Sedimentology and Palaeontology of the Withycombe Farm Borehole, Oxfordshire, England

By

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Abstract

The pre-trilobitic lower Cambrian of the Withycombe Formation is a 194 m thick siliciclastic succession dominated by interbedded offshore red to purple and green pyritic mudstone with minor sandstone. The mudstone contains a hyolith-dominated small shelly fauna including: orthothecid hyoliths, hyolithid hyoliths, the rostroconch *Watsonella crosbyi*, early brachiopods, the foraminiferan *Platysolenites antiquissimus*, the coiled gastropod-like *Aldanella attleborensis,* halkieriids, gastropods and a low diversity ichnofauna including evidence of predation by a vagile infaunal predator.

The assemblage contains a number of important index fossils (*Watsonella, Platysolenites, Aldanella* and the trace fossil *Teichichnus*) that enable correlation of strata around the base of Cambrian Stage 2 from Avalonia to Baltica, as well as the assessment of the stratigraphy within the context of the lower Cambrian stratigraphic standards of southeastern Newfoundland.

The pyritized nature of the assemblage has enabled the study of some of the biota using micro-CT, augmented with petrographic studies, revealing pyritized microbial filaments of probable giant sulfur bacteria. We aim to produce the first complete description of the core and the abundant small pyritized fossils preserved in it, and develop a taphonomic model for the pyritization of the "small" shelly fossils.

Acknowledgements

It is important to acknowledge and thank the many people who supported me and contributed to the successful completion of this thesis. Firstly, a tremendous thank you to my supervisor Dr. Duncan McIlroy. I am beyond grateful for your guidance, experience, expert knowledge, mentorship, and your personal support during the course of this degree. Without your supervision and encouragement, this thesis would not have been possible. Thank you to my Co-supervisor Dr. Liam Herringshaw for your assistance in the UK, for the making of my thin sections, and for your constructive critique. I would also like to thank Dr. Suzanne Dufour, my supervisory committee member, for your contribution.

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Many other people made this research possible and helped with the collection and analyses of the required material. I would like to express my gratitude to the folks at the British Geological Survey for hosting me, in particular Ms. Tracy Gallagher. Thank you to those at the University of Bristol (Dr. Alex Liu, Frankie Dunn, and Tom Davies) for your assistance in the CT scanning of my specimens. Thank you to Dr. David Wacey at the University of Western Australia for your collaboration and the analyses you provided. I

am also grateful to Duncan's former graduate students Katie Power and Chris Boyd for helping teach me to process and understand some of this data. Thank you to Dylan Goudie and David Grant at the MUN CREAIT lab for your help with the SEM. I also cannot forget to thank my many officemates: Melissa Cook, Roddy Campbell, Jessica Hawco, and Chris McKean. Thank you guys, for putting up with my foolishness and for drinking far too many coffees with me. Your friendship, collaboration, and support meant so much to me during the entirety of this project.

Lastly, a huge you to all of my family and friends, particularly my mom, dad, Keegan and Steve for their phenomenal emotional support throughout the last few years, I honestly could not have done this without you.

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Co-authorship Statement

This master's thesis is composed of five chapters. The first is an introductory and overview chapter that contains relevant literature that provides appropriate background knowledge and context for the subsequent chapters, as well as discusses the primary objectives of the project. This chapter was written by me, receiving editorial assistance from Dr. Duncan McIlroy. Chapters two, three, and four are presented in manuscript format and are to be submitted to scientific journals. These chapters were written collaboratively between me, as primary author, and Dr. Liam Herringshaw and Dr. Duncan McIlroy as co-authors, as well as with support from others documented below. Chapter five summarizes the previous four chapters and amalgamates the material and objectives of each chapter in a cohesive way. This chapter was written by me with the editorial assistance of Dr. McIlroy.

Chapter two entitled "Palaeontology of the lower Cambrian Withycombe Formation of Oxfordshire, UK." is to be submitted to the journal *Papers in Palaeontology.* The core was logged by me and the specific samples chosen for analysis were selected by myself at the British Geological Survey and discussed with Dr. Herringshaw. Dr. Herringshaw prepared thin sections at the University of Hull and the CT scanning of the material was completed at the University of Bristol with the assistance of Dr. Alex Liu and Frankie Dunn. I was primarily responsible for the analysis and interpretation of data. Dr. McIlroy provided expert knowledge, major editorial comments, and supervisory assistance, and Dr. Herringshaw also provided thorough editorial comments during the preparation of the manuscript.

Chapter 3, entitled "Taphonomy of the lower Cambrian, Withycombe Farm Borehole, Oxfordshire, England", is to be submitted to the journal *Papers in Palaeontology*. As with chapter 2, the core was logged by myself and the specific samples chosen for analysis were selected by me at the British Geological Survey and discussed with Dr. Herringshaw. Dr. Herringshaw prepared thin sections at the University of Hull and the CT scanning of the material was completed at the University of Bristol with the assistance of Dr. Alex Liu and Frankie Dunn. Additional analysis of the fossils required collaboration with Dr. David Wacey. He completed the sample preparation and stable sulfur isotopic analysis at the University of Western Australia. I was responsible for analysing and interpreting the data. I prepared the manuscript with editorial comments and supervisory assistance provided by Dr. McIlroy.

Chapter 4 entitled "Pyritized microbial filaments from the Cambrian Stage 2 Withycombe Formation, Oxfordshire, UK" is also to be submitted to the journal *Papers in Palaeontology*. As with chapters 2 and 3, the core was logged by myself and the specific samples chosen for analysis were selected by me at the British Geological Survey and discussed with Dr. Herringshaw. Dr. Herringshaw prepared thin sections at the University of Hull and the CT scanning of the material was completed at the University of Bristol with the assistance of Dr. Alex Liu and Frankie Dunn. I was responsible for analysing and interpreting the data. I prepared the manuscript and Dr. McIlroy provided expert knowledge, major editorial comments, and supervisory assistance during preparation of the manuscript.

Chapter 1

Introduction and Overview

1.1 Introduction

The early Cambrian was a time of rapid evolution and marks a profound change in life on Earth. The early evolution of metazoan life has been the focus of many scientific studies and many aspects of it are not well constrained. Excellent preservation of fossils in various locations worldwide have provided scientists with the means to study and generate a better understanding of life at that time.

The purpose of this dissertation is to improve an understanding of the evolution of the earliest Cambrian (Fortunian and/or Cambrian Stage 2) fauna of Avalonia, by studying the sedimentology and paleontology of a section of the Withycombe Farm Borehole near Banbury, Oxfordshire, England. The aim is to better understand the Withycombe Formation stratigraphically, and to generate a better understanding of the phylogenetic placement of some of the fossils present. Initially there were two main components to this study. The first component is a sedimentological and paleontological study of the Withycombe Formation based on core logs, description and redescription of pyritized small shelly fossils (SSF), and possible trace fossils. The second part of the project involves the development of a taphonomic model for the pyritization of these earliest shelled fossils. During the course of this research we discovered pyritized microbial filaments that have not previously been described. An additional chapter is included to discuss the characterization and description of these filaments.

The Withycombe Formation is dominated by a hyolith-rich small shelly fauna preserved in pyrite, which includes orthothecid hyoliths, hyolithid hyoliths, rostroconchs, brachiopods, foraminifera, halkieriids, gastropods or possible monoplacophorans, as well as a low-diversity ichnofauna. These fossils provide important evidence for the timing of the evolution of the main groups of marine invertebrates and is important for understanding the overall pattern of early Cambrian evolution. This dissertation presents a methodical description of the macrofauna and trace fossils present in the Withycombe Formation, discusses the chronostratigraphic position of the fauna based on the comparison to similar strata in southeastern Newfoundland, as well as discusses the unique taphonomy of the assemblage.

1.2 Analytical Methods

Core from the Withycombe Farm borehole is held at the British Geological Survey (BGS) facility in Keyworth, England, where it was logged and photographed. Eight samples were collected for micro CT scanning and thin sectioning. Samples with the prefix BDF or BDG are museum specimens of the BGS in Keyworth.

Five samples were scanned using the Nikon XT H 225 ST computed tomography system at the University of Bristol Life Sciences Facility. Some of the advantages of this CT scanner include its ability to facilitate the scanning of a wide range of materials and sample sizes, especially those that are large or heavy and non-destructive, high-resolution scans (Nikon Metrology Inc, 2017). An X-ray beam is focused on a fixed, slowly rotating sample, collecting magnified projection images at each rotation. The computer then synthesizes a stack of cross section slices through the sample based on these angular views. Due to the pyritic preservation of the fossils, they exhibit a clear mineralogical contrast in the images. It is these images that are then processed and reconstructed to create realistic models. The CT scans are saved as TIFF stacks for the purpose of processing and reconstruction. Programs used for processing and reconstruction include: Adobe Lightroom, Adobe Photoshop CS4, and VG Studio Max. The TIFFs are initially loaded into Lightroom for editing. The contrast and white balance are adjusted for the best visible contrast of fossil to background rock. These images are then exported as JPEGs into Adobe Photoshop. Using Photoshop, the most interesting and best-preserved specimens are isolated from the original image. Once the picking is complete in Photoshop, these new image stacks are then loaded into VG Studio Max to build a 3D reconstruction. These steps are repeated for each sample resulting in several 3D models.

Three samples were selected for thin sectioning and were described at Memorial University, before being sent to the University of Western Australia for stable isotopic analysis of the pyritized fossils using a Cameca 1280 SIMS microprobe at their Centre for Microscopy, Characterisation & Analysis. In SIMS, a high-energy ion beam ablates material from a sample surface and secondary ions are then separated according to mass/charge (m/z) ratio in a mass spectrometer. Although capable of imaging at sub-mm spatial resolution, it is typically operated using a 10–20 mm beam in order to optimise sensitivity (UWA, CMCA website). Sulfur isotope analyses of sulphide minerals can provide information about age or biological activity, helping generate a better understanding of, in this case, the pyritization of the Withycombe Formation fossils. These data will ultimately contribute to understanding the role of microbes in the taphonomic model of preservation in the Withycombe Formation.

1.3 Literature Review

1.3.1 Geological history

During the late Neoproterozoic, southern Britain and south-east Ireland formed part of the crustal block known as Eastern Avalonia, which was located along the edge of Gondwana (Fig. 1.1), which is supported by palaeomagnetic data (Holdsworth *et al.* 2000). The Neoproterozoic rocks of Eastern Avalonia record the development of volcanic arcs and marginal basins produced by oceanic plate subduction. A similar geological history is recorded in age-equivalent rocks in Atlantic Canada and northeastern USA (Strachan, 2000). The Midlands Microcraton in southern Britain was formed as a result of this arc volcanism during the Precambrian. The stable Midlands Microcraton is where the majority of sedimentary shelf deposits are preserved. During the early Cambrian, a eustatic sea-level rise resulted in marine transgression, depositing marine sediment across the eroded Precambrian basement (Brenchley *et al.* 2006).

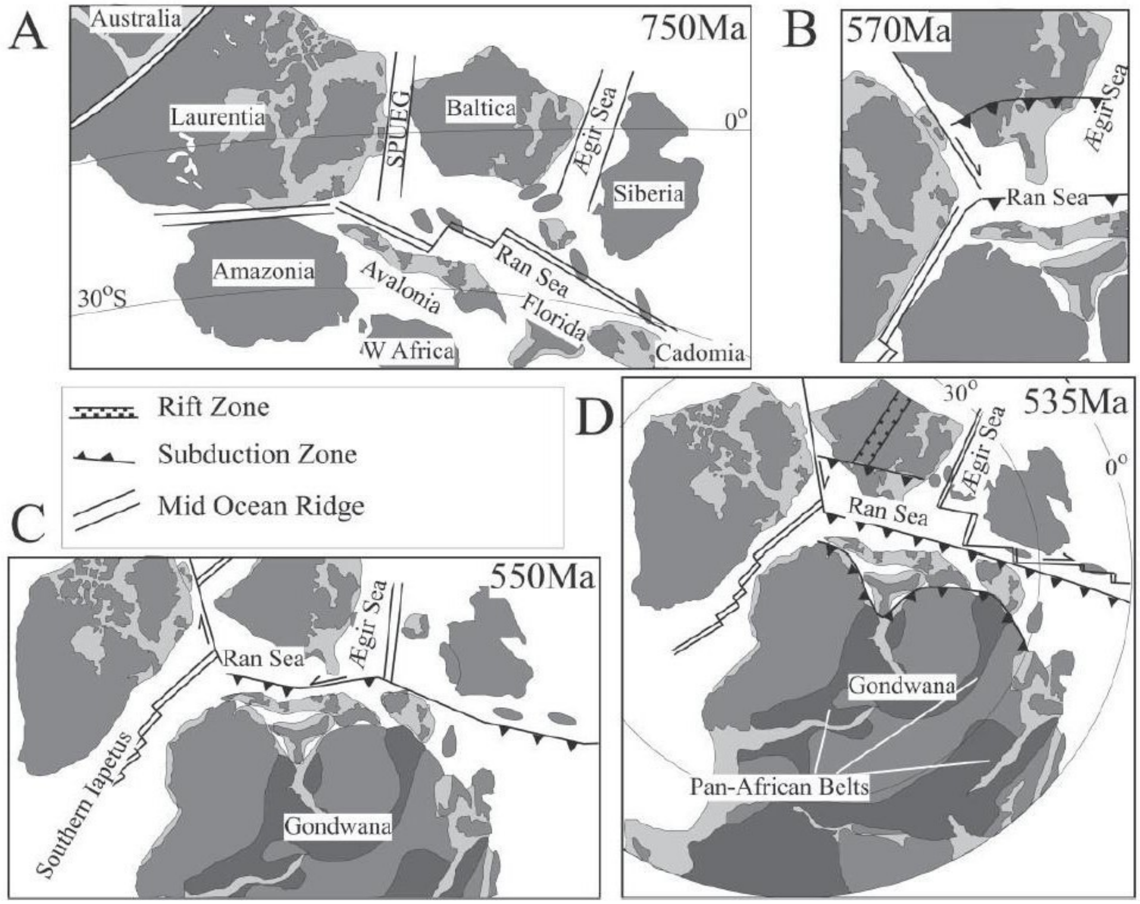

Figure 1.1. Neoproterozoic palaeogeography of Avalonia and related areas showing the location of Avalonia relative to major tectonic boundaries from the Neoproterozoic 700 Ma to lower Cambrian 530 Ma (McIlroy & Horák, 2006 - redrawn from Hartz & Torvik 2002).

In southern Britain, five distinct terranes of eastern Avalonia have been recognized as a result of characterization of the basement rocks (**fig. 1.2**). These are known as the Wrekin Terrane, the Monian Composite Terrane, the Cymru Terrane, the Fenland Terrane and the Charnwood Terrane (Gibbons & Horák 1996; Pharaoh & Carney 2000).

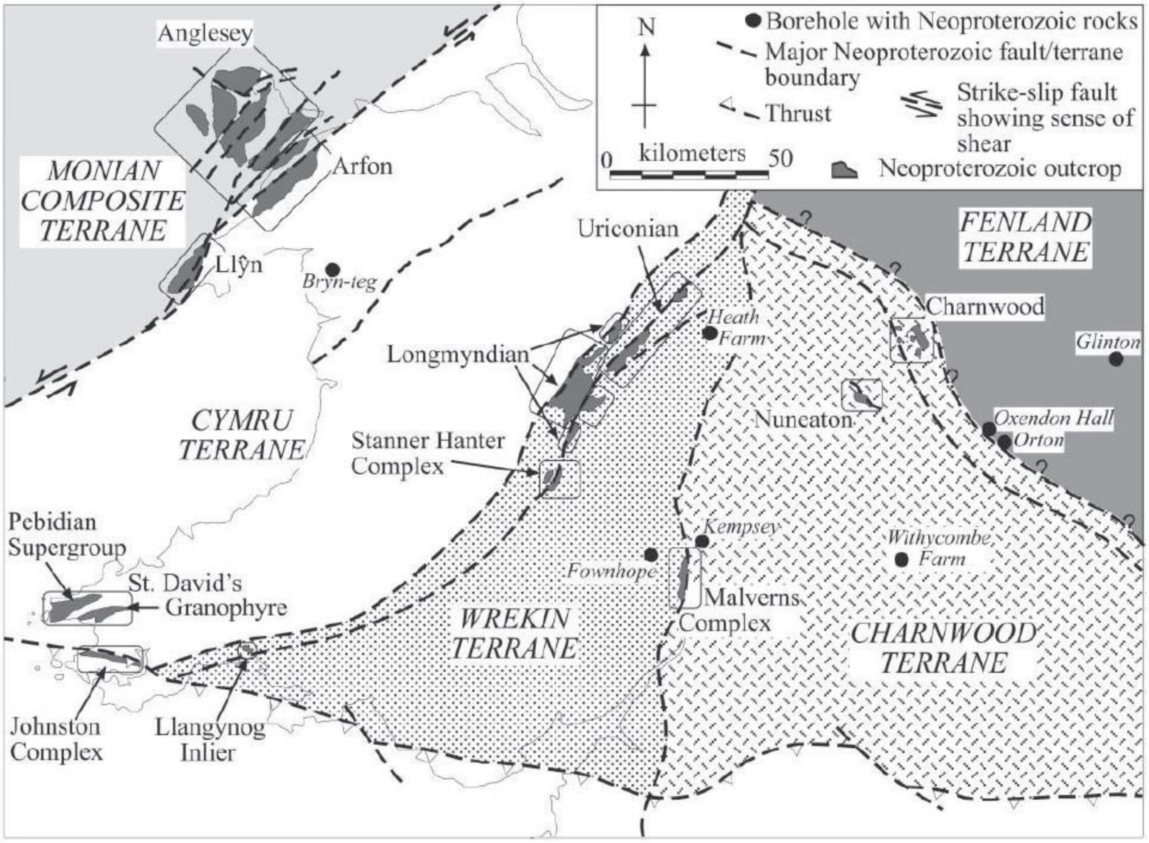

Figure 1.2. The distribution of Neoproterozoic rocks in England and Wales with respect to Neoproterozoic terrane boundaries (McIlroy & Horák, 2006 - redrawn from Carney *et al*. 2000).

Within the Charnwood Terrane, at Nuneaton and Charnwood Forest, there are two major outcrops of volcano-sedimentary successions and plutonic intrusions (McIlroy & Horák, 2006). Additionally, cores from the Kempsey and Withycombe Farm boreholes reveal the southern extent of the Charnwood terrane (McIlroy & Horák, 2006). The volcano- sedimentary succession consists of six formations and includes strata from the mid-Neoproterozoic through to the lower Cambrian (Brasier *et al*. 1978; Brasier & Hewitt 1979; Bland & Goldring 1995; McIlroy *et al.* 1999) that were deposited in a marine basin (McIlroy & Horák, 2006).

The successions at both Charnwood Forest and Nuneaton are located at a distance of approximately 20 km, and have long been compared to one another (McIlroy *et al.* 1999; McIlroy & Horák, 2006). The approximately 130 m thick volcanic succession at Nuneaton is lithologically and geochemically most akin to the Bradgate Formation at Charnwood Forest (Carney & Pharaoh 1993; McIlroy *et al.* 1999; Carney *et al.* 2000). Granophyric diorites cut the volcano-sedimentary successions at both locations and the Nuneaton diorites have yielded a U–Pb age of 603 Ma (Tucker & Pharaoh 1991). The dikes are linked to the South Charnwood diorites and Withycombe volcanics. This correlation is based on their similar εNd(t) isotopic values (Thorogood 1990; McIlroy *et al*. 1998).

The siliciclastic Withycombe Formation lies unconformably upon weathered, altered basaltic lavas of the Precambrian Midlands Microcraton that are geochemically comparable to the diorites of Nuneaton and Charnwood Forest (Wills & Shotton 1934, Brasier *et al*. 1978, Brasier 1992b, McIlroy *et al.* 1999; McIlroy & Horák 2006).

1.3.2 Small Shelly Fossils

The Withycombe Formation contains an abundance of small shelly fossils, as well as some trace fossils. Small shelly fossils were originally given this colloquial name due to their abundance in the pre-trilobitic Cambrian, their predominantly small size, diversity, and uncertain taxonomic affinities (Matthews & Missarzhevsky 1975). Since then, many studies of small shelly fossils have been completed globally, and they have been biostratigraphically for the recognition of the Precambrian–Cambrian boundary and for subdividision of the lower Cambrian.

The Withycombe Farm Borehole was drilled by British Coal in 1972–1973 near Banbury, Oxfordshire, through an upper Carboniferous (Pennsylvanian) to lower Jurassic sedimentary succession. The borehole penetrates the deeper Withycombe Formation and the even older weathered, altered, basaltic basement rocks of the Precambrian Midlands Microcraton. The Withycombe Formation was originally given a Silurian age by Poole (1978), based on his description of poorly preserved chitinozoa, but has since been determined to be lower Cambrian (Rushton & Molyneux 1980). This redetermination of age was supported by the discovery of various fossils including: the foraminifera *Platysolenites antiquissimus*, sclerites of halkieriids (Conway Morris *et al*. 1998), and the putative mollusc *Aldanella attleborensis* (Brasier 1992). The Withycombe Formation is composed of a succession of clastic rocks, approximately 194 m thick. The unit consists of interbedded red-purple and green mudstone and sandstone, interpreted to have been deposited below the storm wave base in the Midland Basin, within the English Midland Platform (Brasier *et al.* 1992b). The detailed sedimentological description of the Withycombe Formation is presented in Chapter 2.

Small shelly fossils are found globally, but there are only a few locations (particularly Russia, Australia, China, and Canada) where they have been studied extensively. They are used for subdivision of the lower Cambrian. Based on a faunal comparison with the middle to upper part of the lithologically similar Chapel Island Formation in southeastern Newfoundland, the strata of the Withycombe Formation have previously been given a *Watsonella crosbyi* zone age (Brasier, 1992). The other fossils recovered from the Withycombe, such as the abundant hyoliths, are also consistent with an early Cambrian depositional age, and have been compared with some lower Cambrian hyoliths in Siberia (Poole, 1978).

It has more recently been suggested that the strata of the Withycombe Formation may in fact be more similar to the slightly younger Cuslett Formation of southeastern Newfoundland, as the Withycombe biota includes more "Bonavista/Brigus elements" such as ostracods, brachiopods, and hyoliths, and specifically the hyoliths *Burithes alatus* and *Allatheca degeeri* (Conway Morris *et al.* 1998). This study further discusses the age of the Withycombe Formation within the Cambrian (see stratigraphic column in Chapter 2 of this thesis).

The affinities of many early Cambrian shelly fossils are still unknown and are not completely taxonomically understood. Though work on lower Cambrian lagerstätte has provided a number of important insights (Conway Morris *et al.* 1987; Hou & Bergström 2003; Paterson *et al*. 2015), there is much debate about where some of these fossils sit phylogenetically. Some of the fossils that are incompletely understood include the hyoliths and *Watsonella crosbyi*.

Since no extant group currently exists that resembles the extinct hyoliths, it has long been unclear where they belong phylogenetically and how to interpret their ecological and evolutionary importance. Hyoliths have previously been referred to as *incertae sedis*, related to molluscs, or assigned to their own phylum (Moysiuk *et al.* 2017). A recent study looking at extremely well-preserved hyoliths from the Burgess Shale supports the idea that hyoliths are lophophorates, exhibiting "an extendable, gullwing-shaped, tentacle-bearing organ surrounding a central mouth", which was interpreted as a lophophore identifying these hyoliths as suspension feeders (Moysiuk *et al.* 2017). More recent studies debunk this interpretation (Li *et al*. 2019; Fan *et al*. 2020) and the feeding strategy of the extinct Hyolitha as well as their phylogenetic placement remains controversial.

Watsonella crosbyi is an important fossil as it is widespread and present in both carbonate and siliciclastic facies in South China, Siberia, Mongolia, Avalonia, and West and East Gondwana. It is for this reason that it is used as an early Cambrian index fossil, demarcating the *Watsonella crosbyi* zone, and has been proposed as a marker for the base of the Cambrian Stage 2 (Li *et al*. 2001; Brock *et al*. 2015; Jaquet *et al.* 2016). It is widely thought to be a micro-mollusc, specifically of the class Rostroconchia. However, there are some authors who consider *Watsonella* to be a helcionelloid gastropod (Li *et al*. 2011). Based on functional morphological analysis, some suggest that *Watsonella* is a univalved mollusc, with a laterally compressed shell that represents an evolutionary transition from helcionelloids to rostroconchs and bivalves (Carter *et al*. 2000). This is would suggest that *Watsonella* is much more primitive than a true rostroconch, as it lacks a rostrum and a true pegma (Li *et al.* 2011). In an effort to confirm or disprove this, we collected a specimen of *Watsonella* from the Withycombe Formation, which was scanned with the micro-CT scanner for analysis. However, due to a lack of contrast in the CT-images, our analysis was inconclusive.

1.4 Relevance of the study

Due to the relatively continuous record of small shelly fossils, and their presence in the pre-trilobitic lower Cambrian strata, they can provide important insights into the early part of the Cambrian explosion, and enable us to determine the patterns of early animal evolution as a whole. The purpose of this study is to produce the first complete description of the Withycombe Farm Borehole core and the abundant small pyritized fossils preserved within it, and develop a taphonomic model for the pyritization of the small shelly fossils. Since the majority of the small shelly fossil biotas are found in carbonate, the taphonomic window of pyritic preservation in green silty mudstone provides a complementary dataset from a different facies. Completing some spatially constrained stable sulfur isotopic analyses provided the appropriate data that enabled us to develop a taphonomic model for the pyritization of the fossils.

It is also important to note that the Withycombe assemblage contains a number of important index fossils (*Watsonella, Platysolenites, Aldanella* and the trace fossil *Teichichnus*) that enable correlation of strata around the base of Cambrian Stage 2 from Avalonia to Baltica. This provides regional biostratigraphic ground-truthing.

Literature exists for small shelly fauna from locations such as the Siberian Platform (Syssoiev, 1962; Matthews and Missarzhevsky, 1975; Komentovsky and Karlova, 1993; Kruse *et al.* 1995; Kouchinsky, 2000b; Kouchinsky *et al.* 2017), southeastern Newfoundland (Landing, 1992; Landing, 1994; Narbonne *et al.* 1987; Hiscott, 1982; Myrow, 1987; Myrow & Hiscott 1993; Benus 1988), China (Qian, 1978; Zhu Mao- yan *et al.* 2001; Qian *et al.* 2001; Gabbott *et al.* 2004; Guo *et al.* 2012), as well as Australia (Berg-Madsen and Peel, 1978; Hinz-Schallreuter, 1997; Kruse, 1990;, Bengston *et al.* 1990; Brock and Cooper, 1993; Brock and Paterson, 2004; Parkhaev, 1998, 2001, 2004, 2017; Topper *et al.* 2009; Vendrasco *et al.* 2010; Jacquet & Brock, 2016; Jacquet *et al.* 2014; Betts *et al.* 2017). This study of the Withycombe Formation fills a gap in knowledge as it provides data from the only known section of lowermost Cambrian strata in the UK. The small shelly fauna are pivotal for understanding the evolution of the main groups of marine invertebrates, particularly the overall pattern of early Cambrian evolution.

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Chapter 2

Palaeontology of the lower Cambrian Withycombe Formation of Oxfordshire, UK.

Palaeontology of the lower Cambrian Withycombe Formation of Oxfordshire, UK.

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Abstract

The Withycombe Formation of Oxfordshire, UK, is a 194 m thick, pre- trilobitic lower Cambrian siliciclastic succession dominated by interbedded offshore red–purple and green pyritic mudstone with minor sandstone. The mudstone contains a hyolith-dominated pyritized small shelly fauna, including orthothecid hyoliths, hyolithid hyoliths, the rostroconch *Watsonella crosbyi*, early brachiopods, the foraminiferan *Platysolenites antiquissimus*, the coiled gastropod-like mollusc *Aldanella attleborensis,* halkieriids, gastropods, and a low diversity ichnofauna. The assemblage includes a number of important index fossils (*Watsonella, Platysolenites, Aldanella* and the trace fossil *Teichichnus*), indicating that the succession was most probably deposited early in Cambrian Stage 2. The pyritized nature of the biota has allowed micro-CT study of some specimens, which reveals the presence of abundant, sub-vertical, branching pyritized tubes, likely formed by the activity of giant sulfur bacteria.

2.1 Introduction

The Withycombe Formation found only in subcrop around Banbury, Oxfordshire, UK (**Fig. 2.1**), is a 194-metre-thick sedimentary succession of offshore sandstone and mudstone, deposited below storm wave base. The succession lies unconformably upon weathered, altered basaltic lavas of the Precambrian Midlands Microcraton that are geochemically comparable to the diorites exposed in outcrop to the northwest at Nuneaton and Charnwood Forest (**Fig. 2.1**; Wills & Shotton 1934; Brasier *et al*. 1978; Brasier 1992b; McIlroy *et al.* 1999; McIlroy & Horak 2006).

Initial investigation of the fauna of the Withycombe Formation suggested that it represented a Silurian succession, possibly part of an unusual nearshore facies (Poole 1978). Subsequent study of the Withycombe Formation yielded specimens of the diagnostically early Cambrian fossils *Platysolenites antiquissimus, Watsonella* sp. *Aldanella* sp., and halkieriid sclerites (Rushton & Molyneux 1990; Conway Morris *et al.* 1998). We present herein a complete description of the macrofauna and ichnology of the Withycombe Formation, and consider the stratigraphic implications of the biota by comparison with the lower Cambrian stratigraphic standard sections of southeastern Newfoundland (Hiscott 1982, Myrow 1987, Narbonne *et al*. 1987, Benus 1988; Landing 1992, 1994; Myrow & Hiscott 1993).

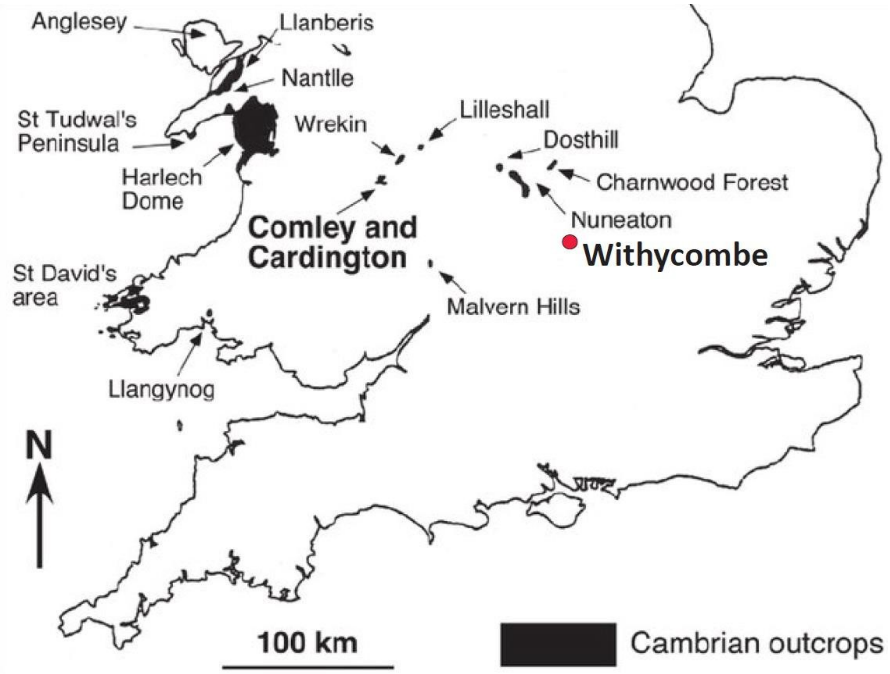
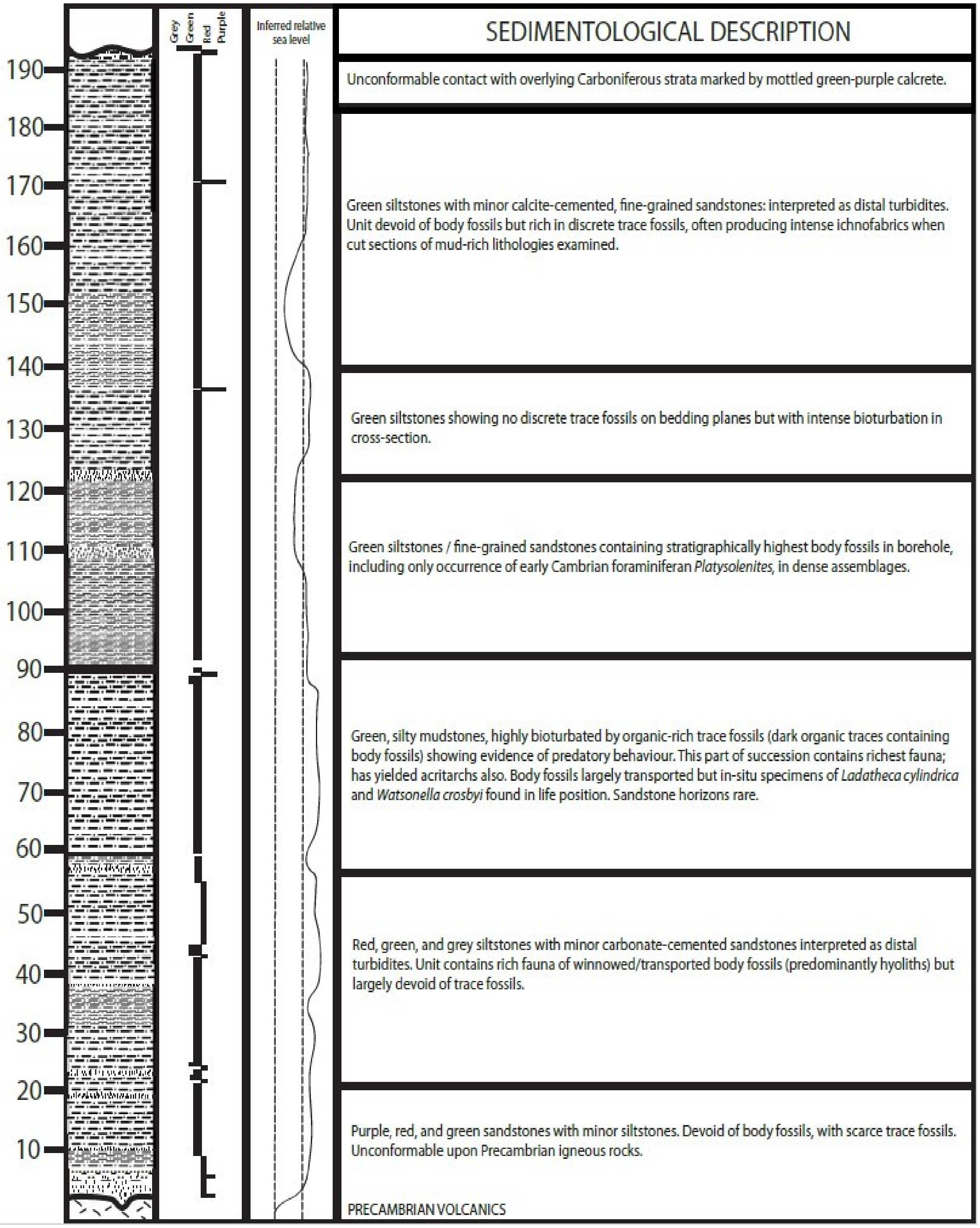


Figure 2.1. Distribution of Cambrian outcrops in England and Wales. The Withycombe Farm Borehole is located near Banbury, Oxfordshire approximately 50 km south of Nuneaton. (Modified from Rushton *et al.* 1999).

2.2 Sedimentology of the Withycombe Formation

The basal unit of the Withycombe Formation is a red, silty to sandy mudstone with fissure infill of the basaltic/dioritic basement (Wills & Shotton 1934; Brasier et al. 1978; McIlroy *et al.* 1998). The basal part of the succession contains several coarse- grained sandstone beds that grade upwards into green/grey mudstone with purple mottling and sparse phosphate nodules. These graded sandstone beds die out stratigraphically ~90 m above the base of the formation. The upper part of the Withycombe Formation (from 90 to 190 m) is a heavily bioturbated, mudstone-rich succession containing a hyolith-dominated pyritized fauna. The uppermost (~50 m) part of the formation is marked by an increase in the abundance of thin sandy horizons, and the interbeds of green silty mudstone are sparsely bioclastic, but contain well-preserved trace fossils. The top of the Withycombe Formation is marked by the sub-Carboniferous unconformity of the Oxfordshire Coalfield, and is likely to have been subject to pedogenesis and weathering, forming a red and green blotchy horizon 0.25 m thick (**fig. 2.2**).

The lower Cambrian stratigraphy of the palaeocontinent Avalonia is remarkable for its lithological similarities over very large lateral distances, with the junctions between mudstone- and limestone-rich lithostratigraphic units being marked by periods of relative sea-level rise, and consequent sediment-starved hiatuses during which limestone formed. The stratigraphy of the lowermost Cambrian is divided by thin quartzites that may result from transgressive ravinement, and thick progradational sandstone units (Landing 1992, 1994, 1996, 2004; Brasier 1992; Brasier *et al*. 1994; McIlroy & Horak 2006). The lithologies— and also the faunas—of the Withycombe Formation invite comparison with the Chapel Island Formation (Members 3-4) of the Ediacaran–Cambrian Global Boundary Stratotype Section and Point (GSSP) in Fortune, Newfoundland (Narbonne *et al.* 1989; Landing 1992b, 1994; Myrow & Landing, 1992; Landing *et al.* 2018), but also the Cuslett Formation of southeastern Newfoundland (Landing & Benus 1988). No similar lower Cambrian facies are known from outcrop or subcrop in England, but in Wales, the deep marine, fine grained slate of the Cymru Terrane are similarly green and red/purple in colour (McIlroy & Logan 1999).



Unconformable contact with overlying Carboniferous strata marked by mottled green-purple calcrete.

Green siltstones with minor calcite-cemented, fine-grained sandstones: interpreted as distal turbidites. Unit devoid of body fossils but rich in discrete trace fossils, often producing intense ichnofabrics when cut sections of mud-rich lithologies examined.

Green siltstones showing no discrete trace fossils on bedding planes but with intense bioturbation in cross-section.

Green siltstones / fine-grained sandstones containing stratigraphically highest body fossils in borehole, including only occurrence of early Cambrian foraminiferan *Platysolenites*, in dense assemblages.

Green, silty mudstones, highly bioturbated by organic-rich trace fossils (dark organic traces containing body fossils) showing evidence of predatory behaviour. This part of succession contains richest fauna; has yielded acritarchs also. Body fossils largely transported but in-situ specimens of *Ladatheca cylindrica* and *Watsonella crosbyi* found in life position. Sandstone horizons rare.

Red, green, and grey siltstones with minor carbonate-cemented sandstones interpreted as distal turbidites. Unit contains rich fauna of winnowed/transported body fossils (predominantly hyoliths) but largely devoid of trace fossils.

Purple, red, and green sandstones with minor siltstones. Devoid of body fossils, with scarce trace fossils. Unconformable upon Precambrian igneous rocks.

Figure 2.2. Summary sedimentological graphic log of the Withycombe Formation.

2.3 Material and Methods

The Withycombe Farm borehole was drilled in 1972 to 1973 by British Coal and the cores are housed at the British Geological Survey (BGS) in Keyworth, UK (Poole 1978). The original core descriptions of Poole (1978) have been used along with new observations to create a sedimentological framework for this study. Micro-CT scanning of pyritized fossils was carried out using a Nikon XT H 225 ST computed tomography system at the University of Bristol, UK. Samples with the prefix BDF or BDG are museum specimens from the BGS collections.

2.4 Systematic Palaeontology

PROBLEMATICA

Phylum, Class, Order uncertain

Family COLEOLIDAE Fisher, 1962

Genus *Coleolella* Missarzhevsky, 1981

Type species: *Hyolithellus billingsi* Syssoiev, 1962, p. 56-57; by monotypy.

Diagnosis: Conical, originally calcareous, shells with very low angle of taper and rounded cross-section; straight except in juvenile part which may be curved; surface of shell bears many ribs parallel to aperture; inside of conch smooth.

Coleolella sp.

Figure 2.6a

1962 *Hyolithellus billingsi* Syssoiev, p.56-57; by monotypy
1973 *Coleolella billingsi* (Syssoiev); Cowie & Rosanov, pp. 241, fig 3
1982 *Coleolella billingsi* (Syssoiev); Yusheng *et al.* pp. 80, Table 2
1985 *Coleolella billingsi* (Syssoiev) McMenamin p.1417
1993 *Coleolella billingsi* (Syssoiev); Khomentovsky & Karlova, pp. 39, fig. 9
1995 *Coleolella billingsi* (Syssoiev); Kruse *et al.* pp. 321, Appendix 1
2016 *Coleolella billingsi* (Syssoiev); Yang *et al.* pp.205, fig. 2

Material: Figured specimen BDF 9977 and 9978 (63m) (part and counterpart).

Description: A single uncompressed, pyritized straight conch with an apical angle of 6^{O} that tapers to a point. Surface ornamentation is restricted to numerous prominent annular ribs, the spacing of ribs increases towards the aperture: around 7-8 per mm in the apical portion and 3 per mm in the apertural region. The ribs bear a fine central depression that is not known in any similar taxa. There is no operculum associated with the specimen, nor is any operculum small enough for this taxon known in the borehole.

Remarks: This specimen differs from the type species in the lack of apical curvature and in the style of ribbing. Other similar taxa, such as *Coleoloides* Walcott, 1889 and *Coleolus* Hall, 1879, differ in the presence of oblique ribbing. This specimen also differs from the narrow orthothecid *Ladatheca cylindrica* (Grabau, 1900) in the possession of a strong ornament, which is absent in the *Ladatheca*. The assignment of this specimen to the Tentaculitida by Poole (1978, p. 19, pl. 2, fig. 17.) is rejected on the grounds of the small apical angle. A newly described species *Rugatotheca daibuica* sp. nov. (Yang *et al.* 2016) also closely resembles *Coleolella billingsi* (Syssoiev).

Occurrence: Specimens were recovered from a layer 55.5 m above the base of the Withycombe Formation in the Withycombe Farm Borehole.

Stratigraphic distribution: Widely known from Cambrian Stage 2 of the Siberian Platform and South China (Rozanov & Sokolov 1984; Rozanov *et al.* 2008; Yang *et al*. 2016).

Phylum, Class, Order and Family uncertain

Ichnogenus *Oikobesalon* Thomas and Smith 1998

Type species: *Trachyderma crassituba* Chapman, 1909, p. 105; by subsequent designation.

Discussion: Allen (1927) gave the name *Keilorites* to Australian material that had been described under the generic name *Trachyderma* Phillips, 1848 (*non Trachyderma* Latreille, 1829). Allen's specific references to Australian material preclude the idea that he might have been proposing a *nomen novum*, though, as Bather (1927, p. 286) pointed out, Allen had not diagnosed his new genus, nor had he indicated the generic position of Phillips' species *Trachyderma squamosa*. Brood (1979, 1980) adopted the view that "*Keilorites"* is a *nom. nov.* for *Trachyderma*, with the implication that the species

"*Keilorites" squamosus* and "*Keilorites" crassituba* are congeneric. *Oikobesalon* nom.

nov. was erected as a replacement name for *Trachyderma* Phillips (Thomas & Smith 1998), based on its distinctive structure and was interpreted as the thin organic lining of a terebellid polychaete dwelling burrow (Thomas & Smith 1998).

Oikobesalon (Phillips, 1848)

1848	*Trachyderma squamosa* Phillips, p. 332, fig. 4:3,4
1888	*Trachyderma squamosa* (Phillips) Etheridge, p. 37
1895	*Trachyderma* sp. Lindström, p. 11
1909	*Trachyderma cf. squamosa* (Phillips) Chapman, pp. 104, fig. 27:5
1980	*Keilorites cf. squamosus* (Phillips, 1848) Brood, p. 281, fig. 1A
1998	*Oikobesalon* (Phillips, 1848) Thomas & Smith, p. 320, fig. 2
2014	*Oikobesalon* Vinn *et al.* p.119
2016	*Oikobesalon* Buatois *et al.* p.105, Table 1

Fig. 2.8e

Material: BDF 9523 (154m) and ?BDF 9978 (55.5 m)

Description: The present specimens of *Oikobesalon* are organic-walled structures found oriented horizontally and obliquely in the sediment. The wall is variably pyritized and has a cross-hatched bandage-like structure. This may be produced by the oblique overlaying of bandage-like strips in two directions, to generate the regular triangular structure.

Remarks: Although *Oikobesalon* has been regarded as a body fossil (Williams, 1916), the general consensus is that it is in fact a trace fossil (Phillips, 1848; Chapman, 1910;

Thomas and Smith, 1998; Buatois *et al*. 2016). It is herein considered an ichnofossil. The similarity of this specimen to Silurian specimens from the Malvern Hills is evident, though the larger size of the Silurian *Oikobesalon* may be grounds for caution.

Occurrence: From 154 m above the base of the Withycombe Formation; in the Withycombe Farm Borehole, a second possible specimen is known from 55.5 m above the base of the Formation.

Stratigraphic distribution: *Oikobesalon* has been recognized from: the Cambrian of the Withycombe Borehole; the Silurian of Shropshire (Phillips 1848; Allen 1927; Thomas and Smith 1998); the Silurian of Australia (Chapman 1910 as *Trachyderma* sp.) and Burma (Reed 1906); and the Ordovician of Baltica in Estonia (Vinn *et al.* 2014).

Phylum **SARCODINA** Schmarda
Class RETICULARIA Lankester
Subclass FORAMINIFERA d'Orbigny
Superfamily ASTRORHIZACEA Brady
Family HYPERAMMINACAE Loeblich & Tappan
Genus *Platysolenites* Pander, 1851

Type species: *Platysolenites antiquissimus* Eichwald, 1860, p. 32-33, pl. 2; by monotypy.

Diagnosis: Cylindrical, straight to slightly curved, gently tapering, non-septate siliceous, agglutinated tubes commonly compressed into a figure eight. The test breaks easily along irregularly spaced transverse annulations that are expressed both internally and externally.

Almost complete specimens are up to 5 cm in length. The test is variable in thickness, consisting of silt to fine siliciclastic sand, which is graded within the test, coarsest grains outermost, showing a sharp difference in grain size between the test and enclosing sediment (from McIlroy *et al*. 2001).

Platysolenites antiquissimus Eichwald, 1860

Fig. 2.8f

1860 *Platysolenites antiquissimus* Eichwald, pp. 678, fig. 33:19

1881 *Platysolenites antiquissimus* (Eichwald) Schmidt, pp. 13, fig. 1

1888 *Platysolenites antiquissimus* (Eichwald) Schmidt, pp. 26, fig. 2:32,33

1890 *Platysolenites antiquissimus* (Eichwald) Walcott, pp. 522, fig. 8

1908 *Platysolenites antiquissimus* (Eichwald) Moberg, pp. 29, fig. 1:2

1918 *Platysolenites antiquissimus* (Eichwald) Holdetahl, pp. 129, fig. 17:2

1924 *Platysolenites antiquissimus* (Eichwald) Vogt, pp. 289, fig. 4

1926 *Serpulites (?) petropolitanus* Yanischevsky, pp. 108, fig. 6

1962 *Platysolenites antiquissimus* (Eichwald) Howell , pp. W105, fig. 104.4

1962 *Platysolenites antiquissimus* (Eichwald) Hecker & Ushakov, pp. 444, fig. 3:9

1963 *Platysolenites antiquissimus* (Eichwald) Glaessner, pp. 9

1967 *Platysolenites antiquissimus*(Eichwald) Hamar, pp. 89-95, fig. 1,3,5-7; 2:1,3,4,7,8

1968 *Platysolenites antiquissimus* (Eichwald) Kiryanov, pp. 23, fig. V 21-23

1968 *Serpulites (?) petropolitanus* (Yanischevsky) Kiryanov, pp. 23, fig. V 24

1971 *Yanichevskyites petropolitanus* (Yanischevsky) Korkutis

1972 *Serpulites (?) petropolitanus* (Yanischevsky) Lendzion, pp. 560-561, fig. 2:5,6;3:7,8

1973 *Yanichevskyites petropolitanus* (Yanischevsky) Jankauskas & Posti, pp. 146

1977 *Platysolenites antiquissimus* (Eichwald) Mens & Pirrus, pp. 90, fig. I 1,3,5-7; II 1,3,4,7,8

1978 *Yanichevskyites petropolitanus* (Yanischevsky) Aren & Lenzion, pp. 37, fig. 1:2

1978 *Platysolenites antiquissimus* (Eichwald) Glaessner, p. 62, Figs 1–6.

1979 *Platysolenites antiquissimus* (Eichwald) Føyn & Glaessner, pp. 30-33, fig. 4A-D, 5A

1979 *Platysolenites antiquissimus* (Eichwald) Rozanov, pp. 86

1979 *Platysolenites lontova* (Öpik) Rozanov, pp. 86

1980 *Platysolenites antiquissimus* (Eichwald) Tynni, pp. 17-22, fig. 3, 5 A-E

1983 *Platysolenites antiquissimus* (Eichwald) Rozanov, pp. 94-100, fig. 1.19-1.20

1984 *Yanichevskyites petropolitanus* (Yanischevsky) Brasier, pp. 243, fig. 2O, P

1987 *Platysolenites antiquissimus* (Eichwald) Loeblich & Tappan, pp. 22-23, fig. 14:4-8

1989 *Platysolenites antiquissimus* (Eichwald) Landing et al. pp. 390, fig. 5.2

1989 *Platysolenites antiquissimus* (Eichwald) Brasier, pp. 134, fig. 7.2:5

1992 *Platysolenites antiquissimus* (Eichwald) Lipps, pp. 238, fig. 5.7.1. A-C

1992 *Platysolenites antiquissimus* (Eichwald) Lipps, pp. 4-7, fig. 5A, B

1994 *Platysolenites antiquissimus* (Eichwald) McIlroy *et al*. pp. 13-15, Figs 1A-E, 2A, D-F & 3A-E

1995 *Platysolenites antiquissimus* (Eichwald) Palacios *et al.* pp. 122-123

1996 *Platysolenites antiquissimus* (Eichwald) Lipps & Rozanov, pp. 679-685, fig. 1-8

1999 *Platysolenites antiquissimus* (Eichwald) Vidal *et al.* pp. 139, fig. 3A, B

2001 *Platysolenites antiquissimus* (Eichwald) McIlroy *et al.* pp. 14, fig. 1A, E-J

2006 *Platysolenites antiquissimus* (Eichwald) Winchester-Seeto & McIlroy, pp. 78

2008 *Platysolenites antiquissimus* (Eichwald) Kontorovich *et al.* pp.937

2013 *Platysolenites antiquissimus* (Eichwald) Hogstrom *et al.* pp. 100

2015 *Platysolenites antiquissimus* (Eichwald) Iglikowska & Pawlowska, pp. 97

2017 *Platysolenites antiquissimus* McIlroy & Brasier, p. 353, fig. 2

Material: BDG84 Thin section and BDF 9644 A, B and C (120 m) (several specimens in one block).

Diagnosis: Cylindrical, untapered, agglutinated tube of siliceous particles, usually broken along transverse wrinkles into short sections. Cross-sections are most commonly circular in smaller tubes but are generally compressed to an elliptical- or U-shape in larger forms (McIlroy *et al*. 2001). *Platysolenites* showing a high specificity of agglutination of quartz and feldspar; proloculus bulbous (emended diagnosis of McIlroy *et al.* 2001).

Description: Large, cylindrical, slightly tapering, finely agglutinated straight tubes, which are up to 3 cm in length. Several specimens occur in close stratigraphic proximity at ~160 m above the base of the section, in an unusual light-green micaceous mudstone facies. Thin section analyses have demonstrated that the test is made of quartz, commonly with a pyrite infill (McIlroy *et al*. 2001).

Remarks: *Platysolenites antiquissimus* has been reported in both Avalonia and Baltica, and it is one of the earliest known skeletal fossils from above the Neoproterozoic–Cambrian boundary (e.g., Brasier 1989a, b; McIlroy *et al.* 2001; McIlroy & Brasier 2017).

Phylum **UNCERTAIN**

Class HYOLITHA Marek

Order ORTHOTHECIDA Marek

Family CIRCOTHECIDAE Missarzhevsky

Genus *Ladatheca* (Syssoiev, 1968)

Type species: *Circotheca annae* Syssoiev, 1959, p. 85, pl. 5, fig. 1; by the subsequent designation of Syssoiev (1968. p. 23).

Diagnosis: Small conical shells with a circular or oval cross section, sharply elongated and ornamented by fine growth lines.

Ladatheca cylindrica (Grabau, 1900)

Fig 2.6e

1900 *Orthotheca cylindrica* Grabau, p. 646-655, pl. 32, fig. 8a-g.

1988 *Ladatheca cylindrica* (Grabau, 1900); Landing, p. 685, figs. 7.8, 7.12, 9.1 & 9.4. (includes synonymy).

1993 *Ladatheca cylindrica* (Grabau, 1900); Landing, p. 335

1994 ?*Ladatheca* (Syssoiev, 1959); Dzik p. 269, fig. 14.

Diagnosis: Calcareous elongate conchs with fine transverse growth laminae on inner and outer surfaces, cross section circular to ovate, the operculum is low and flat with concentric growth lines and no internal processes.

Material: Numerous specimens; figured specimen is BDF 9952 (58m).

Description: Cylindrical, straight tubes showing a very low angle of taper, preserved in full relief as pyritized tubes, infilled with early diagenetic calcite or epitaxial pyrite or compressed composite moulds. The surface is ornamented by fine, transverse growth lines parallel to the straight aperture. The apical angle is 4° and maximum length is 4 cm.

Commonly, small opercula are found at levels adjacent to *Ladatheca cylindrica,* which also closely resemble the *Ladatheca cylindrica* opercula known from acid residues from the limestone of Member 4, Chapel Island Formation, southeastern Newfoundland (Landing *et al.* 1989).

Remarks: The cross-section of the tubes is initially circular and becomes slightly flattened ventrally during ontogeny. This is seen in vertically oriented (interpreted as being *in situ* by Landing *et al*. 1989) tubes of *Ladatheca cylindrica* in the Withycombe Formation, as well as the Chapel Island Formation and the Bonavista Group of southeastern Newfoundland (Landing *et al.* 1989).

Distribution: *Ladatheca cylindrica* was also recognized from the lower Cambrian of Nova Scotia (Landing 1995), Norway (Crimes & McIlroy 1999), Nevada (Hollingsworth 1999), Finnmark (McIlroy & Brasier 2017) and Cambrian Stage 2 of the Siberian Platform (Dzik 1994). *Ladatheca* was first described from the Fortunian *Purella antiqua* assemblage of Siberia (Khomentovsky & Karlova 1993).

Genus *Turcutheca* Missarzhevsky, 1969

Type species: *Turcutheca crasseocochlia* Syssoiev, 1962, p. 52; by original designation.

Diagnosis: Narrow shells with lateral curvature, which is more pronounced in the juvenile portion, oval-rounded cross section, surface ornamented by faint growth lines.

Turcutheca cf. *crasseocochlia* Syssoiev, 1962

Fig. 2.6b

1962 *Turcutheca crasseocochlia* nov. sp. Syssoiev, p. 52, pl. 6, fig. 2.

1966 *Circotheca crasseocochlia* Rozanov & Missarzhevsky, p. 111, pl. 12, fig., 9.

1969 *Turcutheca crasseocochlia* Missarzhevsky *in* Rozanov *et al.* p. 109, pl. 13, fig. 1.

1974 *Turcutheca crasseocochlia* Meshkova, p. 23, pl. 10, fig. 3.

1978 'Scaphopod?' Poole, p. 19, pl. 2, fig. 10.

1981 *Turcutheca crasseocochlia* Missarzhevsky *in* Rozanov *et al.* p. 130, pl. 13, fig. 1.

1993 [?] "*Ladatheca" cylindrica* Rabu *et al.* p. 384 (*pars*), pl. 1, fig. 9 only; *non* pl. 1, fig. 8.

1994 [?] "*Ladatheca" cylindrica* Rabu *et al*. p. 39, pl. 1, fig. 1.

1995 *Turcutheca crasseocochlia* Syssoiev*;* Dzik, pp.260, fig 14.

2017 *Turcutheca crasseocochlia* Syssoiev; Kouchinsky *et al.* pp. 315, fig. 2

Material: Opercula BDF9967 (56m), BDF9930 (61m), and figured specimen BDF 9886 (64m).

Description: Small, narrowly tapering gently curved conchs, up to 4 cm in length. The cross section may be round to slightly ovate, with an apical angle of c.10°. Preserved as pyritized internal moulds and composite moulds display very fine transverse ribbing.

Remarks: Small specimens of *Turcutheca* are reminiscent of *Torellella* Holm, 1893, which differs in having a phosphatic composition. *Ladatheca cylindrica* differs in the absence of a marked curvature of the long axis, as in *Turcutheca,* which also has a greater apical angle than *Ladatheca*. The operculum of *Turcutheca* has processes on the base and a sub-central apex. The typical folded upper surface present in some operculae of an appropriate size to be that of *Turcutheca* (*see* Hinz 1987; pl. 8). Ventral processes could not be unequivocally demonstrated in any *Turcutheca* operculum from the Withycombe Formation, however this is likely preservational. The juvenile parts of several straight hyoliths, such as *Ladatheca cylindrica,* may also be gently curved (Landing, 1988), but the persistence of this condition into the adult stage is typical of *Turcutheca*.

Distribution: *Turcutheca* is also recorded from Massachusetts, U.S.A. (Landing 1988), China (Qian *et al*. 1979; Xing *et al*. 1983), Shropshire, UK (Hinz 1987), and the lowest occurrence of *Turcutheca crasseocochlia* in Siberia is in the *Purella antiqua* Zone (Khomentovsky & Karlova 1993).

Orthotheca sp.

Fig. 2.6d

Material: BDF9897 (63m), BDF9898 - Holotype (63m), and BDF9977b (55.5m)

Description: Very large straight shells, up to 10cm long. Transverse ornamentation consists of very fine ribs parallel to the straight aperture. These are dissected by more pronounced longitudinal ribs that are continuous over the length of the shell and run parallel to its long axis. The conch tapers evenly to a conical apex. CT scans reveal a possible (mm-scale width) gut trace visible towards the apical portion of one conch (**Fig 2.3).** Morphologically similar digestive tracts have been identified in orthothecids from the lower Cambrian of France (Devaere *et al.* 2014).

Remarks: These conchs are some of the largest hyoliths described from the lower Cambrian to date. The reasons for the absence of this hyolith elsewhere in Avalonia might be due to the unusual preservation, faunal provincialism, and the ecology of the Withycombe biota. Large hyoliths – the more tumid *Doliutus inflatus* Syssoiev, 1968, and the ventrally flattened *Hyolithes princeps* Billings, 1888 – are known from the West Centre Cove Formation of Newfoundland, whilst Holm (1893) described *Hyolithes (Orthotheca) hermelini* from younger *Olenellus* Zone strata in Scandinavia.

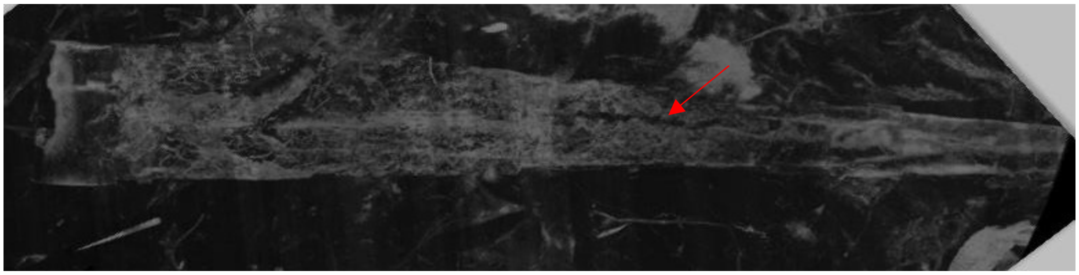


Figure 2.3 CT scan exhibiting a possible mm-scale (width) gut trace towards the apical end of *Orthotheca* sp., which is approximately 8 cm in length.

Family ALLATHECIDAE Missarzhevsky

Genus *Allatheca* Missarzhevsky, 1969

Type species: *Allatheca corrugata* Missarzhevsky, 1969, p. 138, pl. 1, fig. 6; pl. 12, fig. 10-11; by original designation.

Diagnosis: "Comparatively large, narrow, straight thick-walled shells having symmetrically oval to well-rounded triangular section. Dorsal side arcuately convex, ventral side slightly convex. Concave septa exist in the initial part of the shell. Shell sculpture is monotonous throughout the perimeter and is limited to transverse structures parallel to the aperture, in cases with slightly protruding dorsal edge" (Missarzhevsky 1969. English translation by the U.S. Department of the Interior, 1981).

Allatheca concinna Missarzhevsky, 1969.

Fig. 2.6c

1969 *Allatheca concinna* Missarzhevsky in Rozanov *et al.* p. 117, pl. 1, fig. 3 & pl. 12, figs. 14 & 15.

1974 *Allatheca concinna* Meskova, p. 29, pl. 1, fig. 3 & pl. 2, figs, 3, 5 & 10.

1978 'Conch of Orthothecidae' Poole, p. 19, pl. 2, fig. 5.

1981 *Allatheca concinna* Missarzhevsky in Rozanov *et al.* p. 117, pl. 1, fig. 3 & pl. 12, figs. 14 & 15.

Type material: Holotype GIN/3593/34 from the Tommotian strata at Kotui River, Ary-Mas-Yuryakh River mouth, Siberia.

Diagnosis: "Straight shells with oval cross section, small angle of divergence surface ornamented with uniform transverse folds (denser near the aperture), which curve slightly onto the dorsal side. Ribs are expressed faintly on the inside of the shell and contain convex sporadically distributed septa" (condensed translation from Missarzhevsky (1969)).

Material: Figured specimen is BDF 9986 (54 m); also, BDF 9958 (57.5 m).

Description: Straight conch with coarse, closely packed, transverse annulations and a conical apex. The cross section is sub-circular and the aperture straight. The maximum length of shell is 4 cm, with an apical angle of 13°. Shells are preserved exclusively as compressed, pyritized moulds.

Remarks: This species compares closely with *Allatheca corrugata* Missarzhevsky, 1969, and only differs in its very regular distribution of the slightly less pronounced transverse ornament. No operculum could definitely be ascribed to this taxon in the Withycombe Formation based either on size comparisons or by common association. *Allatheca concinna* has never been ascribed an operculum previously.

Distribution: Withycombe Formation, England and the *Aldanocyathus sunnaginnicus* Zone of Siberia (Khomentovsky & Karlova 1993).

Allatheca degeeri (Holm, 1893)

Fig 2.6f

1888 ?*Hyolithes billingsi* Walcott; Shaler & Foerste, p. 34, pl. 2, fig. 20.

1893 *Hyolithus* (*Orthotheca*) *de Geeri* Holm, p. 54-56, pl. 1, figs. 25-27.

1893 *Hyolithus* (*Orthotheca*) *johnstrupti* Holm, 1893, p. 56-57, pl. 1, figs. 28-33.

1898 *Orthotheca de Geeri* Holm; Lapworth, p. 345.

1919 *Hyolithus* (*Orthotheca*) *de Geeri* Holm; Cobbold, p. 150, pl. 4, figs. 1a-9b.

1969 *Allatheca degeeri* (Holm); Missarzhevsky, p. 117, pl. 10, figs. 5a, 8 & 9, 15; pl. 14, fig. 5; pl. 15, fig. 2b.

1978 *Allatheca degeeri* (Holm); Brasier *et al.* p. 29.

1978 'Conch of Hyolithidae' Poole, p. 19, pl. 2, fig. 2 & 3.

1978 'Hyolith conch and operculum' Poole, p. 19, pl. 2, fig. 4.

1979 *Allatheca degeeri* (Holm); Brasier & Hewitt, p. 30-32.

1984 *Allatheca degeeri* (Holm); Brasier, p. 246, fig. 3o.

1988 *Allatheca degeeri* (Holm); Landing, p. 675-677, figures 7.1?, 7.2?, 7.3, 7.4, 7.6, 7.9, 7.11?, 8.1, 8.2, 9.6 & 9.8.

1989 "*Allatheca*" *degeeri* (Holm); Landing *et al.* p. 755, fig. 8.1-8.4 (considers *Obolus*? *major* as a possible senior synonym).

1991 "*Allatheca*" *degeeri* (Holm); Landing, fig. 7.2.

1999 *Allatheca degeeri* (Holm); Malinky & Berg-Madsen, p. 27, table 1.

2012 *Allatheca degeeri* (Holm); Landing & Kröger, p.26. fig. 5.

Type material: Not indicated by Holm (1893).

Diagnosis: Elongate, generally straight hyoliths, aperture straight or with slight ventral lip; dorsal surface flat to concave in adult specimens, ventral surface tumid, lateral edges smoothly rounded; shell surface ornamented by very fine growth lines and inside of the shell smooth (Modified from Landing & Kröger 2012).

Material: BDF 9775 (82m) and BDF 9904 (62.5m).

Description: Large elongate, straight shells with an apical angle of 16°, up to 5 cm in length that taper smoothly to a conical apex. The surface of the conch is ornamented by very fine growth lines that may be curved anteriorly in ventral view. Figured specimen BDF 9775 shows an associated operculum with a strong annular ornament, central apex and a slight fold on one side (presumably ventral). The large diameter of the hyoliths means that they have suffered badly from compression. The conch is flattened to a degree where the cross section is best determined by comparison with the opercular morphology, making the explicit assumption that the operculum matched the aperture of the hyolith.

Discussion: Three of the hyoliths figured by Poole (1978 plate 2, figures 2, 3 & 4) represent this species. No cross-section was available from any of the preserved material in the core, but the distinctive operculum associated with figured specimen BDF 9775 is common and diagnostic. This species first appears in the *Aldanella attleborensis* Zone of southeastern Newfoundland (Landing *et al.* 1989) and in the Tommotian of Siberia (*Dokidocyathus regularis* Zone; Khomentovsky & Karlova 1993). Marusin and Grazhdankin (2018) have also compared large orthothecid conchs from the Terreneuvian of Arctic Siberia to *Allatheca degeeri* of the Cambrian Stage 2 Cuslett Formation of southeast Newfoundland.

Distribution: *Allatheca degeeri* can be found upper Cuslett Formation, Newfoundland, in peritidal limestone beds in such Avalonian regions as England, elsewhere in southeastern Newfoundland, Nova Scotia, New Brunswick, and eastern Massachusetts (Brasier, 1984; Landing, 1988, 1993b, 2004; Landing et al., 1989).

Order HYOLITHIDA Matthew

Family SULCAVITIDAE Syssoiev

Genus *Burithes* Missarzhevsky, 1969

Type species: *Linevitus distortus* Syssoiev, 1962, p.27-28 pl. 7 by the subsequent designation of Missarzhevsky (1969, p. 155).

Burithes alatus (Cobbold, 1919)

Fig 2.6g, 2.7a,c

Holotype. BU 186 figured by Cobbold (1919, pi. 4, fig. 13), housed at the Lapworth

Museum of Geology, University of Birmingham, UK.

1919	*Hyolithes* (*Hyolithus*) *alatus* Cobbold, p. 152, pl. 4, figs. 13-15, ?16.
1969	*Burithes alatus* (Cobbold); Missarzhevsky, pl. 15, fig. 2a.
1978	*'Hyolithes' alatus* (Cobbold); Brasier & Hewitt, p. 29-30.
1984	*Burithes alatus* (Cobbold); Brasier, p. 247, fig. 3p.

Material: BDF 9870 (65.5m) is the figured specimen; also, BDF 9835 (68 m) and BDG 83 (37 m) and opercula BDG 74 (37.5 m), BDG 73 (37.5 m), BDF 9943 (58.5 m) & BDF 9944 (58.5 m).

Description: Hyoliths up to 5 cm in length with an apical angle of around 14°, which compare closely with that of the holotype (Cobbold 1919, pl. 4 fig. 13). The relatively open conch of this species makes complete infilling with pyrite improbable. Hence, all specimens are crushed such that no accurate impression of the cross-section of the shell could be determined. The ventro-lateral carinae of *Burithes* described by Missarzhevsky (1969, pl. 15, fig. 2a) are indicated by the unusual compression of the sides of the shell. The growth lines on the ventral side of the shell follow the pronounced lip and are parallel to the straight margin on the dorsal side. The operculum of *Burithes alatus* is also found in the Withycombe Farm section, and these are generally small, with a sub-central apex and a much sharper inflexion of the ventral side than the similar-sized opercula of *Allatheca degeeri*. The sharp inflexion was presumably to facilitate complete occlusion of the aperture, which is extended by the lip on the ventral surface of the conch. The operculae are identical to those referred to as '*Hyolithes' alatus* in the Cobbold collections (Cobbold 1919, pl. 4 fig.16) at the Lapworth Museum (University of Birmingham).

Distribution: *Burithes* is not known from strata older than the *Dokidocyathus regularis* Zone and *Lapworthella tortuosa* Subzone of Siberia (Cambrian Stage 2). *Burithes* ranges from Cambrian Stages 2 to 3 (Tommotian to Atdabanian) in Siberia (Missarzhevsky, 1969).

?hyolith operculum indet.

Fig. 2.8b

Material: BDF 9878 & 9879 (64.5m).

Description: A single specimen of this taxon is known, in part and counterpart. It has a circular outline with a central apex that appears to be broad and flat. The surface is ornamented by fine concentric growth lines and is slightly compressed, such that it becomes divided into three equal parts. The most noticeable feature of this fossil is a triradiate impression. It is not centered precisely on the disc, and it is tentatively interpreted as a product of compaction, either of the shell itself or, in the case of the broadest radial feature, possibly by compaction onto an underlying burrow. Nearer the margin there is another elongate area of relief. In this case it is almost certainly superimposed, perhaps by distortion associated with an underlying trace fossil. Evidence for incremental growth exists close to the shell margin (Conway Morris *et al*. 1998). Poole (1978, pl. 2, fig. 8) suggested the fossil was a hyolithid operculum.

Remarks: The circular shape of the operculum suggests that it belongs to a hyolith, although it cannot confidently be assigned to any of the above taxa.

Phylum **MOLLUSCA** Cuvier

Class & Order UNCERTAIN

Genus *Aldanella* Vostokova, 1962

Type species: *Pleurotomaria attleborensis* Shaler & Foerste, 1888, p. 30-31, pl. 2, fig. 2; by the original designation of Vostokova (1962, p. 66).

Diagnosis: Small discoidal shells with up to three whorls, aperture oval, surface ornamented with folds and fine growth lines; growth lines on the outer side of the whorls form a wide antispiral sinus (after Missarzhevsky 1981).

Aldanella attleborensis (Shaler & Foerste, 1888).

Fig 2.8d

1888 *Pleurotomaria attleborensis* Shaler & Foerste, p. 30-31, pl. 2, fig. 2.

1962 *Aldanella attleborensis* (Shaler & Foerste); Vostokova, p. 30.

1988 *Aldanella attleborensis* (Shaler & Foerste); Landing, p. 673-674, fig. 5.1-4 & 5.15 (includes extensive synonymy).

1989 *Aldanella attleborensis* (Shaler & Foerste); Landing *et al.* p. 755, fig. 7.14-15.

1996 *Aldanella attleborensis* (Shaler & Foerste); Culver *et al.* p. 4, fig. 5.4.

2011 *Aldanella attleborensis* (Shaler & Foerste); Parkhaev & Karlova, fig 1-6.

2012 *Aldanella attleborensis* (Shaler & Foerste); Parkhaev *et al.* p. 180, fig. 1.

2013 *Aldanella attelborensis* (Shaler & Foerste); Dzik and Mazurek.

2014 *Aldanella attleborensis* (Shaler & Foerste); Parkhaev, p. 103, fig. 1.

2017 *Aldanella attleborensis* (Shaler & Foerste); Kouchinsky *et al*. pp. 350-353, figs. 20-22

Holotype: MCZ, no. 101331, shell with broken apical part; United States, Massachusetts, Nahant section; Lower Cambrian, Weymouth Formation.

Diagnosis: "Shell with low spire and two or three abruptly flattened, keeled whorls, elongate to oval in section. Upper part of whorls convex, lower part flattened, so that lower surface of shell is funnel shaped. Surface bears growth lines and folds parallel to them" (Missarzhevsky 1969).

Material: BDF 9885 (64 m), BDF 9873 (64.5 m), BDG 36 (44 m), BDG 37 (44 m) & BDG 84 (36.5 m).

Description: Small (2–4 mm wide) steinkerns of a dextrally coiled depressed shell, with a moderate rate of whorl expansion and a wide, open umbilicus. The apex shows a blunt, rounded termination. No growth lines, muscle scars or ornamentation are evident, nor is there any indication of uncoiling as in material from Massachusetts (Landing 1988).

Remarks: The small size of these specimens is similar to *Aldanella rozanovi* Missarzhevsky, 1969 (p. 104, pl. 1, figs. 1a-4) and *Aldanella operosa* Missarzhevsky, 1966 (p. 104-106, pl. 10, figs. 7-9) from Siberia. This work follows Landing (1988) in placing these species in synonymy with *Aldanella attleborensis* Shaler & Foerste, 1888, because of the wide variation of morphology documented by Landing (1988). Early gastropods such as the Ordovician *Maclurites logani* Salter, 1859 often have associated opercula (*see* Yochelson 1990) but none of the opercula described from the Withycombe

Formation are of a suitable size or shape to fit the aperture. Due to a wide geographical range and strict stratigraphic occurrence, the species *A. attleborensis* was proposed as an index species for the Tommotian Stage, or Cambrian Stage II (Rozanov *et al.* 2008a; Parkhaev *et al.* 2011, Parkhaev *et al.* 2012).

Distribution: *Aldanella attleborensis* is well-distributed geographically, with records from the Siberian Platform (Khomentovsky & Karlova 1993), South China (Parkhaev *et al.* 2014), Avalonia (Landing 1988), and Baltica (Mens *et al.* 1990).

Superphylum Lophotrochozoa

Family Halkieriidae Poulsen, 1967

Genus *Halkieria* Poulsen, 1967

Type species: *Halkieria obliqua* Poulsen, 1967, p. 30, pl. 2.4-5; original designation.

Diagnosis: "Bilaterally symmetrical lepidote metazoans with calcareous sclerites disposed in several longitudinal zones. Principal types include lateral cultrates and dorsal palmates and at least sometimes ventro-lateral siculates and perhaps dorso-lateral spiniforms. Sclerites housed soft-tissue in central cavity that extended into lateral canals of varying length and was connected to body via basal foramen of restricted diameter. Sclerites consist of a blade and basal region. Blade compressed in cultrates and palmates, sub-cylindrical in siculates. Base usually sharply folded towards lower side of cultrates and palmates, more continuous with blade in siculates. Surface ornamentation comprises longitudinal ribs and sometimes transverse ribbing or tubercles on upper side of blade, on lower side more subdued with transverse striations" (Conway Morris & Peel 1995, p. 310).

Halkieria stonei (Landing *et al*. 1989)

Fig. 2.9

Material: BDG 9 (47.5 m), BDG 80 (37 m), BDG100 (35 m), BDG147 & BDG147A (23 m), BDF 9878 & BDF 9879 (64.5 m), BDF 9977c-d, (55.5 m) & BDF9892 (63.5 m) from between 47.5 and 63.5 m from the base of the Withycombe Formation, Withycombe Farm Borehole, Banbury, Oxfordshire.

Description of sclerites:

Form 'a': sub-triangular, gently convex palmate sclerites up to 4 mm in length, only preserved in dorsal expression. This form displays a 'left-handed' basal process at 95° to

the long axis of the sclerite. The surface is ornamented with prominent longitudinal striae; the central strand is markedly more pronounced than the rest (Conway Morris *et al.* 1998). The small size and basal process suggest that this is the 'palmate sclerite' morphology of Bengtson & Conway Morris (2007).

Form 'b': Dorsal surface of an elongate almost planar sclerite, slightly longer than form 'a'. The surface is ornamented by a prominent central longitudinal ridge, and six subsidiary ridges (Conway Morris *et al.* 1998). Although the base is obscured, gross morphology and size bear strongest resemblance to cultrate halkieriid sclerites (cf. Bengtson & Conway Morris 1984).

Form 'c': Dorsal surface of a very elongated scythe like element. The surface is ornamented by fine striae and the midline is marked by a prominent rib (Conway Morris *et al.* 1998). This specimen is tentatively interpreted as a cultrate halkieriid sclerite such as those that typify the lateral margins of halkieriid animals (Conway Morris & Peel 1995).

Form ‘d: ?Spinose sclerite. Although incomplete at both ends, this possible sclerite is considerably more elongate than the previous three forms (Conway Morris *et al*. 1998).

Description of operculae/shells:

Operculum/shell ‘A’: moderately high, ovate operculum with a sub-central apex and concentric growth lines. The growth lines of the juvenile part of this operculum are sub-circular in outline, although based on the preserved geometry they became ovate through ontogeny. The length of the disk is 9.6 mm and the width 8.4 mm; the apex of the operculum is located ~3.3 mm from the anterior margin. Comparison with material from the Sirius Fauna of Greenland suggests that this may be the anterior shell (Conway Morris & Peel 1990; Conway Morris *et al.* 1998).

Operculum/shell ‘B’: oval operculum 11.2 mm long and 8.9 mm wide, with the apex placed centrally. The anterior margin is extended by two lobes that are divided by a shallow groove. The surface is ornamented by fine concentric growth lines but no radial ornament. It has been tentatively interpreted as the posterior operculum of the same halkieriid animal (Conway Morris *et al.* 1998).

Remarks: The discovery of articulated halkieriids from the Sirius Passet fauna of Greenland (Conway Morris & Peel 1995) allowed reinterpretation of otherwise problematic opercula in the Burgess Shale (Conway Morris 1995) and the Withycombe Formation (Conway Morris *et al.* 1998). The sclerites differ from forms previously reported from the lower Cambrian of Avalonia, which are normally only represented by steinkerns in acid digestion of carbonate. The species *Halkieria stonei* was erected by Landing *et al.* (1989) when describing specimens from the Chapel Island Formation of Southeastern Newfoundland.

Distribution: Between 23 and 63.5 m from the base of the Withycombe Formation in the Withycombe Farm Borehole, and the Chapel Island Formation of SE Newfoundland (Landing *et al*. 1989).

Class HELCIONELLOIDA Peel, 1991

Order and Family UNCERTAIN

Genus *Watsonella* Grabau, 1900

Type species: *Watsonella crosbyi* Grabau, 1900, p. 632-633, pl. 1, fig. 9a-f; by original designation.

Diagnosis: "Generally bilaterally symmetrical univalves in which the calcareous shell is usually coiled through up to several whorls; the whorls may be in contact or open coiled and are often laterally compressed. The aperture is oval, without re-entrant but the subapical surface may develop a median sinus which is occasionally deep and slit-like or even trematose, with a single perforation at the end of an elongate tube termed the snorkel. In some forms, the lateral areas of the aperture may become prosocyrt, extended into weak lateral fields and producing broad emarginations in both the supraapical and subapical surfaces astride the plane of symmetry. Ornamentation may include both comarginal and spiral elements; prominent comarginal rugae are common" (Devaere *et al*. 2013, p. 40).

Watsonella crosbyi Grabau, 1900

Fig 2.7a,b,d & Fig 2.8c

1900 *Watsonella crosbyi* Grabau, p. 632-633, pl. 1, fig. 9a-f.

1935 *Heraultia varensalensis* Cobbold, p. 38-40, pl. 2, figs. 1a-10b.

1975 *Heraultia varensalensis* Cobbold; Müller, 1975, p. 168-180, pl. 13, figs. 1-11.

1976 *Watsonella crosbyi* Grabau; Pojeta & Runnegar, pl. 3, figs. 1-4.

1976 *Heraultipegma varensalensis* (Cobbold); Pojeta & Runnegar, p. 54, pl. 2, figs. 9-12.

1976 *Heraultipegma varensalensis* (Cobbold); Runnegar & Jell, fig. 8, C1-8.

1978 Bivalved shells; Poole, fig. 14.

1980 *Heraultipegma* sp.; Yin *et al.* p. 158, pl. 14, figs. 6 & 7.

1987 *Heraultipegma* sp.; Yu, p. 214-215, pl. 60, figs, 1-8.

1982 *Watsonella crosbyi* Grabau; Luo *et al.* pl. 21, figs. 9-12 & 15.

1983 "*Heraultipegma* " n. sp. Bengtson & Fletcher fig. 2d.

1983 *Watsonella crosbyi* Grabau; Xing *et al.* pl. 10, figs. 16 & 17.

1983 *Watsonella crosbyi* Grabau; Runnegar, fig. 9A-H.

1985 *Watsonella crosbyi* Grabau; Runnegar & Pojeta, fig. 20.

1988 *Watsonella varensalensis* (Cobbold); Kerber, p. 159-60, pl. 4, figs. 1-13.

1988 *Watsonella crosbyi* Grabau; Landing, p. 691-692, figs. 5.16, 5.17 & 5.20.

1989 *Watsonella crosbyi* Grabau; Landing, p. 566-573, fig. 3.1-3.4.

1989 *Watsonella crosbyi* Grabau; Landing *et al.* p. 765, figs. 8.5 & 8.8.

1993 *Watsonella crosbyi* Grabau; Rabu *et al.* p. 384, pl. 1, fig. 2.

1994 *Watsonella crosbyi* Grabau; Rabu *et al.* p. 38, pl. 1, fig. 4.

2001 *Watsonella crosbyi* Grabau; Parkaev p. 187.

2011 *Watsonella crosbyi* Grabau; Li *et al.* p. 311-312, fig. 1.

2013 *Watsonella crosbyi* Grabau; Devaere *et al.* p. 37, figs 14.1-33, 15.1-14

2017 *Watsonella crosbyi* Grabau; Kouchinsky *et al*. pp. 343, fig 16

2017 *Watsonella crosbyi* Grabau; Jacquet *et al.* p. 1098-1099, fig 7.

2020 *Watsonella crosbyi* Grabau; *Guo et al*. p. 43, fig. 4.

Material: Numerous specimens including BDG 96 (35.5 m), BDG 102 (35 m), BDF 9974a (55.5 m) & BDF 9938 (60 m).

Description: Bi-symmetrical, roughly oval shells, ornamented by very fine growth lines and in cases a flat marginal flange (*see* figure 14 in Poole 1978). Specimens are up to 7 mm long with a low convexity index and pronounced anterior and posterior gapes. Preserved as composite moulds with a fine epitaxial coating of pyrite crystals. No visible pegma present in any Withycombe specimen.

Remarks: *Watsonella* has been generally assigned to the phylum Mollusca.The question of which class it falls under has been under heavy debate. It was widely thought to belong to the class Rostroconchia since it has a strong curved ventral margin and was suggested to have an internal pegma in the subapical region (e.g. Pojeta and Runnegar, 1976; He and Yang, 1982; Yu, 1987; Landing, 1989; Qian, 1989). Due to the shell microstructures on steinkerns and similarities to the shells of certain bivalves, however, Jacquet *et al.* (2016) proposed that *Watsonella* is closer to the bivalve crown group than typical rostroconchs. Alternatively, Li *et al*. (2011) considered *Watsonella* to be a helcionelloid, rather than a rostroconch, based on its univalved conch being untorted, endogastric, and lacking a rostrum and true internal pegma. In a most recent study, a "pair of muscle attachment sites below the apex provide new soft part information about *Watsonella*, confirming that *Watsonella* is an untorted helcionelloid (mollusc) with endogastrically coiled shell" (Guo *et al*. 2020).

Distribution: *Watsonella crosbyi* occurs in the siliciclastic successions across Avalonia including Massachusetts, Newfoundland, England and France, Mongolia and China, South Australia, and first occurs in the *Aldanocyathus sunnaginicus* Zone of Siberia ("Tommotian" or ?Cambrian Stage 2; Khomentovsky & Karlova 1993).

?Monoplacophoran indet.

Fig. 2.7g

Material: BDG80; 37m from the base of the Withycombe Formation.

Description: A single specimen of a high, univalved shell preserved concave up in the sediment, which makes extraction impossible. The shell shows fine growth lines and is broadly circular in basal profile. Width at the base is ~7 mm (Conway Morris *et al*. 1998, Fig. 3a). Specimen found immediately adjacent to two halkieriid sclerites, although its association with the sclerites may be coincidental (Conway Morris *et al*. 1998).

Discussion: The monoplacophorans *Bemella* Missarzhevsky (1969, p. 163), *Randomia* Matthew (1889b, p. 190), and *Prosinuites* Poulsen (1967, p. 19) are relatively common at similar stratigraphic levels. There is no evidence for the strong cancellate ornamentation of the shell, as seen in *Randomia*. Both *Bemella* and *Prosinuites* are generally much smaller than this specimen, and consequently it seems prudent to leave this material in open nomenclature.

Phylum **BRACHIOPOD**A Dumeril, 1806

Subphylum LINGULIFORMEA Williams, Carlson, Brunton, Holmer, & Popov, 1996

Class LINGULATA Gorjansky & Popov, 1985

Order LINGULIDA Waagen, 1885

Family OBOLIDAE King, 1846

Genus UNCERTAIN

Obolidae indet.

Fig 2.7e

Material: BDF 9859 & BDF 9860 (66m from the base of the Formation).

Description: A single complete valve with a rounded triangular outline and blunt marginal apex, situated posterior of the highest point of the shell from the commissural plane. The length of the shell is ~3 mm. The surface is ornamented with numerous very fine concentric ridges. Preserved as an external mould with a very fine covering of pyrite.

Remarks: “Obolid shells are subcircular, subtriangular to subpentagonal, moderately convex and thick-shelled, with a more or less pointed ventral beak and rounded dorsal apex” (Mergl *et al.* 2018,. p.1023). Obolid shells often have deeply impressed muscle scars, thickened visceral platform and a prominent pedicle groove (Mergl *et al.* 2018). The absence of internal shell details in the Withycombe Formation material precludes confident specific identification.

Genus *Lingulella* Salter, 1866, p. 333.

Type species: *Lingulella davisii* McCoy 1851, p. 405; by the subsequent designation of Dale (1870, p. 159).

Diagnosis: "Elongate oval to sub-triangular in outline, subacuminate; thin shelled, external ornament of concentric growth lines, inner layers of shell with fine radial striae, visceral area may be pustulose. Musculature apparently like *Obolus*" (from Rowell 1965).

?*Lingulella* sp.

Fig 2.7h

Material: BDF 9938a (60m from the base of the Formation).

Description: A single complete valve preserved as an internal mould covered by a fine layer of pyrite, which is concentrated in the more prominent growth lines. The shell is sub- triangular in outline and covered in fine growth lines that became more prominent through ontogeny. The maximum height of the shell is attained halfway along its length, with the umbo gently recurved toward the posterior margin.

Remarks: The outline of the Withycombe specimen differs from *Lingulella viridis* Cobbold, 1921, in being much broader anteriorly. The lack of details of internal morphology, due to the absence of any shelly material, precludes species level assignment, but the presence of the genus alone is of stratigraphic importance.

Order PATERINIDA Rowell, 1965

Paterinidae indet.

Fig. 2.7f

Material: BDG 39 (44 m from the base of the Withycombe Formation).

Description: The single specimen is almost sub-circular in outline. Several growth lines terminate against the anterior margin owing to compression and over-folding. The shell is strongly convex with a fine irregularly distributed ornamentation of growth lines. The specimen has a broad, open pseudodeltidium characteristic of the Paterinida.

Discussion: The lack of internal detail precludes the confident specific assignment of this Specimen. Originally described as a monoplacophoran by Poole (1978), the specimen bears no resemblance to any known lower Cambrian monoplacophoran. The identification as *Paterinidae indet*. is simply due to the lack of preservation of the musculature, characteristic external ornament and mantle canals.

Distribution: Paterinids are not known from before the Cambrian Stage II, the oldest examples being from the *Aldanocyathus sunnaginicus* Zone of Siberia (Khomentovsky & Karlova 1993).

?*Paterina* sp.

Fig. 2.7c

Material: BDF 9970 (56m from the base of the Withycombe Formation).

Description: Large, strongly convex sub-oval shell with anteriorly directed posterior margin, ornamented with numerous fine concentric growth lines. The apex is marginal, recurved and lies above a small deltidial opening.

Discussion: This specimen was also described by Poole (1978) as a ?monoplacophoran. The morphology is inconsistent with that of any known monoplacophoran and the state of preservation precludes thorough taxonomic treatment, though it appears brachiopod-like.

?Arthropod cuticle indet.

Material: BDG 158; 20m from the base of the Withycombe Formation.

Description: A large valve of poorly preserved phosphate in a red sandy siltstone. The shape is broadly similar to the rostroconch *Watsonella crosbyi* but differs in having a bulge in the anterior of the valve and the ventral margin bears a small process.

Discussion: The specimen has broad morphological similarities with the Bradoriida in size and shape. However, this specimen bears no resemblance to any of the bradoriids documented from the relatively ostracod-rich Comley Limestone Formation of Shropshire, UK (cf. Cobbold 1921), or from any other lower Cambrian section. Bradoriids and the first trilobites co-occur on several continents (Williams *et al.* 2007), but appear slightly earlier than the first recorded trilobite (*Abadiella*) in southern China (Hou *et al.* 2002; Williams *et al.* 2007; Zhang, 2007; Zhang, *et al.* 2008).

2.5 Trace fossils from the Withycombe Formation

Trace fossils from the Withycombe Formation have not previously been described in detail. The traces form a rather restricted assemblage, comparable to that of Members 3 and 4 of the Chapel Island Formation of southeastern Newfoundland. This formed part of the reasoning behind Brasier (1992) and Brasier *et al.*'s (1992) interpretation that the Withycombe Formation is roughly coeval with the Chapel Island Formation of southeastern Newfoundland.

The trace fossils present in the Withycombe Formation include bi-lobed horizontal traces devoid of internal structure and lacking lateral bevels, attributable to *Didymaulichnus lyelli* (Rouault, 1850); unlined vertical pipes of *Skolithos linearis* Haldemann, 1840; and horizontal, mud-lined tubes of *Palaeophycus*. Less common taxa include: possible *Treptichnus triplex* Palij, 1976, which is a tri-lobed trace fossil showing alternate branching in a 'feather stitch' pattern; *Gordia ?meandria* Jiang, 1982, which is a looping trace which shows self-crossing. Lastly, the ichnogenus *Teichichnus* is present in two forms: the first is the typically large and relatively shallow *Teichichnus rectus* Seilacher, 1955; and a second form that is only 3–4 mm wide and is much deeper in proportion to its width. The latter form, referred to as *Teichichnus* sp. A., has also been recognized in southeastern Newfoundland and Charnwood Forest (Landing *et al.* 1989; Bland and Goldring 1995; McIlroy *et al*. 1998; Herringshaw *et al.* 2017) and has been proposed as a possible index fossil for its first common occurrence as an ichnofabric-forming trace fossil at around the base of Cambrian Stage 2 (Landing *et al.* 1994; Brasier & McIlroy 2017; Herringshaw *et al.* 2017) Specimens BDF 9775, 9791, 9792, 9860, 9946A, 9960, 9973, 9988 and BDG 83 97, 98, 99, 100, 101, and 103 appears to be dark, organic-rich traces up to 30 mm in diameter, preserved as trails consisting of concentric layers of organic matter and green siltstone, which produce a darker trace in the matrix of green siltstone (**Fig. 2.7).** Specimens in this section (between ~60-90 m) commonly contain high concentrations of fossils, but with a relatively low diversity of prey taxa, as the vast majority are hyoliths. The apertural orientations of hyoliths show no common direction within the traces, similar to material from the middle Cambrian Burgess Shale in which hyolithids were found in the gut traces of a priapulid worm documented by Babcock & Robison (1988). These large organic traces containing body fossils (predominantly hyoliths) provide evidence for predation. However, the Withycombe assemblage does not contain any skeletal evidence for a candidate predator. The lack of skeletal fossil evidence for a possible predator in the Withycombe Farm Formation implies a soft-bodied animal that, from the morphology of the trace, would appear to be vermiform. A candidate trace-maker would be a priapulid worm as these have been shown to be a common hyolith-eating element of Cambrian faunas (Conway-Morris 1977), and have been considered to be common trace-makers at this stratigraphic level (Jensen *et al.* 2017).

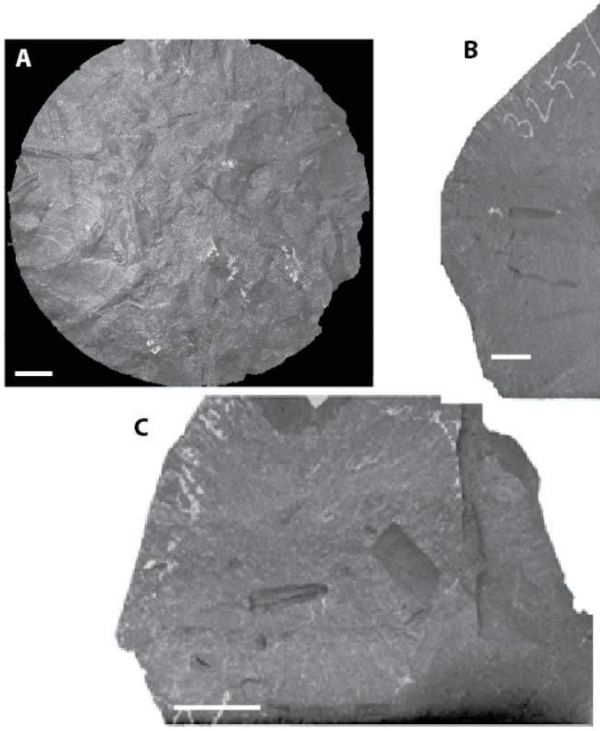


Figure 2.4. a: Bi-lobed horizontal traces. **b-c:** Predatory trace fossils showing dark organic rich trails containing body fossils. Scale bars equivalent to 1 cm.

2.6 Palynology of the Withycombe Formation

The palynology of the Withycombe Formation has been discussed by Rushton & Molyneux (1990), and Downie (*in* Poole 1978). The preservation of the acritarchs is very poor and only the long-ranging *Granomarginata squamacea* Volkova, 1968 and ′sphaeromorph acritarchs′ have been reported (Rushton & Molyneux, 1990). A form tentatively referred to as ‘*Granomarginata ?rigida*’ (Potter unpubl. thesis 1974) has also been recovered (Rushton & Molyneux 1990), which is otherwise only known from an occurrence in the Hollybush Sandstone Formation of the Malvern Hills, England. Flask shaped bodies in the Withycombe Formation (Poole 1978), previously attributed to chitinozoans, were re-examined by Dr. S. Molyneux, but did not allow confident referral of this material to the Chitinozoa (Rushton & Molyneux 1990). Re-examination of the Withycombe specimens may be prudent, especially considering the bulbous, chitinozoan-like morphology of the proloculus of *Platysolenites* documented by McIlroy *et al.* (2001).

2.7 Possible pyritized giant sulfur bacterial sheaths

Thioploca and *Beggiatoa* are genera of filamentous sulfur-oxidizing bacteria that inhabit marine and freshwater environments, commonly with high levels of hydrogen sulfide (Teske and Nelson, 2006). The type species of *Beggiatoa* is *Beggiatoa alba* (Vaucher, 1803). It is described as being "colorless, filamentous, gliding bacterium consisting of disk-shaped or cylindrical cells. Filament widths ranging from 12-160 μm have been observed in native material and are assumed to belong to this genus (Jorgensen, 1977; Klas, 1937; Nelson *et al.* 1989b), but a single phylogenetic affinity group is by no means proven"(Teske and Nelson, 2006). *Thioploca* is a closely related genus of filamentous sulfur-oxidizing bacteria and differs morphologically from *Beggiatoa* by only one characteristic: *Thioploca* filaments occur in bundles surrounded by a common sheath, whereas *Beggiatoa* filaments occur as individual filaments, and do not form this structure (Teske and Nelson, 2006). CT scans of the Withycombe material were completed to better characterize some of the body fossils present and unexpectedly revealed pyritized cylindrical microbial filaments with consistent width over the entire length of the filaments (BDF 9977; **Fig. 2.5**). The average width of the filaments is ~150 μm and average length is 4-5 cm. These filaments are preserved in a subvertical orientation within the sediment.

These pyritized filaments invite comparison with the *Thioploca* and *Beggiatoa* giant sulfur bacterium, which occur on top of sulfidic substrates such as sediment, bones, or decaying vegetation (Salman *et al.* 2013).

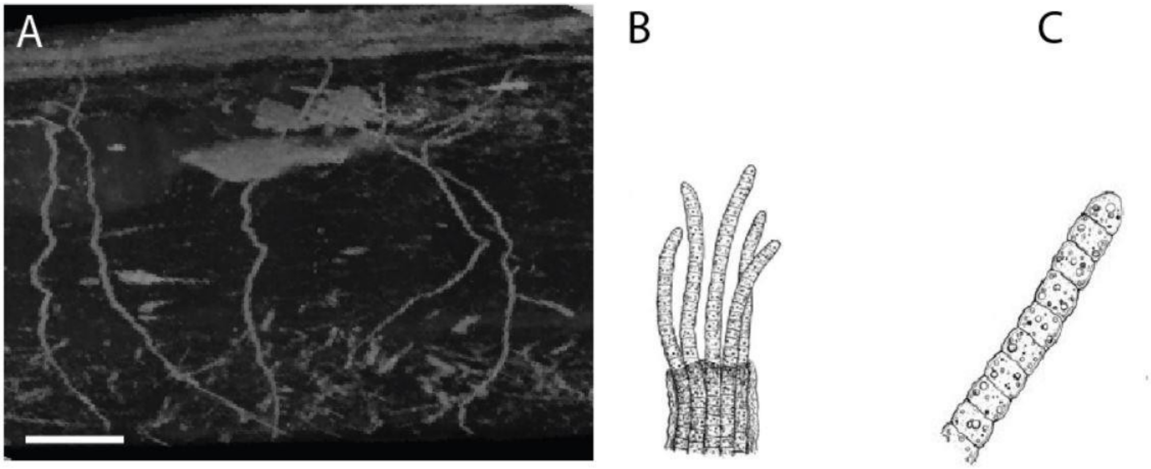


Figure 2.5. a: 3D reconstruction of CT scan (using VGSTUDIO MAX volume graphics software) showing near vertical possible giant sulfur bacteria (*Thioploca* or *Beggiatoa*-like). Specimen - BDF 9977. **b:** Illustration of a single, free-living filament of *Beggiatoa* (Illustration from Salman *et al.* 2013). **c:** Illustration of a bundle of *Thioploca* filaments surrounded by a common thick mucus sheath (Illustration from Salman *et al.* 2013).

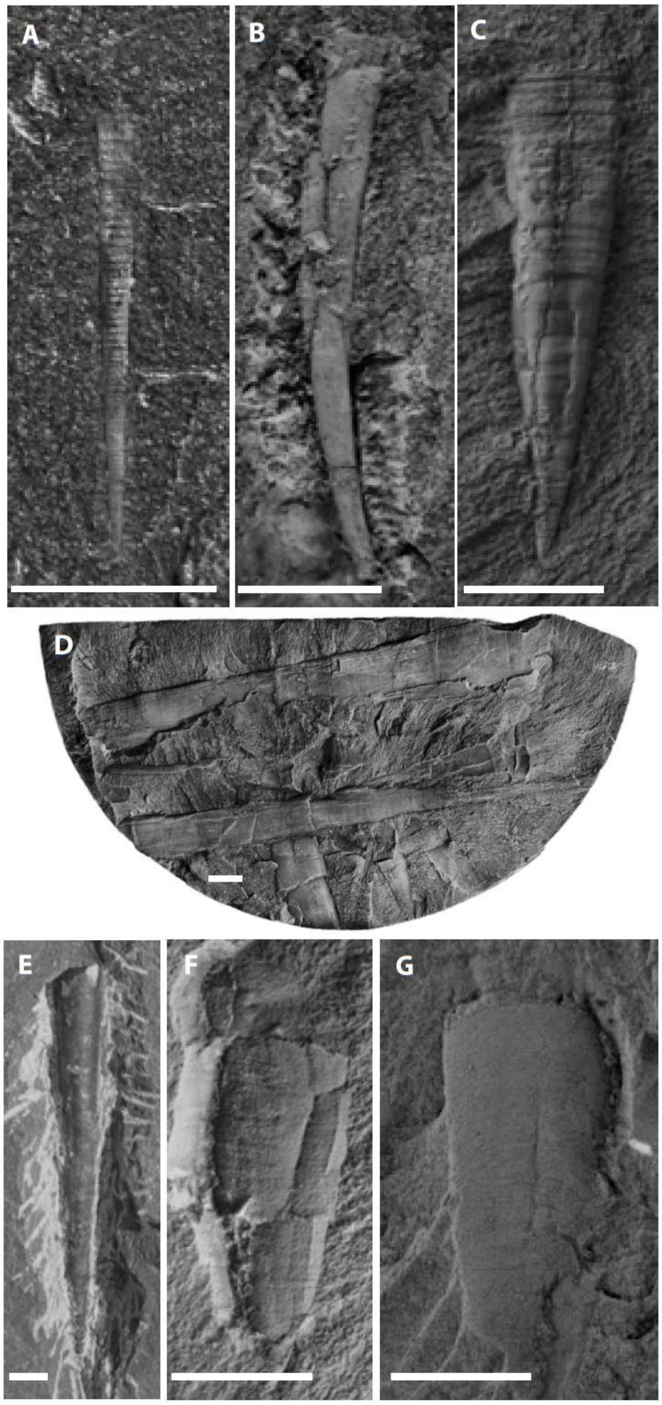


Figure 2.6. a: *Coleolella,* BDF 9977, Withycombe Formation, UK. **b:** *Turcutheca,* BDF 9886, Withycombe Formation, UK. **c:** *Allatheca concinna,* BDF 9986, Withycombe Formation, UK. **d:** *Orthotheca* sp. BDF 9898, Withycombe Formation, UK **e:** *Ladatheca cylindric*a Withycombe Formation, UK. **f:** *Allatheca degeeri*. BDF 9775, Withycombe Formation, UK. **g:** *Burithes alatus,* BDF 9870, Withycombe Formation, UK. Scale bars equivalent to 1cm.

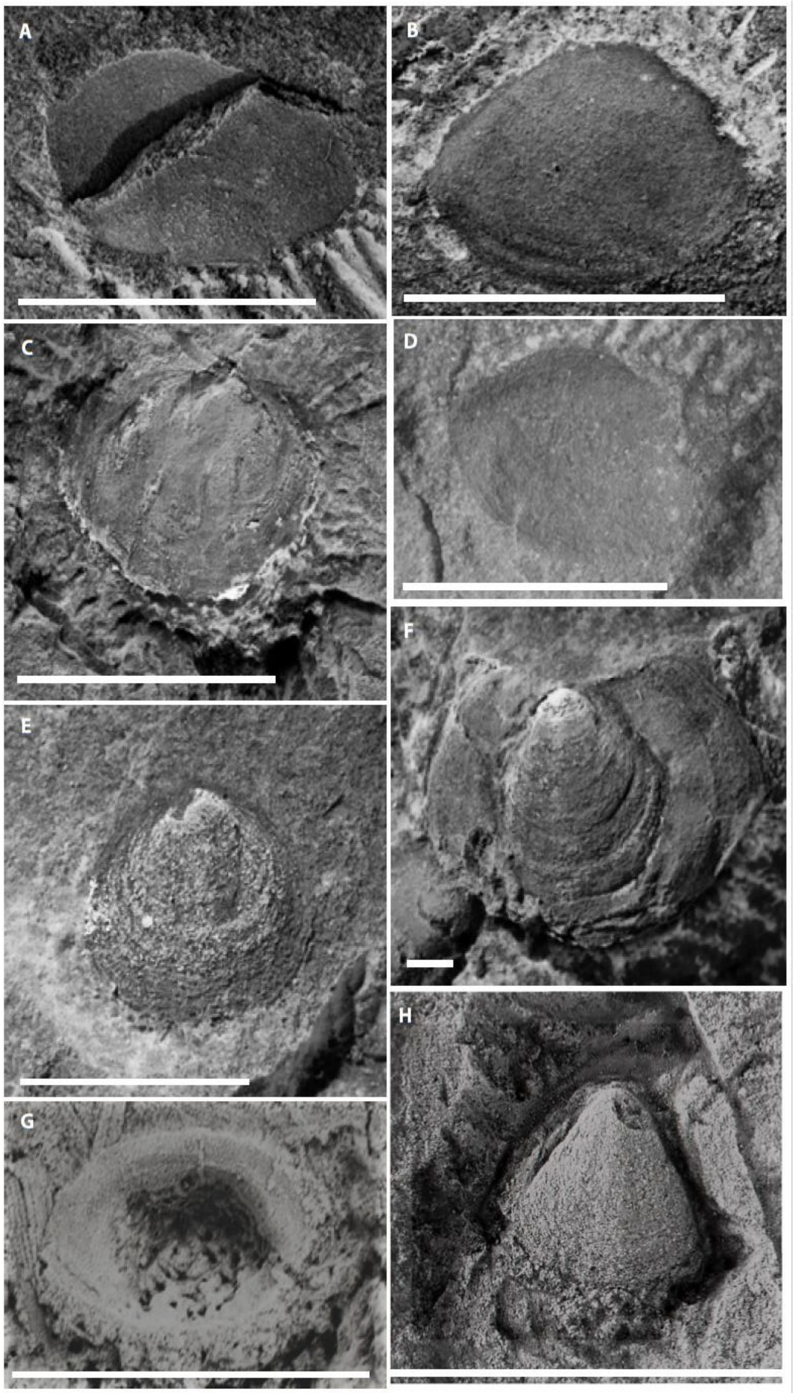


Figure 2.7 a: BDF 9774, Withycombe Formation, UK. **b:** *Watsonella Crosybi,* BDG 102, Withycombe Formation, UK. **c:** *Paterina* sp. BDF 9970, Withycombe Formation, UK. **d:** *Watsonella crosbyi*, BDG 96, Withycombe Formation, UK. **e:** Obolid brachiopod. BDF 9859, Withycombe Formation, UK. **f:** *Paterinidae indet.* BDG 39 Withycombe Formation, UK. **g:** Monoplacophoran indet. BDG 80, Withycombe Formation, UK. **h:** ?*Lingulella sp.* BDF 9938a, Withycombe Formation, UK. Scale bars equivalent to 500μm.

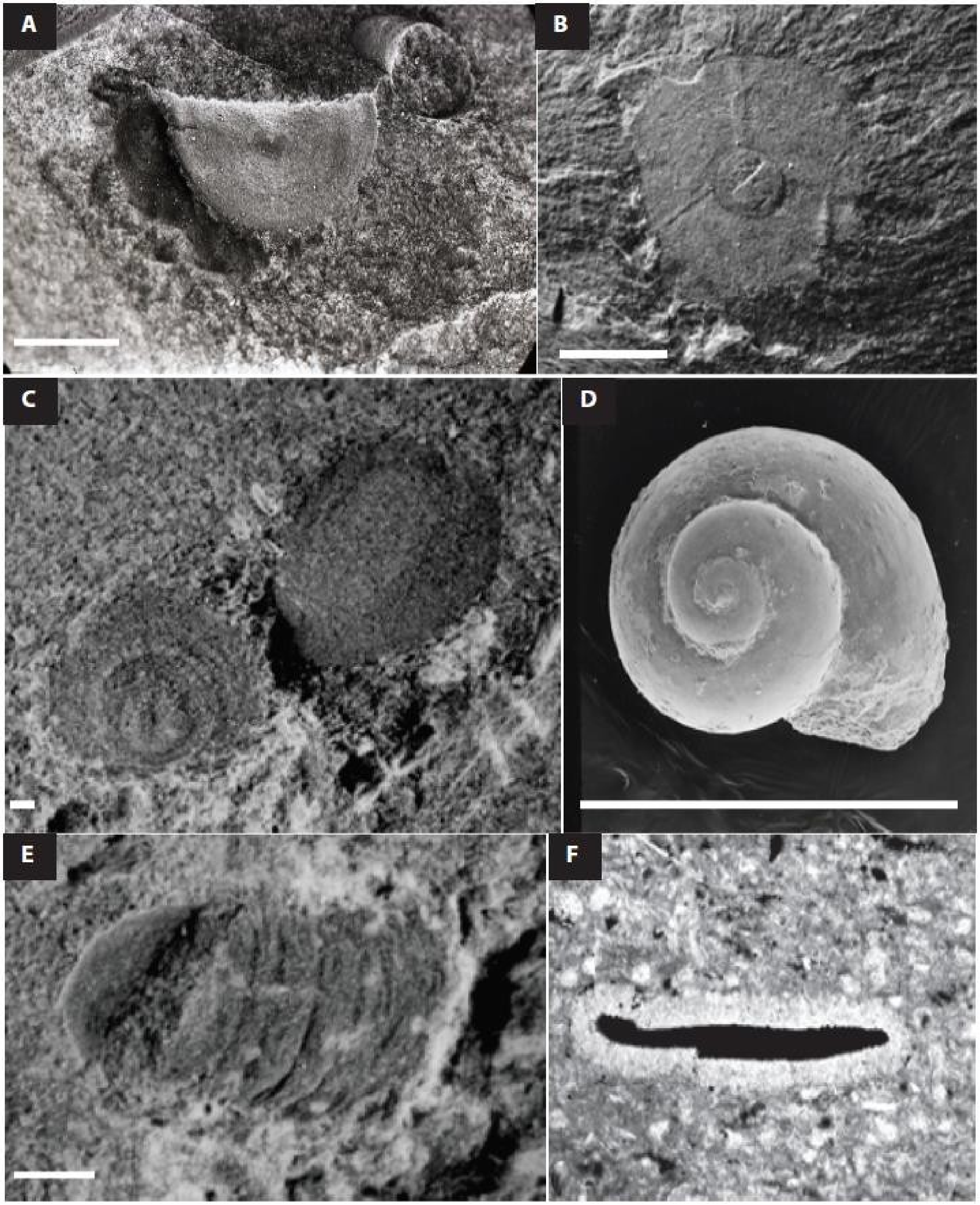


Figure 2.8 a: Hyolith operculum (*?Burithes*), BDF 73, Withycombe Formation, UK. **b:** hyolith operculum indet., BDF 9878, Withycombe Formation, UK. **c:** BDG 74, Withycombe Formation, UK. **d:** *Aldanella attleborensis,* BDF 9885, Withycombe Formation, UK. **e:** *Oikobesalon*, BDF 9523, Withycombe Formation, UK. **f:** Test of *Platysolenites antiquissimus*, BDG 84 (thin section), Withycombe Formation, UK. Scale bars equivalent to 100µm.

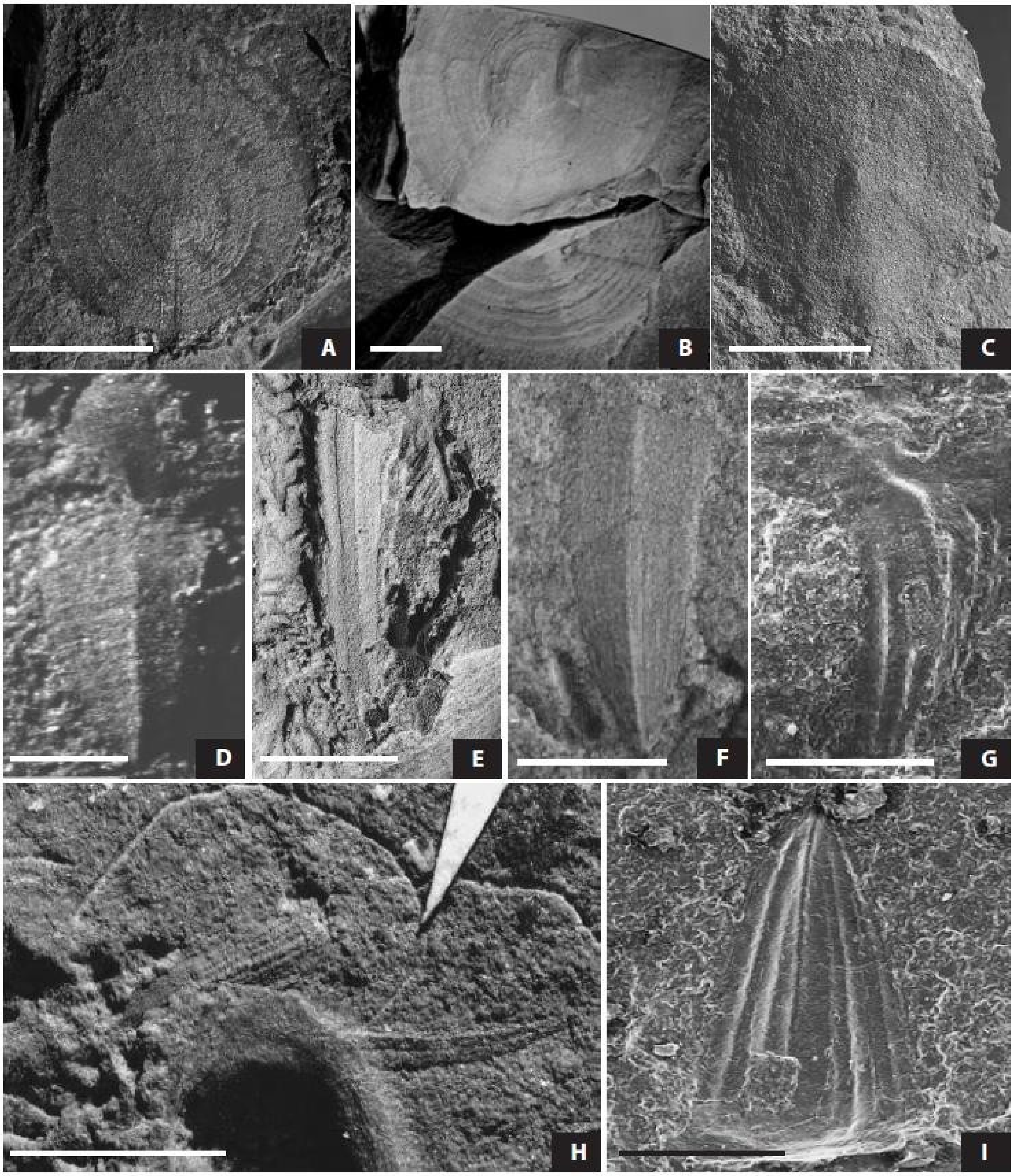


Figure 2.9 Halkieriid opercula (a-c) and sclerites (d-i). **a:** Halkieriid operculum type A, BDG 9, Withycombe Formation, UK. **b:** Halkieriid operculum type A, BDF 9973, Withycombe Formation, UK. **c:** Halkieriid operculum type B, BDG 147a, Withycombe Formation, UK. **d:** BDF 9977d **e:** Spinose sclerite, BDF 9892, Withycombe Formation, UK. **f:** BDF 9977c, Withycombe Formation, UK. **g:** Impression associated with BDG100a, BDG 100b, Withycombe Formation, UK. **h:** The upper sclerite possibly represents a cultrate, the lower may be a siculate, BDG 80, Withycombe Formation, UK. **i:** Symmetrical, form B sclerite displaying the dorsal surface, BDG 100a, Withycombe Formation, UK. Scale bars equivalent to 5mm (a-f, h) and 100μm (g-i).

2.8 Significance of the macroscopic nature of the assemblage

The lower Cambrian is dominated by a heterogeneous group of small enigmatic fossils colloquially termed the “small shelly fauna”. In contrast to the normally diminutive nature of early Cambrian body fossils, the larger nature of the body fossils in the Withycombe Formation, as well as the coeval trace fossil assemblage, indicates the presence of large bilaterians. There are other reports of early Cambrian fossil assemblages with large fossils comparable in size to those of the Withycombe Formation (Missarzhevsky 1969; Dzik 1991; Marti Mus *et al*. 2008). These occurrences bring into question our understanding of the average size of the oldest metazoans, which may be biased towards preservation of the small, phosphatic small shelly fossils that dominate fossil residues from limestone (Dzik 1991, 2005; Marti Mus *et al*. 2008; Mángano and Buatois 2014; Nagovitsin *et al*. 2015; Shahkarami *et al.* 2017; Zhang *et al.* 2017).

There is also the suggestion that the early Cambrian small shelly fauna is an artifact of the selective preservation of early ontogenetic stages of much larger macroscopic organisms (Dzik 1991; Marti Mus *et al.* 2008). Recent discovery of large tubular fossils from the Terreneuvian of Arctic Siberia have been considered to be due to an unusual taphonomic window that allows preservation of the adult stages of the more familiar small shelly fossils (Marusin and Grazhdankin, 2018). The discoveries in Siberia and the Withycombe Formation suggest that larger biomineralized organisms may have been relatively common in quiescent offshore marine environments below storm wave base. Perhaps it is possible that the Withycombe Formation preserves a rare occurrence of the preservation of the adult stage of many of these taxa previously known. However, comparable biotas are absent elsewhere in Newfoundland in well studied highly comparable facies (Landing 1992b; Landing 1994; Narbonne *et al.* 1989; Landing *et al.* 2018).

2.9 Stratigraphic and ecological distribution of the macrofossils.

Ladatheca conches are the most ubiquitous element of the macrobiota and are commonly in very high concentrations that may be current-winnowed assemblages. There are no apparent ecological trends recorded in the section, except the increased abundance of the large hyoliths *Allatheca* and *Orthotheca* high in the section. The distribution of the less prolific taxa cannot be related to either facies or linked to other metrics, such as palaeontological diversity. The predatory, organic rich trace fossils described previously (**fig. 2.4),** along with the types of foodstuff present in the trace that are generally closely related to the relative abundance of shelly taxa, suggest that there was no preferred diet for the tracemakers. It can be inferred that the traces conferred increased preservation potential to the small shelly fauna, allowing lightly biomineralized taxa to be preserved. This may probably be related to the higher proportion of organic matter in the traces, which increased the potential for pyritization. The stratigraphic distribution and ranges within the Withycombe borehole of all the taxa mentioned is summarized in **fig. 2.10**.

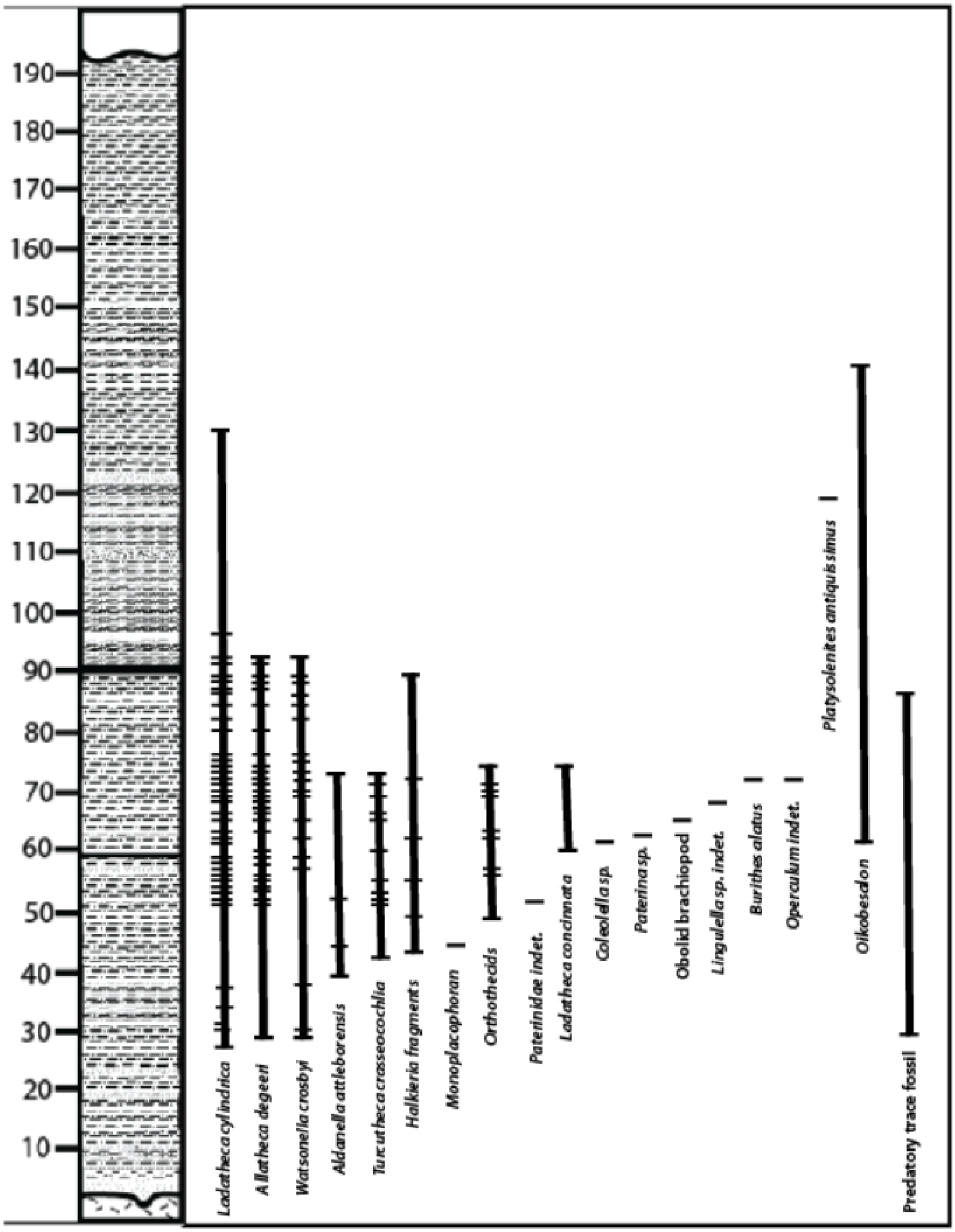


Figure 2.10. Stratigraphic distribution and ranges of taxa and trace fossils within the Withycombe Farm borehole.

2.10 Biostratigraphic implications of the fauna

The rich, hyolith-dominated fauna re-described in this section includes both orthothecid and hyolithid hyoliths, a helionelloid, brachiopods, a foraminiferan, halkieriid sclerites and plates, tubular problematica and a gastropod-like mollusc, along with a low diversity ichnofauna, as described above.

The Withycombe Formation has previously been assigned to the *Watsonella crosbyi* Zone, based on comparison with the fauna of the lithologically similar Chapel Island Formation of southeastern Newfoundland (Brasier 1992). However, it contains several taxa that are typical of the Cuslett and Brigus Formations in the reference sections in Newfoundland (Landing and Benus 1988a, b; Landing *et al.* 1989, 2013a; Myrow and Landing 1992). Withycombe Formation taxa that are common in the Cuslett and Brigus formations include brachiopods, and the hyoliths *Burithes alatus* and *Allatheca degeeri.* There are some longer ranging genera that typify the whole of the Placentian Series of Avalonia, such as *Watsonella*, *Platysolenites*, *Aldanella* and *Ladatheca* (Landing *et al.* 1989).

The Chapel Island Formation of southeastern Newfoundland is dominated by leiosphaerids and filamentous sheaths (Palacios *et al*. 2017) and has also yielded specimens of *Granomarginata squamacea* (Strauss *et al.* 1992) like the Withycombe Formation (Poole 1978; Rushton & Molyneux 1990). This palynological data is further support for correlation of the Withycombe Formation with the Fortunian Chapel Island Formation and the 'Nemakit-Daldynian'/Fortunian of Siberia (Vidal *et al.* 1995). Strata at the the top of a unit in New Brunswick, Canada that Landing correlates to the Chapel

Island Formation in Newfoundland are dated at c. 530 Ma by Landing (1994) (from the U-Pb zircon date of Isachsen *et al.* (1994)); and the top of the 'Nemakit-Daldynian'/? Fortunian in Siberia has been dated at ca. 534 Ma by Bowring *et al.* (1993), both of which are equivalent to the Fortunian stage. This infers that the fossil assemblage of the Chapel Island Formation may contain elements of younger Cambrian Stage 2 or ‘Tommotian’ faunas, or that the first occurrences of 'Tommotian-type' small shelly fossils may be markedly diachronous (Landing *et al.* 1989). In terms of its regional lithostratigraphic correlation, the Withycombe Formation could, therefore, still be equated with the Chapel Island Formation despite the presence of some 'Tommotian-type' elements to the fauna (*sensu* Khomentovsky & Karlova 1993).

A second stratigraphic approach would be to disregard the rather scant palynological evidence (since *Granomarginata squamacea* is in any case a long-ranging taxon) and interpret the age of the Withycombe Formation on the basis of small shelly fossil stratigraphy alone. This would suggest correlations with the Bonavista sedimentary cycle where it may be compared with the Cuslett Formation of southeastern Newfoundland (**fig. 2.11)**. Although lithologically different, the Cuslett Formation contains large hyoliths and brachiopods in carbonate facies and this seems to be the most parsimonious biostratigraphic correlation with the Withycombe Formation.

Finally, it could also be argued that there are slightly younger Branchian-type elements (cf. Landing *et al.* 1980) (i.e., the lingulellid brachiopods) in the Withycombe Formation fauna and, as such, it could be considered to be of *Callavia* Zone age (Cambrian Stage 3?). However, the conspicuous lack of trilobites (despite suitable facies, and the good preservation of their exoskeletons in similar facies) is notable, and potentially significant. The delicate pyritization, which preserved the brachiopods, might otherwise suggest that there are taphonomic biases to the first occurrences of brachiopods, and the Withycombe Formation material would therefore constitute very early examples of the Brachiopoda. The identification of these specimens as lingulellids should be considered with caution due to the poor preservation and difficulty in confirmed taxonomic identification. The second interpretation of the fauna is preferred herein.

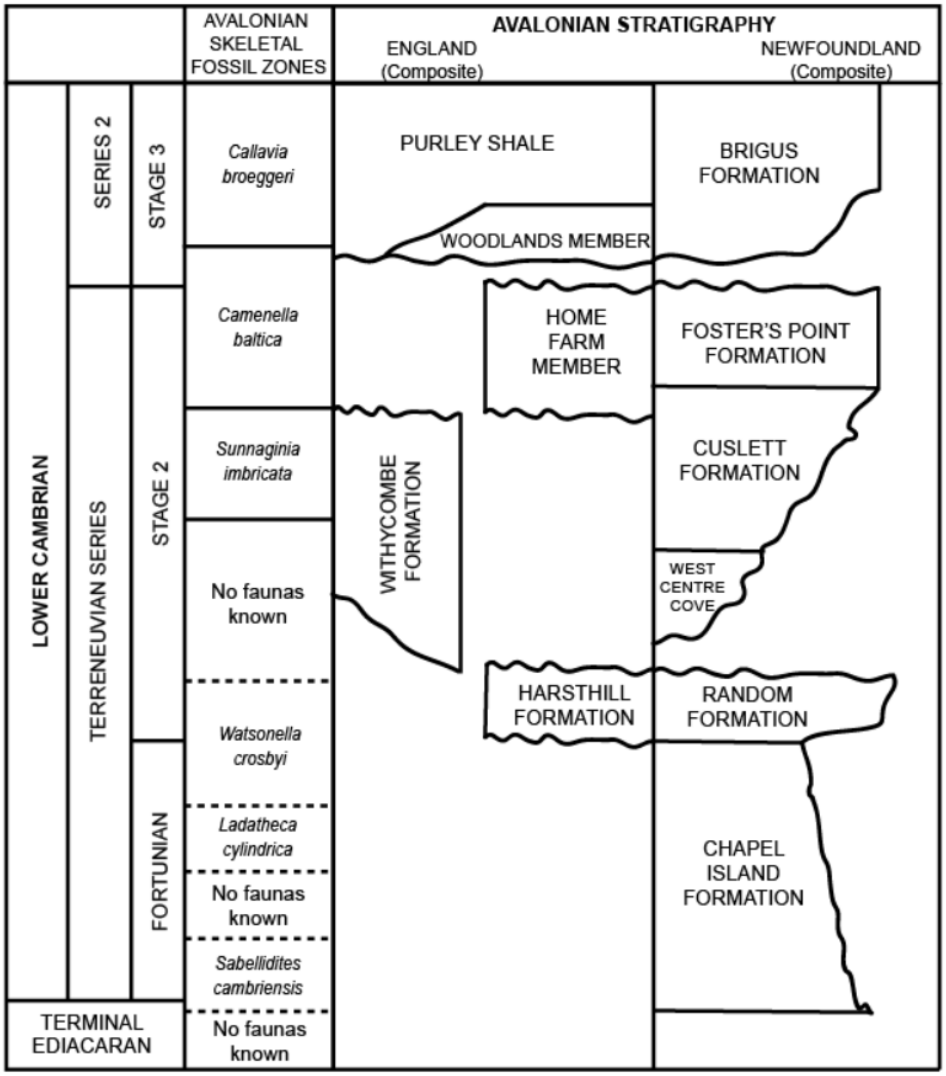


Figure 2.11. Correlation chart of the lower Cambrian successions in Avalonian regions of central England and southeast Newfoundland. Modified from Conway Morris *et al.* (1998) & Landing *et al.* (2017).

2.11 Conclusions

The pre-trilobitic lower Cambrian Withycombe Formation is a siliciclastic succession containing a hyolith-dominated small shelly fauna including orthothecid hyoliths, hyolithid hyoliths, the rostroconch *Watsonella crosbyi*, early brachiopods, the foraminiferan *Platysolenites antiquissimus*, the coiled gastropod-like *Aldanella attleborensis,* halkieriids, and a low diversity ichnofauna including evidence of predation by a vagile infaunal predator. The pyritized nature of the assemblage enabled the study using micro-CT revealing pyritized microbial filaments of probable giant sulfur bacteria that have not previously been described.

Based on the macroscopic scale of these “not so small shelly fossils” in comparison with studies completed in the Arctic of Siberia, it is possible that the Withycombe Formation preserves a rare occurrence of the preservation of the adult stage of many of these taxa previously known, although this cannot be confirmed at this time.

Particularly interesting in the Withycombe assemblage is the presence of possible early brachiopods and an absence of trilobites. This brings into question the timing and evolutionary history of these early forms of brachiopods. There is no evidence of trilobites in the Withycombe Formation, yet there are possible lingulellids. The nearby Purley Shale Formation (lower Cambrian Stage 3) of Nuneaton is located within the same basin and is known to yield trilobites (Williams et al. 2013). Together these suggest that the Withycombe Formation is older, and it is more plausible that the Withycombe Formation preserved an early form of brachiopod. The lingulellids at the Withycombe are preserved with such a thin coating of pyrite, perhaps the early brachiopods were chitinous rather than thick-walled and phosphatic, with the pyritization of the Withycombe Formation being a type of konservat lagerstätte.

The Withycombe assemblage contains a number of important index fossils (*Watsonella crosbyi, Platysolenites antiquissimus,* and *Aldanella attleborensis*) that enable correlation of strata around the base of the Cambrian Stage 2 within and between Avalonia and Baltica. Biostratigraphically, given the lack of palynological evidence, we suggest that the Withycombe Formation is contemporaneous with the lithologically similar Cuslett Formation of Southeastern Newfoundland.

This provides a better understanding of the earliest Cambrian (Fortunian and Cambrian Stage 2) of Avalonia through analysis of the small and not-so-small shelly fossils of the Withycombe Formation. Identifying the fossils present, some of them rather enigmatic, we were able to better constrain the formation biostratigraphically and assign the formation to the Cambrian stage 2. This study of the Withycombe Formation fills a gap in knowledge as it provides data from the only known section of the lowermost Cambrian strata in the UK. Understanding the small shelly fauna is pivotal in understanding the evolution of the main groups of marine invertebrates, particularly the overall pattern of early Cambrian evolution.

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Chapter 3

Taphonomy of the lower Cambrian, Withycombe Farm Borehole, Oxfordshire, England

Taphonomy of the lower Cambrian, Withycombe Farm Borehole, Oxfordshire, England

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Abstract

Fossil pyritization primarily occurs as a result of the metabolism of sulfur reducing bacteria, and the rate and extent of pyritization is largely controlled by the availability of iron, sulfur, and microbiota in porewaters. For pyritization of calcitic shells to occur, the carbonate skeleton must act as a nucleation substrate for the formation of pyrite in porewaters that are undersaturated with respect to carbonate. Studies of modern sediment suggest that these conditions occur during the early stages of sulfate reduction and methanogenesis. Sulfur isotopic data provide support for these associations of porewater chemistry and style of fossil pyritization.

The pre-trilobitic lower Cambrian of the Withycombe Formation is a 194 m thick siliciclastic succession dominated by interbedded offshore red-purple and green pyritic mudstone with minor sandstone. The mudstone contains a hyolith-dominated “small shelly fauna” preserved as pyrite. Petrographic observations and sulfur isotopic analyses allow the development of a model for pyritization of these “small shelly fossils”, the oldest biomineralized fossils in the UK.

3.1 Introduction

The Withycombe Formation of Oxfordshire sub-crop represents the lowermost Cambrian of Central England. The sandstone and mudstone of the Withycombe Formation unconformably overlie weathered, altered basaltic lavas of the Precambrian Midlands Microcraton, which are comparable to the diorites of Nuneaton and Charnwood Forest (Wills & Shotton, 1934; Brasier *et al*. 1978; Brasier, 1992b; McIlroy & Horak 2006). The significance of the Withycombe biota stems from the presence of a variety of these enigmatic early Cambrian small shelly fossils, their pyritic preservation, and their unusually large size. Some of the biota present in the Withycombe Formation include large hyoliths, early brachiopods, putative gastropods, and rostroconches, as well as the sclerites of multi-scleritome halkieriids. The palaeontology is fully described in Chapter 2.

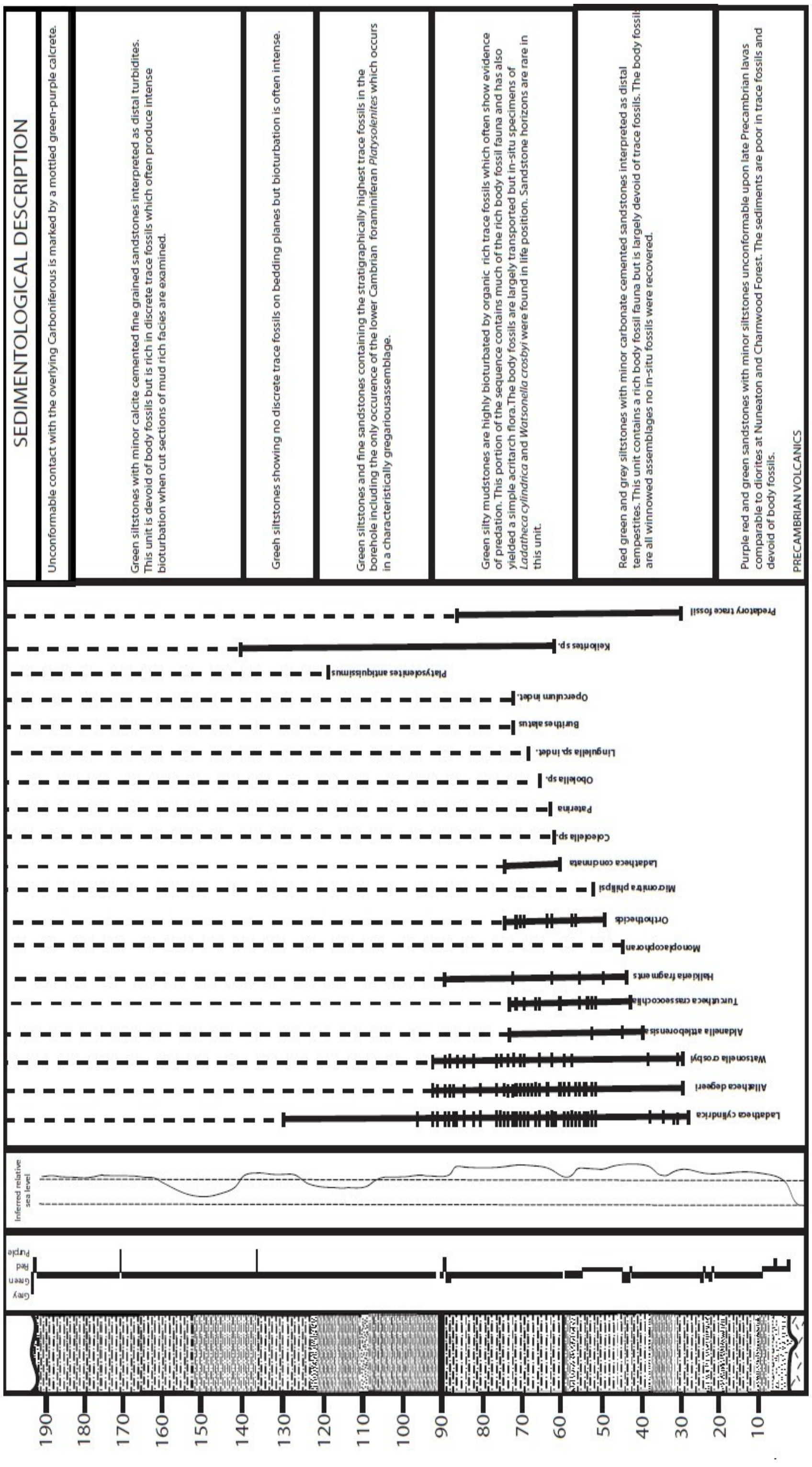
The strata have previously been assigned a *Watsonella crosbyi* Zone age based on comparison with the fauna of the lithologically similar Chapel Island Formation of southeastern Newfoundland (Cambrian Stage 2; Brasier *et al.* 1992). Our reinvestigation concludes that there are several typical Cambrian Stage 2 elements to the Withycombe biota (brachiopods, and the hyoliths *Burithes alatus* and *Allatheca degeeri*), along with some longer-ranging genera that typify the whole of the Placentian in Avalonia, such as *Watsonella*, *Platysolenites*, *Aldanella* and *Ladatheca*. This assemblage of fossils thus constitutes the oldest Palaeozoic body fossils in the UK.

3.2 Sedimentology

The Withycombe Formation of Oxfordshire is a 194 m thick siliciclastic sedimentary succession of sandstone and heavily bioturbated mudstone that is interpreted to have been deposited below storm wave base in the Midlands Basin. The mudstone-rich part of the succession contains a hyolith-dominated assemblage of early skeletal fossils that are the focus of this study (Rushton & Molyneux 1990; Conway Morris *et al*. 1998).

The basal unit of the Withycombe Formation is a red mudstone that fills fissures in the basaltic basement, and contains several coarse sandy horizons that grade into green/grey mudstone with purple mottling and, in the lower 90 m of the formation there are sparse phosphate nodules (Wills & Shotton, 1934; Brasier *et al*. 1978; Power *et al*. 2019, in prep). The 104 m thick upper Withycombe Formation is composed of abundant thin sandstone beds that fine upward into highly bioturbated green mudstone with sparse body fossils, but which contain well-preserved trace fossils. The top of the Withycombe Formation is delineated by the sub-Carboniferous unconformity of the Nottinghamshire Coal Field, pedogenesis and weathering along the unconformity created a 0.25 m thick red and green mottled calcrete (**Fig.3.1; Poole 1978; Chapter 2**).

Due to increased focus on the palaeontology of the Withycombe Farm Borehole, a more detailed sedimentological study including a more detailed breakdown of facies distributions is lacking. Therefore, we were unable to discuss the application of biofacies models developed for oxygen-stratified basins. Our approach to develop a taphonomic model for the Withycombe assemblage included understanding the biogeochemical processes of pyritization of the small shelly fossils which is discussed herein.



SEDIMENTOLOGICAL DESCRIPTION

Unconformable contact with the overlying Carboniferous is marked by a mottled green-purple calcrete.

Green siltstones with minor calcite cemented fine grained sandstones interpreted as distal turbidites. This unit is devoid of body fossils but is rich in discrete trace fossils which often produce intense bioturbation when cut sections of mud rich facies are examined.

Greeh siltstones showing no discrete trace fossils on bedding planes but bioturbation is often intense.

Green siltstones and fine sandstones containing the stratigraphically highest trace fossils in the borehole including the only occurence of the lower Cambrian foraminiferan *Platysolenites* which occurs in a characteristically gregariousassemblage.

Green silty mudstones are highly bioturbated by organic rich trace fossils which often show evidence of predation. This portion of the sequence contains much of the rich body fossil fauna and has also yielded a simple acritarch flora.The body fossils are largely transported but in-situ specimens of *Ladatheca cylindrica* and *Watsonella crosbyi* were found in life position. Sandstone horizons are rare in this unit.

Red green and grey siltstones with minor carbonate cemented sandstones interpreted as distal tempestites. This unit contains a rich body fossil fauna but is largely devoid of trace fossils. The body fossil are all winnowed assemblages no in-situ fossils were recovered.

Purple red and green sandstones with minor siltstones unconformable upon late Precambrian lavas comparable to diorites at Nuneaton and Charnwood Forest. The sediments are poor in trace fossils and devoid of body fossils.

PRECAMBRIAN VOLCANICS

Figure 3.1. Sedimentological descriptions and stratigraphic distribution and ranges of taxa.

3.3 Taphonomy

The presence of large benthic organisms in the lowermost Cambrian of Avalonia is unexpected and raises the question as to whether this is an endemic biota, or a rare taphonomic window that preserves a normal, but seldom preserved element of early benthic assemblages. Understanding the taphonomy of the Withycombe Formation is important in determining the conditions under which the fauna was preserved, and might provide a basis for a search for similar facies elsewhere in Avalonia, particularly the thick units of southeastern Newfoundland, which have been previously described (Landing 1992; Myrow & Landing 1992; Landing 1994; Narbonne *et al*. 1987; Hiscott, 1982; Myrow 1987; Myrow & Hiscott 1993;).

3.3.1 Biostratinomy

Biostratinomy is one of the important subdisciplines of taphonomy involving the study of the environmental factors that affect organic remains for the time between an organism's death and final burial (Lawrence, 1979). There are many biostratinomic processes to consider when discussing the various mechanical and biogenic agents that act to disturb, break down, and destroy skeletal hard parts in marine environments (Brett *et al.* 1986).

Due to the rubbly, non-oriented nature of the Cambrian part of the Withycombe Farm Borehole core, no palaeocurrent information could be gathered for comparison between core slabs. Many of the fossiliferous horizons are, however, heavily bioturbated. *Ladatheca cylindrica* and *Turcutheca crasseocochlia* are considered to have been sessile endobenthos that had a vertical attitude in the sediment (Landing *et al*. 1989), and as such, their almost ubiquitous horizontal orientation in the Withycombe Formation suggests post-mortem winnowing and reorientation, possibly due to current action. Some of the body fossils in the Withycombe Formation occur within dark organic-matter rich burro with concentrations of fossil material that suggests concentration by predation (**Fig. 3.2b**). The shells and conches preserved within the burrows of predatory organisms are typically sediment-filled and compressed, rather than sub-circular in cross section and filled with early diagenetic minerals.

In contrast to the abundant horizontal shelly fossils, MicroX-ray imaging reveals a range of pyritized filaments (**Fig. 3.2h**) that have a strong vertical component, which appear to have been created after deposition (Chapter 4). It is possible that these bacterial sheaths were preserved during vertical migration, perhaps in search of available nutrients, not too dissimilar from the behaviour of the sediment-dwelling sulfur bacteria *Thioploca* that migrate vertically to overcome diffusion limitations (Huettel *et al.* 1996).

Compaction: It is noted there are some taxon-specific compaction trends in the Withycombe Formation assemblage, which are considered to be the result of a combination of shell dimensions, shell/conch thickness, and timing of lumen-filling cement relative to compaction. Some of the narrow tubular shells and conches are filled with early diagenetic calcite and pyrite that provided support to the shell during burial. Examples of this mode of preservation can be seen in taxa with a long, narrow, tubular shells such as *Coleolella* sp. (**Fig. 3.3h**), *Ladatheca cylindrica* (**Fig. 3.3 d,i**), *Turcutheca crasseocochlia* (**Fig. 3.2e**) and *Aldanella attleborensis* (**Fig. 3.3i**).

Larger, broader hyoliths with a relatively large apical angle, are typically compressed. The apertural end of some narrow conches are more likely to be compressed (**Fig. 3.2**), and thus in some cases taxa that are commonly unfractured/compressed develop longitudinal fractures. Such brittle deformation is most common in *Ladatheca cylindrica* and *Turcutheca crasseocochlia*, which in this study were completely or partly filled with sediment, rather than those specimens with early diagenetic cements of pyrite and/or calcite. Broad conches that are always compressed include the large orthothecid hyoliths (**Fig. 3.3a**), and the hyolithid hyolith *Allatheca degeeri* (**Fig. 3.2c**). Specimens of *Platysolenites antiquissimus* commonly show plastic deformation of the agglutinated quartzose test from its original circular morphology to a compressed u-shape (McIlroy *et al.* 2001), though post-mortem fracturing also took place (**Fig. 3.2g**). Petrographic thin sections through the test of *Platysolenites antiquissimus* demonstrate that it has a siliceous test with framboidal pyrite infill in the lumen and wall (see McIlroy *et al.* 2001).

Many of the *Watsonella* specimens (**Fig. 3.2j**), palmate sclerites, and halkieriid operculae (**Fig. 3.3 c, d**) in the Withycombe Formation are partly compressed and fractured in a manner comparable to that seen in the broad hyolith shells.

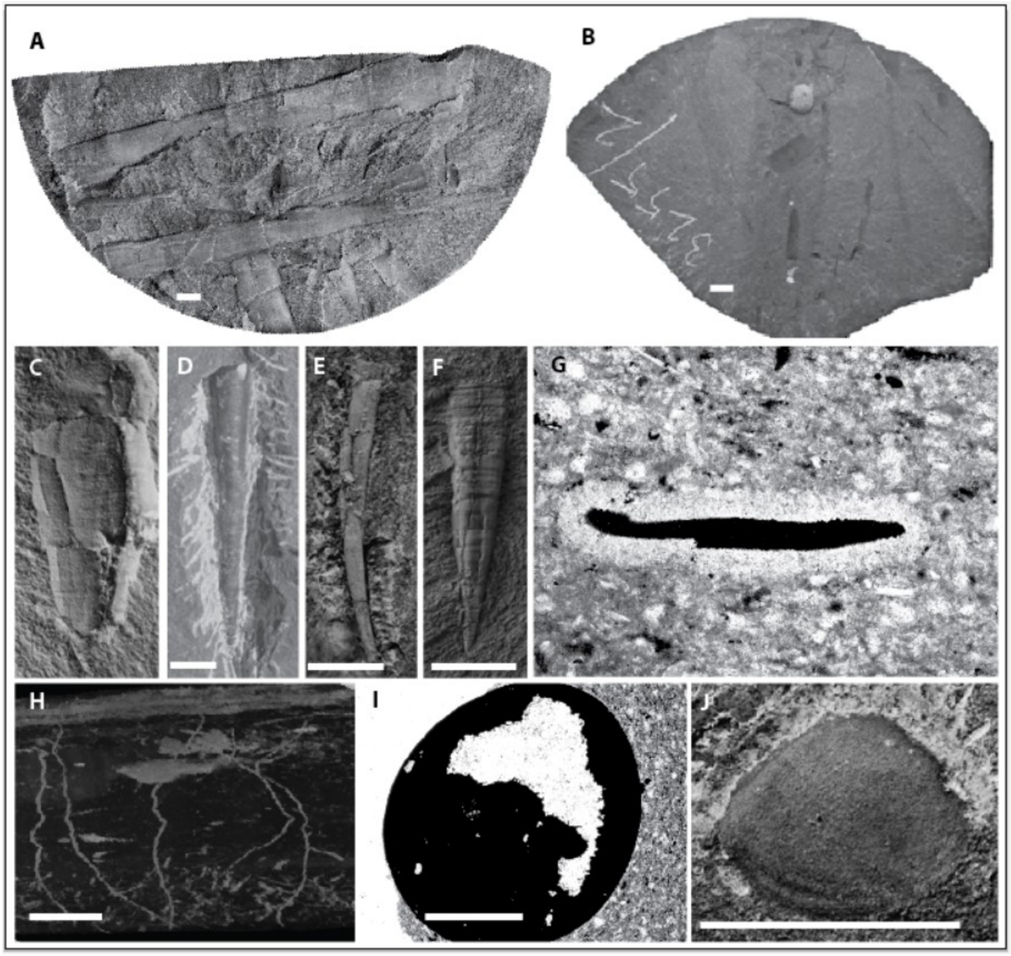


Figure 3.2 a) BDF 9898. Large, compressed orthothecid hyolith conches orientated longitudinally in sediment. b) Dark organic-matter rich predatory trace fossil containing longitudinally orientated hyolith body fossils and small pyritic concretion. Other organic-matter rich trace fossils are non-fossiliferous. c,e,f) Compressed hyolith conchs of c) BDF 9775 *Allatheca*, e) BDF 9886 *Turcutheca*, and f) BDF 9986. *Allatheca*. d) *Ladatheca cylindrica* conch preserved in full relief. i) Petrographic thin section of sample BDG 84 showing an uncompressed hyolith conch filled with early diagenetic pyrite, preserved in full relief. g) Petrographic thin section sample of BDG 84 showing an agglutinated test of *Platysolenites antiquissimus* with framboidal pyrite fill h) 3D reconstruction of CT image showing subvertical orientated probable giant sulfur bacteria. j) Compressed shell of *Watsonella crosbyii.* Scale bars equivalent to 1 cm (a-f, h), and 500 µm (g, i, j).

3.3.2 Diagenetic Re-mineralization

The majority of the fossils of the Withycombe Farm Borehole were, by analogy with specimens of those taxa that are preserved in limestone (Landing, 1992; Landing, 1994; Narbonne *et al*. 1987; Hiscott, 1982; Myrow, 1987; Myrow & Hiscott, 1993), probably originally calcitic (the hyoliths, gastropods, rostroconchs), or organo-phosphatic (brachiopods and a possible bradoriid). The tests of the agglutinated foraminiferan *Platysolenites* are not replaced by pyrite, but typically have a pyritic fill (McIlroy *et al.* 2001), and palynomorphs are preserved as organic matter (Rushton & Molyneux, 1990). In order to determine the taphonomic pathway that allowed preservation of the calcitic and some of the organo-phosphatic components of the Withycombe Farm Borehole biota in pyrite, we completed petrographic studies augmented with sulfur isotopic analysis.

Preservation as Pyritic Coatings

Many of the larger hyoliths (with broader conchs) and those with a relatively large apical angle, consistently succumbed to the forces of compression. In such cases, preservation of the shell wall often did not occur, and the fossil took the form of a non-mineralized compression. This in many instances is covered with a coating of finely disseminated pyrite (**Fig. 3.3 a-d**), possibly as a result of the breakdown of periostracum-like organic matter (Fisher and Hudson, 1985; Seilacher *et al.* 1985). This mode of preservation is most common in the orthothecid hyoliths and the hyoliths *Ladatheca cylindrica*, *Turcutheca crasseocochlia*, and *Allatheca degeeri* specimens. The same mode of preservation as external molds exists in many of the smaller elements of the fauna such as the *Watsonella crosbyi*, the palmate sclerites and operculae of *Halkieria stonei,* and some of the brachiopods.

Void fill and Shell/Conch Replacements

Many of the shells in the Withycombe Formation were filled with early diagenetic calcite and pyrite (**Fig. 3.3e**), and as such were not subject to burial compaction. The shell wall is often preserved around this central core of pyritic void-fill (**Fig. 3.3g**), subsequent to the dissolution of shell material. Examples of this mode of preservation include specimens with long, narrow, tubular shells such as *Coleolella* sp., *Ladatheca cylindrica*, and *Turcutheca crasseocochlia.* The long, tubular shape of the conch provides an ideal micro-environment for the generation of pyrite by sulfate reducing bacteria, especially if traces of organic matter remained in the shell. A similar condition was also met within the originally hollow, palmate sclerites of halkieriids (Landing e*t al*. 1989). It has been inferred that the pyritic fill of *Platysolenites* (**Fig. 3.3f**) is the product of biodegradation of the inner organic sheath, such as in many agglutinated foraminiferans (McIlroy *et al.* 2001; Fig. 1I, J).

Pyritic Steinkerns (**Fig. 3.3 h-j**)

Another style of preservation in the Withycombe Farm Borehole is that of internal moulds in which the internal structure of the organism is preserved. Examples of this mode of preservation includes the *Aldanella attleborensis* pyritic steinkerns, similar to those preserved in the Chapel Island Formation of southeast Newfoundland (Myrow and Landing, 1992; **Fig. 3.3i**), and paterinid brachiopods exhibiting the internal structure of the shell including potential muscle scars (**Fig. 3.3j**).

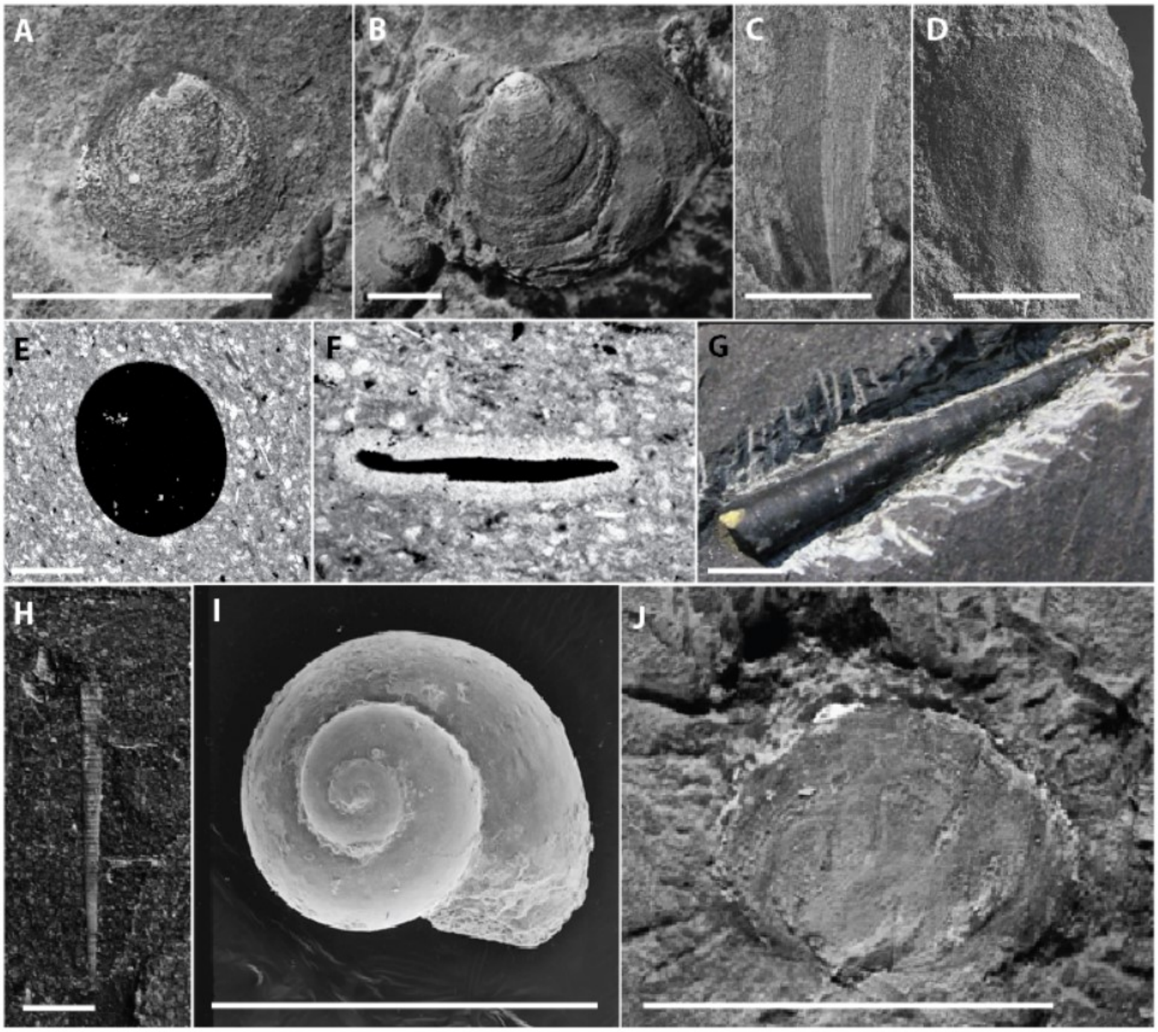


Figure 3.3. Styles of pyritic preservation present in the Withycombe Formation. a-d) Pyritic patina - fine coating of disseminated pyrite. a) BDF 9859 – Obolid brachiopod. b) BDG 39 – *Paterinidae indet.* c) BDF 9977c - Halkierid sclerite. d) BDG 147a halkieriid operculum. e) Void fill of pyrite during sulfate reduction followed by diagenetic calcite during methanogenesis. Thin shell wall is partially preserved in places (thin grey line on bottom right of conch). f) BDG 84 - *Platysolenites antiquissimus* displaying a siliceous test with framboidal pyrite infill in the lumen and wall. g) *Ladatheca cylindrica* conch infilled with diagenetic pyrite and calcite, preserved in full relief. h,i,j) Steinkerns exhibiting internal structure of: h) BDF 9977 - *Coleolella* i) SEM image of BDF 9885 - *Aldanella attleborensis.* j) BDF 9970 - *Paterina* sp. with visible muscle scars. Scale bars equivalent to 500 μm (a,b,h,j), 5mm (c-e, g), 100 μm (i).

3.3.3 Biogeochemistry of pyrite formation

Stable sulfur isotopic analysis was completed on three samples of the Withycombe Formation using a Cameca 1280 at the Centre for Microscopy Characterisation and Analysis, University of Western Australia by Dr. David Wacey. We received successful data from two of the thin sections: BDG 120 and BDG 84. The BDF 9952 sample was unsuccessful as the individual grains of pyrite are much smaller than the beam size and therefore the beam hit the matrix at the same time. The mount for these analyses is provided in Appendix 1.

Sample BDG 120 has a range of $\delta^{34}S$ mostly between -20 to -23‰, but also contains a couple of heavier isotopic values, which may suggest that this was the last region to be pyritized (Raiswell 1997). In sample BDG 84, six pyritized structures were analysed. All are heavier than BDG120 and are mostly between $\delta^{34}S$ = -3 to -11‰ (though each structure has specific $\delta^{34}S$ ranges). The largest of the BDG 84 structures (labelled area b in Appendix 1) has a few anomalous values that are much heavier. A couple of these could be real, but the others have large errors and are likely artefacts in which the beam hit non-pyritic inclusions. The detailed results of the analyses are given in the tables and graphs of Appendix A.

While data on the isotopic composition of pyritized shells are scant, some examples of previous studies found a large range in $\delta^{34}S$ values from -54 to +44‰ in the Lower Jurassic Amaltheus Clays, and -22 to +14‰ in the Middle/Upper Jurassic Oxford Clay (Hudson, 1978). A much smaller range was found for pyritized brachiopods (-34 to - 37‰; Beier & Feldman 1991), as well as for pyrite associated with graptolites (-17 to -

30‰; Underwood & Bottrell 1994). The most negative $\delta^{34}S$ values represent very large fractionations from seawater sulfate (about 75‰; using seawater values from Claypool *et al.* 1980) and the most positive values represent reduction from an almost completely sulfate-depleted closed system. The highly negative $\delta^{34}S$ values of samples BDG 84 and BDG 120 of the Withycombe Formation are consistent with open system in which microbial sulfate reduction was dominant (i.e., a porewater system in which sulfate was introduced at the same rate at which reduction occured; Raiswell 1997).

3.4 Full Taphonomic Model

The preservation of the shells in the Withycombe Formation can be subdivided on the basis of their original composition and degree of compression. The majority of the fossils of the Withycombe Farm Borehole were originally calcitic, although some had organo-phosphatic shells. In addition, there are agglutinated foraminifera and microfossils. Only the originally calcitic and organo-phosphatic shells are replaced by pyrite. Major taphonomic pathways include:

- Preservation of originally calcitic shells as pyrite replacements in full relief;
- Preservation of originally calcitic shells as pyritic compressions;
- External and internal molds of probable organo-phosphatic brachiopods;
- Agglutinated foraminiferal tests as partially pyrite filled U or 8 shaped compressions.

I herein present a taphonomic model (**Fig. 3.4**) to show the pyritization of thin organic layers and void fill of calcite and pyrite in narrow conchs, carbonate dissolution and pyritization of shell voids, and late pyritic void fill.

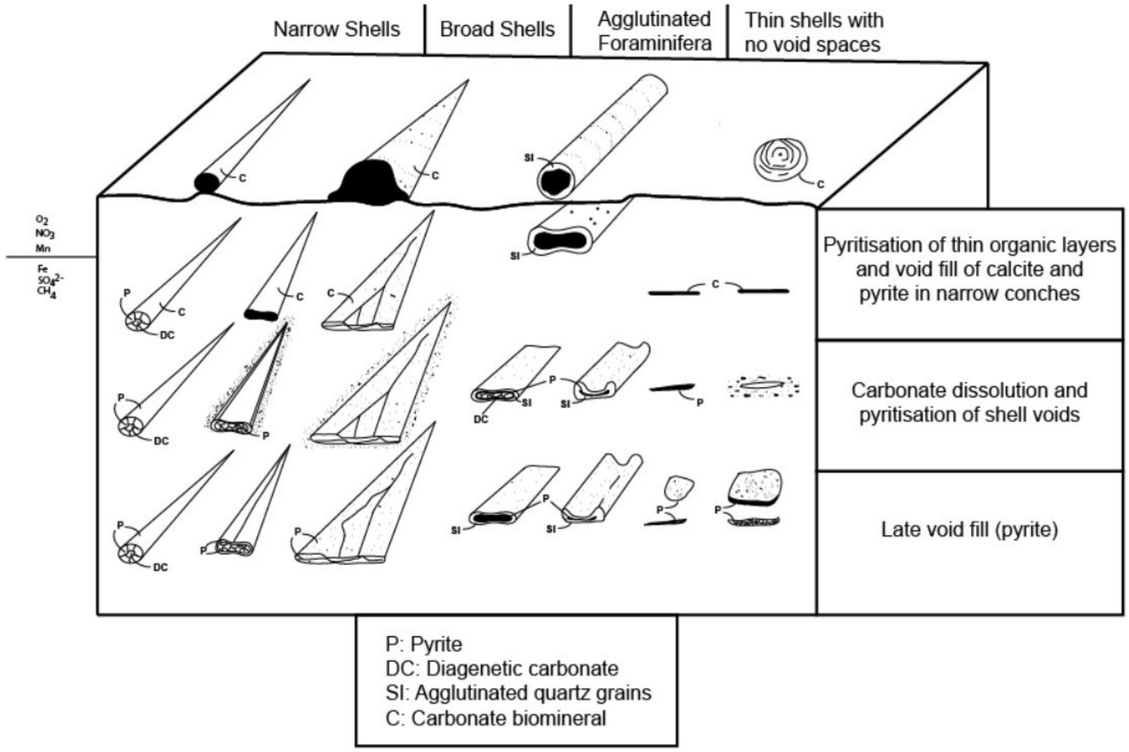


Figure 3.4. Taphonomic model explaining the relationship between the degree of compression and diagenetic phenomena seen in the Withycombe assemblage.

3.5 Discussion

The early Cambrian was a time of rapid evolution and marks a profound change in life on Earth. Our understanding of the evolution of life during the earliest Cambrian has been vastly improved through excellent preservation in various locations worldwide, including parts of the former Avalon Terrane of eastern Newfoundland and southern Britain. However, the lower Cambrian Withycombe Formation of Oxfordshire constitutes the oldest Palaeozoic body fossils in the UK, therefore providing the only information on life at that time for this area. Studying the sedimentology and palaeontology of the Withycombe Farm Borehole has provided insights into the seafloor conditions in the Midland Basin at that point in history.

The unusual preservation of the brachiopods at Withycombe is noteworthy.
Lingulid brachiopods are among the first known members of their phylum (Williams *et al.* 1994; Cusack *et al.* 1997; Cusack *et al.* 1999; Cusack and Williams, 2007; Cusack *et al.* 2008; Kowalewski, 1996; Kowalewski and Flessa, 1996; Zabini *et al.* 2010a) and although the morphological conservatism of the lingulid shell is a well-known feature (e.g., Cusack and Williams 1996; Kowalewski *et al.* 1997; but see Emig 2003), the chemical composition and biomineralization patterns of early lingulids have not been well documented (Zabini *et al.* 2012). The early lingulids were inferred to have been originally organo-phosphatic (Forchielli *et al.* 2012). The pyritization of the specimens described from the Withycombe is unexpected, and therefore it is possible that these earlier forms of brachiopods were not yet well mineralized and were largely organic or chitinous in composition. If so, upon burial, this organic matter would have been replaced with pyrite under low pH diagenetic conditions within the green siltstone. In this case, the phosphate of the shell would have been leached, leaving a void that subsequently became infilled with pyrite (this might incidentally be the source of some of the phosphate nodules in the section). This is consistent with Zabhini *et al.'s* (2012) study, in which they document pyritization of Devonian lingulides and infer that it took place with organic matter in the shell serving as a substrate for bacterial sulfate reduction, generating the H2S for the precipitation of pyrite. Quite possibly a combination of the previous two hypotheses could be responsible for the

pyritization of the inarticulate brachiopods of the Withycombe Farm assemblage.

This study on the taphonomy of the Withycombe Formation has also provided insight into the sedimentary environments and basin conditions at the time of deposition. In order for pyrite formation to occur, the following sources are required: iron, sulfate, and organic matter. In modern sediment, pyrite forms during shallow burial through the reaction of reduced iron with H_2S. The H_2S is produced by sulfur-reducing bacteria that use sedimentary organic matter as a reducing agent and energy source (Berner, 1984). The following formula represents the formation of pyrite:

$Fe^{2+} + H_2S + R$ (organic compounds) $= FeS_2 + 2HR$

The availability and concentrations of these sources largely influence the rate of pyritization. Three major modes of taphonomy dominate the rise of the Metazoa: 1) molds; 2) early authigenic mineralization/replication; 3) carbonaceous compression. It is also possible that two or more modes of taphonomy are present in an individual specimen.

The small shelly fossils of the Withycombe Farm borehole, Oxfordshire, England exhibit various styles of pyritic preservation. Petrographic observations, as well as S isotopic analyses, enabled the study of the pyritized nature of the assemblage. This aided in the development of an understanding of the genesis of this pyrite and a taphonomic model for the pyritization of these “small” shelly fossils, and it provided some insight into basin conditions at that time.

Diagenetic fossil pyritization occurs as a result of the decay of organic matter, which provides an energy source and reducing agent for sulfur reducing bacteria to generate sulfide that subsequently reacts with sedimentary iron to form pyrite (Berner, 1970, 1984;

Canfield & Raiswell, 1991). The duration that a decaying organism spends in different microbial zones of the sediment column is considered to be fundamental in modulating fossil pyritization, and this in turn is contingent on post-burial sedimentation rates and/or microbial zone thicknesses (Schiffbauer *et al.* 2014). A requirement for pyrite replacement of carbonate shells is undersaturation of porewaters with respect to carbonate, which would be expected in siliciclastic systems between sulfate reduction and methanogenesis (Raiswell, 1997).

Sulfur systematics

The mechanisms and relative timing of different fossil pyritization events can be studied using sulfur isotopes, as the presence of sulfate is directly related to pyrite formation. As previously stated, the following steps led to the pyritization of the fossils within the Withycombe Formation:

1. Bacterial reduction of sulfate resulting in the formation of H_2S and elemental S
2. Reaction of H_2S with Fe ions resulting in FeS
3. Reaction of FeS with elemental S resulting in the formation of pyrite FeS_2

The systematics of sulfur isotopes has been widely documented (e.g. Krouse 1977; Chambers and Trudinger 1979; Thode 1991; Raiswell 1997). McConville *et al.* (1999) stated that “the S isotope composition of pyrite is affected by: (1) kinetic isotope fractionation between H_2S and sulfate during reduction; (2) the 34S/32S ratio of the sulfate ($\delta^{34}S$ ~+16‰ for Jurassic seawater and $\delta^{34}S$ ~+21‰ for modern seawater; Claypool et al. 1980); and (3) the open or closed nature of the system with respect to sulfate and H2S (Ohmoto & Rye, 1979).” $\delta^{32}S$- and the $\delta^{34}S$- bearing molecules react at different rates. The lighter isotope of sulfur $\delta^{32}S$ generally reacts faster, which is why isotope fractionation occurs. Sulfur reducing bacteria preferentially metabolize $\delta^{32}S$, therefore through time, with microbial activity in the porewaters, in the absence of any other limiting factor, the sulfate pool becomes increasingly heavier as it is the $\delta^{34}S$ that is left behind (Raiswell, 1997).

The highly negative δ34S values in samples BDG 84 and BDG 120 of the Withycombe Formation are consistent with open system microbial sulfate reduction, in which sulfate is replaced at the same rate at which it is reduced. The pyritization of the Withycombe Formation likely occurred during early diagenesis in a shallow burial, iron-rich, anoxic pore water environment below normal marine seawater. Pyrite replacement of carbonate shells was likely due to the acidic porewaters having been saturated with iron sulphide and undersaturated with respect to calcium carbonate. The porewaters must have been significantly rich in iron in order to have confined the pyritization to the fossils/decay sites themselves, much like that of the Ordovician Beecher's Trilobite Bed in New York (Farrell *et al.* 2009).

This study provides a taphonomic window into the early biomineralized Cambrian faunas, which is seemingly similar to that faunas of the latest Ediacaran, and uncommon through the rest of the Phanerozoic. There is an ample record of non-biomineralizing fossils throughout the Proterozoic–Cambrian transition and it is expressed in a variety of taphonomic modes, one of which in particular is pyritization. Exquisite biological detail can be retained as a result of exceptional preservation of soft tissue by means of pyritization (Schiffbauer *et al.* 2014). This information provides our clearest views into the rise of the Metazoa across the Ediacaran–Cambrian transition (Schiffbauer *et al.* 2014). The

Withycombe pyritization occurred as a result of similar processes as the pyritized, Ediacaran Gaojiashan fossils of South China transition (Schiffbauer *et al.* 2014). Geochemical analyses of the Gaojiashan fossil *Conotubus hemiannulatus* revealed that pyrite precipitation was stimulated by the degradation of labile tissues through bacterial sulfate reduction (Schiffbauer *et al.* 2014). The fossils of the Gaojiashan biota exhibit a preservational gradient from pervasive pyritization to compressed kerogenization, including three- dimensional pervasive pyritization, incomplete pyritization, and carbonaceous compression with associated pyritization (Schiffbauer *et al.* 2014). In comparison with the Gaojiashan, many of the shells of the Withycombe assemblage are pyritized, preserved in full relief, and some consequently succumbed to the forces of compression and were consequently preserved as non-mineralized compressions. Due to the exceptional pyritic preservation of both the Ediacaran Gaojiashan biota and the lower Cambrian Withycombe assemblage, we have been able to study in detail the taphonomic processes that took place. Only by understanding the taphonomy can we begin to examine the many fundamental questions regarding early life, some of which include the morphologies of poorly understood organisms, taphonomic biases imparted by the various paleoenvironments in which the organisms lived, and the relationships between organisms and their environments.

3.6 Conclusion

The shelly taxa of the Withycombe Farm Borehole were preserved by several different modes of pyritization, based on their original shell composition and degrees of compression. These styles of pyritization include shell replacement, pyritic compressions, and internal moulds. Sulfur isotopic analysis of the pyrite revealed highly negative δ^{34S}

values, consistent with open system microbial sulfate reduction (sulfate replaced at the same rate in which reduction occurred). The pyritization of the Withycombe Formation likely occurred during early diagenesis in a shallow burial, iron-rich, anoxic pore water environment.

The unique taphonomy recorded in the Withycombe Formation differs from equivalent stratigraphic sections globally with the exception of the Chapel Island Formation in Newfoundland, in which there are pyritic steinkerns of small shelly fossils in siliciclastic facies similar to that of the Withycombe assemblage. Equivalent Siberian sections contain phosphatic small shelly fossils preserved in carbonate facies (Rozanov & Missarzhevsky 1966; Rozanov *et al.* 1969; Zhuravleva *et al*. 1969) and equivalent sections in South China also reveal phosphatized small shelly fossils (Conway Morris & Chen 1992). In some cases, these small shelly fossils are described as being “over-phosphatized”, resulting in a loss of preservational detail (Conway Morris & Chen 1992) unlike the well-preserved fossils of the Withycombe Formation.

The pyritization in the Withycombe Formation, not unlike the pyritization recorded in uppermost Ediacaran strata, was responsible for preservational detail, providing valuable insights into a spectrum of paleobiological questions. The Cambrian explosion is an event recognized exclusively from the fossil record, so it is imperative that the processes responsible for fossilization be well understood, as understanding the small shelly fauna is pivotal in understanding the evolution of the main groups of marine invertebrates and especially the overall pattern of early Cambrian evolution as a whole.

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Chapter 4

Pyritized microbial filaments from the Withycombe Formation, Cambrian Stage 2 of Oxfordshire, UK

Pyritized filaments from the Cambrian Stage 2 Withycombe Formation, Oxfordshire, UK

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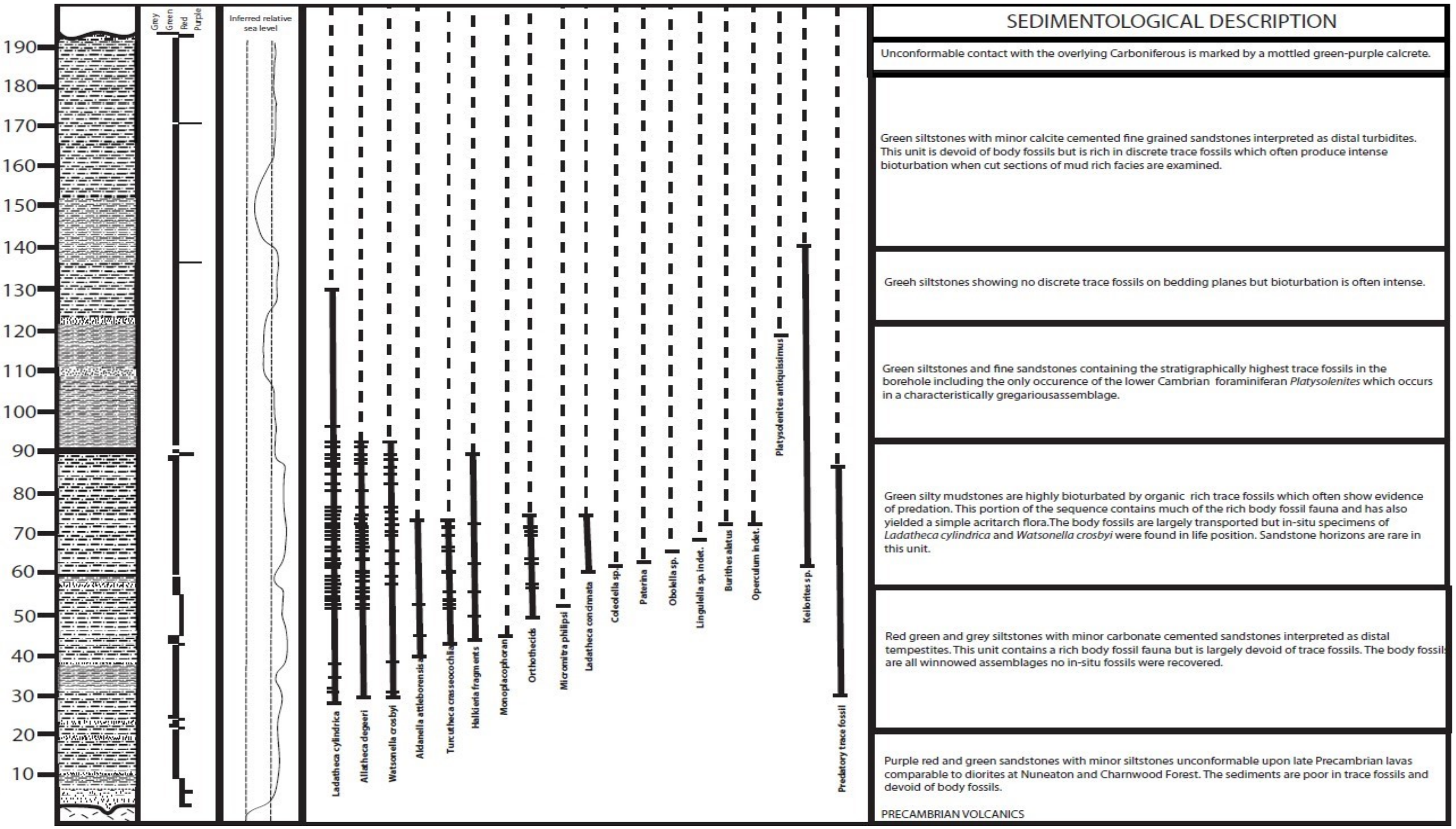
Abstract

The Withycombe Formation of Oxfordshire sub-crop represents the lowermost Cambrian of Central England. The pre-trilobitic lower Cambrian of the Withycombe Formation is a 194 m thick siliciclastic succession dominated by fossiliferous interbedded offshore red-purple and green pyritic mudstone with minor sandstone. Micro-CT scanning of a part of the core reveals filaments of possible giant sulfur bacteria, which invite comparison to the family of giant sulfur bacteria *Beggiatoaceae.* Herein, we investigate the origin of the filamentous structures and consider the validity of this comparison.

4.1 Introduction

The early Cambrian was a time of rapid evolution and marks a profound change in life on Earth. Assemblages of mineralized filaments and tubes in ancient rocks are considered in some studies to be fossil microbes, and in others as trace fossils. Although recent studies suggest that assemblages of mineralized tubular structures represent some of the oldest body fossils (Dodd *et al.* 2017), including the oldest fungi (Bentson *et al.* 2017), and the best analogues for fossils that might form in the basaltic Martian subsurface (Hoffman *et al.* 2000; Hoffman *et al.* 2008; Onstott *et al.* 2019), proving their biogenicity is challenging and their biogenic origin has been heavily debated (Brocks *et al*. 1999; Brasier *et al.* 2015; Nutman *et al*. 2016; Dodd *et al.* 2017; Schopf *et al*. 2018). Following the work of Schopf & Walter (1983) and Buick (1990), the key criteria for the interpretation of fossil bacteria are (1) the proposed fossil must be biogenic; (2) the proposed fossil must be indigenous to the host sediment; and (3) the proposed fossil must occur in an environment consistent with the presence of such bacteria. The most controversial of the criteria is the question of its biogenicity. Biogenic origin can be determined by "size, shape, cellular complexity (e.g., cell division) and organization (e.g., association of cells enclosed in a sheath, as is common in cyanobacteria), and colonial distribution" (Westall, 1999). Many authors agree that morphological indicators are too presumptuous and do not provide enough evidence to support the biogenicity of some of the world's oldest putative fossils. Therefore, one should not accept a feature as biogenic without critical analysis and rejection of alternative non-biological hypotheses (Brasier *et al.* 2006). In recent years analytical techniques have been employed to study various biosignatures in an effort to confirm the biogenicity of putative fossils. These include Raman Spectroscopy, X-ray Diffraction, X-ray Tomography, Electron Microscopy, nanoscale secondary ion mass spectrometry (Nano SIMS), as well as synchrotron light (Callefo *et al.* 2019).

Micro CT scans from a study of the Withycombe Formation revealed pyritized filaments that invite comparison with the *Thioploca* and *Beggiatoa* sulfur bacterium. This comparison and the biogenicity of the filaments are discussed herein. The Withycombe Formation pyritized filaments come from a succession of offshore sandstone and mudstone, deposited below the storm wave base (**Fig. 4.1; Chapter 1, 2**). The succession lies unconformably upon weathered, altered basaltic lavas of the Precambrian Midlands Microcraton (Wills & Shotton 1934, Brasier *et al*. 1978, Brasier 1992b, McIlroy *et al.* 1998; McIlroy & Horak 2006).



SEDIMENTOLOGICAL DESCRIPTION

Unconformable contact with the overlying Carboniferous is marked by a mottled green-purple calcrete.

Green siltstones with minor calcite cemented fine grained sandstones interpreted as distal turbidites. This unit is devoid of body fossils but is rich in discrete trace fossils which often produce intense bioturbation when cut sections of mud rich facies are examined.

Greeh siltstones showing no discrete trace fossils on bedding planes but bioturbation is often intense.

Green siltstones and fine sandstones containing the stratigraphically highest trace fossils in the borehole including the only occurence of the lower Cambrian foraminiferan *Platysolenites* which occurs in a characteristically gregariousassemblage.

Green silty mudstones are highly bioturbated by organic rich trace fossils which often show evidence of predation. This portion of the sequence contains much of the rich body fossil fauna and has also yielded a simple acritarch flora.The body fossils are largely transported but in-situ specimens of *Ladatheca cylindrica* and *Watsonella crosbyi* were found in life position. Sandstone horizons are rare in this unit.

Red green and grey siltstones with minor carbonate cemented sandstones interpreted as distal tempestites. This unit contains a rich body fossil fauna but is largely devoid of trace fossils. The body fossils are all winnowed assemblages no in-situ fossils were recovered.

Purple red and green sandstones with minor siltstones unconformable upon late Precambrian lavas comparable to diorites at Nuneaton and Charnwood Forest. The sediments are poor in trace fossils and devoid of body fossils.

PRECAMBRIAN VOLCANICS

Figure 4.1. Sedimentological descriptions and stratigraphic distribution and ranges of taxa.

Initial investigation of the fauna of the Withycombe Formation suggested that the succession was Silurian, and possibly part of an unusual nearshore facies (Poole 1978). However, reinvestigation of the Withycombe Formation pyritized biota (Chapter 3) shows it is consistent with a Cambrian Stage 2 age (Rushton & Molyneux 1990; Conway Morris *et al.* 1998; Chapter 2). During 3D micro-CT scanning of hyolithid specimens, it was discovered that the sedimentary succession is rich in pyritized filamentous structures. The pyritization of the Withycombe Formation probably occurred during early diagenesis in a shallow burial, iron-rich, anoxic pore water environment, as indicated by sulfur isotopic analysis, which revealed highly negative δ34S consistent with open system microbial sulfate reduction (Chapter 3). Based on this environmental interpretation, we postulate that these filamentous structures are the sheaths of giant sulfur bacteria.

4.2 Materials and Methods

Our samples were collected from the Withycombe Farm Borehole, which is housed at the British Geological Survey in Keyworth, UK. These samples were selected for micro-CT scanning using a Nikon XT H 225 ST computed tomography system at the University of Bristol Life Sciences Facility. The technique was used in order to examine the small shelly fossils contained within the core. Due to the pyritic preservation of the fossils, they exhibit a clear X-ray attenuation contrast in the CT images.

4.3 Filamentous Structures of the Withycombe Assemblage

As these filamentous structures were discovered fortuitously, material containing evidence of these filaments is currently scant. The descriptions herein are based on Micro CT scans of samples BDG 44 (55.5 m above base of log) and BDF 9977. The filamentous microbial structures discovered in the siltstone and mudstone of the Withycombe Formation are pyritized, cylindrical filaments exhibiting consistent width over the entire length of the filament, that cut sedimentary laminae, are relatively uncompressed, and thus appear to have been formed after deposition. The morphology of the filamentous structures is similar to the sheaths of the giant sulfur bacteria *Thioploca.* The average width of the pyritic filaments is ~150 μm and the average length is 4–5 cm **(Fig. 4.2)**. The majority of the filaments are isolated from nearby filaments and are preserved in a near-vertical position within the surrounding sediment layers, consistent with that of *Thioploca*.

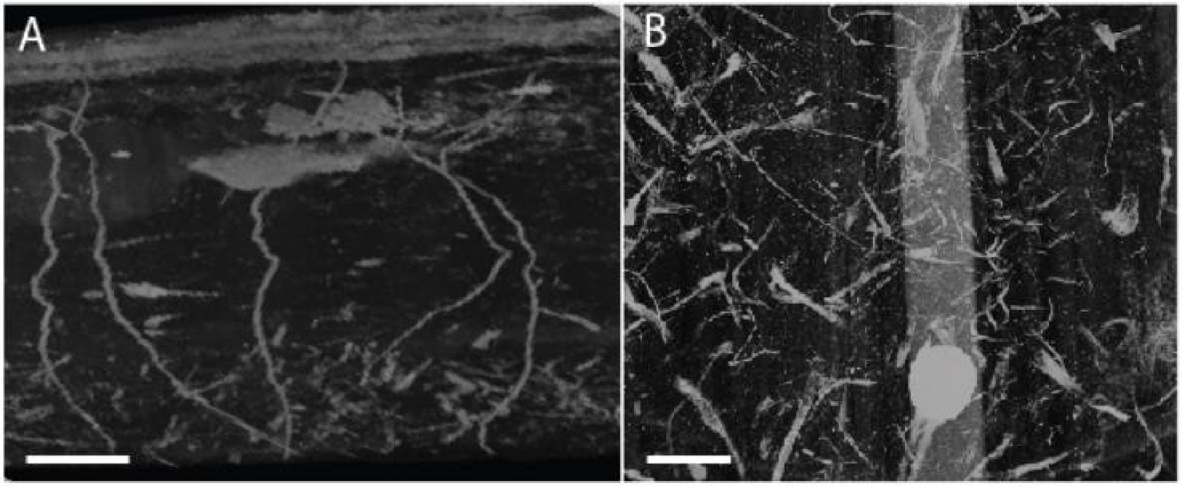


Figure 4.2. Micro-CT scans exhibiting pyritized microbial filamentous structures: a) Cross sectional view of sample BDF 9977, Withycombe Formation, UK; b) Plan view of sample BDG 44, Withycombe Formation, UK. Note: Light grey vertical stripe is an artifact from the CT-scan. Scale bars equivalent to 1cm.

4.4 Discussion

One possible interpretation of the pyritized filaments in the Withycombe Formation, based on gross morphological comparison with the modern sulfur bacterium *Thioploca* and *Beggiatoa,* is that they represent pyritized filaments of giant sulfur bacteria. A second theory is that these filaments could possibly be trace fossils, and a third possibility is that they are abiogenic in origin.

4.4.1 Fossil microbes and the genera *Thioploca* & *Beggiatoa*

The genera *Thioploca* and *Beggiatoa* are principally recognized on the basis of their filamentous morphology. Filament lengths range from a few µm to 10 cm, and the cell and filament diameter range between ~1–200 µm (Teske & Nelson 2006). *Beggiatoa* are described as being composed of colorless cells that are either disk-shaped or cylindrical, and arranged in long filaments (Teske & Nelson 2006). They are interpreted to be free-living motile organisms that live on top of sulphidic substrates such as sediment, bones, or decaying vegetation (Teske & Nelson 2006). *Thioploca* is a closely related genus of filamentous sulfur-oxidizing bacteria. It differs morphologically from *Beggiatoa* by one characteristic: *Thioploca* filaments occur in bundles surrounded by a common sheath, whereas *Beggiatoa* filaments occur as individual filaments (Teske and Nelson, 2006). They are anaerobic chemolithotrophs, meaning that they obtain their energy from the oxidation of inorganic compounds such as sedimentary sulfur (Teske & Nelson 2006). These filamentous sulfur oxidizers live within the sediment at oxic/anoxic interfaces where sulphide comes into contact with oxygen or nitrate in the overlying water column (Jørgensen & Revsbech, 1983a; Nelson *et al.* 1986b). *Thioploca* and *Beggiatoa* live in fresh, brackish, and marine water (Teske & Nelson 2006), and grow in a wide range of habitats including organic-rich, coastal marine settings (Jørgensen, 1977; Mussmann *et al.* 2003); hydrothermal vents (Jannasch *et al.* 1989b; Nelson *et al.* 1989c; Fig. 3); oxygen-depleted bays (Graco *et al.* 2001); salt marshes (Nelson *et al.* 1982b); natural and anthropogenic eutrophic, oxygen-depleted marine settings (Williams and Reimers, 1983; Kuever *et al.* 1996); geothermally active submarine caves (Mattison *et al.* 1998); cold sulfide seeps (Sassen *et al.* 1993); hydrocarbon seeps (Larkin *et al.* 1994); and sulfidic sediment above gas hydrates (Sahling *et al*. 2002).

Descriptive Palaeontology

Modern giant sulfur bacteria of the family *Beggiatoaceae* are colorless, filamentous, gliding bacteria consisting of disk-shaped or cylindrical cells (**Fig. 4.3**). Filament widths range from 1-200 µm (Jorgensen, 1977; Klas, 1937; Nelson *et al.* 1989b), but it is unclear whether the Beggiatoacea is monophyletic. These giant sulfur bacteria are commonly free living on top of sulfidic substrates, such as sediment, bones, or decaying vegetation (Salman *et al.* 2013).

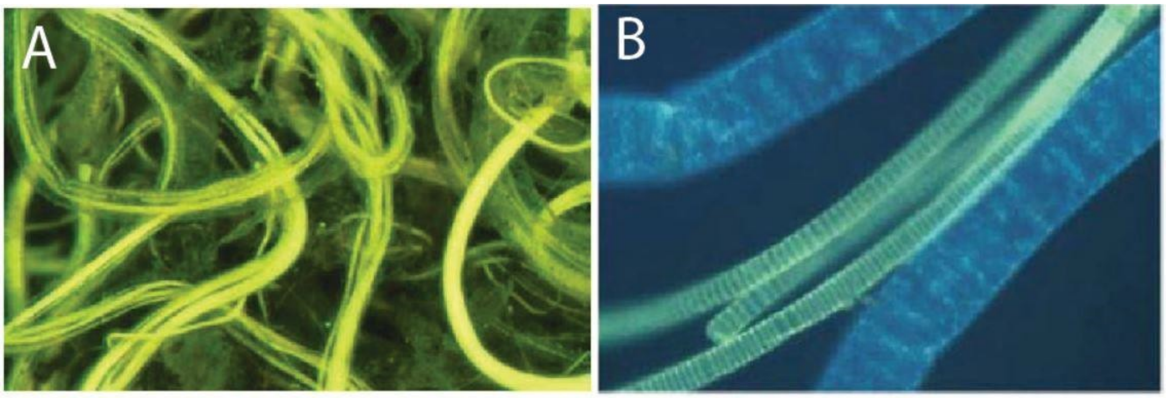


Figure 4.3 a) Rinsed *Thioploca* bundles from the Chilean Coast. The gelatinous, transparent sheaths harbor white *Thioploca* filaments (Teske and Nelson 2006; Fig. 4). b) Two *Beggiatoa* spp. from Guaymas under ultraviolet (UV) light. The larger species (ca. 100µm filament diameter) is fluorescing blue, the smaller species (ca. 35µm filament

diameter) yellow orange (Teske & Nelson 2006, Fig 8B).

The strata of the Withycombe Formation are interpreted to have been deposited in an offshore marine environment, which is favourable for giant sulfur bacteria, though it would appear that the fossils in this study were endogenic organisms rather than those living in mats. However, the size and morphology of the Withycombe filaments are consistent with that of *Thioploca* and *Beggiatoa*, and sulfur isotopic analysis of various samples of pyritized shells from the Withycombe Formation provided highly negative δ^{34}S values, which is consistent with open system microbial sulfate reduction (Chapter 3). The pyritization of the Withycombe Formation fossils likely occurred during very early diagenesis in a shallow burial, iron-rich, anoxic pore water environment. It is not unreasonable to postulate that such a porewater environment would be suitable for the growth of sulfur bacteria (Huettel *et al.* 1996). It is possible that the bacterial sheaths were preserved during vertical migration of the sulfur bacteria, perhaps in search of available nutrients, not too dissimilar from the behaviour of the sediment-dwelling sulfur bacterium *Thioploca* spp., which migrate vertically to overcome diffusion limitations (Huettel *et al.* 1996).

Although in cases it can be difficult to distinguish between fossil bacteria, trace fossils, and abiotic filaments, fossil bacterial filaments and tubes have been discovered in rocks of all ages. Precambrian examples have recently been presented as candidates for Earth's oldest fossils (Brasier *et al*. 2002; Dodd *et al*. 2017) and Earth's oldest fossil eukaryotes (Bengtson *et al*. 2017). In some sudies, carbonaceous matter and identifiable biopolymers that contain iron minerals within filaments are present (Ivarsson *et al.* 2012; Ivarsson *et al*. 2013) and provide non-morphological evidence to support the interpretation of their biogenicity (MacMahon, 2019). Unfortunately, such evidence is not always present.

4.4.2 Discriminating between fossil microbes and trace fossils

Despite there being convincing morphological similarities between the pyritized filaments of the Withycombe Formation and modern filamentous bacteria, and despite the existence of cases of fossilized bacterial filaments in various locations and in rocks of diverse ages globally, it could still be argued that these filaments are in fact trace fossils left behind by some form of thin vermiform organism. A study by Parry *et al.* (2017) describes three-dimensionally preserved traces ranging from 50 to 600 μ m in diameter, indicative of small-bodied, meiofaunal tracemakers from siltstones of the Ediacaran–Cambrian Tamengo and Guaicurus formations, Corumbá Group, central western Brazil. They suggest that the ichnofossils were created by a nematoid-like organism that moved through the sediment using an undulating locomotion (Parry *et al.* 2017). We do not have evidence to eliminate the possibility that the filamentous structures of the Withycombe Farm Borehole are trace fossils rather than bacterial filaments.

It is confirmed that the strata of the Withycombe Formation contain a diverse assemblage of trace fossils (Chapter 2). This includes bi-lobed horizontal traces devoid of internal structure and lacking lateral bevels, attributable to *Didymaulichnus lyelli* (Rouault, 1850); unlined vertical pipes of *Skolithos linearis* Haldemann, 1840; and horizontal, mud-lined tubes of *Palaeophycus*. Less common taxa include ?*Treptichnus triplex* Palij, 1976, a tri-lobed trace fossil showing alternate branching in a 'feather stitch' pattern; *Gordia ?meandria* Jiang, 1982, which is a looping trace that shows self-crossing, as well as two forms of the ichnogenus *Teichichnus* (Chapter 2). It is therefore the case that during deposition of the Withycombe Formation the sediment was appropriate for bioturbating organisms. The lack of skeletal fossil evidence for a possible predator in the Withycombe Farm Formation implies a soft-bodied animal that, from the morphology of the structures, would appear to be vermiform (Chapter 2).

We also must consider that filamentous bacteria such as *Thioploca* move within their sheaths. Perhaps it is possible that the original cells migrated out of their sheaths during life or decayed or oxidized away after death. It is therefore difficult to determine whether or not, without further evidence, these pyritized filaments are traces. The trace fossil *Trichichnus* (Frey 1970) is particularly interesting when assessing the pyritized filamentous structures of the Withycombe assemblage, as it is a commonly pyritized cylindrical structure reported from the Cambrian (Stachacz 2012) to the Holocene (Wetzl 1983). It is described as being branched or unbranched, straight to winding, mostly 0.1–0.7 mm in diameter, commonly pyritized, oriented at various angles (mostly vertical) with respect to the bedding (Kędzierski *et al.* 2017). *Trichichnus* is omnipresent in some fine-grained facies, and has been reported from both shallow- and deep- sea environments (Frey, 1970; Wetzel, 1983). It was previously interpreted as a deep-tier burrow formed by invertebrates (Kędzierski *et al.* 2017), but is now interpreted as being remnant of a fossilized intra-sediment bacterial mat burrow and is proposed as being an indicator of fossil bioelectric bacterial activity at the oxic–anoxic interface zone of marine sediment (Kędzierski *et al.* 2017). SEM studies and micro-CT analyses were completed on samples of *Trichichnus,* revealing different spatial organizations, density, diameters and shapes of the *Trichichnus*, which were reported to correspond to different parts of vertical system of *Thioploca* mats in sediment (Kędzierski *et al.* 2017). The pyritization of *Trichichnus* in the study is said to be related to sulfate-reducing bacteria (Kędzierski *et al.* 2017), like δ-proteobacteria *Desulfovibrio* spp., which can co-occur with sulfur-oxidizing bacteria, such as *Beggiatoa* or *Thioploca* (e.g., Jiang *et al*, 2012), and based on this and morphological comparisons, it is interpreted that *Trichichnus* is a trace fossil formed by *Thioploca*-like, mat forming, large sulfur bacteria (Kędzierski *et al.* 2017). Despite the endogenic nature of the Withycombe material, perhaps the pyritized filamentous structures of the present material are not too dissimilar from *Trichichnus* in that they could possibly be traces left behind by *Thioploca*-like sulfur bacteria.

Further evidence as a result of a more analytical approach is required to confirm or disprove that the filamentous structures of the Withycombe Formation are trace fossils.

4.4.3 Questioning the biogenicity of iron-mineralized filaments and tubes

Some authors question the biogenicity of some of the putative fossils interpreted as the Earth's earliest tubes and filaments, and postulate that they could in fact be abiotic microstructures (McMahon, 2019). Previous evidence to suggest that the filaments are biogenic is exclusively morphological. Studies have shown that abiotic processes can also produce very similar filaments. A study concluded that inorganic chemical reactions can morphologically, and compositionally similar, iron-mineralized filaments that were previously thought to be fossil microorganisms in diverse rocks of all ages (McMahon 2019).

McMahon (2019) ran an experiment involving the dissolution of a "seed" metal salt into an alkaline carbonate or silicate solution. This produced a pocket of acidic fluid, enclosed by a gelatinous membrane of hydrous metal carbonate or silicate together with metal (oxyhydr)oxides. This membrane pocket grew and eventually ruptured, due to the increase in internal pressure caused by an osmotic flow. This rupture caused an ejection of fluid, which was quickly enclosed by a new tube-like membrane. As this process continued, subsequent ruptures occurred, which generated further extensions of these tubes, yielding filaments with life-like morphologies (McMahon, 2019). Many of the diagnostic features that were previously used as evidence for a biological origin of these putative fossils including hollow circular cross-sections, branching, anastomosis, and nested geometries within 'sheaths', and these were all replicated by this experiment, proving that chemical gardening can result in biomorphs that exhibit the same morphological features that were previously proposed to establish biogenicity. Although chemical gardening is likely to occur in nature (McMahon, 2019), and such filamentous structures should not be assumed to represent fossil microbes without further corroborating evidence, it would be rash to conclude that chemical gardening was responsible for the production of all of the geologic assemblages containing these microstructures, which have previously been interpreted as fossil microbes. The study did however conclude that an abiotic origin must be "considered as a 'null hypothesis' to be rejected or not on a case-by-case basis depending on the evidence" (McMahon, 2019).

Other studies have even disproved the biogenicity of some of the world's oldest putative fossils, such as in the case of the self-organizing structures (SOS) of the carbonaceous Apex Chert (Brasier *et al.* 2002). This study concluded that the putative beggiatoan *Eoleptonema apex* (Schopf 1993) could be explained as a self-organizing structure resulting from the breaking of polygonal symmetry during crystal growth (Brasier *et al.* 2002). Some authors (Brasier *et al.* 2002) support the idea that the co-occurrence of biological morphology and carbonaceous chemistry in ancient, microfossil-like objects simply does not provide enough evidence to support a biogenic origin. They consider that in order to correctly comprehend the fossil record, it is essential to understand SOS and complexity as the majority of reports of early microfossils and stromatolites (e.g., Hoffmann et al. 1999) are not easily discernible from self-organizing structures (Brasier *et al*. 2006).

In most of the cases in which abiotic processes were proven responsible for the formation of these fossil-like structures, the material studied was either formed in, or influenced by, a hydrothermal environment (Brasier *et al*. 2002; Brasier *et al.* 2006; MacMahon 2019). In contrast to this, the Withycombe assemblage was deposited in a quiet offshore marine environment in which bioturbating organisms lived. Although chemical gardening and an abiotic origin in the case of the Withycombe filaments is possible, this explanation may not be as easily comparable or relevant due to the discrepancy in depositional history. Until further analysis and study are completed to validate this hypothesis, we postulate that these pyritized filamentous structures are most likely that ofgiant sulfur bacteria.

4.5 Conclusion

It is possible to distinguish fossil bacteria from non-biological biomorphs despite ambiguities associated with their interpretation. Such fossils have been identified in rocks of all ages from the early Archean to Recent despite the difficulties of proving biogenicity. Morphological evidence can be used in conjunction with corroborating evidence such as a suitable biological environment, when considering the biogenicity of potential fossils. Further biogeochemical analysis is, however, undoubtedly useful in confirming such biogenic origins.

Based on the scant evidence that has been discussed hitherto, we cannot preclude with certainty the possibility that these filamentous structures are traces or abiotic in nature, however, until evidence either way is produced, we surmise that the pyritized filamentous structures of the Withycombe Formation are most likely fossilized filaments of sulfur bacteria. This interpretation is based on morphological comparison with the modern bacterium *Thioploca* and *Beggiatoa*, in conjunction with the interpreted favourable depositional/biological environment. Due to the ambiguities that can ensue during the interpretation of fossil microorganisms, future work is recommended to determine the origin of the pyritized filamentous structures of the Withycombe Formation. Methods could potentially include a detailed study of the filament's internal texture, wall texture, and spatial arrangements, as well as C isotopic analysis and biomarker analysis.

4.6 References

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Chapter 5

Summary

5.1 Introduction

The early Cambrian was a time of rapid evolution and marks a profound change in life on Earth. Our understanding of the evolution of life during the earliest Cambrian has been vastly improved through excellent preservation in fossil sites worldwide, including parts of the former Avalon terrane of eastern Newfoundland and southern Britain. To provide a greater understanding of the earliest Cambrian (Fortunian and Cambrian Stage 2) of Avalonia, this project was devised to study the sedimentology and palaeontology of a section of the Withycombe Farm Borehole near Banbury, Oxfordshire, England. Through thorough description and logging of core samples, micro CT scanning, and petrographic studies, this thesis provides the first complete sedimentological and palaeontological description of the Withycombe Formation of Oxfordshire, which represents the lowermost Cambrian of Central England.

The importance of studying the Withycombe Formation stems from the presence of its diverse assemblage of its not-so-small shelly fossils and its intriguing pyritic preservation of the assemblage. The Withycombe Formation also contains a number of important index fossils, which enabled the assessment of the stratigraphy within the context of the lower Cambrian stratigraphic standards of southeastern Newfoundland. This project provides better stratigraphic constraints on the Withycombe Formation, helps to generate a better understanding of the phylogenetic placement of some of the fossils present, and provides a taphonomic model for the pyritization of these earliest shelled fossils.

5.2 Outcomes of Chapter 2

Core logging, petrographic studies, as well as micro-CT scanning enabled the study of the pyritized assemblage of with Withycombe Formation, and we conclude that it is a pre-trilobitic, lower Cambrian, siliciclastic succession that contains a hyolith- dominated small shelly fauna. Most common taxa include orthothecid hyoliths, hyolithid hyoliths, the rostroconch *Watsonella crosbyi*, early brachiopods, the foraminiferan *Platysolenites antiquissimus*, the coiled gastropod-like *Aldanella attleborensis,* halkieriids, gastropods and a low diversity ichnofauna including evidence of predation by a vagile infaunal predator.

Particularly interesting in the Withycombe assemblage is the possible presence of early brachiopods in the absence of trilobites. This brings into question the timing and evolutionary history of these early forms of brachiopod. There is no evidence of trilobites in the Withycombe Formation, yet it is possible lingulellids are present. The nearby Purely Shale Formation (lower Cambrian Stage 3) of Nuneaton is located within the same basin and is known to yield trilobites. Together these suggest that the Withycombe Formation is older, and it is more plausible that the Withycombe Formation preserved an early form of brachiopod. The lingulids at the Withycombe are preserved with a thin coating of pyrite. Perhaps these early brachiopods were chitinous rather than thick-walled and phosphatic.

The Withycombe assemblage also contains a number of important index fossils (*Watsonella crosbyi, Platysolenites antiquissimus,* and *Aldanella attleborensis*) that enabled correlation of strata around the base of the Cambrian Stage 2 within and between Avalonia and Baltica. Biostratigraphically, given the lack of palynological evidence, we suggest that the Withycombe Formation is contemporaneous with the lithologically similar Cuslett Formation of Southeastern Newfoundland, and we assign it to Cambrian Stage 2.

Micro-CT images were initially completed to study the macroscopic small shelly fossils present within the succession. These scans revealed the presence of pyritized filamentous structures that have not previously been described.

5.3 Outcomes of Chapter 3

Stable sulfur isotopic analyses were completed at the University of Western Australia to aid in the development of a taphonomic model for the pyritization of the Withycombe Farm Borehole assemblage. These analyses revealed that the taxa of the Withycombe Farm Borehole were preserved by several different modes of pyritization based on their original shell composition and degrees of compression. These styles of pyritization include shell replacement, pyritic compressions, and internal moulds. Sulfur isotopic analysis of the pyrite revealed highly negative δ^{34S} values with a range of mostly -20 to -23‰ for sample BDG 120 and a range of $\delta^{34}S$ = -3 to -11‰ for sample BDG 84.

These highly negative values are consistent with open system microbial sulfate reduction (sulfate replaced at the same rate in which reduction occurs). We therefore conclude that the pyritization of the Withycombe Formation likely occurred during early diagenesis in a shallow burial, iron-rich, anoxic pore water environment.

5.4 Outcomes of Chapter 4

It is possible to distinguish fossil bacteria from non-biological biomorphs despite the ambiguities associated with their interpretation. They have been identified in deposits of all ages from the Early Archean to Recent, despite the arduous nature of their interpretation. Morphological evidence can be used in conjunction with corroborating evidence such as a favourable biological environment, when considering the biogenicity of potential fossils. However, further biogeochemical analysis is unquestionably useful in confirming such biogenic origins.

The pyritized filamentous structures in the Withycombe Farm Borehole core are pyritized, cylindrical, microbial filaments exhibiting consistent width over the entire length of the filament and appear to have been formed after deposition. Morphologically, these filamentous structures are comparable to the giant sulfur bacterium *Thioploca* and *Beggiatoa.* The average width of the filaments is ~150 µm and the average length is 4-5 cm. Most of these filaments are individual, free-living filaments, preserved in a near-vertical position within the surrounding sediment layers, consistent with that of the *Thioploca* and *Beggiatoa*.

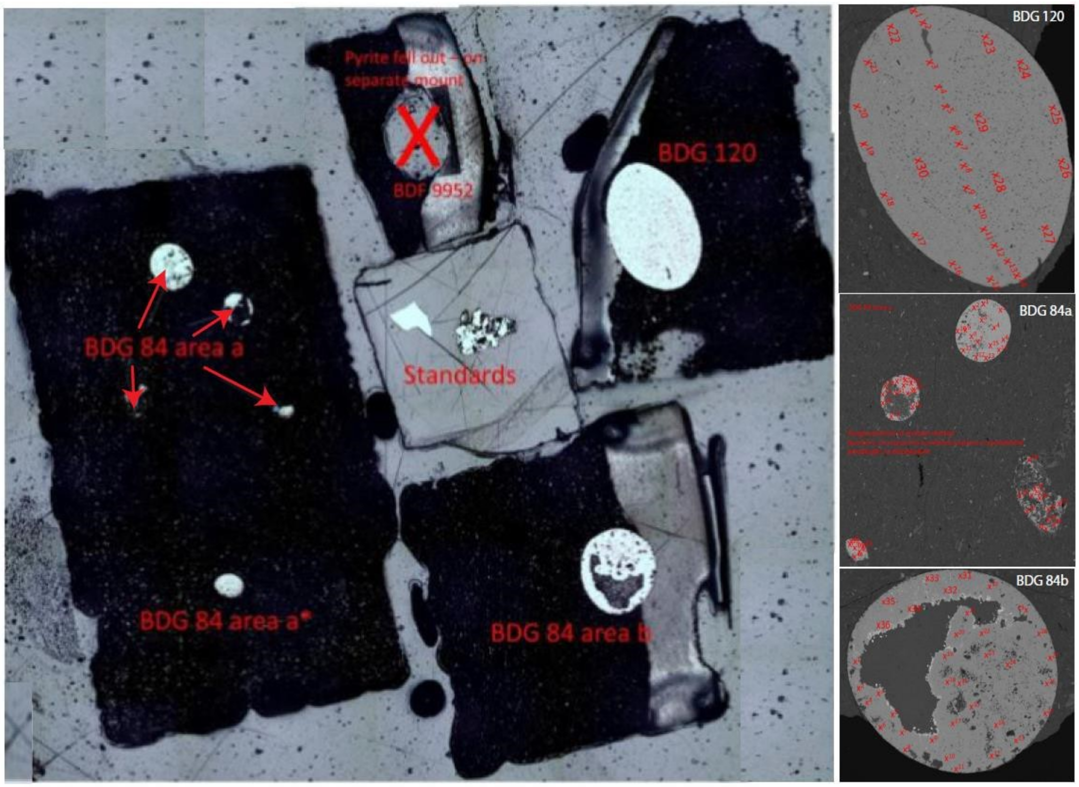
Due to the lack of evidence, we cannot exclude the possibility that these filamentous structures are traces or abiotic in nature however, until evidence to contradict this hypothesis is produced, we surmise that the pyritized filamentous structures of the Withycombe Formation are fossilized filaments of sulfur bacteria. This interpretation is based on morphological evidence comparable to the family of modern *Beggiatoaceae*, in conjunction with the interpreted favourable depositional/biological environment. Future work could be completed to further deduce the origin of the pyritized filamentous structures and to confirm their biogenicity, as the current conclusion is based solely on morphological substantiation. Methods could include a detailed study of the filament's internal texture, wall texture, spatial arrangements, as well as possible Carbon isotopic analysis to further deduce their origin.

5.5 Concluding Statement

Our understanding of the evolution of life during the earliest Cambrian has been vastly improved through excellent preservation in various locations worldwide, including parts of the former Avalon terrane of eastern Newfoundland and southern Britain. This project provides a better understanding of the earliest Cambrian (Fortunian and Cambrian Stage 2) of Avalonia by studying the small and not-so-small shelly fossils of the Withycombe Formation. Identifying the fossils present, some of them rather enigmatic, and by understanding the taphonomic processes that occurred, we were able to better constrain the formation stratigraphically and assign the formation to the Cambrian stage 2. This study of the Withycombe Formation fills a gap in knowledge as it provides data from the only known section of the lowermost Cambrian strata in the UK. Understanding the small shelly fauna is pivotal in understanding the evolution of the main groups of marine invertebrates and especially the overall pattern of early Cambrian evolution.

Appendix A

Appendix 1

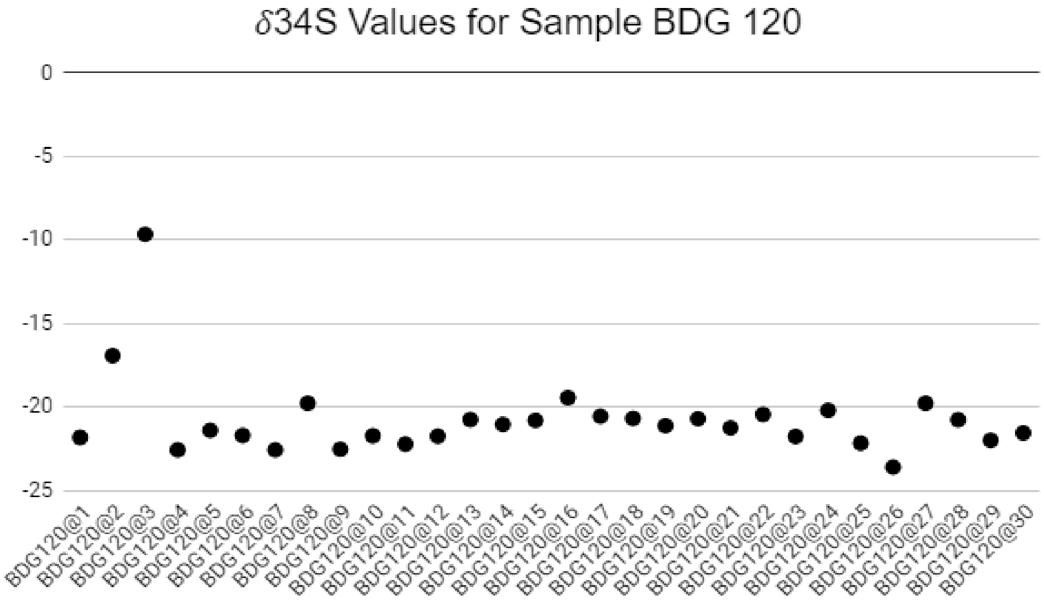


Mount demarcating positions of analyzed pyrite grains in samples BDG 84a, BDG 84b, BDG 120, and BDF9952.

Appendix 2

Analysis name (BDG120)	**δ34S**
3S-DWKP-FullMount-BDG120@1	-21.83
3S-DWKP-FullMount-BDG120@2	-16.93
3S-DWKP-FullMount-BDG120@3	-9.67
3S-DWKP-FullMount-BDG120@4	-22.57
3S-DWKP-FullMount-BDG120@5	-21.41
3S-DWKP-FullMount-BDG120@6	-21.71
3S-DWKP-FullMount-BDG120@7	-22.57
3S-DWKP-FullMount-BDG120@8	-19.78
3S-DWKP-FullMount-BDG120@9	-22.53
3S-DWKP-FullMount-BDG120@10	-21.73
3S-DWKP-FullMount-BDG120@11	-22.23
3S-DWKP-FullMount-BDG120@12	-21.75
3S-DWKP-FullMount-BDG120@13	-20.76
3S-DWKP-FullMount-BDG120@14	-21.05
3S-DWKP-FullMount-BDG120@15	-20.81
3S-DWKP-FullMount-BDG120@16	-19.45
3S-DWKP-FullMount-BDG120@17	-20.56
3S-DWKP-FullMount-BDG120@18	-20.69
3S-DWKP-FullMount-BDG120@19	-21.13
3S-DWKP-FullMount-BDG120@20	-20.71
3S-DWKP-FullMount-BDG120@21	-21.26
3S-DWKP-FullMount-BDG120@22	-20.45
3S-DWKP-FullMount-BDG120@23	-21.77
3S-DWKP-FullMount-BDG120@24	-20.2
3S-DWKP-FullMount-BDG120@25	-22.17
3S-DWKP-FullMount-BDG120@26	-23.61
3S-DWKP-FullMount-BDG120@27	-19.78
3S-DWKP-FullMount-BDG120@28	-20.77
3S-DWKP-FullMount-BDG120@29	-22
3S-DWKP-FullMount-BDG120@30	-21.56

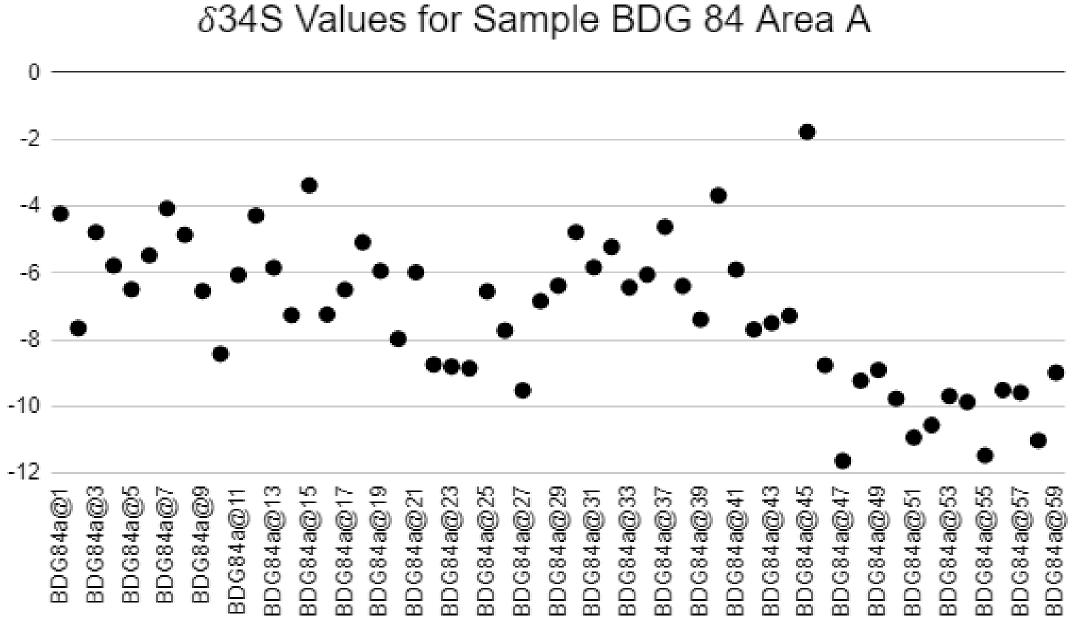
Table 1: δ34S results for sample BDG 120. The poor/suspect data is highlighted in blue.



Graph 1: δ34S results for sample BDG 120

Analysis name (BDG84a)	**δ34S**	**Analysis Name (BDG84a)**	**δ34S**
3S-DWKP-FullMount-BDG84a@1	-4.23	3S-DWKP-FullMount-BDG84a@30	-4.78
3S-DWKP-FullMount-BDG84a@2	-7.65	3S-DWKP-FullMount-BDG84a@31	-5.83
3S-DWKP-FullMount-BDG84a@3	-4.78	3S-DWKP-FullMount-BDG84a@32	-5.22
3S-DWKP-FullMount-BDG84a@4	-5.78	3S-DWKP-FullMount-BDG84a@33	-6.43
3S-DWKP-FullMount-BDG84a@5	-6.49	3S-DWKP-FullMount-BDG84a@34	-6.05
3S-DWKP-FullMount-BDG84a@6	-5.47	3S-DWKP-FullMount-BDG84a@37	-4.62
3S-DWKP-FullMount-BDG84a@7	-4.07	3S-DWKP-FullMount-BDG84a@38	-6.39
3S-DWKP-FullMount-BDG84a@8	-4.86	3S-DWKP-FullMount-BDG84a@39	-7.39
3S-DWKP-FullMount-BDG84a@9	-6.54	3S-DWKP-FullMount-BDG84a@40	-3.68
3S-DWKP-FullMount-BDG84a@10	-8.42	3S-DWKP-FullMount-BDG84a@41	-5.9
3S-DWKP-FullMount-BDG84a@11	-6.06	3S-DWKP-FullMount-BDG84a@42	-7.69
3S-DWKP-FullMount-BDG84a@12	-4.28	3S-DWKP-FullMount-BDG84a@43	-7.5
3S-DWKP-FullMount-BDG84a@13	-5.84	3S-DWKP-FullMount-BDG84a@44	-7.28
3S-DWKP-FullMount-BDG84a@14	-7.26	3S-DWKP-FullMount-BDG84a@45	-1.78
3S-DWKP-FullMount-BDG84a@15	-3.38	3S-DWKP-FullMount-BDG84a@46	-8.76
3S-DWKP-FullMount-BDG84a@16	-7.24	3S-DWKP-FullMount-BDG84a@47	-11.62
3S-DWKP-FullMount-BDG84a@17	-6.5	3S-DWKP-FullMount-BDG84a@48	-9.22
3S-DWKP-FullMount-BDG84a@18	-5.08	3S-DWKP-FullMount-BDG84a@49	-8.9
3S-DWKP-FullMount-BDG84a@19	-5.94	3S-DWKP-FullMount-BDG84a@50	-9.76
3S-DWKP-FullMount-BDG84a@20	-7.97	3S-DWKP-FullMount-BDG84a@51	-10.92
3S-DWKP-FullMount-BDG84a@21	-5.98	3S-DWKP-FullMount-BDG84a@52	-10.55
3S-DWKP-FullMount-BDG84a@22	-8.74	3S-DWKP-FullMount-BDG84a@53	-9.68
3S-DWKP-FullMount-BDG84a@23	-8.8	3S-DWKP-FullMount-BDG84a@54	-9.86
3S-DWKP-FullMount-BDG84a@24	-8.85	3S-DWKP-FullMount-BDG84a@55	-11.46
3S-DWKP-FullMount-BDG84a@25	-6.55	3S-DWKP-FullMount-BDG84a@56	-9.5
3S-DWKP-FullMount-BDG84a@26	-7.72	3S-DWKP-FullMount-BDG84a@57	-9.58
3S-DWKP-FullMount-BDG84a@27	-9.51	3S-DWKP-FullMount-BDG84a@58	-11.01
3S-DWKP-FullMount-BDG84a@28	-6.84	3S-DWKP-FullMount-BDG84a@59	-8.98
3S-DWKP-FullMount-BDG84a@29	-6.38		

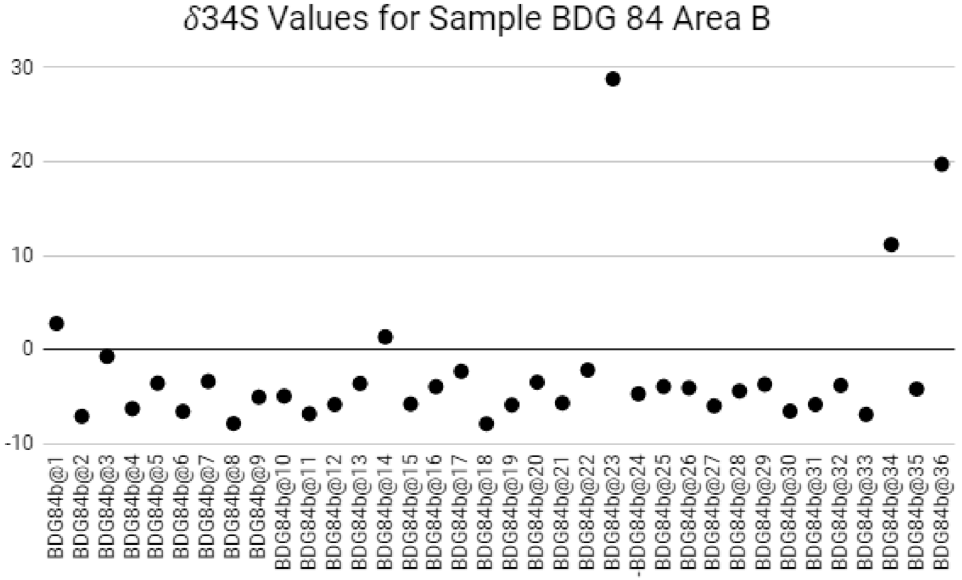
Table 2: δ34S results for sample BDG 84 area A.



Graph 2: δ34S results for sample BDG 84 area A.

Analysis name (BDG84b)	δ34S
3S-DWKP-FullMount-BDG84b@1	2.76
3S-DWKP-FullMount-BDG84b@2	-7.11
3S-DWKP-FullMount-BDG84b@3	-0.74
3S-DWKP-FullMount-BDG84b@4	-6.29
3S-DWKP-FullMount-BDG84b@5	-3.6
3S-DWKP-FullMount-BDG84b@6	-6.6
3S-DWKP-FullMount-BDG84b@7	-3.4
3S-DWKP-FullMount-BDG84b@8	-7.88
3S-DWKP-FullMount-BDG84b@9	-5.07
3S-DWKP-FullMount-BDG84b@10	-4.97
3S-DWKP-FullMount-BDG84b@11	-6.85
3S-DWKP-FullMount-BDG84b@12	-5.85
3S-DWKP-FullMount-BDG84b@13	-3.63
3S-DWKP-FullMount-BDG84b@14	1.33
3S-DWKP-FullMount-BDG84b@15	-5.8
3S-DWKP-FullMount-BDG84b@16	-3.96
3S-DWKP-FullMount-BDG84b@17	-2.33
3S-DWKP-FullMount-BDG84b@18	-7.91
3S-DWKP-FullMount-BDG84b@19	-5.9
3S-DWKP-FullMount-BDG84b@20	-3.49
3S-DWKP-FullMount-BDG84b@21	-5.7
3S-DWKP-FullMount-BDG84b@22	-2.19
3S-DWKP-FullMount-BDG84b@23	28.79
3S-DWKP-FullMount-BDG84b@24	-4.72
3S-DWKP-FullMount-BDG84b@25	-3.94
3S-DWKP-FullMount-BDG84b@26	-4.09
3S-DWKP-FullMount-BDG84b@27	-6
3S-DWKP-FullMount-BDG84b@28	-4.42
3S-DWKP-FullMount-BDG84b@29	-3.72
3S-DWKP-FullMount-BDG84b@30	-6.57
3S-DWKP-FullMount-BDG84b@31	-5.85
3S-DWKP-FullMount-BDG84b@32	-3.82
3S-DWKP-FullMount-BDG84b@33	-6.92
3S-DWKP-FullMount-BDG84b@34	11.17
3S-DWKP-FullMount-BDG84b@35	-4.21
3S-DWKP-FullMount-BDG84b@36	19.71

Table 3: δ34S results for sample BDG 84, area b. The poor/suspect data is highlighted in blue.



Graph 3: δ34S results for sample BDG 84, area b.