosion: Ichnodiversity and biodiversity from intertidal to bathyal depths (Azores)	10.1111/j.1472-4669.2011.00299.x
Wisshak	2006	High-latitude bioerosion: The Kosterfjord experiment	10.1007/978-3-540-36849-6
Wisshak	2008	Two new dwarf *Entobia* ichnospecies in a diverse aphotic ichnocoenosis (Pleistocene/Rhodes, Greece)	10.1007/978-3-540-77598-0
Wisshak, Gektidis, Freiwald et al.	2005	Bioerosion along a bathymetric gradient in a cold-temperate setting (Kosterfjord, SW Sweden): An experimental study	10.1007/s10347-005-0009-1
Wisshak, Tribollet, Golubic et al.	2011	Temperate bioerosion: Ichnodiversity and biodiversity from intertidal to bathyal depths (Azores)	10.1111/j.1472-4669.2011.00299.x.
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Young, Nelson	1988	Endolithic biodegradation of cool-water skeletal carbonates on Scott shelf, northwestern Vancouver Island, Canada	10.1016/0037-0738(88)90123-6
Zebrowski	1936	New genera of Cladochytriaceae	10.2307/2394150
Zeff, Perkins	1979	Microbial alteration of Bahamian deep-sea carbonates	10.1111/j.1365-3091.1979.tb00350.x
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13.2 Summary of the results of the semi-quantification of all study sites

Producer	Ichnotaxon	Svalbard								Canadian Arctic						Ross Sea												
		0	0–20	25	38	50	75	100	125	62	74	80	86	90–91	93–94	37	154	277	321	466	538	620	770	879	980	1130	1310	1680
Cyanobacteria	*Fascichnus frutex*															--												
(Cyanobacteria)	*Fascichnus* isp. I	--																										
(Cyanobacteria)	*Fascichnus* isp. I				--																							
Cyanobacteria	*Planobola* cf. *microgota*	--	--		--																							
Chlorophytes	*Cavernula pediculata*	--																										
Chlorophytes	*Ichnoreticulina elegans*		++	++	--	++	-									++												
Rhodophytes	*Conchocelichnus seilacheri*		+	+	-	-																						
(Sponge)	*Entobia mikra*					--	+	+	-																			
(Fungi)	*Flagrichnus baiulus*	--	--	--	-	--	+	+	+	--		--		--	-		+	-	-	--	-	-	--	--	--	-	+	-
(Fungi)	*Flagrichnus* cf. *baiulus*	-	--		--	--	--	--									--	--	--	--	-	--				--	--	--
(Fungi)	*Flagrichnus* cf. *profundus*		-	--	-	--	--	-					--	--	--													
(Fungi)	*Flagrichnus*-form I																	--		--	--		--					
(Fungi)	Large tongue-form										--	-		-	--													
Fungi	*Saccomorpha clava*							--													--			--		--	++	--
(Fungi)	*Saccomorpha guttulata*			--		--	-	+	-	--	--	--	--	--	--		-	--	--	++	-	--	--	-	--	-	++	
(Fungi)	*Orthogonum*-form I *sensu*				--	--	--	--												--		--	--					
(Fungi)	*Orthogonum lineare*				--	--	-	-	--											--				--		--	--	
(Fungi)	*Orthogonum tubulare*			--	--	--	+	+	-																			
(Fungi)	*Orthogonum giganteum*		--					--	--							--		--		--								
Fungi	*Polyactina araneola*																			-			--	-		-	-	
(Foraminifera)	*Pyrodendrina villosa*		--		-	--	-	-	--							--	--	--		-								
(Foraminifera)	*Pyrodendrina arctica*		--	--		--	-	-	--																			
Foraminifera	*Nododendrina europaea*		--	--	--	-	-	+	-	+	--	-	--	+	-													
Bacteria	*Scolecia serrata*	--	--	--	--	-	+	-	-	--								--										
Unknown	Finger-form															--	--	--		--				--				--
Unknown	Nidus-form															--						--						
Unknown	Proturbero-form																			--								
Unknown	Clavate-form																		--									
Acrothoracid barnacles	*Rogerella* isp.																			-								
		6	11	9	13	14	13	14	10	4	3	4	3	5	5	6	5	8	4	12	5	5	5	6	2	6	6	4
Number of trace	**29**					**20**								**6**									**18**					

euphotic zone
dysphotic zone
aphotic zone

exclusive to Svalbard
exclusive to the Canadian Arctic
exclusive to the Ross Sea

occurence at both poles
exclusive to the Arctic

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Publication list

M. Wisshak, **N. Meyer**, G. Radtke & S. Golubic (2018) Saccomorpha guttulata – *a new marine fungal microbioerosion trace fossil from cool- to cold-water settings*. Paläontologische Zeitschrift 92. 525–533, https://doi.org/10.1007/s12542-018-0407-7.

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M. Bertling, L. A. Buatois, D. Knaust, B. Laing, M. G. Mángano, **N. Meyer**, R. Mikuláš, N. J. Minter, C. Neumann, A. K. Rindsberg, A. Uchman, M. Wisshak (submitted) *Names for trace fossils 2.0: theory and practice in ichnotaxonomy*. Lethaia.

Versicherung an Eides Statt
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