Cambro-Ordovician Microorganisms: Acritarchs and Endoliths

MARTIN STOCKFORS
Abstract

Organic-walled microfossils are abundant and taxonomically diverse in Cambrian-Ordovician strata; some are important for biostratigraphy and for the correlation of geological successions. New assemblages of Cambrian-Ordovician acritarchs from Kolguev Island, Arctic Russia and Middle Cambrian ichnofossils of endoliths from Peary Land, North Greenland are studied. Twenty-seven acritarch species are described in detail and 10 taxa are left under open nomenclature. The diagnosis of one genus is restricted, and two other are emended. New combinations are proposed for three species and one new species is recognised. The studied acritarch assemblages are taxonomically rich and age-diagnostic and used to recognise Upper Cambrian and Tremadoc strata on Kolguev Island. The sedimentologically continuous successions provide for the first time palaeontological evidence of Cambrian strata in the northeastern sector of Europe. The exact level of the Cambrian-Ordovician boundary was distinguished together with stratigraphic intervals equivalent to the *Peltura* and *Acerocare* zones of the Upper Cambrian of Baltica. The newly established relative age of the lowermost sedimentary succession overlying the Timanian unconformity allows verification of the minimum age of the Timanian deformation and the time-span of the hiatus bound to this unconformity. Endoliths occur in the fossil record from the Early Archean and they played an important role in the formation of stromatolites and the process of bioerosion and biodegradation. Endoliths that have actively bored into brachiopod shells or carbonate grains (euendoliths), and some that inhabited the cavities inside brachiopod shells (cryptoendoliths) are described. Borings within the carbonate grains extended with a dendritic pattern, whereas those within the brachiopod shells were formed by a multifilamentous euendolith which produced characteristic longitudinally ridged galleries. The cryptoendolithic morphologies include indeterminate coccoid masses and at least two filamentous forms. However, considerable variation in the dimensions of the currently phosphatised diagenetic crusts of the cryptoendoliths hinders discrimination.

Keywords: Cambrian. Ordovician, acritarch, endolith, Kolguev Island, North Greenland, stratigraphy

Martin Stockfors, Department of Earth Sciences, Palaeobiology, Norbyvägen 22, Uppsala University, SE-75236 Uppsala, Sweden

DISCLAIMER
This manuscript is printed only for public examination as a doctoral thesis.

© Martin Stockfors 2005


Printed in Sweden by Geotryckeriet, Uppsala 2005
Till
min familj
List of Publications


V. Stockfors, M. & Peel, J.S., 2005: Euendoliths and cryptoendoliths within late Middle Cambrian brachiopod shells from North Greenland. *GFF*, submitted manuscript.

Reproduction of papers I-III was made with permission of the copyright holder.

Paper I © 2004 Elsevier
Paper II © 2004 AASP Foundation
Paper IV-V © 2005 by the authors, submitted to GFF
Contents

List of Publications ........................................................................................................v
Introduction .....................................................................................................................1
  Early life and microorganisms .............................................................................1
  The Cambrian Explosion and diversification of microorganisms ..............3
  Aims ............................................................................................................................4
Acritarchs .............................................................................................................5
  Geology of Kolguev Island and the Pechora Basin ..................................7
  Palaeogeography ..................................................................................................9
Endolithic microorganisms ...........................................................................11
  Euendoliths .........................................................................................................11
  Cryptoendoliths ..................................................................................................12
  Bioerosion ............................................................................................................13
  North Greenland .................................................................................................14
Results & Discussion ..........................................................................................16
  The Acritarch Study ..........................................................................................16
  The Endolith Study .............................................................................................17
Sammanfattning på svenska: .............................................................................19
  Kambro-ordoviciska mikroorganismer: acritarcher och endoliter ..............19
  Tidigt liv och mikroorganismer ..........................................................................19
  Den kambriska explosionen och diversifieringen av mikroorganismer ........21
Acknowledgements ..............................................................................................23
References .............................................................................................................24
Introduction

Early life and microorganisms

Life has existed on Earth for almost four billion years. Until recently its history has been recognised exclusively from the study of fossils but is now also supported by molecular data, geochemical signatures and isotopic fractionations of some organic compound. The earliest known microfossils, of probable cyanobacterial origin, are from the Apex Cherts, Western Australia and of Early Archean age, approximately 3.5 Ga (Schopf & Packer 1987, Schopf et al. 2002; see discussion in Brasier et al. 2002). Fossils of microborers from the same period have also been found in pillow lava from South Africa (Furnes et al. 2004). The degree of complexity of the earliest microorganisms probably required a substantial period to develop, suggesting that life must have existed for a long time before its first appearance in the geological record. Crustal rocks older than 3.5 Ga are intensely metamorphosed, hence lacking recognisable organic remains and fossils once preserved in them. However, biotic activity is inferred from geochemical signatures of carbon isotopes preserved in the approximately 3.8 Ga meta-sediments from the Isua Formation exposed on Akilia Island, southwest Greenland (Mojzsis et al. 1996; see also Whitehouse et al. 2001; Fedo & Whitehouse 2002). In rocks younger than 3.5 Ga, in particular after the appearance of eukaryotic organisms at 2.7 Ga (Brocks et al. 1999), the increasing amount of microfossils provides evidence of progressive evolution and diversification of the biota.

The earliest microbiota known from the geological record was unicellular prokaryotes, lacking a cell nucleus and advanced organelles, and inhabiting marine environments. They have been described as photosynthesizing cyanobacteria that used sunlight as the source of energy for their metabolic processes. The cyanobacteria, together with other bacteria, could form microbial mats (stromatolites) in near-shore tidal environments, or live a planktonic mode of life in the oceans. They probably occupied various marine environments down to a maximum depth dependent on the availability of sunlight. Today cyanobacteria and other bacteria also thrive in lacustrine and other fresh water environments, but such ancient environments are poorly
preserved in the geological record and the time of bacterial colonisation of land is uncertain.

The first evidence of eukaryotes, i.e. cells with a differentiated and membrane-bound cell nucleus, comes from molecular fossils of biological lipids, approximately 2.7 Ga (Brocks et al. 1999, see also Javaux et al. 2004), whereas morphological fossils appeared in the geological records at 2.1 Ga (Runnegar 1994). One group of single celled marine organisms which is among the earliest and most common microfossils from 1.9-1.8 Ga (Hofmann & Schopf 1983; Zhang 1986; Jankauskas 1989; Mendelson and Schopf 1992), is referred to as acritarchs. This is a group of microfossils named and taxonomically defined by their uncertain origin. Acritarchs are considered to be resting cysts of phytoplankton which accumulated in the bottom sediments where they may be buried and fossilised. Since the affinity of most acritarchs is now related to eukaryotic photosynthesising plankton, the status as a group of ‘uncertain origin’ has diminished. Although not so ancient, the Cambrian-Ordovician acritarchs of an approximate age of 500-480 Ma are the major subject of the present studies.

This thesis also describes endoliths, a group of microorganisms which may be representative of various biological clades, such as bacteria, cyanobacteria, algae and fungi that are characterised by their mode of life, i.e. living within rocks by inhabiting small cavities in carbonate substrates either by boring actively or using existing cavities. It is well known that endoliths penetrate shells of metazoans and they are recorded from the Cambrian period onwards (Golubic & Seong-Joo 1999). Nonetheless, they appeared long before the shell secreting metazoans in the geological record. The earliest endolithic microorganisms have been described by Furnes (2004) from Archaeaean pillow lava in South Africa, but they are more commonly found from the Late Proterozoic (700-800 Ma) onwards (cf. Knoll et al. 1986).

From our own ‘homocentric’ point of view, the species Homo sapiens is often alleged to be the most prominent creature on Earth. However, the microbes (e.g. archea, bacteria, cyanobacteria and algae) exhibit the greatest species diversity on Earth and constitute the frontiers of the biosphere expansion, inhabiting an enormous array of environments down to depth of several kilometres into the hydrosphere and the lithosphere. The unicellular organisms exhibit far more complex metabolic processes and this is because they perform all their life functions in a single cell, whereas true multicellular organisms have specialised cells and tissues for different life functions. The latter cells are not capable of a surviving on their own.

The biosphere has a profound influence on the Earth system and generates driving mechanisms for a global environmental change (Lovelock 1979; Lenton 1998). The most significant effect of the early microbial life on Earth was the gradual oxidation of the initially reducing atmosphere through a continuous release of free oxygen as the by-product of photosynthesis that has evolved among cyanobacteria in the early Proterozoic. The release of free oxygen into the atmosphere was a prerequisite for the development of
eukaryotes and subsequently the ‘higher’ organisms, and the colonisation of land. The Earth’s continual environmental change is the result of the interaction between living organisms, and underlying tectonic processes, all combining to create the Dynamic Earth we know today.

The Cambrian Explosion and diversification of microorganisms

The Cambrian Period (543-490 Ma) is known for a remarkable diversification of marine shelly metazoans, also known as The Cambrian Explosion. Several distinct clades of protoctists (unicellular eukaryotes) both organic walled and with mineralised tests or skeletons, such as algae (including acritarchs), foraminiferans and radiolarians also radiated rapidly throughout the Cambrian (Vidal & Moczydłowska 1997; Moczydłowska 1998; Won & Below 1999; McIlroy et al. 2001; Moczydłowska 2002) forming an integrated part of this evolutionary event.

Most Cambrian metazoans were suspension feeders and grazers dependant on organic matter provided by the photosynthesising microbiota, predominantly algal acritarchs at this time. Thus they are tightly linked to the primary producers in the trophic web. The coeval evolution of autotrophic microbiota and heterotrophic metazoans established complex marine ecosystems and was a result of the interplay between genetic and environmental factors, among which the nutrient-generating phytoplankton played a significant role (Moczydłowska 2002).

The studies of endolithic microborers is still at an initial stage, although the first endolithic trace fossils have been found as far back as the Early Archean (Furnes et al. 2004). The endoliths are also experiencing selective pressure from grazers, feeding on endolithic and epilithic (inhabiting the surface of shells, corals and other carbonate substrates) cyanobacteria, green algae and fungi. A strong selective pressure may also produce a great diversification among primary producers, suggesting that many new forms of microphytoplankton and cyanobacteria appear in conjunction with the Cambrian Explosion.

The fossils studied here are neither closely related biologically nor belonged to the same biocenosis, but they were a part of the extended and diverse community of single celled biota that rapidly radiated in the Cambrian and showed a variety of modes of life and ecological adaptations. This was one of the signs of the Cambrian evolutionary and ecological explosion.
Aims

The aim of this thesis is to document two interesting and distinct groups of microorganisms from the late Middle Cambrian to Early Ordovician periods: the algal acritarchs and cyanobacterial endoliths. Although differing in many ways, they evolved through the Cambrian and were a part of the great diversification event. The thesis is based on two separate studies. The first study deals with the group Acritarcha, which is defined by the uncertain origin of the fossil organisms. Well preserved acritarch assemblages from Kolguev Island, Arctic Russia, are described in detail and referred to valid and revised taxa and higher systematic ranks. The Cambrian-Ordovician boundary is also identified for the first time in this region. The second study constitutes a group of microorganisms with an endolithic mode of life, fossilised in rock cavities and brachiopod shells. Well preserved material associated with hardgrounds from the Henson Gletscher Formation and Holm Dal Formation of North Greenland consists of trace fossils of a diverse flora of endoliths from an area that so far has a poorly known microfossil record.
Acritarchs

As early as in the nineteenth century palaeontologists developed an interest in organic-walled microfossils, but it took more than half a century before a more systematic research was undertaken. The first palynomorphs classified as acritarchs are almost certainly those described by White (1862) from the Ordovician to Devonian strata of New York State, U.S.A. The term acritarch originates from the Greek words *acros* and *tarchos*, and simply means *uncertain origin*. In the 1930’s, Eisenack described many acritarch species and eventually he regarded them to be of phytoplanktonic origin (Eisenack 1969). Together with co-authors, he produced a monumental taxonomic catalogue (Eisenack *et al*. 1973, 1976). At the same time Wetzel (1933) assigned many Mesozoic microfossils to the group Hystrichosphaera that consisted both of acritarchs and dinoflagellates. This was later divided into two different groups by Evitt (1961) to distinguish fossil cysts of dinoflagellates from fossil cysts of unknown origin. Subsequently, Evitt (1963) proposed the group Acritarcha that today is defined principally as *organic walled cysts of uncertain origin*. Consequently, any acritarch of which the biological affinity has been determined should be transferred from the group Acritarcha to their true systematic group (Tappan 1980). Certain taxa of the former acritarchs have also been transferred, e.g. the genus *Tasmanites* and *Pterospermella*, and are today referred to the Family Prasinophyceae of the algal Phylum Prasinophyta. The group Acritarcha is a polyphyletic and informal group (Deflandre 1947; Downie *et al*. 1963; Evitt 1963), and its taxonomy is entirely phenetic and based on morphological features. Despite the acritarch’s uncertain biological affinity and they are all classified under the International Code of Botanical Nomenclature (Downie 1961). Acritarchs exhibit many different morphologies (Fig. 1) and are classified primarily by their vesicle shape, the shape and size of the processes.

Acritarchs and many other microfossils have become very important tools in biostratigraphic correlation. The application of microfossils to biostratigraphic correlation was developed by researchers in the petroleum industry at an early stage of micropalaeontological studies. Improved modern microscopes enable better interpretations of morphological features of the microfossils. Scanning Electron Microscopes (SEM) improved the possibilities to distinguish ultrastructures and recently acritarchs were studied in Transmission Electron Microscope (TEM) (e.g. Talyzina & Moczydlowska 2000). The Laser Confocal Microscope enables studies of the internal structures of organic walled fossils, but also allows creation of three dimensional images.
This permits more precise classifications of microfossils and to improve the systematic and biostratigraphical interpretations.

Figure 1. Acritarchs from the Upper Cambrian-Tremadocian strata in Kolguev Island illustrating the diversity of cyst morphologies.

4. *Saharidia fragilis* (Downie, 1958) Combaz, 1967. All specimens are from Kolguev Island, Arctic Russia. Scale bar in 1 is 12 µm for 1, 2; 15 µm for 3; 20 µm for 4.
Geology of Kolguev Island and the Pechora Basin

Kolguev Island is located on the Barents Sea shelf near the northern coast of Arctic Russia and geologically it is a part of the Pechora Basin (Fig. 2). The Pechora Basin extends between the Timan Range and the Polar Urals, which are the two fold belts amalgamated to the East European Craton during the Ediacaran (formerly Vendian) Timanian and the late Palaeozoic Uralian orogenies, respectively (see review by Gee et al. 2000). The Pechora Basin is a crustal block defined by deep faults and it consists of a pre-Ediacaran basement of deformed and metamorphosed sedimentary and volcanic rocks, intruded by igneous bodies, approximately 620 and 560 Ma, and the overlying terminal Neoproterozoic-Phanerozoic platform cover (Bogatsky et al. 1996; Olovyanishnikov 1998; Gee et al. 2000).

The angular, so-called Timanian unconformity that separates basement and sedimentary cover is a major tectonic feature in the region, yet the time interval of the hiatus is not accurately recognized because of the deficiency of reliable fossil records and/or isotopic datings. The maximum age of the platformational succession has been estimated roughly to be late Neoproterozoic in the Timan Range and early Ordovician in the Pechora Basin (Preobrazhenskaya et al. 1995; Olovyanishnikov 1998; Melnikov 1999). However, the supposed Neoproterozoic age of the strata in the Timan Range (Bogatsky et al. 1996; Olovyanishnikov 1998) lacks supporting evidence. Recent studies
of acritarchs from Kolguev Island have proved the existence of Upper Cambrian rocks (Moczydłowska et al. 2004).

The Phanerozoic sedimentary strata on Kolguev Island are almost 5000 m

Figure 3. Sedimentary successions in the Bugrino 1 and North-Western 202 boreholes with sample locations and proposed biostratigraphic subdivision.
thick and logged in several boreholes. However, the lowermost part of the succession is recognised exclusively in the Bugrino 1 and North-Western 202 boreholes, although the basement rocks are not yet reached (Preobrazhenskaya et al. 1995; Fig. 3). This succession is composed predominantly of fine-grained siliciclastic rocks with thin interbeds of conglomerates and it underlies the pre-Devonian regional paraconformity. The strata are almost horizontal, un-metamorphosed and consist of laminated organic-rich claystones and siltstones with a maximum thickness of 1280 m in the Bugrino 1 borehole. Formations are not yet distinguished in the two studied successions and only brief descriptions of the lithology and sedimentary structures are available (Bro et al. 1988; Preobrazhenskaya et al. 1995; Moczydlowska et al. 2004). Fossil records of acritarchs, brachiopods and phyllocarid arthropods have been interpreted previously to indicate an early Ordovician age (Rudavskaya & Popov in Preobrazhenskaya et al. 1995), whereas the new studies of acritarchs reveal assemblages which are diagnostic for both the late Cambrian and Tremadocian time intervals. These Upper Cambrian-Lower Ordovician sediments accumulated in open marine environments on a stable shelf flooded by a transgression prograding over the peneplaned basement (Preobrazhenskaya et al. 1995; Malyshev 2000; Moczydlowska et al. 2004). The deposition of platformal sediments on the passive margin extending along the northern and north-eastern (in present day coordinates) edge of the Baltica palaeocontinent has been interrupted by several episodes of regional uplift and submergence as well as some volcanic activity, but it continued throughout the Palaeozoic.

Palaeogeography

Acritarchs play an important role in global palaeogeographic reconstructions. Based on palaeontological, palaeomagnetic, palaeoclimatic, tectonic and stratigraphic evidence, several models of Cambrian and Ordovician palaeogeography are available today. The Cambrian model by Scotese and McKerrow (1990) has been used (Moczydlowska 1997) to plot the fossil records and to test the possible bioprovincial distribution of acritarchs. More time restricted Ordovician palaeomaps have recently been published by Cocks (2001) and Li & Powell (2001). Bergström (1990) presented an oceanic current circulation model for the Early Ordovician whereas Christiansen and Stouge (1999) published a palaeo-oceanographic model for the Arenigian epoch. Servais et al. (2003) summarised different palaeobiogeographical distribution of Ordovician organic-walled microphytoplankton, such as acritarchs, prasinophytes and related microorganisms. Cramer (1968) made the first bioprovincial interpretation of two major acritarch assemblages to be dependent on palaeo-latitudes. Cramer & Diez (1977) distinguished two acritarch ‘provinces’ in the Ordovician; one controlled by cold water regimes and the other of warm water regimes. During
the Late Cambrian and Early Ordovician, the supercontinent Gondwana (including South Africa, America, Antarctica, Australia, India and several micro-continents) occupied higher palaeolatitudes and was dominated by cold water provinces, whilst Laurentia (including North America and Greenland) was located in the equatorial zone and was dominated by warm water assemblages. Vavrdová (1974) distinguished two other provinces; the Mediterranean province dominated by diacromorphic acritarchs and the Baltic province dominated by acanthomorphic acritarchs. Studies on recent marine phytoplankton show that ocean currents play an important role for their global distribution (Matthiessen 1995; Mudie and Harland 1996), suggesting that palaeo-ocean currents must have played an important role for the distribution of acritarchs (Vidal & Moczydłowska 1996; Servais et al. 2003).
Endolithic microorganisms

Cyanobacteria form a very diverse group of Eubacteria (true bacteria) and its constituent members range in morphology from minute unicellular to large multicellular organisms. Most cyanobacteria are photosynthesising, producing oxygen as a by-product and most of them contain chlorophyll $a$, together with various proteins called phycobilins, which give the cells a typical blue-green colour. Cyanobacteria have a known geological record from the Archaean, approximately 3.5 Ga (Schopf & Packer 1987, Schopf et al. 2002; see discussion in Brasier et al. 2002), to the present day. Certain cyanobacteria are characterised by an endolithic mode of life. Such endoliths may be classified as chasmoendoliths that colonize existing cracks and fissures, cryptoendoliths that occupy structural cavities in the rock and euendoliths that actively penetrate the interior of rocks (Golubic et al. 1981).

The earliest described endolithic microorganisms have been found in Archaean pillow lava from South Africa (Furnes 2004) but cyanobacteria appear more frequently from the late Proterozoic (Knoll et al. 1986) onwards.

Euendoliths

A variety of names has been applied to fossils and ichnofossils of euendolithic organisms (e.g. Green et al. 1988; Guoxiang 1997). One such form, with branching linear cell series, has been described as *Eohyella* Zhang & Golubic, 1987, emend. Green et al., 1988 and it is a morphological counterpart of the recent living genus *Hyella* Bornet & Flahault, 1888 (Fig. 4). *Hyella* has been described as one of the morphologically most complex genera of coccoid cyanobacteria (Golubic et al. 1987), combining properties of both unicellular and multicellular organisms (LeCampion-Alsumard & Golubic 1985). Cyanobacterial taxonomy has been based mainly on morphology, which is also the only parameter applicable to fossil specimens. Several attempts to compare boring patterns and cell shapes of fossil euendolithic morphospecies with recent living *Hyella* species have been made to find modern morphological counterparts to the fossil *Eohyella* and other early ichnofossils (e.g. Campbell 1982; Knoll et al. 1986; Green et al. 1988; Al-Thukair & Golubic 1991a; Golubic & Seong-Joo 1999). However, it is also possible to reconstruct palaeoenvironments by comparing fossil cyanobacteria with their modern counterparts (Golubic & Seong-Joo 1999). Re-
cently, our understanding of the fossil endoliths has been improved by the description of many new euendolithic *Hyella* species, especially from the Arabian Gulf (Al-Thukair & Golubic 1991a, 1991b, 1996; Al-Thukair *et al.* 1994).

![Figure 4. FEG SEM images of different endoliths from North Greenland. A. Etched out “mould” of a euendolithic organism actively bored into a carbonate grain and resembling the modern genus *Hyella*. B. Cryptoendolith, with long encrusted filament that inhabit the inside of a brachiopod shell. Scale bars = 100µm.](image)

**Cryptoendoliths**

Another group of endoliths is the *cryptoendoliths* (Golubic *et al.* 1981), which inhabit a cavity, e.g. the inside of shells or cracks and fissures in the rocks (Fig 4). Schroeder (1972) described the growth of calcareous crusts on algal filaments in cavities within present day Bermuda reefs, recognising its contribution to synsedimentary submarine cementation. The cavity-dwelling filaments, or cryptoendoliths in the terminology of Golubic *et al.* (1981), formed the locus for deposition of a crust of radiating bladed or fibrous calcite crystals, such that individual cavities were crossed with a mesh of calcified fibres. Schroeder (1972) also recognised algal borings within shell fragments, euendoliths in the sense of Golubic *et al.* (1981), noting that these euendolithic filaments extended from their galleries to form the cryptoendolithic meshworks. Schroeder (1972) attributed his modern endolithic algal threads to the green alga *Ostreobium*, although this was not previously known to change between euendolithic and cryptoendolithic life styles. Riding & Voronova (1985) stressed that the true affinities of Cambrian so-called ‘algae’ are often contentious, giving as examples the familiar *Renalcis, Epi-*
phyton and Chabakovia which were interpreted as Rhodophyta by Vologdin (1962) and Cyanobacteria by Luchinina (1975). Riding (2001) noted that two thirds of the 30 principal genera of calcified Cambrian microbes were most likely cyanobacteria, while only 3 genera were interpreted as calcified algae.

Unlike the modern Bermudan examples described by Schroeder (1972) and the Greenland forms described in this thesis, many of these Cambrian microbes described by Riding (2001) developed calcification of the enclosing sheath during life.

Figure 5. Multifilamentous, bundle forming euendolith from the samples of Holm Dal Formation. The endolithic galleries may show very acute angles or soft bends in the brachiopod shell. The bundles vary greatly in diameter. The individual filaments also vary in diameter in concordance with the diameter of the bundle. Scale bar = 5µm.

Bioerosion

Endolithic organisms are commonly and widely known to play a major role in bioerosion and biodegradation (e.g. Mao Che et al. 1996; Vogel et al. 1996; Radtke et al. 1997; Vogel et al. 2000; Tribollet & Payri 2001). By dissolving and perforating carbonate rocks, endoliths have a great impact on micritization in shallow marine and intertidal environments. Vogel et al. (2000) studied the rate of bioerosion due to endolithic activity and pointed out its palaeoecological importance. Metazoans grazing on endoliths not only increase coastal destruction (Torunski 1979), but also enhance the micritization process immensely. Nevertheless, it has been suggested that endolithic Cyanobacteria not only destroy original grain textures, but also play a constructional role in stromatolite growth by forming lithified layers of welded grains (Macintyre et al. 2000). Present day endolithic Cyanobacteria are restricted to the upper photic zone, whereas the lower photic zone is inhabited by green and red algal endoliths. Thus, endolithic Cyanobacteria can be important bathymetric indicators (Budd & Perkins 1980) and may con-
North Greenland.

The endolithic material treated in this thesis comes from two separate areas and three different localities in Peary Land, North Greenland. The first study reported in Paper IV is based on material collected from one locality in the Løndal area, marked locality 1 in Figure 6, belonging to the Henson Gletscher Formation. The Henson Gletscher Formation forms part of the Brønlund Fjord Group of late Early-Middle Cambrian age (Ineson & Peel 1997) which represents the development of a carbonate platform on the currently southern margin of the mainly Lower Palaeozoic Franklinian Basin of the Canadian Arctic Islands (Peel & Sønderholm 1991). Off-platform strata of the Brønlund Fjord Group show an alternation of pale, carbonate-dominated units (Aftenstjerneso and Sydpasset Formations) with darker, mixed siliciclastic and carbonate units (Henson Gletscher and Ekspedition Bræ Formations). The former represent extensive sheets of carbonates shed from the strongly prograding platform during highstands of sea level (Surlyk & Ineson 1987; Ineson & Surlyk 1992, 1995). The mixed siliciclastic-carbonate sediments of the Henson Gletscher and Ekspedition Bræ Forma-
tions were deposited during lowstands of sea level during which much of the carbonate platform was exposed. The phosphatised sediments forming the upper few metres of the Henson Gletscher Formation in Løndal represent a lowstand wedge of wackestones which accumulated prior to the ensuing highstand represented by the Sydpasset Formation.

The samples in Paper V were all collected from two localities around Holm Dal, marked locality 2 in Figure 6, and are all from the Gustav Holm Dal Formation of central North Greenland (Peel 1988). The formation was defined by Ineson (1988) as part of the Tavsens Iskappe Group which is fully described by Ineson & Peel (1997); see also Peel & Sonderholm (1991). The formation is about 155 m thick in its type section (Fig. 6, locality 2) but pinches out entirely some 5 km to the south in Fimbuldal. In the area around Gustav Holm Dal, the formation typically forms recessive, dark-weathering outcrops of mainly thin, parallel and wavy bedded argillaceous lime mudstones and grey laminated dolomites that are interbedded with thin bedded packstones and grainstones. The latter dominate the upper third of the formation where they are frequently dolomitised. Beds of carbonate breccia and slumped horizons occur sporadically throughout the formation.

A hardground composed of a finely laminated phosphatised surface, a few millimetres in thickness, is conspicuous on frost-heaved slabs derived from the lower 10 m of the formation at the type locality at Holm Dal. The same, or a similar surface, was also located at one of the Holm Dal localities, some 11 m above the base of the formation. The hardground is encrusted with minute, crater-like, echinoderm holdfasts and is associated with winnowed shell lags of phosphatic brachiopods, which also display the currently described endolith associations.
Results & Discussion

The thesis is based on two separate studies on different groups of microorganisms from late Middle Cambrian to the earliest Ordovician. The first study is based on fossil acritarchs from late Cambrian-early Ordovician material from Kolguev Island in Barents Sea in the Arctic region of Russia and comprises three papers. The second study deals partly with euendoliths that extends with dendritic patterns into carbonate grains, partly with Bundle-forming euendoliths penetrating brachiopod shells with complex galleries in combination with encrusted filaments of cryptoendoliths inhabiting brachiopod shells. All associated with the late Middle Cambrian hardground preserved in geological successions in Peary Land, central North Greenland.

The Acritarch Study


The first paper (Paper I) ‘Upper Cambrian-Ordovician successions overlying Timanian complexes: new evidence of acritarchs and brachiopods from Kolguev Island, Arctic Russia’ focuses on new material from the Kolguev Island. The studies on acritarch microfossils from the lowermost part of the Palaeozoic succession (c. 4500 m depth) revealed diverse assemblages that are biostratigraphically very significant. The position of the Cambrian-Ordovician boundary is recognised in the off-shore marine sedimentological
succession at a level where the age-diagnostic Ordovician taxa appeared. The Upper Cambrian strata of the *Peltura* and *Acerocare* trilobite zones are distinguished on the basis of taxa known from adjacent areas in the East European Platform, in general from Baltica and other palaeocontinents, Avalonia and Gondwana. Invertebrate faunas, including brachiopods, problematic mollusc and phyllocarid arthropods, are revised taxonomically and they are indicative for the Tremadocian and Arenigian stages in the upper part of the succession.

The second paper (Paper II) ‘Acritarchs from the Cambrian-Ordovician boundary interval on Kolguev Island, Arctic Russia’ is a major taxonomic revision of the diverse fossil association from the Bugrino 1 and Northwestern 202 boreholes. Age-diagnostic acritarchs were used to identify Upper Cambrian and Lower Ordovician (Tremadocian) strata and were evaluated in the context of regional stratigraphy and interregional correlation. The boundary between Cambrian and Ordovician is established in a sedimentologically continuous succession, as are the *Peltura* and *Acerocare* trilobite Zones of Cambrian from Baltica. In this paper we describe the acritarch association from Kolguev Island in great detail, its taxonomy and biostratigraphic interpretation. We propose several new combinations and emendations of species and genera commonly known from Cambrian-Ordovician successions. The aim of the revision is also to verify and establish a more consistent morphological key to identify acritarchs taking into consideration their intraspecific variations and their morphologically evolutionary diversification.

The third paper (Paper III) ‘Late Cambrian age constrains on the post-Timanian deposition on Kolguev Island, Arctic Russia’ summarizes the recently established acritarch dating of the relative age of the lowermost sedimentary succession known on Kolguev Island (Moczydłowska & Stockfors 2004) and re-evaluates the microfossil record by Rudavskaya (in Preobrazhenskaya et al. 1995) deriving from the same section as well as the invertebrate faunas. The newly documented relative age of the base of the post-Timanian platform succession is significant for interpreting the timing of the Timanian orogeny (its minimum age) and establishing the passive margin setting and onset of deposition. The previous assessment on the age of the post-Timanian unconformity in the context of the regional occurrence of Cambrian rocks is also summarized and critically reviewed.

The Endolith Study
Stockfors, M. & Peel, J.S., 2005: Endolithic Cyanobacteria from the Middle Cambrian of North Greenland, GFF, submitted manuscript. (Paper IV)
Two papers describe endolithic microorganisms from the Henson Gletscher Formation and the Holm Dal Formation. Two different kinds of endoliths were present in the study; 1 euendoliths that actively penetrates the substrate or shell by boring (chemically dissolving calcium carbonates), obtaining complex boring patterns and galleries that, in recent studies on living cyanobacterial endoliths, suggest that they are species specific; 2 cryptoendoliths inhabiting cracks and fissures, or any other cavity in the rock, e.g. cavities between brachiopod shells.

In the first paper (Paper IV) ‘Endolithic Cyanobacteria from the Middle Cambrian of North Greenland’, we describe borings in carbonate grains, attributed to the euendolithic cyanobacteria *Eohyella*, from the Middle Cambrian Henson Gletscher Formation of North Greenland. Four morphotypes are recognised, both in thin section and as three-dimensional phosphatic replicas etched from the host rock with acetic acid. While comparisons are made with living species of *Hyella* and fossil *Eohyella*, the lack of details concerning the cell shape and size allows description under open nomenclature only.

The second paper (Paper V) ‘Euendoliths and cryptoendoliths within late Middle Cambrian brachiopod shells from North Greenland’ is focused on describing both euendoliths and cryptoendoliths. At least in some cases it is possible to infer a combination of the two living modes for some of the described ichnofossils. Traces of an association of microscopic endoliths are described within the shell wall and internal cavity of phosphatic brachiopods with conjoined valves from the Holm Dal Formation (late Middle Cambrian) of Peary Land, central North Greenland. Ridged galleries which also penetrate early diagenetic, phosphatised, fibrous crusts on the shell interior are borings excavated by a multifilamentous euendolith. Meshworks of strands crossing the shell interiors are phosphatised encrustations seemingly originally deposited as radiating, acicular, aragonite crystals on cryptoendolithic filaments prior to their degradation. The identity of the endoliths from the Holm Dal Formation is unknown, but they were probably cyanobacteria.
Sammanfattning på svenska:

Kambro-ordoviciska mikroorganismer: acritarcher och endoliter

Tidigt liv och mikroorganismer
Liv har existerat på jorden i nästan fyra miljarder år. Det tidiga livet har främst beskrivits genom fynd av fossila organismer vilka på senare tid även kompletteras av moleylära och geokemiska data. De äldsta kända mikrofossilien har man funnit i Apex Cherts, västra Australien, och var troligtvis cyanobakterier och av tidigarkeisk ålder, ca. 3,5 Ga (Schopf & Packer 1987, Schopf et al. 2002; se även diskussion i Brasier et al. 2002). Nyligen har dessutom fossila spår av borrande mikroorganismer av samma ålder upptäckts i kuddlava från Sydafrika (Furnes et al. 2004). De äldsta kända organismerna måste haft en längre tid att utveckla den komplexitet de påvisar, vilket också innebär att livet är mycket äldre än dessa. All berggrund äldre än 3,5 Ga har utsatts för så kraftig metamorfos och deformation att inga fossil finns bevarade. Däremot visar geokemiska fynd (av kolisotop $^{13}$C) på biologisk aktivitet i 3,8 Ga metasediment från Isua Formation, Akiliaön, sydvästra Grönland (Mojzsis et al. 1996; se även Whitehouse et al. 2001; Fedo & Whitehouse 2002). I berggrund yngre än 3,5 Ga, framför allt efter eukaryoternas första uppträdande omkring 2,7 Ga (Brocks et al. 1999), visar den ökande mängden mikrofossil på en progressiv evolution och större diversitet bland mikroorganismer.

De tidigaste mikroorganismerna var prokaryota och levde i marina miljöer. De flesta fossil har beskrivits som fotosyntetiserande cyanobakterier, men även andra fototrofa, såväl som heterotrofa bakterier existerade vid denna tid. Cyanobakterier kunde forma strandnära stromatoliter (algmattor) eller leva ett planktiskt liv i alla marina miljöer ner till ett djup som endast begränsades av tillgången på solljus. Idag florerar cyanobakterier och andra bakterier även i sötvattensmiljöer. Emellertid är sådana miljöer dåligt bevarade i den geologiska lagerföljden och tidpunkten för mikroorganismernas kolonisation av landområden är därför osäker.

En annan grupp av mikroorganismer som behandlas i avhandlingen är endoliter, vilka representerar olika biologiska klader, t.ex. Archea, bakterier, cyanobakterier, alger och svampar. Endolitiska organismer karakteriseras av att de ”lever i berg” och då främst i hårda karbonatsubstrat, i spickor och håligheter, antingen genom att aktivt borra sig in, alternativt att bebo redan existerande håligheter (t.ex. mellan brachiopodskal). Endoliter finns, som redan nämnts, beskrivna från 3,5 Ga, men återfinns mer frekvent från sen-proterozoikum, 800-700 Ma, (Knoll et al. 1986) och är väl kända som skalbollande organismer från kambrium och framåt (Golubic & Seong-Joo 1999).

Oftast ser vi livets mångfald främst bland de högre djuren och växterna. Men faktum är att mikroberna (Archea, bakterier, cyanobakterier, alger och svampar) påvisar den största diversiteten bland alla organismer på jorden. De utgör de yttersta gränserna av biosfären och existerar på flera kilometers djup i hydrosfären och litosfären, samt lever i de mest extrema miljöer. De encelliga organismerna består av mer komplexa celler på grund av att alla deras livsfunktioner måste inrymmas i en enda cell, emedan de flercelliga organismerna har specialiserade celler för olika funktioner i organismen. Biosfären har en grundläggande påverkan på systemet jorden och genererar drivmekanismer för globala miljöförändringar (Lovelock 1979; Lenton 1998). Den mest påtagliga effekten som det tidiga livet hade på jorden, var att det påbörjades en oxidation av den tidigare reducerande atmosfären, främst p.g.a. av att fritt syre släpptes ut i atmosfären. Syret var en biprodukt av fotosyntesen som utvecklades hos cyanobakterier under tidig-proterozoikum. Tillförseln av syre till atmosfären blev också förutsättningen för den utveckling av eukaryoter och sedemera ”högre liv” som följde och därmed även förutsättningen för kolonisationen av landmassorna.
Den kambriska explosionen och diversifieringen av mikroorganismer

Kambrium (543-490 Ma) är bland annat känt för den snabba utvecklingen och diversifieringen av skalbärande marina djur, den sk. "kambriska explosionen". Parallellt med denna skedde dock även en anmärkningvärd diversifiering av encelliga mikroorganismer från olika framträdande grupper, dels de som är inneslutna endast av organiska cellväggar, såsom alger (inkl. acritarcher), cyanobakterier och andra bakterier, dels de som utsöndrar ett hårt skal utanför cellmembranet, t.ex. foraminiferer (skalamöbor) och radiolarer och kalkalger.

Syftet med denna avhandling är att beskriva två av dessa intressanta och distinkta grupper av mikroorganismer från sen-mellankambrium till tidig-ordovicium, nämligen de planktiska acritarcherna och de cyanobakteriella endoliterna. Trots att de skiljer sig avsevärt åt i många avseenden har de gemensamt att de är encelliga (cyanobakterierna visar dock "primitiv flercellighet" med celler i serie) och fotosyntetiserande organismer. Dessutom var de en del av den stora evolutionshändelsen under kambrium.

Avhandlingen baseras på två separata studier.


Den andra studien behandlar mellankambriskt, tidigare obeskrivet material från Peary Land i norra Grönland och handlar om endolitiska mikroorganismer. I två olika artiklar beskrivs dels euendoliter som aktivt borrar sig in i skal av brachiopoder och/eller karbonatkorn genom att kemiskt lösa upp karbonater. De tidigare skapar komplexa mönster och nätverk av gångar inuti skalet, medan de senare sprider ut sig i ett trädlikat mönster. Dels beskrivs kryptoendoliter vilka utnyttjar de redan existerande håligheterna mellan brachiopodskalen och som fossilit består av långa kalcifierade filament med radiell kristallväxt.

Endoliter spelar bland annat en viktig roll för bildningen av stromatoliter (Macintyre et al. 2000) såväl som för bioerosionen och biodegradation (t.ex. Mao Che et al. 1996; Vogel et al. 1996; Radtke et al. 1997; Vogel et al. 21
Acknowledgements

Thanks to all the members of the Palaeobiology Program at the Department of Earth Sciences, Uppsala University. Special thanks to my supervisors Małgorzata Moczydłowska-Vidal and John S. Peel for help, guidance and cooperation in my quest to complete this work. My co-authors Małgorzata Moczydłowska-Vidal and Leonid Popov who provided the Kolguev Island material for the acritarch study and John S. Peel, apart from co-authorship, also provided the Greenland material for the endolith study. Thanks to Sebastian Willman for variable comments and coffee-break discussions; Jonas Ahnesjö and Joakim Eriksson for recreational debates on natural science during weeks of fishing and sailing etc. I would also like to thank my family, Jenny and Malte for great support as well as my mother Birgitta for entertaining Malte.

Scanning electron microscoping was carried out in the microscopy centre, Evolutionary Biology Centre, Uppsala University. Financial support from The Swedish Research Council (Vetenskapsrådet) to Małgorzata Moczydłowska-Vidal and John S. Peel and scholarship from The Royal Swedish Academy of Sciences (Kungl. Vetenskapsakademien) is gratefully acknowledged, as is the award of a faculty postgraduate research scholarship.
References


Brasier, M.D., Green, O.R., Jephcoat, A.P., Kleppe, A.K., Van Kranendonk, M.J., Lindsay, J.F., Steele, A. & Grassineau, N.V. 2002: Questioning the evidence for Earth’s oldest fossils


Knoll, A.H., and Barghoorn, E.S. 1977: Archean microfossils showing cell division from the Swaziland System of South Africa. Science 198, 396-398.


Preobrazhenskaya, V.I., Ustritskiy, V.I., & Bro, E.G., 1995: Paleozjskie otlozheniya ostrova Kolguev (Barentsevo morie) [The Palaeozoic deposits of the Kolguev Island (Barents Sea)]. Stratigrafiya, Geologicheskaya korrelatsiya.3, 75-85.


Schopf, J.W. & Packer, B.M., 1987: Early Archean (3.3 billion to 3.5 billion-year-old) microfossils from Warrawoona Group, Australia, Science 237, 70-73.


