

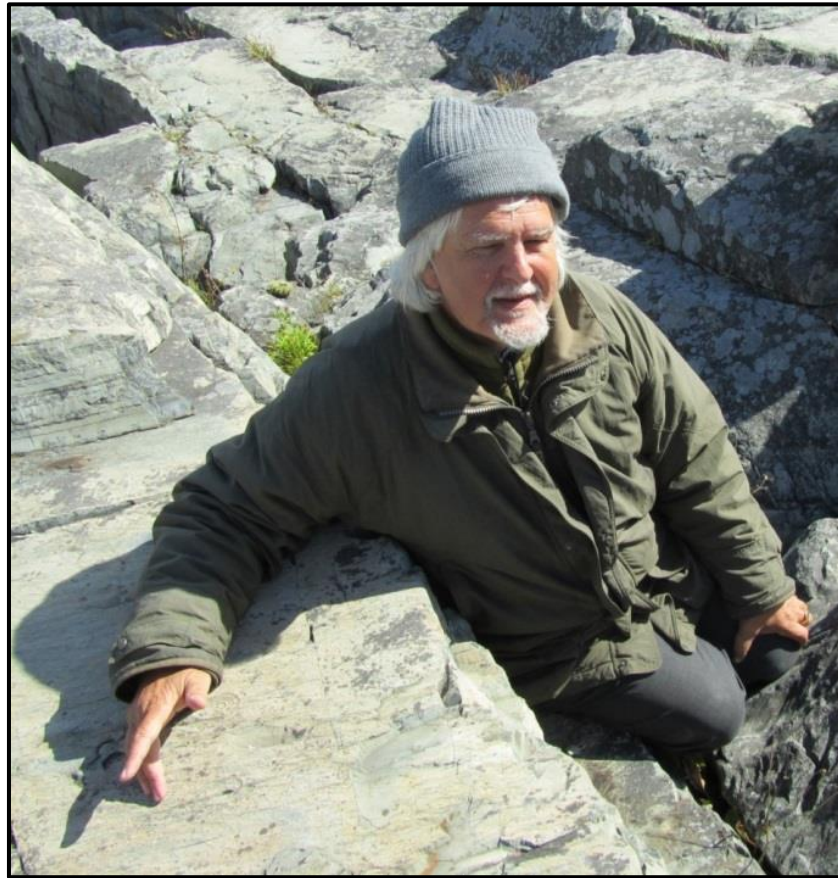
**EDIACARAN DISCOIDAL
IMPRESSIONS
AND RELATED STRUCTURES FROM
NEWFOUNDLAND, CANADA AND
THE LONG MYND, SHROPSHIRE, UK:
THEIR NATURE AND BIOGENICITY**

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*To the memory of Martin Brasier, who introduced me to these rocks,
but was not there to read my thesis.*

R.I.P.

Image: Professor Martin Brasier, on fieldwork, Upper Island Cove, Newfoundland.

Frontispiece: Left to right, *Charniodiscus*, Mistaken Point E surface, Newfoundland; cross-section through “Longmyndian *Medusinites*”, Long Mynd, UK; Discoidal impression on bed sole, Fermeuse Formation, Ferryland, Newfoundland; *Hiemalora*, Murphy’s Cove, Newfoundland.

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ABSTRACT

The nature of the Ediacaran macrobiota (c. 580-541 Ma) remains puzzling. These first assemblages of large, complex fossils may have included early animals; giant microbial forms; and organisms representing radically different body plans that went extinct. Discoidal impressions – some forming the base of Ediacaran fronds but most found as isolated discs – dominate the Ediacaran macrobiota. However round markings may also be formed in a variety of abiogenic ways. This study investigates the nature and biogenicity of discoidal impressions from two Ediacaran successions: the c. 560-Ma upper Burway Formation, Longmyndian Supergroup, Shropshire, UK; and several sites on the Bonavista and Avalon Peninsulas, Newfoundland, Canada, ranging in age from 565–c. 560 Ma.

The investigation involved fieldwork, photography, serial grinding through cross-sections, and optical and scanning electron microscopy. It concludes that several Longmyndian discoidal forms are pseudofossils formed by sediment injection resulting from small-scale fluid escape inferred to be driven by microbial mat sealing. Turning to clearly biogenic impressions, comparison of the varied morphologies of holdfast discs associated with fronds preserved under ash and sand from several Newfoundland sites leads to a generic model of their architecture as consisting of enclosed chambers, a complex construction perhaps for strength or possibly symbiosis. Detailed observations of the rayed disc *Hiemalora* suggest that it may have had an amoeboid lifestyle. Finally, the key Ediacaran taxon *Aspidella* is separated from the discs *Ediacaria* and *Spriggia*, with which it has been

synonymized, and interpreted as a possible polyp-like animal capable of limited movement. This thesis thus demonstrates that the earliest reported Ediacaran discoidal impressions are abiogenic, produced by mat-influenced processes particularly relevant to the Precambrian, and proposes models and interpretations for several key Ediacaran forms that have important implications for both the nature and diversity of the Ediacaran macrobiota, and early animal evolution.

EXTENDED ABSTRACT

The Ediacaran Period (635–541 Ma) represents a critical time for the evolution of life on Earth. Lying between the major glaciations of the Cryogenian Period, and the rapid radiations of modern phyla in the early Cambrian, the Ediacaran Period saw the rise of the first assemblages of large, complex biological forms – the enigmatic, soft-bodied Ediacaran macrobiota.

The nature of these Ediacaran organisms, known only from their impressions in sediment, remains unresolved, despite the discovery of Ediacaran fossil assemblages on almost every continent. They may have included early animals, or represented giant colonies of microbes, or a radically different body plan that was to disappear without trace. Whether a failed experiment or part of the “long fuse” of the Cambrian Explosion, interpretation of the Ediacaran biota is central to understanding the origins and evolution of complex life.

Much research has been conducted on the architectures of frondose Ediacaran forms such as *Charnia* and *Beothukis*, but relatively little attention has been paid to the discoidal impressions that dominate Ediacaran assemblages. Some form the bases of Ediacaran fronds, but most occur as isolated impressions. Preferentially preserved by being partially buried in sediment in life position, discoidal impressions, or “discs”, are the sole fossils on many Ediacaran bedding planes.

Interpreting discs is challenging, since round impressions may be formed in many ways, a number of them abiogenic, and the impressions have few characters. Variations of size and ornament have led to the naming of many discoidal taxa. Yet understanding the nature and variety of organisms represented by discoidal impressions is central to the interpretation of the Ediacaran biota. This study seeks to assess the biogenicity and shed light on the nature of discoidal impressions from two early Ediacaran assemblages – the Ediacaran succession of the Bonavista and Avalon Peninsulas of Newfoundland, Canada (~580–560 Ma); and the upper part of the Burway Formation of the Ediacaran Longmyndian Supergroup, Long Mynd, Shropshire, UK (~560 Ma).

The approach taken is one of critical assessment of the limited information available from discoidal impressions, with the null hypothesis of abiogenic possibilities at the forefront. The methods used have been primarily field observation and photography; systematic hand grinding of cross-sections of hand specimens using 16- μm carborundum powder; examination of surface features and polished cross-sections of hand specimens under the binocular microscope; study of petrographic thin sections; examination of surfaces with the scanning electron microscope (SEM); and element mapping using electron-dispersive X-ray analysis (SEM-EDX).

Establishing the biogenicity of simple discs forms an important component of the work. After introducing discs in the context of the Ediacaran biota, Chapter 1 therefore summarizes the variety of ways in which abiogenic discoidal impressions

may form, from weathering out of mineral grains to fluid escape, as well as the different biological causes, from microbial colonies to trace fossils. Key criteria for assessing the biogenicity of discs are enumerated. This introductory chapter concludes by setting out the aims of the thesis in the form of several specific questions to be explored in the following chapters.

Chapter 2 focuses on the discoidal impressions found in the Long Mynd, Shropshire, specifically those of the c. 560-Ma upper Burway Formation, which contains the greatest variety of such impressions in the Longmyndian Supergroup. Described by John Salter in 1856, and mentioned by Darwin in the *Origin of Species*, the biogenicity of these markings, found on the soles and tops of beds, has been debated for over a century. They have recently been regarded as biological, and described as *Medusinites* aff. *asteroides*, considered a possible trace fossil showing vertical movement through sediment; *Beltanelliformis brunsa* and *B. minutae*; and a form considered similar to *Intrites punctatus* Fedonkin. In the first part of the chapter, evidence from serial grinding is used to show that an unusual suite of mostly sub-millimetric sandstone features observed in cross-section in upper Burway Formation rocks represents small-scale fluid escape, interpreted as resulting from the sealing effect of microbial mat layers. The pattern of sandstone fills observed above and below Longmyndian *Medusinites*, *B. brunsa*, and *B. minutae* is explained as resulting from a combination of sediment injection and loading. All three discoidal impressions are thus demonstrated to be abiogenic, and the result of very small-scale fluid escape which, it is proposed, extends the recognized dynamic

influence of microbial mats on sediments. Fluid escape is well recognized as a process that can result in pustules and sand volcanoes on top surfaces. The model presented here shows that, under some conditions, related sediment injection and loading can also produce discoidal features on bed soles. This possibility is important for the interpretation of ancient discoidal specimens.

In the second part of Chapter 2, preliminary results from close examination of the microbial mats and filaments of the upper Burway Formation rocks are presented. The presence of mineralized microbial filaments in these rocks has previously been noted. Examination of petrographic thin sections and hand specimens ground parallel to bedding, visually and with SEM, together with SEM-EDX element mapping, leads to the conclusion that at least some of the mat-forming filaments are the calcified sheaths of cyanobacteria. Larger, iron-rich tubular filaments are also noted, as well as several different filament morphologies. There are also suggestions of a possible fungal component.

The third and final section of Chapter 2 returns to the remaining form of disc from the upper Burway Formation – that resembling *Intrites*. Serial grinding of cross-sections, together with examination of thin sections, reveals that these apparently simple, mostly incomplete, rings found on both soles and tops of beds have a torus structure with pale internal laminae and fine-grained sediment of unusual texture. They are also sometimes associated with fluid escape structures. A model is presented to explain Longmyndian *Intrites* as a form of torus-shaped

microstromatolite that has built up by trapping and binding of sediment, and precipitation of carbonate by cyanobacteria, on the raised topography of a small sediment volcano. Thus the final form of discoidal impression from the upper Burway Formation is shown to represent a new form of microbially induced sedimentary structure (MISS).

Having established the abiogenicity of the Longmyndian discs, and the microbial influence on their formation, Chapter 3 turns to discoidal impressions from Newfoundland that are clearly biological – the discs attached to the bases of Ediacaran fronds. Such discs are generally interpreted to be holdfasts that were partially buried in sediment. Features observed on holdfast discs, primarily those of *Charniodiscus*, preserved beneath ash and sand in several localities in the Bonavista and Avalon Peninsulas of eastern Newfoundland, and understood as capturing the morphologies of upper and lower surfaces, are interpreted as revealing glimpses of internal architecture. These observations are combined to construct a tentative generic model of the possible internal architecture of frond holdfasts. The model proposes a complex architecture for holdfasts, consisting of several envelopes, presumably enclosing chambers, surrounding the anchor of the frond. This complexity of structure implies that the discs at the base of Ediacaran fronds may have had functions other than simply operating as holdfasts. One possibility, it is proposed, is that the chambers may have housed microbial symbionts.

One discoidal impression that does not appear to conform to this pattern is the rayed disc *Hiemalora*, which forms the subject of Chapter 4. *Hiemalora* has been associated with the frond *Primocandelabrum*, as *Primocandelabrum hiemaloranum*. The nature of this cosmopolitan taxon with ray-like extensions from the disc edge has been under debate, with proposed possibilities for the rays including protoplasmic streams of giant xenophyophores, fungal hyphae, and roots or other structures used for osmotrophy. The relatively recent association of *Hiemalora* with a frond has led to its being perceived as a variant holdfast disc, and *Hiemalora* has come to be considered as forming a continuum with *Charniodiscus* discs, with which it often co-occurs. New observations are presented in this chapter of previously figured and new specimens of *Hiemalora* discs preserved under ash in rocks stratigraphically equivalent to the Mistaken Point and Fermeuse Formations in the Bonavista Peninsula, and under sand in the Fermeuse Formation of the Avalon Peninsula, Newfoundland. The nature of *Hiemalora* preservation is compared with that of co-occurring *Charniodiscus* discs, and it is concluded that *Hiemalora* is distinct from *Charniodiscus* and other holdfasts. *Hiemalora* is regularly preserved in all localities studied as a smooth, low-relief positive disc, and shows no signs of the internal architecture of several envelopes described in Chapter 3 for *Charniodiscus*. Differences are also noted between the basal connection of *Hiemalora* with its frond, and those of typical Ediacaran frondose organisms. The lack of *Hiemalora* discs with rays associated with fronds, beyond the holotype and two paratypes, and the presence of a feature that may represent the growth of a small frond from a rayed disc, leads to the suggestion that the frond may have been a temporary structure

that grew from the *Hiemalora* disc at a life stage when it lacked rays. Detailed views of *Hiemalora* rays from a cast of a well-preserved specimen are presented for the first time. These reveal several mergers and branchings of rays. Together, these observations are considered to point to a possible amoeboid lifestyle for *Hiemalora*, with *Primocandelabrum* as a temporary growth, perhaps associated with reproduction. It is proposed that *Hiemalora* may represent large-scale experimentation with the amoeboid way of life at the dawn of multicellularity.

Chapter 5 considers the nature and limits of *Aspidella terranovica* Billings 1872, which was the first-named Ediacaran body fossil. *Aspidella* is found amid several disc morphologies in the disc-rich outcrops of the Fermeuse Formation on the east coast of the Avalon Peninsula, Newfoundland. In the absence of any definitive fronds, it is not certain whether all or some of these discs were frond holdfasts, and how many types of organism are represented. Although the idiomorphic “Billings” form has a distinctive appearance, with a central furrow from which radiate fine grooves, as observed in positive hyporelief, it was synonymized in a major study in 2000 by Gehling et al. with two other co-occurring types of disc, described as *Ediacaria* and *Spriggia*, and by extension to a number of other similar Ediacaran discoidal forms. As a consequence, the name *Aspidella* has come to be applied to all holdfast discs by the majority of Ediacaran researchers.

A re-examination of the discs of the upper part of the Fermeuse Formation, which shows evidence of slumping and soft-sediment deformation, confirms that the

majority of discs appear to be biogenic, although occasional fluid escape features also occur. *Ediacaria* and *Spriggia* are re-assessed in the light of the model for holdfast architecture proposed in Chapter 3. It is concluded that both discs probably represent holdfasts, but that *Spriggia* captures the eroded tops of holdfasts, revealing the rings formed by the internal envelopes. An examination of idiomorphic *Aspidella* (the form with morphology as originally described by Billings) leads to the conclusion that it represents a separate organism from *Ediacaria* and *Spriggia*. Another discoidal impression from the Fermeuse Formation, the three-lobed form *Triforillonia costellae*, is found to be limited to a few bedding planes in a narrow geographical area of <2 km. Comparison of *Triforillonia* with distorted forms of *Aspidella* found on the same bedding planes leads to the suggestion that *Triforillonia* may not be a separate taxon but a transient variant of *Aspidella*, possibly even a diseased population.

In the final section of Chapter 5, consideration of a range of basal impressions found in close association and regarded as *Aspidella* leads to the suggestion that the *Aspidella*-making organism had a highly flexible base. The morphologies of these impressions are compared with the flexible physa of modern Actiniaria, and it is suggested that the *Aspidella*-making organism may have been a polyp-like form capable of limited muscular movement through sediment. In the second part of this section, evidence is presented for small horizontal trails and vertical equilibrating traces directly associated with *Aspidella*. If the interpretation is correct, the latter represent the earliest vertical traces currently known. It is proposed that *Aspidella*

may have been a polyp-like form of cnidarian grade, an early animal living among the Ediacaran biota.

The final chapter returns to the questions posed at the start of this study, and summarizes the progress made towards answering them.

The aim of this study was to investigate the nature and biogenicity of Ediacaran discoidal impressions and related structures from the Long Mynd and several sites in Newfoundland. It has led to the demonstration that the discoidal markings of the upper Burway Formation of the Longmyndian Supergroup are abiogenic, with the identification of a new way in which microbial mats may dynamically influence sediments, resulting in pseudofossils on bed soles. Investigation of the decidedly biological discs of Newfoundland has led to a new model for disc architecture, a re-assessment of the nature of the rayed disc *Hiemalora*, and a proposed delimiting of the key Ediacaran taxon *Aspidella*, with evidence presented suggesting that *Aspidella* may have been a simple polyp-like animal capable of limited muscular movement. In spite of the challenges of interpreting discoidal impressions, it is shown that their study can bring new insights that will help to elucidate the nature of life in the early stages of the build-up to the Cambrian Explosion.

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CHAPTER 1

INTRODUCTION

1.1 THE EDIACARAN BIOTA AND ITS DISCS

1.1.1 The continuing puzzle of the Ediacaran impressions

The Ediacaran biota, which flourished from *c.* 580-541 Ma, remains deeply enigmatic. In spite of assemblages of well-preserved impressions found on almost every continent (see e.g. Fedonkin et al., 2007), the affinities of the Ediacaran organisms are unclear (Brasier and Antcliffe, 2004). Since the first descriptions by Sprigg (Sprigg, 1947, 1949), interpretations of Ediacaran macrofossils have ranged from sponges and cnidarians (e.g. Glaessner and Wade, 1966; Wade, 1972; Glaessner, 1984; Gehling, 1988; Gehling and Rigby, 1996; Sperling et al., 2010; Liu et al., 2014; Droser and Gehling, 2015), ctenophores (Tang et al., 2011), early molluscs (Fendonkin and Waggoner, 1997; Gehling et al., 2014), giant xenophyophores (Seilacher et al., 2003), fungi (Peterson et al., 2003), and lichens (Retallack, 1994), to a failed evolutionary experiment of “pneu” constructions unconnected with modern phyla (Seilacher, 1989). Among microfossils, the interpretation of exceptionally preserved globular forms from the *c.* 570 Ma Doushantuo assemblage as animal embryos (Xiao and Knoll, 2000) has been questioned by some (Bailey et al., 2007; but see Cunningham et al., 2012; Chen et al., 2014). Many of the typical Ediacaran macrofossils, in particular the rangeomorphs, are thought to have been benthic, sessile organisms (e.g. Narbonne, 2005), although trace fossils are also known from

Ediacaran successions (Jensen et al., 2005, 2006; Liu et al., 2010; Rogov et al., 2012, but see also Brasier et al., 2013a).

Ediacaran fossils, first found almost immediately after the Gaskiers glaciation, which ended *c.* 580 Ma (Bowring et al., 2003), matter because they provide a window on evolution during a key period in the history of life (Fig. 1.1). They are the first major assemblages of macrofossils, potentially including the earliest animals that, by molecular clock estimates, may have emerged in the Cryogenian, by *c.* 800 Ma (Erwin et al., 2011). Fossil evidence for probable bilaterian animals dates back to about 555 Ma, although the major radiation of the Bilateria appears to have occurred only from the early Cambrian onwards (see e.g. Budd and Jensen, 2000; Peterson et al., 2008; Erwin et al., 2011; Gehling et al., 2014). The Ediacaran Period (635-541 Ma) may represent a time during which critical gene regulatory networks were being laid down that would, in combination with environmental changes and new ecological opportunities, eventually allow the Cambrian Explosion (Davidson and Erwin, 2006; Erwin et al., 2011). Although some forms may have been simple metazoans (Liu et al., 2014), many of the typical Ediacaran forms defy easy shoehorning into familiar metazoan taxa (Antcliffe and Brasier, 2007), and by the early Cambrian Period they disappear from the fossil record, perhaps as a result of the activities of the rapidly radiating metazoans (see e.g. Brasier, 1989; Seilacher, 1989; McIlroy and Logan, 1999; Laflamme et al., 2013).

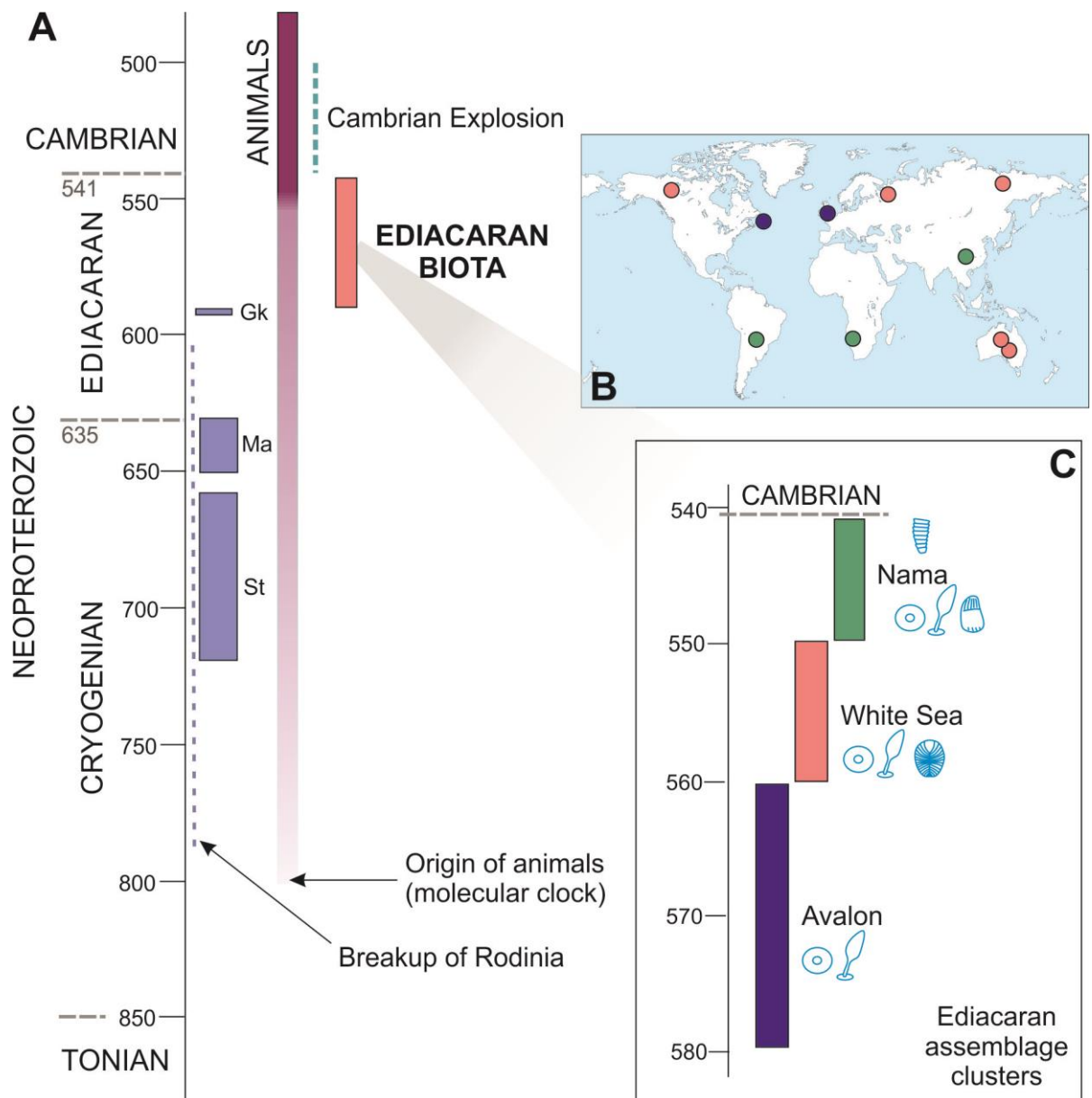


Fig. 1.1. The Ediacaran biota: a pictorial summary of its range and context. **A:** Range of the Ediacaran biota, extending from the end of the Gaskiers glaciation (Gk) to the Ediacaran–Cambrian boundary, in the context of the origin of animals according to latest molecular clock estimates, by *c.* 800 Ma (Erwin et al., 2011); the Cambrian Explosion; the major glaciations of the Cryogenian (Ma = Marinoan; St = Sturtian); and the breakup of the supercontinent of Rodinia. (Ranges of glaciations are uncertain, and the Sturtian may have consisted of several discrete episodes; the ranges shown are broadly based on those illustrated in Mills and Canfield (2014).) **B:** Some of the major Ediacaran fossil localities (circles, colour coded by assemblage clusters in C). **C:** Ranges of the three major clusters of Ediacaran fossil assemblages obtained from Parsimony Analysis of Endemism (Waggoner, 2003): Avalon (mainly England, Newfoundland); White Sea (mainly Russia, Siberia, Ukraine, Australia); and Nama (mainly Namibia, S. China). Frondose taxa and discoidal impressions are found across the entire range. The White Sea assemblages have the greatest diversity of taxa (Shen et al., 2008), including forms such as *Dickinsonia*, *Kimberella*, and *Tribrachidium*. The rather less diverse Nama cluster includes sack-like forms such as *Ernieetta*. Close to the Cambrian boundary, biomineralized forms such as *Cloudina* occur.

Although forms of striking architecture such as *Dickinsonia* and *Charnia* tend to be the focus of most interest in the Ediacaran biota, the majority of Ediacaran body fossils are discoidal impressions. While some discs are found at the base of fronds, the great majority are isolated. To understand the nature and diversity of the Ediacaran biota as a whole, it is essential to decode the much neglected Ediacaran discs.

1.1.2 Tackling the Ediacaran enigma: thesis objectives

The characteristic morphologies and fractal construction of rangeomorphs have allowed exploration of growth patterns and suggested possible lifestyles (Antcliffe and Brasier, 2007, 2008; Laflamme et al., 2009; Hoyal Cuthill and Conway Morris, 2014). By contrast, discoidal impressions have been relatively little studied, although a large number of discs have been described (MacGabhann, 2007). This is perhaps not surprising given the challenges of interpreting such simple forms. The aim of this thesis is to seek to rectify this imbalance by the application of critical observation, inference, and deduction to discoidal forms in the Ediacaran successions of Newfoundland and the Long Mynd, England, in order to ascertain their nature.

Unlike frondose impressions, even the biogenicity of isolated discs, which form the majority, may be far from evident. They have few characters. Statistical analyses attempted on discs have been reliant on assumptions regarding the number of different types of discoidal taxa represented, which characters are intrinsic versus

taphonomic, and even their biogenicity (e.g. Gehling et al., 2000; Peterson et al., 2003; Burzynski and Narbonne, 2014). The methodological approach taken here has been to apply the null hypothesis: to consider biogenicity first; to be cautious with inference while keeping all plausible possibilities open; and to interpret biological forms as being the simplest possible grade that would be consistent with the evidence. By this means, it is hoped that some progress will be made in interpreting the nature of several types of discs that will provide insights into early evolution, and establish a robust basis for future quantitative approaches.

The main methods used, in addition to visual examination in the field and under the microscope, have been serial cross-sectioning and hand grinding; petrographic studies of thin sections; and elemental analysis using SEM-EDX (JEOL JSM-840A SEM with Oxford Instruments Isis 300 EDX system).

The bedding surfaces of the localities discussed here, both in Newfoundland and the UK, have suffered tectonic distortion. Depending on the amount of strain, originally circular forms would be distorted into ellipses, and the angles of felled fronds need to be adjusted to allow for deflection from the original (see e.g. Wood et al., 2003; Ramsay, 1967). It has become commonplace to retro-deform discs on the assumption that they must all have originally been holdfasts and inevitably circular (see e.g. Hofmann et al., 2008). However, such an assumption is often not justified. As will be discussed in Chapters 4 and 5, it is not necessarily the case that all discs are holdfasts, and holdfast discs may co-occur with other forms. Moreover, the

extent of tectonic deformation can vary greatly across bedding planes. The pitfalls of retrodeformation have recently been highlighted by Brasier and Antcliffe (2009) and Liu et al. (2011). Therefore, images in this thesis have not been retro-deformed.

Based on the study of discs in the Avalon and Bonavista Peninsulas of Newfoundland, Canada and the upper Burway Formation of the Longmyndian Supergroup, UK, the thesis poses and seeks to answer the following questions:

- a) What is the nature of the first described Ediacaran fossils, observed by John Salter (Salter, 1856, 1857) in the upper Burway Formation of the Longmyndian Supergroup, UK? The biogenicity of these simple discoidal forms has been debated ever since (Callow et al., 2011b). (Chapter 2)
- b) Turning to obviously biogenic holdfast discs of fronds, commonly termed *Aspidella*, what can we deduce about their construction, and thereby infer about their function? (Chapter 3)
- c) The rayed disc *Hiemalora* does not appear to fit with the holdfast discs discussed in Chapter 3. What is the nature of *Hiemalora*, and what is its relationship - if any - to non-rayed holdfast discs? (Chapter 4)
- d) The disc-dominated Fermeuse Formation of the Avalon Peninsula, Newfoundland, Canada exhibits evidence of slumping and soft-sediment deformation (Gehling et al., 2000; Wood et al., 2003). Are some of its discs abiogenic? Two discoidal taxa that occur here - *Ediacaria* and *Spriggia* - have been synonymized with the other contemporary disc in the Fermeuse

Formation, the first-named Ediacaran body fossil, *Aspidella terranovica* Billings, by Gehling et al. (2000). All three taxa are currently regarded as holdfasts of fronds. Are *Ediacaria* and *Spriggia* in fact “taphomorphs” of Billings-type *Aspidella*? If not, what is the relationship between them? If Billings-type *Aspidella* is a distinct form, what is its nature? (Chapter 5)

1.1.3 The challenge of the discs

The term “disc” or “discoidal impression” is used here in a broad sense to include circular to highly elliptical forms that may be flat to high relief; preserved as casts or moulds, in epirelief or hyporelief; with or without protuberances and ray-like extensions; and a variety of ornamentation such as radial or concentric markings, or none.

While some Ediacaran discoidal forms have distinctive morphological characters and ornamentation, many are relatively simple mounds or annulated discs. Given the possible variation in modes of preservation, and varying levels of compaction, depending on the lithology of the impression-bearing beds and their context, as well as natural biological variation, and the possibility of differing juvenile and adult forms, the identification of distinct taxa among discoidal forms is highly challenging.

Partly as a consequence of the difficulty in differentiating taphomorphs from biological form, a plethora of discoidal taxa have been described, particularly from

the relatively diverse Ediacaran assemblages of the Russian White Sea coast and from Australia (Amadeus Basin and Ediacara Hills), but their taxonomic status and evolutionary/biological inter-relationships have been much debated. Some taxa have come to be recognized as synonymous, with morphological variations such as marginal creasing and relative relief resulting from differences in styles of preservation. An example is the proposed synonymization of *Beltanelliformis brunsa* Menner 1974 (Keller et al., 1974) and *Nemiana simplex* Paliy 1976 as preservational variants by Narbonne and Hofmann (1987). Another is the synonymization by Gehling et al. (2000) of *Aspidella terranovica* Billings with discoidal forms described as *Ediacaria* (Sprigg, 1947) and *Spriggia* (originally *Madigania*; Sprigg, 1949), mentioned above and discussed in Chapter 5. The majority of named discs can be classified as variants within four broad categories based on morphology, leaving a handful of exceptions (Tables 1.1, 1.2).

The challenges to understanding the discoidal Ediacaran taxa are not limited to establishing their taxonomic status and inter-relationships. The biogenicity of some simple discs has been questioned, for example specimens of *Nimbia occlusa* Fedonkin, 1981 (Fendonkin, 1981) described from below glacial diamictites in the Mackenzie Mountains, North West Canada (the “Twitya” discs; Hofmann et al., 1990; see e.g. Dornbos, 2003). The question of disc biogenicity extends beyond the Ediacaran, to the nature of far older discoidal impressions, such as those from the c. 1.8 Ga Sterling biota of south-western Australia (Cruse et al., 1993; Cruse and


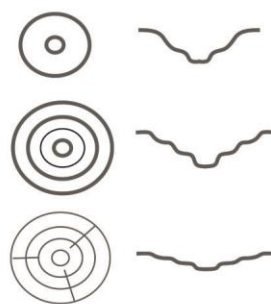
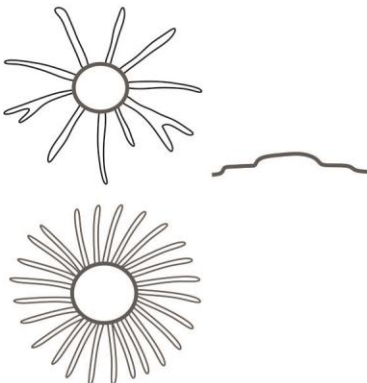
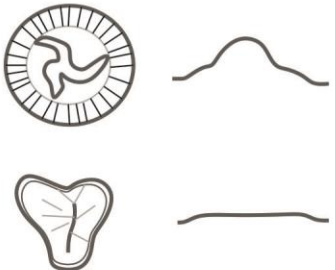
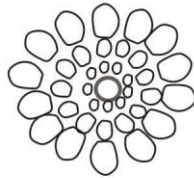
Character	Description	Example taxa
<p>1. Simple discs</p> 	<p>Simple round forms, flat or high-relief, egg-like mounds. Some with fine edging rings or crinkled appearance</p>	<p><i>Nimbia</i> <i>Nemiana</i> <i>Beltanelliformis</i> <i>Chuaria</i></p>
<p>2. Annulated discs with central boss/depression</p> 	<p>Discs of varying relief with central mound or depression, one or several concentric rings, and sometimes showing radial markings. Some show central invagination/ridge</p>	<p><i>Medusinites</i> Longmyndian <i>Intrites</i> <i>Ediacaria</i> <i>Spriggia</i> <i>Cyclomedusa</i> <i>Tirasiana</i> <i>Irridinitus</i></p>
<p>3. Rayed discs</p> 	<p>Low-relief discs with rays, some showing branching, or dense fringe of simple rays</p>	<p><i>Hiemalora</i> <i>Eoporpita</i></p>
<p>4. Discs with three-fold symmetry</p> 	<p>Discs characterized by three arm-like central ridges or lobes, "Trilobozoa".</p>	<p><i>Tribrachidium</i> <i>Albumares</i> <i>Anfesta</i> (<i>Triforillonia</i>)</p>

Table 1.1. Discs grouped by basic morphological characters, with profile views.

Other discoidal forms



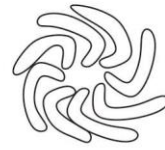
Aspidella
(invaginated
form)



Mawsonites spriggi
(multilobed disc)



Arkarua
(five-point
centre)



Eoandromeda
(eight-armed
form)

Table 1.2. Examples of discoidal forms that do not fit obvious groups in terms of morphology. References to these taxa are given in Appendix 1. (Note: Gehling et al. (2000) would place *Aspidella* with annular discs.)

Harris, 1994; Rasmussen et al., 2002; Bengtson et al., 2007), with important implications for the fossil record of early evolution. Discoidal forms can arise from a range of abiogenic processes, and these possibilities must be kept in mind in any examination of discs. The main abiogenic and biogenic ways in which a discoidal impression might be produced are summarized in the next section.

1.2 HOW TO MAKE A DISC

1.2.1 Abiogenic discs

Abiogenic means by which a discoidal impression might form may involve weathering, mineral growths, gravity, impact, the motion of objects over a surface, and the motion of fluids within sediments. These possibilities, relevant to rocks of any age, will be considered in turn below.

Crystals, pellets, and weathering

A simple way in which small pits may form on a rock surface is by the weathering out of crystals such as pyrite. Such pits may appear in profusion on a surface. Examination of the surface should indicate the origin of the pits, through the observation of unweathered crystals of the same size as the pits on the surface. The pits tend to have an angular appearance which is also telling of mineral weathering rather than a biological origin. Crystals and small pellets of rock can also produce protuberances. The appearance of “numerous small protuberances” on the top surface of dried mud from the Bay of Fundy, Nova Scotia, is described by Lyell (1851). On examination, these were found to contain salt crystals and pellets of shale that had become covered with sediment on the beach and were left as protuberances as the surrounding mud shrank on drying. These abiogenic pits and protuberances are usually easily identified as such.

Mineral growths may also mimic biological impressions. An example is “*Rutgersella truexi*”, from the Lower Silurian Shawangunk (Tuscarora) Formation,

Pennsylvania, North America, interpreted as a medusa and referred to the family Dickinsoniidae Harrington and Moore (Johnson and Fox, 1968). These structures have many radial ridges, in one specimen extending from a narrow central ridge, reminiscent of both the epirelief form of the Ediacaran disc *Aspidella terranovica* Billings and *Dickinsonia* (Johnson and Fox, 1968, fig. 2). The appearance of a sister genus to *Dickinsonia* as late as the Lower Silurian would have been highly significant in evolutionary terms, indicating the survival of a key Ediacaran form well beyond the Cambrian boundary. However, these “Rutgersella” specimens were subsequently re-interpreted as post-depositional pyrite rosettes between beds (Cloud, 1973; see also Cloud, 1968, fig. 4, for example of a similar marcasite growth). This re-interpretation was based on the morphological similarity of the spoke-like ornamentation with pyrite and marcasite growths, and the presence of pyrite both as distinct cubic crystals and as a thin film on the specimens. A pyrite veneer is however also commonly associated with Ediacaran specimens in siliciclastic rocks, representing the decayed remnants of a microbial “death mask” that aided preservation (Gehling, 1999; Mapstone and McIlroy, 2006). The lack of a distinct margin to the “Rutgersella” structures, and the rigidity of the ornamentation are, however, telling.

Load casts

Less obvious abiogenic candidates for disc-making are load casts. These common sedimentary features occur on bed soles as rounded protuberances and can, in Ediacaran strata from which groups of rounded biogenic discoidal forms may be



Fig. 1.2. Load casts on sole of bed, Chapel Island Formation Member 1, uppermost Ediacaran, Grand Banks, Newfoundland.

expected, be misleading (Fig. 1.2). Examination of the broader sedimentary context (presence of flame structures, other soft sediment deformation features) should normally quickly establish the nature of the protuberances. The commonly irregular appearance of load casts generally allows them to be ruled out as biological in origin, but examination in cross-section is essential in uncertain cases. Even when cross-sectioned, in the case of biogenic discoidal forms preserved in “Fermeuse-style”, which involves the casting of external moulds of discoidal forms by an overlying sand layer (Gehling et al., 2000; Narbonne, 2005), differentiation between the cast of a biogenic disc and an ordinary load cast must rely on morphology and the sedimentary context (see Chapter 5, Fig. 5.10, for a good example).

Tool marks

The stationary tool mark left by a pebble or other inanimate object on soft sediment may appear as a simple, isolated disc. In a current, entrapped or partially buried

pebbles will produce a deep scour on the upstream side and a diverging shallow V-shaped scour on the downstream side (Reineck and Singh, 1986), as will a partially buried holdfast disc (see Chapter 3). Evidence for an attached frond, or characteristic ornamentation may be sufficient to identify a biogenic disc, but other cases may be ambiguous.

Tool marks from movement of an object across a soft sediment surface may appear as discs and trails. A striking example is *Kullingia*, a disc with many closely spaced concentric rings originally considered to be evidence of chondrophorines in the latest Neoproterozoic and early Cambrian (Narbonne et al., 1991). A number of Early Cambrian examples, including “*Kullingia delicata*” from the Chapel Island Formation Member 2 in Fortune, Newfoundland, were subsequently shown to be scratch circles formed by the movement of a tubular organism, perhaps a sabellidid, anchored at the centre of the circle (Jensen et al., 2002).

Moving tool marks must also be kept in mind when it comes to evidence for horizontal locomotion in discoidal organisms. A rounded object may slide due to gravity or as a result of a current; it may also produce skip marks if intermittently lifted off the sea bed by a current. These processes can produce a series of marks, either joined in the form of an apparent trail or as a series of discrete impressions. Such tool marks may be confused with a trail left by a moving organism, and it is necessary to look for other indications – for example the form of the trail margins, comparison with other evidence of current direction, and patterns within a group of

trails, in order to establish whether the trail was formed by genuine movement of an organism (see for example Liu et al., 2010a). “Tilting marks”, linear tool marks produced in shallow water by the oscillating movement of waves on stationary objects, can have regular transverse markings which make them similar in appearance to trace fossils, and examples have been documented from the passive movement of jellyfish along the sediment surface (Wetzel, 1999, 2013). Such tool marks are found in shallow water, and sedimentological evidence for a deep marine palaeoenvironment, as well as other considerations such as changes in direction of trails can be used to distinguish genuine trace fossils from tilting marks (see Retallack, 2010; Liu et al., 2010b; and Chapter 5).

Raindrop impressions

Mudstone and fine sandstone beds that had experienced sub-aerial exposure may preserve impressions of raindrops from a passing shower on top surfaces, with casts on the sole of the overlying bed. Raindrop impressions were described in detail by Lyell (1851), who noted that they have prominent narrow rims. He observed that elliptical impressions, resulting from rain that has fallen at an angle, are deeper on one side, with a higher rim on that side. Rain prints merge and sometimes interfere, but in the latter case the drop that fell last preserves its complete rim, partially destroying that of the earlier drops. The detailed morphology of rain imprint features, and their relative shallowness, were used by Lyell to distinguish rain prints from cavities produced by air bubbles that had risen through mud and burst on the surface (see the *Surface bubbles and fluid escape* subsection below). Both Lyell,

and Buckland (1842) before him, recognized the need to differentiate carefully between raindrops and the marks of rising bubbles. Raindrop impressions have been claimed from rocks as old as 2.7 Ga (Som et al., 2012), and have been described from the Synalds Formation of the Longmyndian Supergroup, stratigraphically above the Burway Formation discussed in Chapter 2 (Toghill, 2006).

Surface bubbles and fluid escape

Bubbles and foam on the sediment surface can make contact impressions, usually appearing as clusters of round, shallow depressions of varying size with scarcely any rims (Twenhofel, 1921; Cloud, 1960). Moving bubbles can leave trails with raised edges that can look remarkably like trace fossils (see e.g. Reineck and Singh, 1986). However, while they may curve (Twenhofel, 1921), they do not show sudden changes of direction, which forms a suitable diagnostic feature for biological traces (cf. Liu et al., 2010a,b). Bubble-contact features are restricted to very shallow muddy waters, mud flats, and other intertidal sediments that experience subaerial exposure. Since Ediacaran fossils have only been found in shallow and deep marine environments, a bubble-contact interpretation is not usually relevant.

Of much greater importance in the critical assessment of Ediacaran discs are bubble bursts and other features resulting from fluid escape. Discoidal impressions can result from the escape of gas, either trapped air or gases such as H₂S resulting from microbial activity, as well as water escape. Cavities resulting from air bubbles have long been known, and were discussed by Buckland (1842), Lyell (1851), and others.

By comparison with rainprints, Lyell observed that air bubble bursts resulted in circular impressions, deeper than they were wide, sometimes overarching, with no rim or a slight, very sharp rim (Lyell, 1851). Gas escapes can produce quite complex ringed blisters, sometimes double blisters sharing an outer boundary in muddy sediments (Cloud, 1960), somewhat similar to Ediacaran discs such as *Cyclomedusa*, but lacking the morphological regularity of biological forms.

The rapid settling of mud in salt water can produce vertical currents that result in miniature craters of up to a few millimetres diameter, with central pits, on the sediment surface, known as pit-and-mound structures (Kindle, 1916). Kindle's experiments using fine clay mixed with salt water within glass jars were replicated here, resulting in the formation of pit-and-mound structures on the clay surface after some 8 hours (Fig. 1.3). Such structures are often seen in rapidly deposited muddy sediments as trapped air and water escapes (Shrock, 1948).

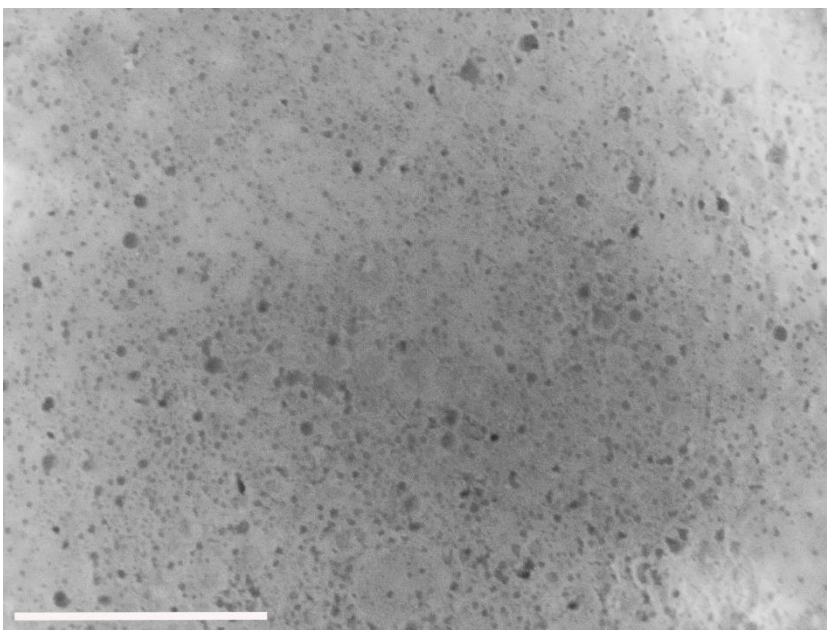


Fig. 1.3. Pit-and-mound structures created artificially by rapid settling of fine clay in salt water, photographed from above, through water. Scale bar: 1 cm.

Surface expressions of rising and bursting bubbles resulting from decaying organic matter were described by Twenhofel (1921), and by Maxson (1940), who described resulting craters with central peaks in submerged mud bars. Similar isolated discs are found in the non-marine sediments of Ferryland Head Formation, Ferryland Head, Newfoundland (Fig. 1.4). Twenhofel noted that the paths created by bubbles can be utilized by subsequent gas effusions and may leave a deep hole. The forms produced when such holes survive compaction, and become filled with calcite, have been discussed by Cloud (1960). The paths produced by bubbles may also draw up pore fluid with entrained sediment in its wake (see Chapter 2). In such cases, examination in cross-section can confirm the abiogenic nature of the resulting surface features. However small-scale gas escape commonly leaves no evidence of escape paths in cross-section, so absence of such structures below, while significant, is not in itself sufficient to confirm the biogenicity of discs.

Sedimentary structures in cross-section resulting from water escape have been explored by various researchers since Cloud's early work (e.g. Lowe, 1975; Nichols et al., 1994; Owen, 1996; Frey et al., 2009). When pore fluid pressures are elevated,



Fig. 1.4. Probable gas-escape crater on top surface, Ferryland Head Formation, Ferryland Head, Avalon Peninsula, Newfoundland. Scale bar: 1 cm.

fine-grained unconsolidated sediment may lose strength as the grain-supported structure gives way to suspension in fluid. Particles become entrained in the migrating fluid, resulting in the development of fluid escape structures such as pillars, dishes, sandstone dykes and sills, and sand volcanoes and sand boils at the sediment-water interface, varying in scale from metres to centimetres or less (Lowe and LoPiccolo, 1974; Lowe, 1975). Sand volcanoes may have both rings and radial markings, and thus may sometimes be mistaken for body or trace fossils, as occurred with the Lower Cambrian “Astropolithon” (Pickerill and Harris, 1979). (Somewhat similar structures with reverse topography have been identified as biogenic (*Astropolichnus*; see Crimes et al., 1977).)

Dewatering structures tend to develop in regions of tectonic or gravitational instability, in association with slumping, in sediments with poor sorting/packing, and rapid sedimentation. Therefore caution is required where there is evidence of such conditions, for example, very thick beds, climbing ripples, and convolute bedding (Farmer et al., 1992). The disc-dominated upper Fermeuse Formation in the Avalon Peninsula, Newfoundland, discussed in Chapter 5, shows evidence of slope instability and rapid sedimentation, thereby adding to the challenge of interpreting its discoidal forms.

1.2.2 Biogenic discs

The following characteristics would support the biogenicity of a discoidal form:

- a) A distinct boundary, margin, or flange, of consistent form. (This is not always reliable, and insufficient on its own, but load structures, for example, tend not to have distinct margins.)
- b) Distortion of boundaries in contact. (This is a strong criterion for biogenicity, indicating flexibility and integrity of form, and mutual avoidance. However, apparent cross-cutting may not necessarily rule out biogenicity: disc boundaries may appear to cross-cut if they are imprinted from a higher stratigraphic level (see e.g. Gehling et al., 2000).)
- c) Complex, consistent ornamentation. (Simple rings and radial grooves are not sufficient, and even simple lobes may result from abiogenic processes (see Chapter 2; Cloud, 1968).)
- d) Folds, creases, and other signs of flexibility.
- e) Signs of post-mortem microbial colonization, or fluid releases into the bed overlying a discoidal impression that occur as pyritic cements, as these are likely to have been associated with the decay of an organism. (This includes overlying microbial threads or the ivesheadiomorph “effaced preservation” of partly decayed forms with microbial overgrowths (see Liu et al., 2011).)

A disc may still be biogenic even if characteristics a), c) and d) are not observed and b) does not apply because it is isolated, as long as there is no evidence for any of the

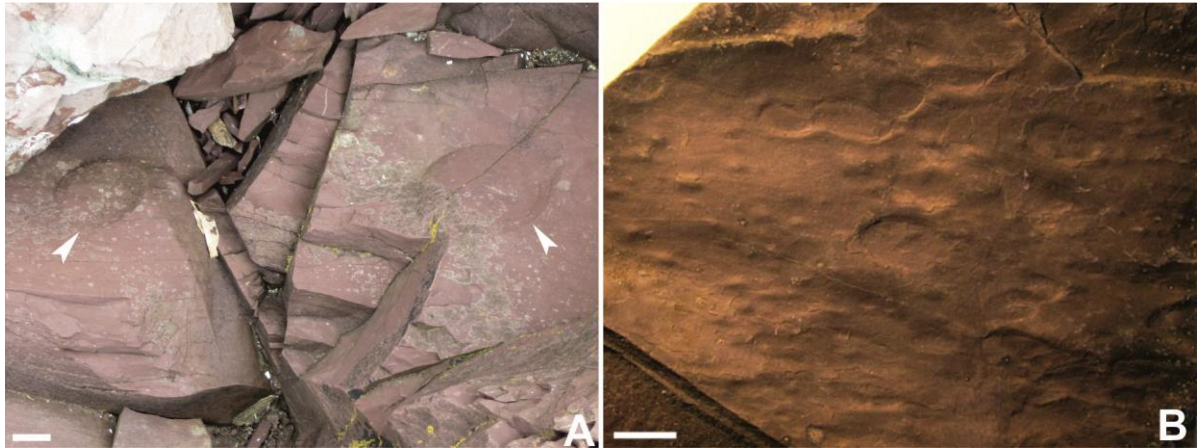


Fig. 1.5. Examples of discs of uncertain nature. **A:** Slightly concave, smooth, unrimmed discs (arrowed) with minute central depression, top surface. Early Cambrian, Chapel Island Formation Member 4, near Fortune, Newfoundland. These may be abiogenic, due to fluid escape, or scratch circles formed by an attached simple tubular form. **B:** Shallow, unrimmed negative discs amid small protuberances on top surface, Synalds Formation, Longmyndian Supergroup. The negative discs may be the result of small bubble bursts, compaction reducing their depth, while the protuberances may be small gas pustules. No structures are visible below on cross-sectioning. OUMNH Á.2540. Scale bars: 1 cm.

abiogenic possibilities described above. However, such a disc must remain suspect, and if in doubt, an abiogenic interpretation must be the null hypothesis. A number of discs, due to lack of access for examination or lack of evidence, must probably forever remain uncertain (Fig. 1.5).

Even if a disc is evidently biogenic, interpretation of its nature is challenging. It may be the impression of a complete organism or colony in itself – for example a giant protist or a microbial colony, fungal or bacterial. Or it may be the impression of the base of a larger organism. Some Ediacaran discs, synonymized under the form taxon *Aspidella* (Gehling et al., 2000) are observed to form the bases of rangeomorphs and are interpreted as holdfasts. A variety of isolated discs are inferred to be holdfasts even when fronds are not observed (Gehling et al., 2000; see Chapters 3, 5). Affinities with various modern phyla, kingdoms, or types of

organism have also been proposed for some forms of isolated discs, including microbial colonies (Grazhdankin and Gerdes, 2007), sponges (Gehling and Rigby, 1996), and organisms of fungal grade (Peterson et al., 2003). A final possibility is that a disc is neither part of an organism nor a body fossil but a simple trace fossil, perhaps resulting from an organism moving up through the sediment (see Chapter 5).

It is apparent from the variety of possibilities listed above that extreme caution should be applied in the interpretation of discoidal impressions. A further complication, in considering any Ediacaran form, is the influence of microbial mats.

1.2.3 The role of microbial mats

In the absence of grazing organisms, microbial mats appear to have been widespread on sediment surfaces in the Ediacaran Period (Seilacher and Pflüger, 1994). Their presence is well attested (e.g. McIlroy and Walter, 1997; Gehling, 1999; Seilacher, 1999; Noffke, 2010; Liu et al., 2011). Characteristic “elephant skin” texture (Gehling, 1999) is observed on many bedding planes, and some surfaces show the larger scale patterns of wrinkling known as *Kinneyia* (Fig. 1.6; Walcott, 1914; Hagadorn and Bottjer, 1997; Pflüger, 1999; Porada et al., 2008). As well as binding and stabilizing the sediment surface, they are now understood to be involved in the production of a range of sedimentary structures, collectively known as “microbially induced sedimentary structures” or MISS (Gerdes et al., 1993; Noffke et al., 2001). Microbial mats may have formed the basis of lifestyles for various Ediacaran

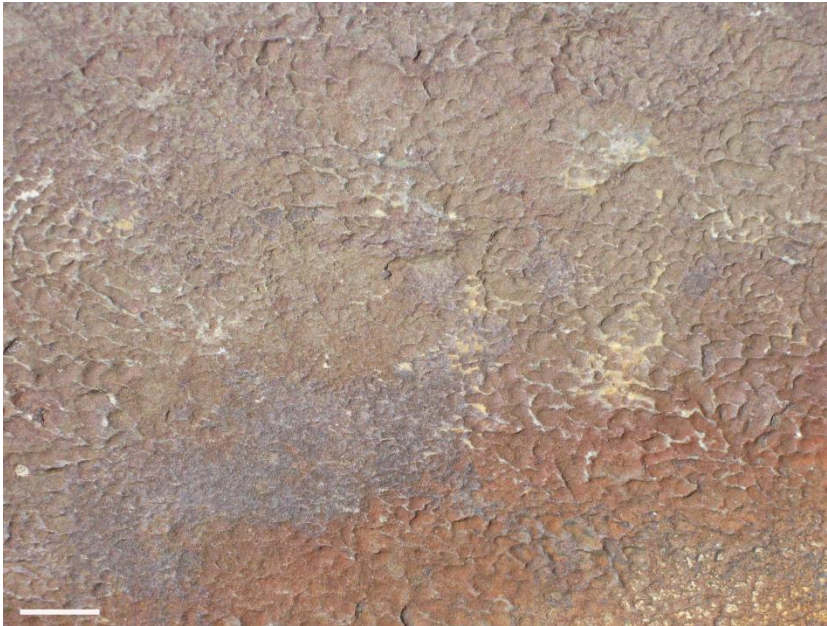


Fig. 1.6. Kinneyia-like microbial mat textures on top surface, lower Fermeuse Formation, Bonavista Peninsula, Newfoundland. Scale bar: 1 cm.

organisms living on, within, or beneath, and exploiting it for nutrients (Seilacher, 1999). The presence of microbial mats is also considered to have played a key role in the preservation of Ediacaran organisms through rapid capture of the upper and lower surface impressions in the “death mask” scenario (Gehling, 1999; Mapstone and McLroy, 2006; Darroch et al., 2012). These microbial mats can show exceptional preservation in the Neoproterozoic and lower Palaeozoic (Callow and Brasier, 2009; Harazim et al., 2013). Matgrounds and MISS are relevant with regard to identifying the morphologies and ornamentation of discs. They may overlie discs, particularly those captured in varying states of decay, so that intrinsic ornamentation is masked or uncertain, or apparent morphological diversity enhanced (Liu et al., 2011; Tarhan et al., 2015b).

Cohesive mat-bound sediments are also likely to influence the surface expression of abiogenic processes such as fluid escape through their resistance, acting as films



Fig. 1.7. Analogy of the response of mat-bound sediment to fluid pressure, using water injected through sand layer into soft plaster bounded by thin plastic film. Note the development of raised lobes of displaced material between the grooves (cf. lobed discs, Chapter 2). Scale bar: 1 cm.

that distort and crease in response to fluid pressure. As an analogy, water was injected through a layer of sand on to an adjoining layer of plaster separated by a thin plastic film, to approximate mat-bound unconsolidated fine sediment. On removal of the sand, the film-bound plaster surface was found to have retained deep depressions at the injection points, each surrounded by radial grooves (Fig. 1.7). While only an approximate analogy, the resultant structures are suggestive of some discs, such as the margin-less *Pseudorhizostomites howchini* (Sprigg, 1949), which was originally considered to be a medusa, but subsequently reinterpreted as a gas escape feature, perhaps from a decaying organism (Glaessner and Wade, 1966; Wade, 1968), and, most recently, as a structure resulting from the uprooting of a holdfast (Tarhan et al., 2010).

In the next chapter, I will look at an example of a disc assemblage that illustrates both the need for a critical evaluation of biogenicity, and the scale of the role played by microbial mats in Ediacaran sediments.

CHAPTER 2

THE DISCS AND MICROBES OF THE LONG MYND

Section 2.1 of this chapter is based on a paper accepted for publication in the Journal of the Geological Society, London (Menon et al., 2015), co-authored with Alexander Liu as well as my supervisors Duncan McIlroy (DMC) and the late Martin Brasier (MDB). The paper was written by me. The reinterpretation of Long Mynd structures according to a sediment injection and loading model is mine. DMC made the key suggestion of microbial mat sealing as influencing the fluid escape, based on work by Harazim et al. (Harazim et al., 2013). I conducted all the experimental work described in the paper except for the images of mechanical grinding through a four-lobed disc and its 3D reconstruction (fig. 7(a-d) in paper), which was conducted by Liu, but the results were reinterpreted by me. Liu's contribution to the paper has been omitted from this thesis chapter.

Section 2.4 is intended to become a paper co-authored with DMC and MDB. It was written by me. I did the experimental work and discovered the unusual structure and texture of Longmyndian Intrites in cross-section. DMC proposed that the Intrites-like structure was a sediment volcano; MDB suggested that the Intrites-like structure resulted from clay-mineral precipitation by microbes. I proposed that failed sediment injections were involved. I devised a model involving all these elements and based on the idea of architectures arising from the congregation on raised topography of cyanobacteria competing for light (Gerdes et al., 1994), suggesting micrite rather than clay-mineral precipitation, but also trapping and binding to build up the lobes on the flanks of a sediment volcano.

2.1 INTRODUCTION

Discoidal forms were first noted in the Burway and Synalds Formations of the Longmyndian Supergroup, Shropshire, UK, in the 19th century (Salter, 1856; Callow et al., 2011b). They were originally inferred to be biological structures of simple animals (Salter, 1856; Darwin, 1859), but this interpretation has subsequently been much debated (e.g. Cobbold, 1900; Greig et al., 1968; Pauley, 1986, 1990; Toghil, 2006; Liu, 2011). The possible interpretation of circular impressions in the Burway Formation as rain-pits is ruled out by the recognition of subaqueous deposition of

this unit (Pauley, 1990), and they have recently been widely regarded as fossils of simple Ediacaran organisms belonging to form taxa *Medusinites* aff. *asteroides* (Sprigg) Glaessner and Wade 1966 (Sprigg, 1949; Glaessner and Wade, 1966), *Beltanelliformis brunsae* Menner 1974 (Keller et al., 1974), *B. minutae* McIlroy et al. 2005, and *Intrites punctatus* Fedonkin 1980 (McIlroy et al., 2005). These discoidal forms are reassessed here in the context of other sedimentary features observed in cross-section, and the widespread evidence for microbial mats.

The abundance and importance of microbial mats on the Ediacaran seafloor was noted in Chapter 1. Microbially mediated sedimentary structures resulting from seafloor biostabilization, and build-up of decay gases below matgrounds (e.g. gas domes, “sponge pore” fabrics), are now well characterized (see Gerdes et al., 1994; Noffke, 2010; Schieber et al., 2007). Most studies have focused on structures formed in association with cyanobacterial mats in intertidal settings, but many of the fundamental properties required to generate such forms are inferred to apply to all types of microbial mat.

In the first section of this chapter, mat-driven processes are shown to provide a physical explanation for at least three forms of discoidal impression observed in the upper Burway Formation: the Longmyndian forms of *Medusinites*, *Beltanelliformis brunsae*, and *B. minutae* (cf. McIlroy et al., 2005). In the second section, the nature of the Long Mynd microbial mats is examined in more detail, and preliminary results presented that shed light on their nature and composition. The third section

discusses the nature of Longmyndian *Intrites*, the remaining type of discoidal impression found in the upper Burway Formation (McIlroy et al., 2005), and proposes a model for its formation. A reassessment of several of John Salter's original specimens from the Long Mynd in the light of the interpretations given in this chapter can be found in Appendix A2.5.

2.2 MICROBIAL-MAT-RELATED DYNAMICS AND PSEUDOFOSILS

2.2.1 Lithology, palaeoenvironmental context, and surface features

The specimens discussed here were collected from a disused quarry in Ashes Hollow, from horizons approximately 75 m below the Cardingmill Grit, close to the top of the Burway Formation, Stretton Group, Longmyndian Supergroup (Fig. 2.1). The discoidal fossils occur in heterolithic facies of mudstone to fine siltstone interlaminated with fine sandstone (Pauley, 1986; McIlroy et al., 2005). The lamination, typically <0.2–1 mm in width, is mostly plane parallel, with some cross-lamination, and contorted laminae in places stretching a few centimetres, with occasional small microfaults. Grains include a significant volcanic and plutonic component from the Uriconian Volcanic Complex underlying the Stretton Group (Pauley, 1986, 1990). The chloritic mudstone and siltstone are greenish-grey in hand specimen, while the amalgamated sandstone is dark brown due to the presence of haematite (Pauley, 1986). Intermittent thin (<0.3 mm), white laminae were previously identified as hosting mineralized microbial mats preserved in a white

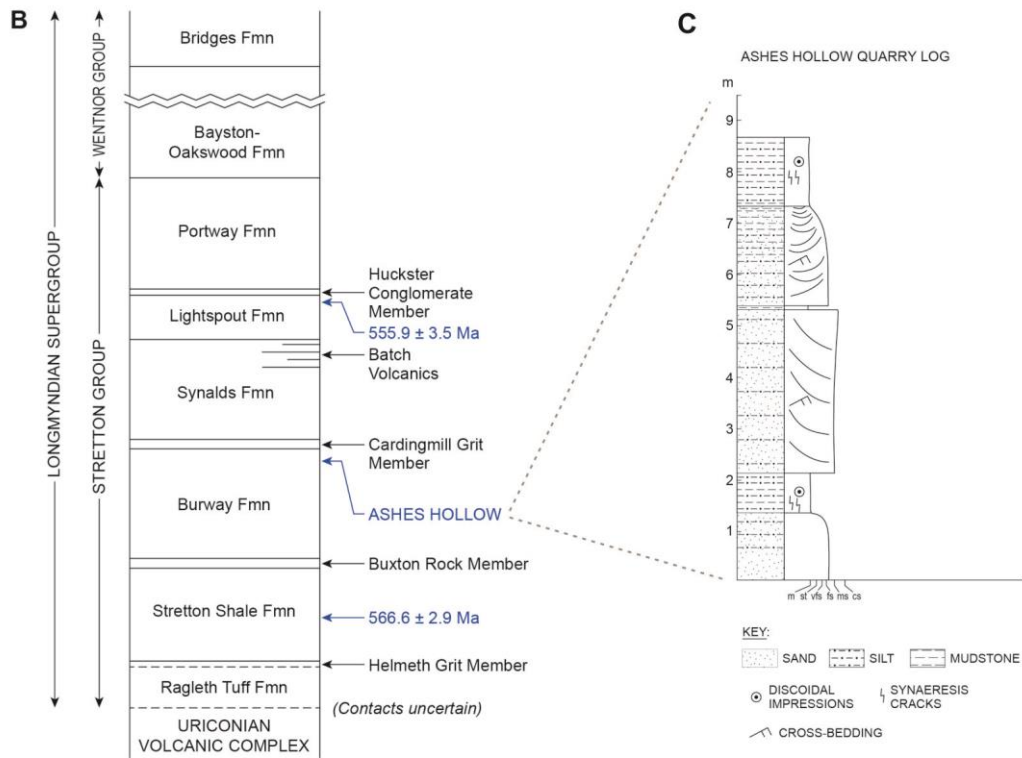
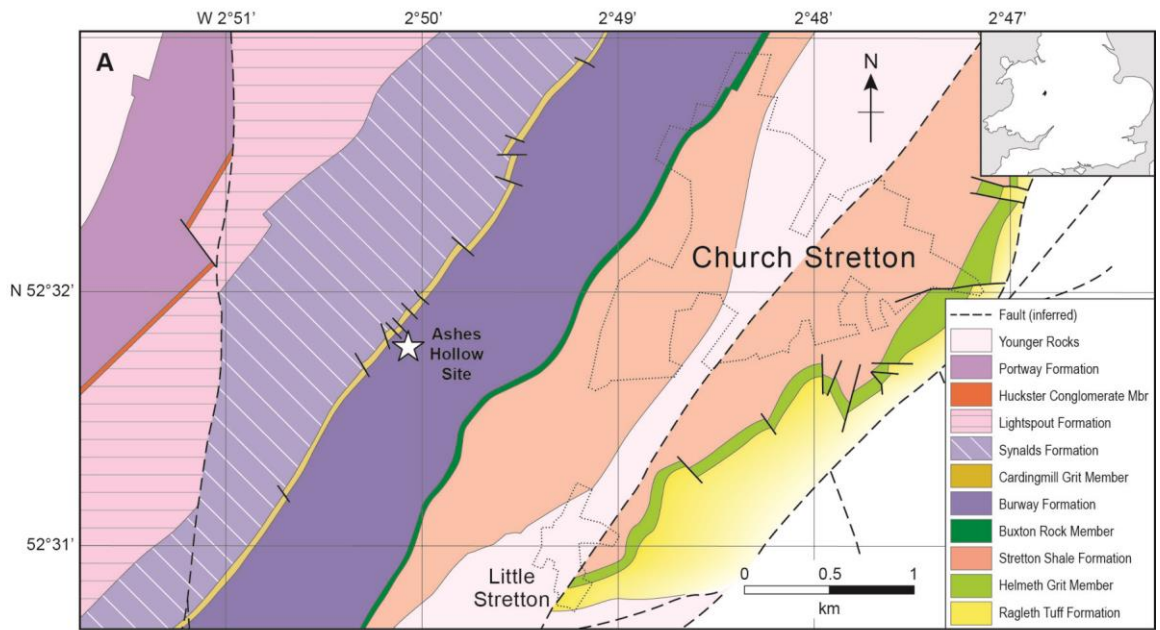


Fig. 2.1. Location and stratigraphic position of Ashes Hollow area of study. **A:** Simplified geological map of area with site of specimens indicated. Inset map shows position of the Long Mynd within Britain. **B:** Stratigraphy of the Longmyndian Supergroup, following the interpretation of Pauley (1990, 1991), with stratigraphic position of Ashes Hollow site marked, together with dates measured by Compston et al. (2002). **C:** Log of Ashes Hollow quarry. See also Appendix A2.1.

aluminosilicate mineral (Callow and Brasier, 2009). The colour contrast between the mudstone and inter-laminated sandstone allows sub-millimetric sediment fabrics to be studied in polished vertical section. The age of the Burway Formation is currently constrained by U/Pb SHRIMP geochronology to between 566.6 ± 2.9 Ma in a lapilli tuff at the base of the underlying Stretton Shale Formation, and 555.9 ± 3.5 in a tuff at the top of the stratigraphically higher Lightspout Formation (Compston et al., 2002).

Sole surfaces of some Ashes Hollow beds are covered with millimetre-scale mounds, typically of 2 mm diameter, and pinhead-like (typically 0.3 mm diameter) protuberances (“pimples”), with rimless counterpart pits on the tops of underlying beds (Fig. 2.2A-C; Table 2.1). Shallow (0.5 mm depth), rimless discoidal depressions, generally larger than and lacking the sharp edges of the counterpart pits, are also found on top surfaces (Fig. 2.2D; Table 2.1).

The most distinctive discoidal fossil from the Burway Formation is Longmyndian *Medusinites aff. asteroides*, a blister-like mound of diameter 1-6 mm, sometimes with a central boss, locally found in large numbers on the soles of beds (Fig. 2.2A).

Longmyndian *Medusinites* mounds in cross-section are typically filled with dark sandy sediment, sometimes with a tube-like extension above, which was thought to represent the passage of either gas or an organism (Cobbold, 1900). Since gas-escape structures are rarely preserved in this way, McIlroy et al. (2005) tentatively concluded that Longmyndian *Medusinites* might be a trace fossil.

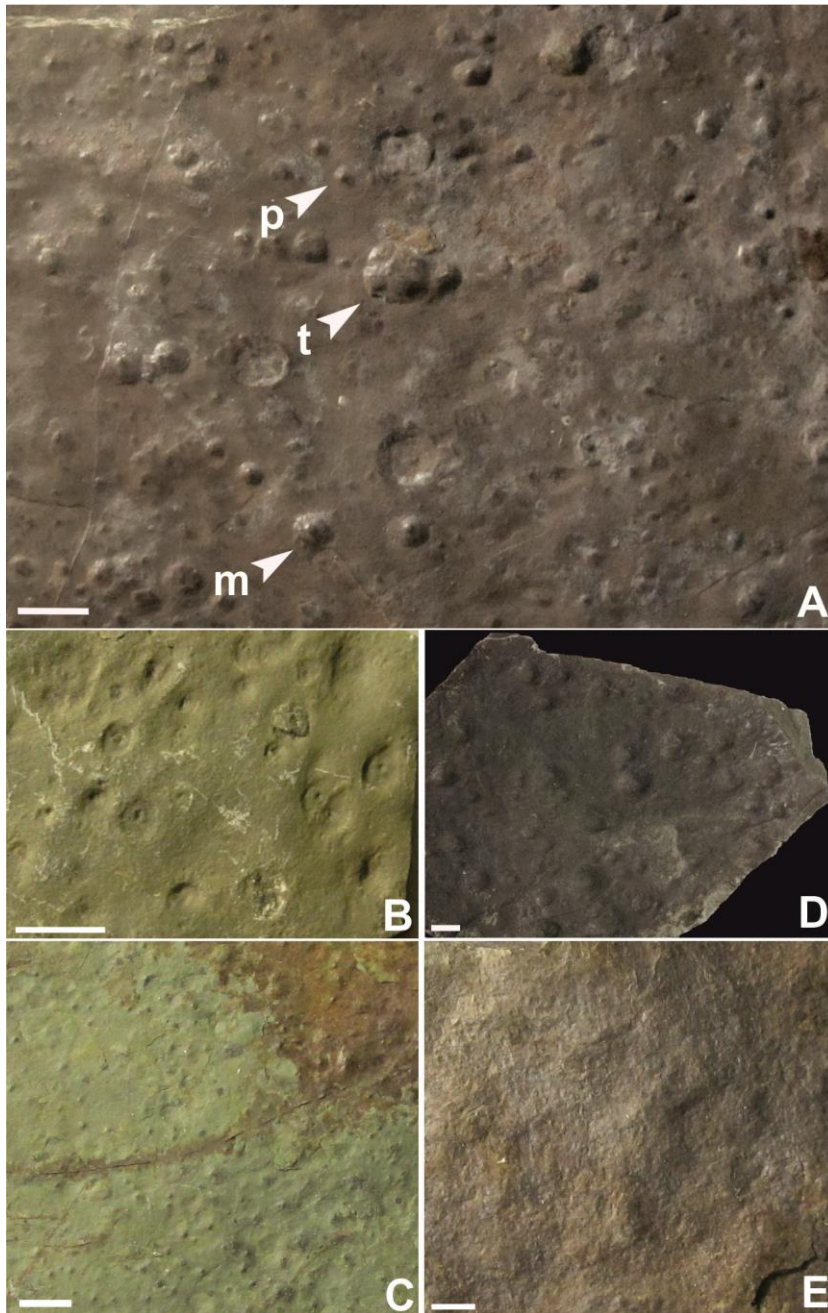


Fig. 2.2. A: Sole of block showing abundant small Longmyndian *Medusinites* ('m'), individual pimple protrusions described as *Beltanelliformis minutae* ('p'), and occasional tetralobate discs ('t'). Specimen no. L-AH/10. (see Appendix 6 for specimen list.) **B:** Negative epirelief counterparts of *Medusinites* on bed top. OUMNH Á.2541. **C:** Sole surface covered with *B. minutae*. OUMNH Á.2542. **D:** Shallow, rimless depressions, described as Longmyndian *B. brunsae*, on top of bed. OUMNH Á.2543. **E:** Microbial-mat-associated texture on top surface. L-AH/3. Scale bars: 5 mm.

Microbial-mat-associated “elephant skin”, wrinkle textures and thread-like markings are also seen on surfaces of Stretton Group rocks in association with discoidal markings (McIlroy et al., 2005; Fig. 2.2E), and widespread filamentous microfossils consistent with mat fabrics have been observed from the Burway and Lightspout Formations (Peat, 1984; Callow and Brasier, 2009; see also Section 2.3).

2.2.2 Upper Burway Formation rocks in vertical section

Serial polished vertical cross-sections through hand samples bearing *Medusinites*, “pimples”, and the *Beltanelliformis*-like shallow depressions were investigated, to examine the discoidal structures, the potential trace fossils, and the associated matground fabrics. Hand specimens were first cut in a series of slices of 1 cm depth and the cross-sections polished, to form a general impression of the features in cross-section. Individual discoidal specimens were then hand-ground with 16- μ m grain size carborundum powder on a glass plate, and photographed at intervals of 1 minute, with the removal of \sim 0.1 mm of rock between grinds, for detailed study. Other specimens were ground at intervals of 5 minutes, with the removal of \sim 0.25 mm of rock between grinds, for confirmation and checking of features.

Examination of beds with crinkly laminae in vertical cross-section revealed a suite of sedimentary features that disrupt laminae at scales of $<$ 0.5 to 10 mm, of which the tube-like extensions of sandstone previously observed above *Medusinites* (Cobbald, 1900; McIlroy et al., 2005) form only a part (Fig. 2.3A; Table 2.1). These features include irregular, often widening, sub-vertical columns of sandstone that have horizontal branches penetrating into associated laminae (Fig. 2.3B). Larger areas of vertical disruption, encompassing over 2 cm of sediment thickness (Fig. 2.3C), with displaced and locally discontinuous laminae, and fragments of green mudstone laminae within the zone of disruption, are associated with strikingly crinkled whitish sedimentary laminae. Serial grinding through one such zone of disruption demonstrated that the disrupted region was less than 5 mm wide.

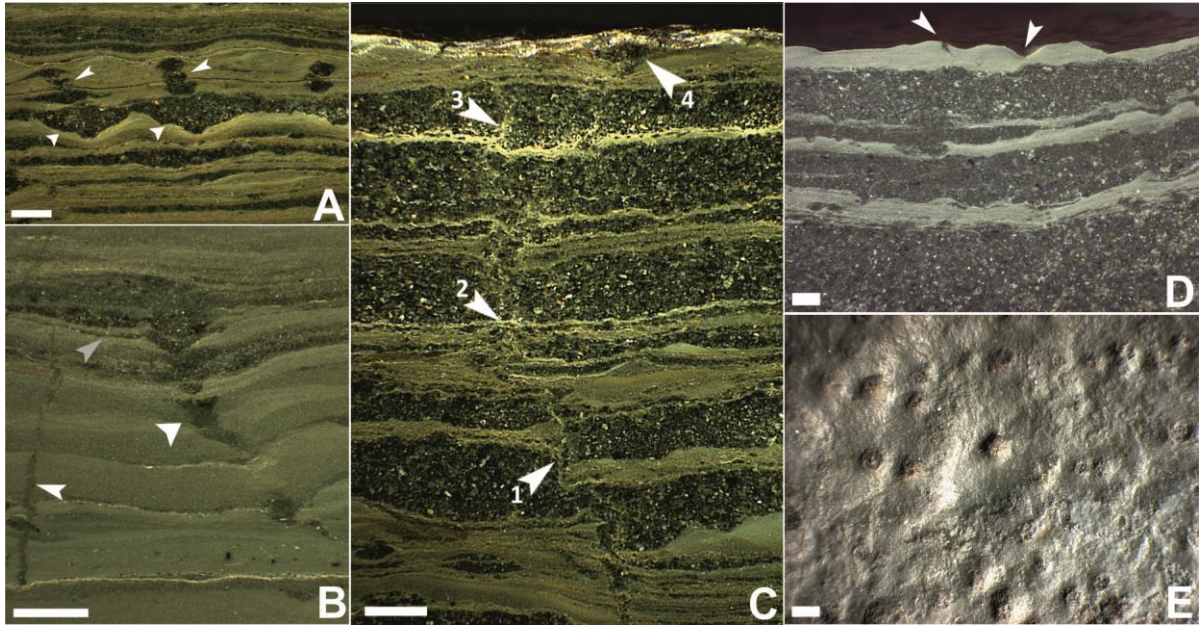


Fig. 2.3. **A:** Two *Medusinites* in ground cross-section (wide arrows) showing columnar extensions of sandstone above (fine arrows), in context amid other sandstone protrusions. **B:** Ground cross-section showing widening vertical sandstone feature (wide arrow) with horizontal branches penetrating into laminae (grey arrow), and a fine zigzag structure (fine arrow). **C:** Ground cross-section showing upper portion of narrow, extended vertical disturbance, with vertically displaced laminae in some parts (1), but not in others (2), and fragments of laminae extending along the line of disturbance (3). The disturbance terminates at the top surface in a small sand volcano (4). **D:** Ground cross-section showing disrupted laminae and craters on top surface (arrows), one with fine sandstone column within. **E:** View of top surface of block in D, showing small craters with dark sandstone within. A,C, L-AH/12; B, OUMNH Á.2542; D, E, RCL-AH/11. Scale bars: 1 mm. Further images of sediment disruption and features in cross-section are given in Appendix A2.2.

Moreover, the laminae cut by the disturbance do not show systematic displacement; some are displaced, others simply discontinuous. This contrasts with microfaults and indicates that the feature results from localized soft-sediment deformation.

Where the sediment columns reach bedding surfaces, (e.g. Fig. 2.3C, D), they are associated with small cones and craters of between 1 and 5 mm in diameter and 0.5–1.5 mm height (Fig. 2.3E).

Feature	Description	Size range and orientation
<i>Discoidal forms:</i>		
Longmyndian <i>Medusinites</i> aff. <i>asteroides</i>	Mound-like forms on bed soles, many with pinhead-like central boss; negative counterparts on tops of beds, unrimmed, with sharply defined outline and pinhole-sized dip at centre of depression. Found in large clusters	1–4 mm diameter; typically 2mm; rarely up to 6 mm. Protruding 0.5–1 mm from sole surface
Lobed form	Mound-like form on bed soles, similar to <i>Medusinites</i> , with central pinhead-like boss, but lobed perimeter. Typically four symmetric lobes, within a depressed rim. However, in some places, up to 20% of <i>Medusinites</i> specimens have 3–5 poorly formed lobes or exhibit a lobate tendency. Negative counterparts on tops of beds. Found in clusters among round <i>Medusinites</i> in patches on some bedding planes only	3–5 mm diameter; typically 3 mm. Protruding 0.5–1 mm from sole surface
“Pimples”	Very small protrusions on bed soles, and counterpart pits on bed tops. Found among <i>Medusinites</i> , or in large clusters	0.2–0.5 mm diameter; typically 0.3 mm. Protruding 0.2–0.3 mm from sole surface
Longmyndian <i>Beltanelliformis</i> -like depressions	Shallow, rimless depressions without clearly defined edges and lacking the central pits of counterpart <i>Medusinites</i> . Found in clusters on tops of beds	4–5 mm diameter; ~0.5 mm depth
<i>Features observed in cross-section:</i>		
Sandstone columns	Columns observed fully within the cross-section or above discoidal impressions on the bed sole; may have horizontal branches extending into sandstone laminae which the columns cross-cut. Columns usually terminate either by converging with a sandstone lamina or just below a white mat layer	Length, highly variable, 0.3–3.8 mm; diameter 0.1–0.65 mm. No typical dimensions. Orientation 40–90°, typically 80°
Inverted sandstone cones	Inverted conical forms, most with thin, meandering sandstone column below, extending into a lower sandstone lamina	Highly variable in dimensions. Cone diameter 0.65–3.00 mm; cone length (above start of thin column) 0.5–1.75 mm. Orientation of cone 80–90°; orientation of columnar extension highly oblique, 10–20°

Table 2.1. Characteristics of discoidal impressions in upper Burway Formation rocks, and main features observed in cross-section.

The highly crinkled whitish sedimentary laminae observed in association with zones of disruption would be conventionally attributed to microbial matgrounds (Noffke, 2010). Petrographic study of these lithologies provides substantial evidence for the former presence of widespread microbial mats, including intermeshed filaments angled at approximately 45° to bedding, trapped and bound sediment grains, and the preferential alignment of muscovite and other elongated grains within the matground facies (cf. Noffke, 2010; Figs 2.4, 2.5; see also Peat, 1984; Callow and Brasier, 2009).

All simple, mound-like *Medusinites* examined in cross-section by serial grinding reveal a protruding mound that is partially or wholly filled with dark sandstone of the same lithology as the surrounding sandstone laminae, frequently with a sub-vertical columnar extension (Fig. 2.6A, B). This sediment column distorts and cuts mudstone laminae above the discoidal impression, and typically terminates at an overlying sandstone bed (Fig. 2.6B). *Medusinites* with a central boss have a partial fill of sandstone, encompassing the boss and widening laterally a little above the centre of the mound (Fig. 2.6C, D). Negative counterparts of *Medusinites* found on the tops of beds (Fig. 2.2B) are underlain by irregular dark-coloured sandstone structures that intersect the centre of the pit (Fig. 2.6E, F). These sandstone features are also of the same lithology and texture as the surrounding sandstone laminae. Cross-sections through the pimple-like impressions on bed soles attributed to *B. minutae* (McIlroy et al., 2005; Fig. 2.2A, C) show narrow columnar features (Fig. 2.6G, H).

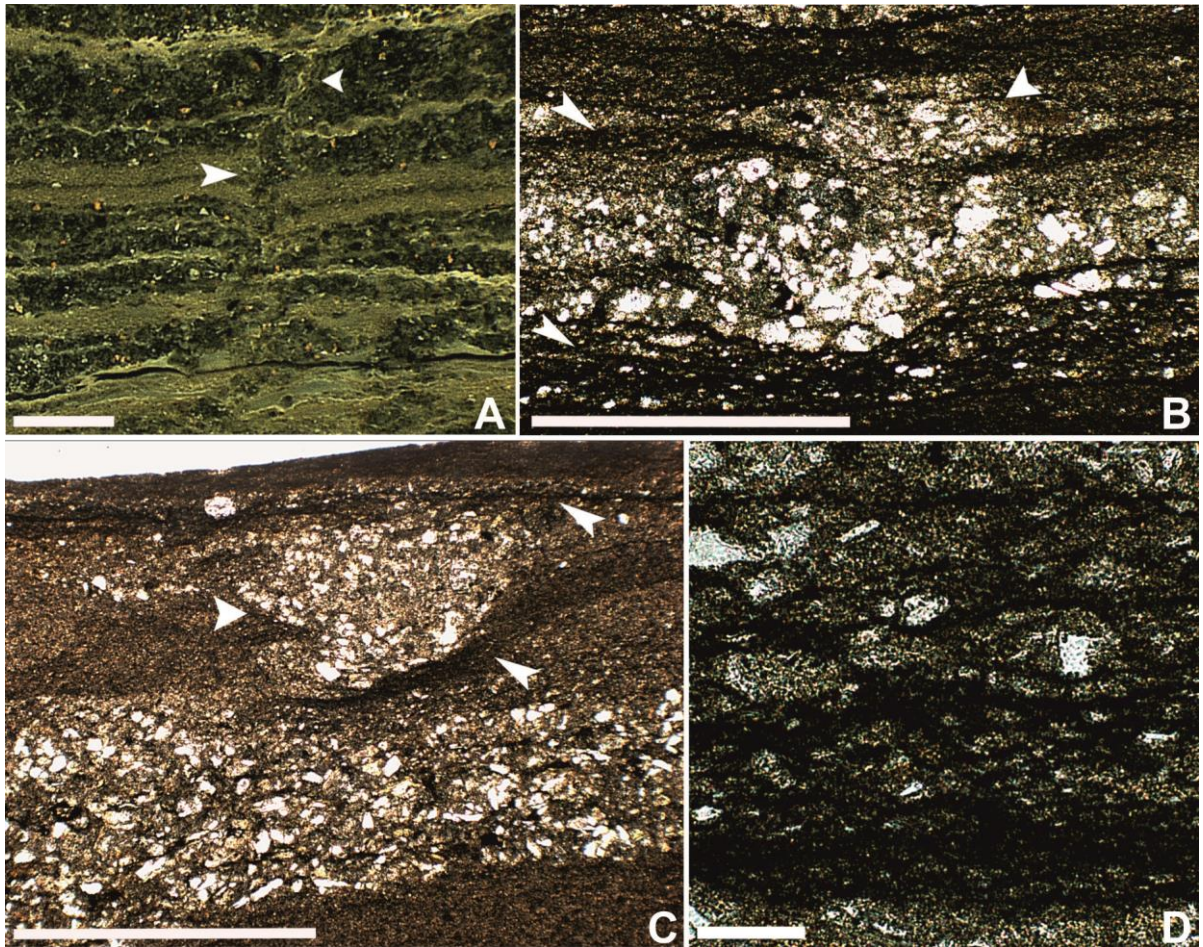


Fig. 2.4. Microbial mats in cross section. **A:** Ground cross-section showing crinkly laminae surrounding a vertical disturbance (disturbance indicated with fine arrow), and fragments of white lamina within disturbance (wide arrow). **B, C:** Photomicrographs of thin sections showing microbial mat layers (fine arrows) constraining sandy sediment structures (wide arrows). Note narrow sinuous connection of V-shaped structure in C to sandstone lamina below. **D:** Photomicrograph of thin section showing trapping and binding of sediment grains by microbial mat. A,B,D, L-AH/12; C, L-AH/1b. Scale bars: A-C, 1 mm; D, 100 μ m.

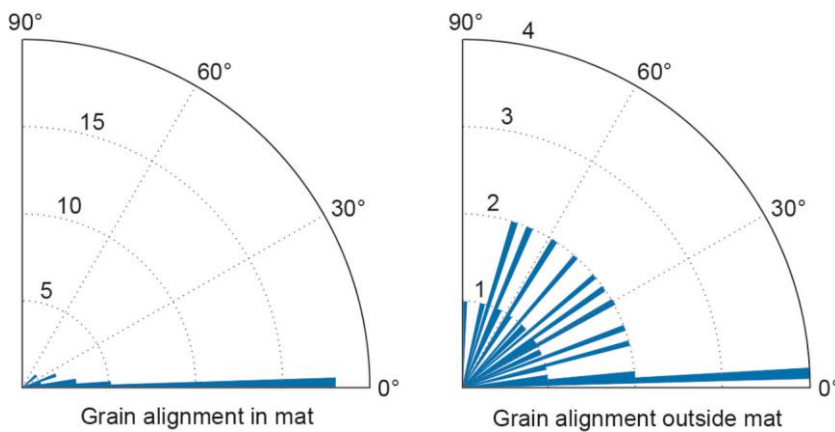


Fig. 2.5. Comparison of angles of grains trapped in proposed microbial mat (left) with those in sandstone layer (right), showing striking grain alignment in the mat layer resulting from trapping and orienting of grains within the mat plane by microbes. Total number of grains $N = 40$.

A tetra-lobate form, comprising a mound divided into four lobes by shallow radial grooves extending from the central pimple (Fig. 2.2A) was also examined by serial grinding. This form is found in association with normal, rounded *Medusinites* in patches on some bedding planes, and has been regarded as a variant of *Medusinites* (Pauley, 1986). The tetra-lobate form appears to represent the most symmetrical example of a wider tendency towards lobe formation in *Medusinites*. Many *Medusinites*, up to ~20% of specimens in some patches, show between 3 and, more typically, 5 poorly formed lobes. In cross-section the lobed forms have sandstone fills very similar to those of non-lobed forms of *Medusinites* (cf. Fig. 2.6C, D) and the lobes are found to be composed of unlaminated mudstone with an admixture of 20–40% sandstone (Fig. 2.7A–D).

Shallow depressions on the tops of beds from the locality with *Medusinites* (Fig. 2.2D), previously described as *Beltanelliformis brunsae* (McIlroy et al., 2005), were also serially ground, both in vertical cross-section and parallel to bedding, revealing roughly apex-down conical structures composed of dark sandstone, again of the same lithology and texture as the surrounding sandstone laminae (Fig. 2.8A–C; Table 2.1). These conical structures do not reach the impression-bearing surface but terminate just below it, as a lopolith-like spread with a central depression (Fig. 2.8C). Such conical structures are seen in vertical cross-section to extend downwards as meandering, tapering columns, often linking the conical structure to a sandstone bed below (Fig. 2.8A, B, D).

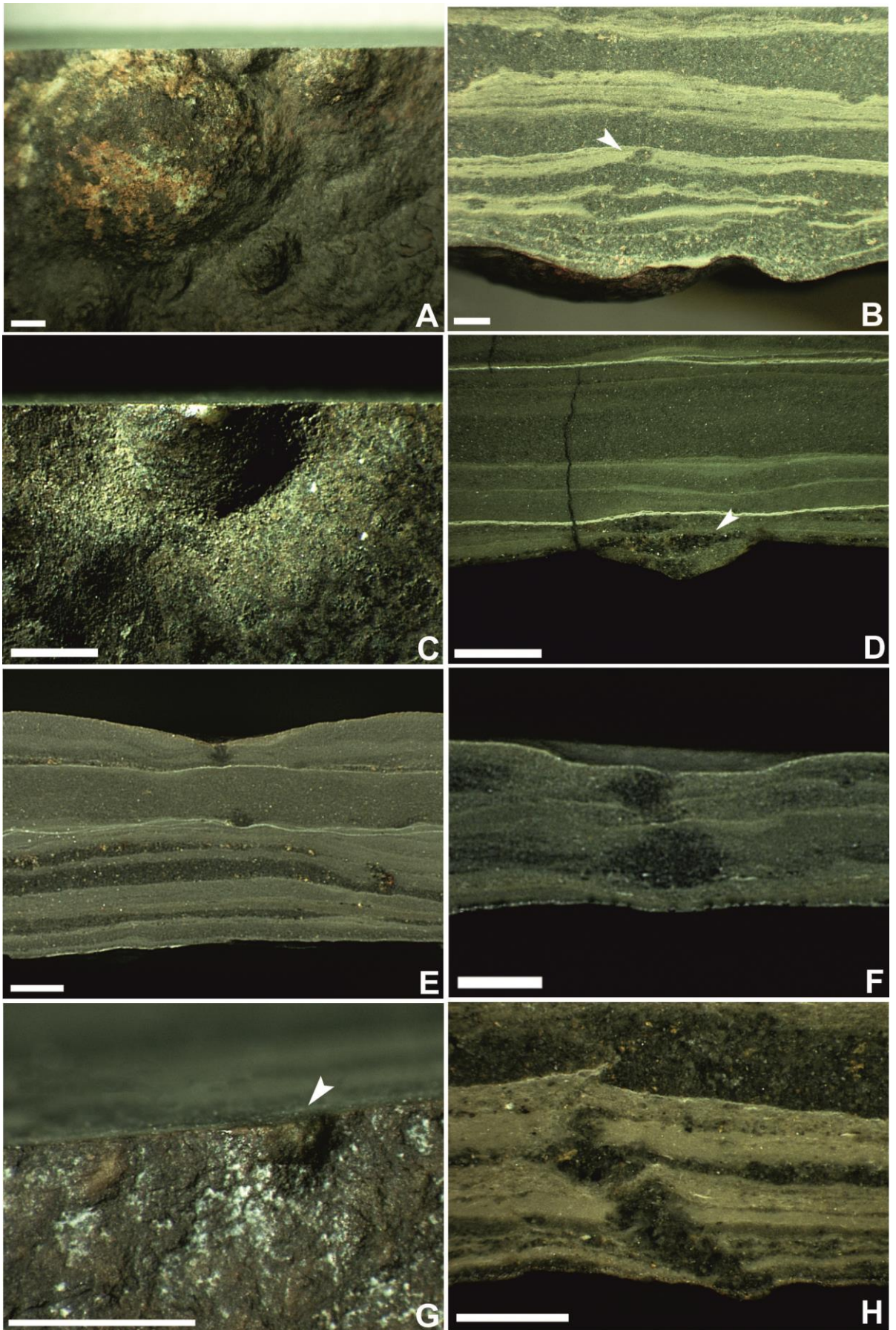


Fig. 2.6.

◀ **Fig. 2.6.** **A:** Large and small mound-like Longmyndian *Medusinites* on bed sole before grinding. **B:** Ground cross-section through *Medusinites* shown in A, illustrating broken and distorted laminae and central oblique sandstone column (arrowed). **C:** Partially ground *Medusinites* with central boss on bed sole. **D:** Ground cross-section through *Medusinites* in C, showing widening sandstone fill centred on boss (arrowed). **E, F:** Ground cross-sections through negative *Medusinites* counterparts on tops of beds, showing sandstone below centre. **G:** “Pimple” or *B. minutae* (arrowed) on bed sole. **H:** Ground cross-section through pimple shown in G. A,B, G, H, OUMNH Á.2543; C,D, L-AH/10; E, L-AH/17; F, OUMNH Á.2541. Scale bars: 1 mm.

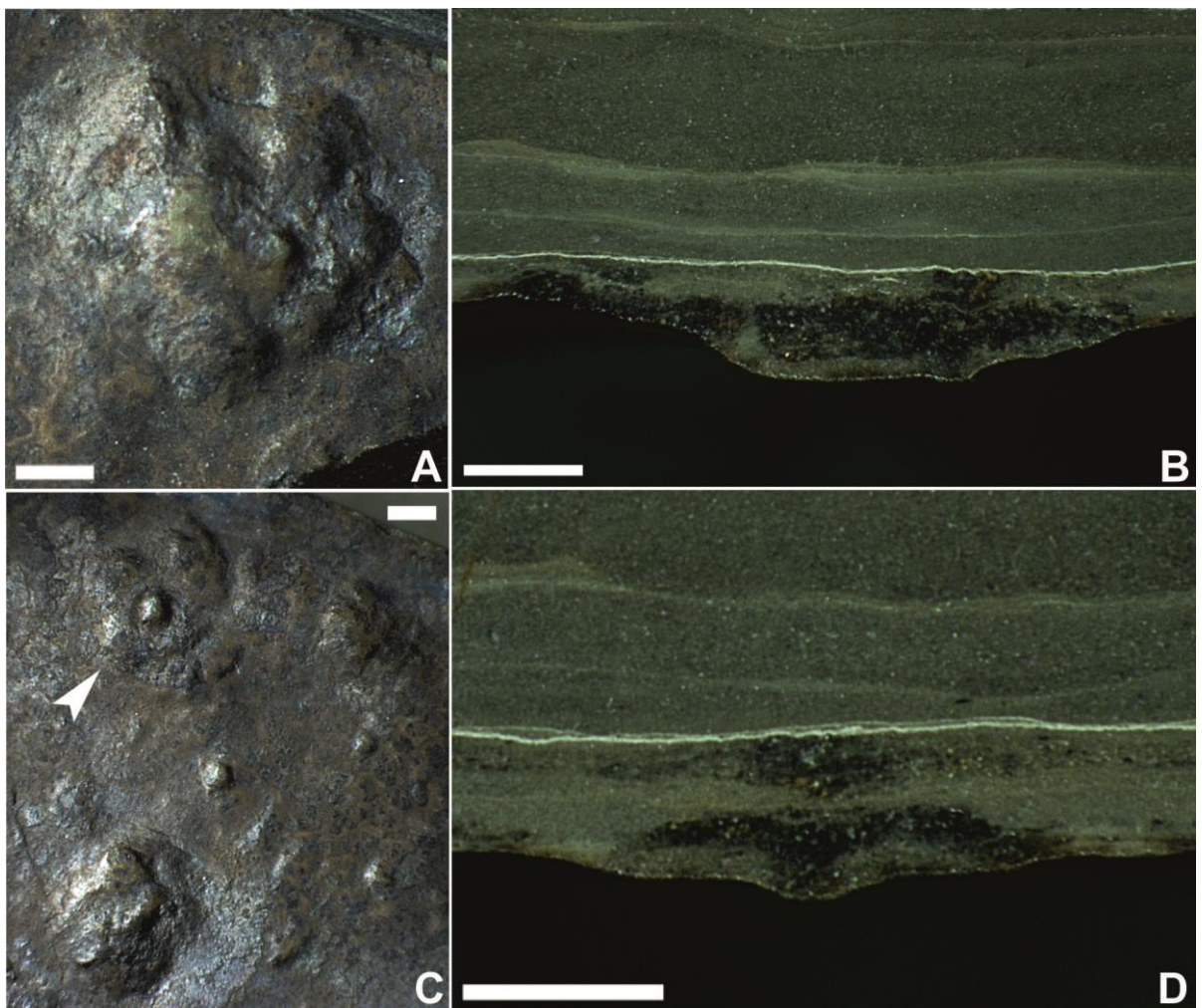


Fig. 2.7. Lobed Longmyndian *Medusinites* on bed soles in cross-section. **A:** Irregular lobed form with five lobes, abutted against mound. **B:** Ground cross-section through disc shown in A. **C:** Several *Medusinites* showing lobate tendency, together with isolated pimples. **D:** Ground cross-section through *Medusinites* with lobes arrowed in C. L-AH/10. Scale bars: 1 mm.

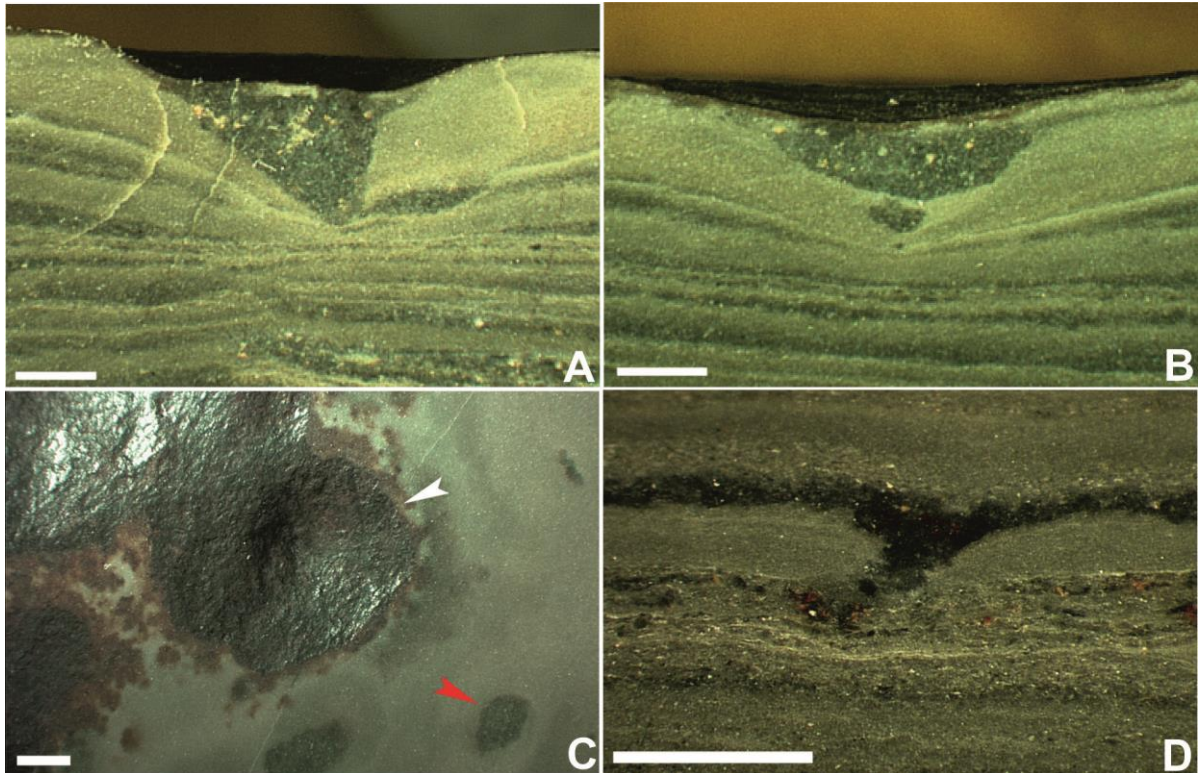


Fig. 2.8. A, B: Ground cross-sections through shallow, rimless depressions (Longmyndian *B. brunsa*), showing conical sandstone structures in laminae just below surface. Note distortion of laminae surrounding cone. **C:** Grinding of top surface parallel to bedding reveals wide top of cone and sill-like spread of sandy sediment directly below (white arrow). Note central dip in top of cone, and also small round dark patches to bottom and right of picture (red arrow), being cross-sections through vertical sand columns. **D:** Similar conical structures observed within ground cross-sections through blocks, such as this example, show cone extending as fine column and often linking to a lower sandstone bed. Note dip in centre of top of cone. OUMNH Á.2543. Scale bars: 1 mm.

2.2.3 Interpretation

The structures observed in cross-section strongly suggest small-scale injection of sand slurries. Features suggesting fluid escape processes include highly disturbed and torn laminae, fragments of green mudstone and white matgrounds entrained in lamina-cutting features filled with sandstone, and small sand volcanoes (Figs 2.3C–E; 2.4A; 2.6B, H; 2.9). The sediment deformation fits the pattern of injected (non-neptunian) clastic dykes and sills (cf. Dżułyński and Walton, 1965), but at a much smaller scale. Clastic dykes occur at scales of centimetres to many metres and are

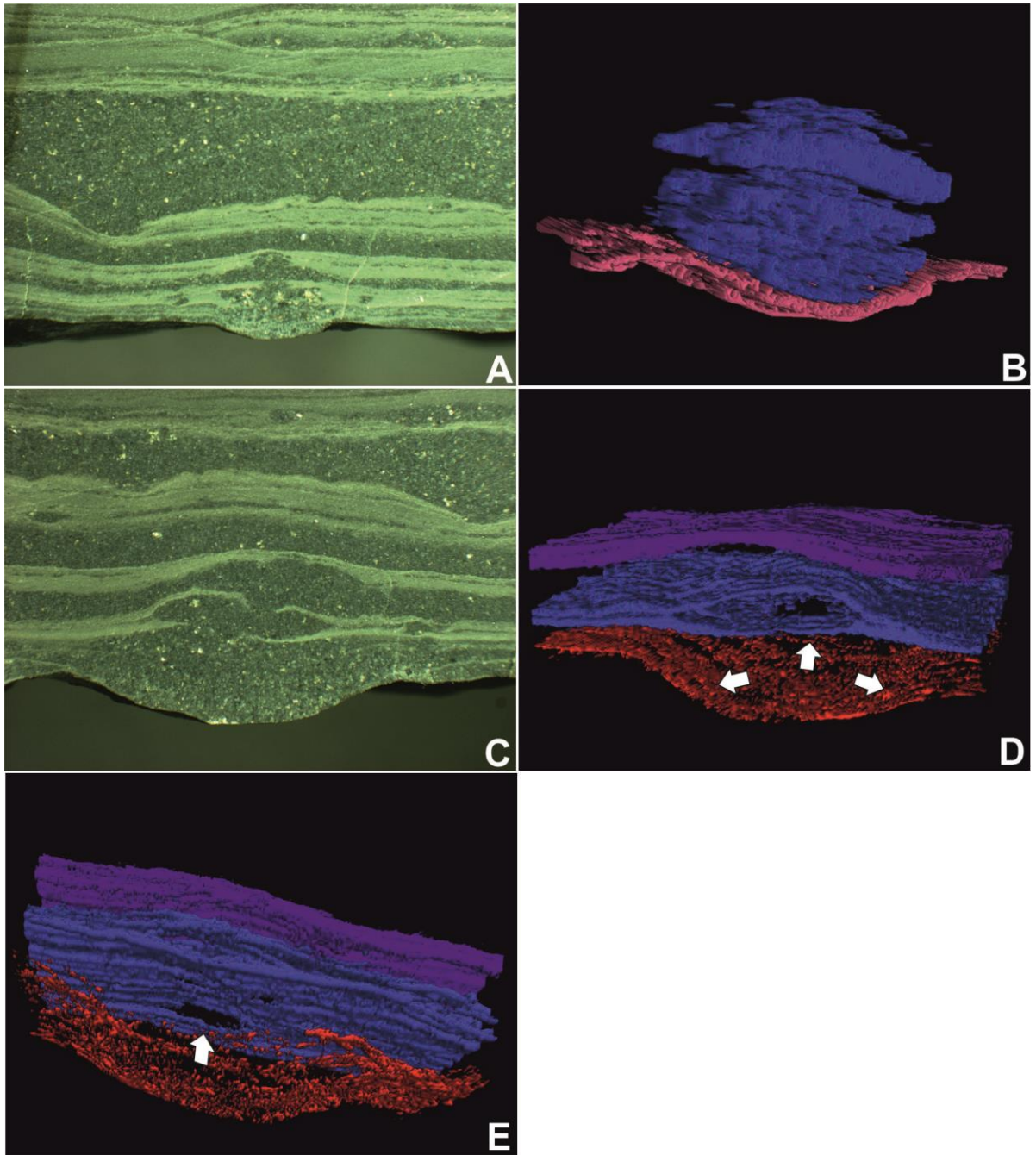


Fig. 2.9. 3D reconstructions of sediment injection features. **A:** Cross-section through small “Longmyndian *Medusinites*”. **B:** 3D reconstruction of central portion of feature in A. Base of block shown in pink; rising column of dark sediment-carrying fluid shown in blue. Note horizontal branches in fluid spread. **C:** Central portion of large mound-like “*Medusites*” shown in Fig. 2.6A, with broken laminae above. **D,E:** 3D reconstructions of central portion of feature in C, viewed from two different angles. Base of block shown in red; mudstone laminae shown in blue and purple. Note upwarping of laminae and hole torn in lower laminae at centre. Arrows indicate inferred movement of fluid, upwards and to sides, causing loading. See Appendix 2, Figs A2.8, A2.9 for images of individual cross-sectional slices through features. OUMNH Á.2543. 3D reconstructions produced using SPIERS software (Sutton et al., 2012). Scale bars: 1 mm.

usually associated with slumping and tectonic instability (Smith and Rast, 1958). Dykes and sills resulting from loading and sediment compaction are also known (e.g. Harazim et al., 2013), but these too are larger in scale. Small-scale dewatering structures on bed tops have been reported from regions of rapid sedimentation in some Ediacaran deposits (e.g. Farmer et al., 1991; Brasier and McIlroy, 1998). There is no evidence of slumping or rapid sedimentation in the upper Burway Formation. Apart from the small-scale disruptions, and occasional examples of low-angle cross-lamination, the laminae are plane parallel and suggest a low-energy, shallow-marine environment (Pauley 1986, 1990). The very small-scale (predominantly submillimetric) fluid injection features are here proposed to result from the influence of the microbial mats.

The effects of microbial mats on sediment sealing and fluid exchange in intertidal settings have previously been noted (Gerdes et al., 1994; Noffke, 2010; Schieber et al., 2007). In marine conditions, microbial mat sealing can also affect pore pressure in unconsolidated sediments, allowing the build-up of overpressure in sub-matground sediments (Harazim et al., 2013). The suite of features described here is considered to result from the dewatering of pore-water-rich unconsolidated sediments, driven by sediment loading and the sealing effect of microbial mats. Sediment injection, which occurs during compaction of sediments, requires the rise of pore waters at sufficient force to mobilize and entrain sediment grains (particulate fluidization), and tends to produce fluid-escape structures in fine-grained sands overlain by cohesive layers such as clay (Lowe 1975; Nichols et al.,

1994; Frey et al., 2009). Here, in spite of relatively quiet and stable conditions of sedimentation, the sealing effect of cohesive matgrounds on sediments that appear, from the examples of soft-sediment deformation, to have been pore-water-rich muds, would have been sufficient, it is proposed, to produce sediment injection on a small scale. The scale may also reflect the thin sedimentary laminae involved (<0.5 mm thick), which may have limited the amount of sedimentary material available for sediment injection during dewatering of any particular horizon.

The correlation of regions of high sediment disruption with indicators of decayed microbial matgrounds (see e.g. Fig. 2.4A) is consistent with the concept that mat sealing operated as a fundamental process in such sediments. In thin section, the interaction between matgrounds and pore-water-rich sediment evinces the role of mats in sediment sealing and in constraining and modifying the features of mobilized sediment (Fig. 2.4B and C). Intermeshed mat filaments are observed to surround loading structures and are inferred to influence their shape (Fig. 2.4B, C). Additionally, matgrounds appear to obstruct the upward injection of sediment columns (e.g. Figs 2.6D; 2.7B, D).

Microbial metabolism and necrosis are known to result in the build-up of gas in association with matgrounds, and may form such features as gas domes and pustules on the sediment surface, some of which may burst before burial (see e.g. Gerdes, 2007). The escape of such gases following sedimentation may have left paths for pore waters subsequently to follow during burial compaction. This may

explain the observation that fluid escape features often originate just above white matground laminae (Fig. 2.10). Another possibility is that, given the ability of matgrounds to block fluid escape from below, the maximum pressure experienced on which the fluid can act occurs just above each matground layer. Both factors may apply.

Upward injection and spread of sand slurries resulting from mat sealing is here inferred to have caused deformation of sedimentary laminae to produce loading structures on bed soles that have previously been attributed to *Medusinites* (Fig. 2.11). If sand slurry is injected with sufficient force to spread at stratigraphically higher levels than the preserved discoidal impression, the injection point may be preserved as a central boss (Figs 2.2A, 2.6C, D). Immediate spread of the sand slurry on injection results in loading of the whole injection area, producing a smooth mound on the bed sole (Fig. 2.6A, B).

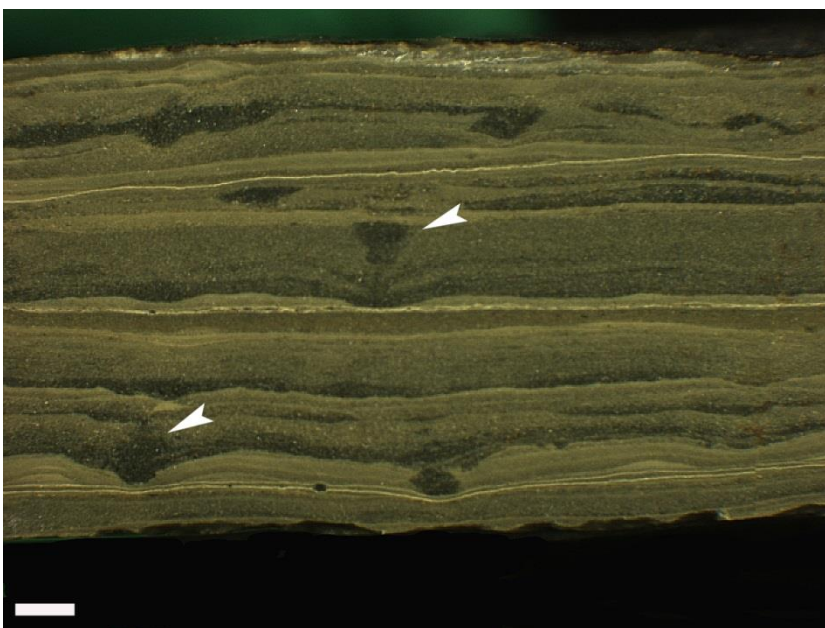


Fig. 2.10. Examples of fluid escape features originating just above white matground laminae (arrowed). For further discussion, see Section 2.4. Other dark sandstone features such as those at the top of the picture may result from loading. L-AH/Y. Scale bar: 1 mm.

Grinding of “*Medusinites*” counterparts from the Longmyndian confirms that a sandstone column extends below the centre of this structure, supporting the abiogenic injection model for creation of these features (Fig. 2.6E, F). Injections that rise without spreading produce isolated pimples on the bed sole (and counterpart pits on the top of the underlying bed) previously identified as *Beltanelliformis minutae* (Fig. 2.2A, C; Fig. 2.6G, H). Lobe formation around the injection point in some “Longmyndian *Medusinites*” is a subtle feature that appears to arise from the particular hydrostatic conditions of these fluid injections and the rheology of the sediment at the bedding plane in question. Without knowledge of the precise conditions of fluid injection, it is difficult to investigate such features experimentally. However, the significant point here is that the irregular and widening spread of sand slurry above the lobate forms rules out the possibility that these impressions are either body or trace fossils of Ediacaran organisms. Their abiogenic origin is hereby established.

The shallow rimless depressions formerly described as Longmyndian *Beltanelliformis brunsa*e and found on some top surfaces of upper Burway Formation beds can also be explained in terms of the same model. Fluid movement and sediment loading above pore-water-rich unconsolidated muds produces the inverted conical sandstone features observed in cross-section in the underlying laminae (Fig. 2.8A, B). The injection of sand slurry into overlying sediment results in

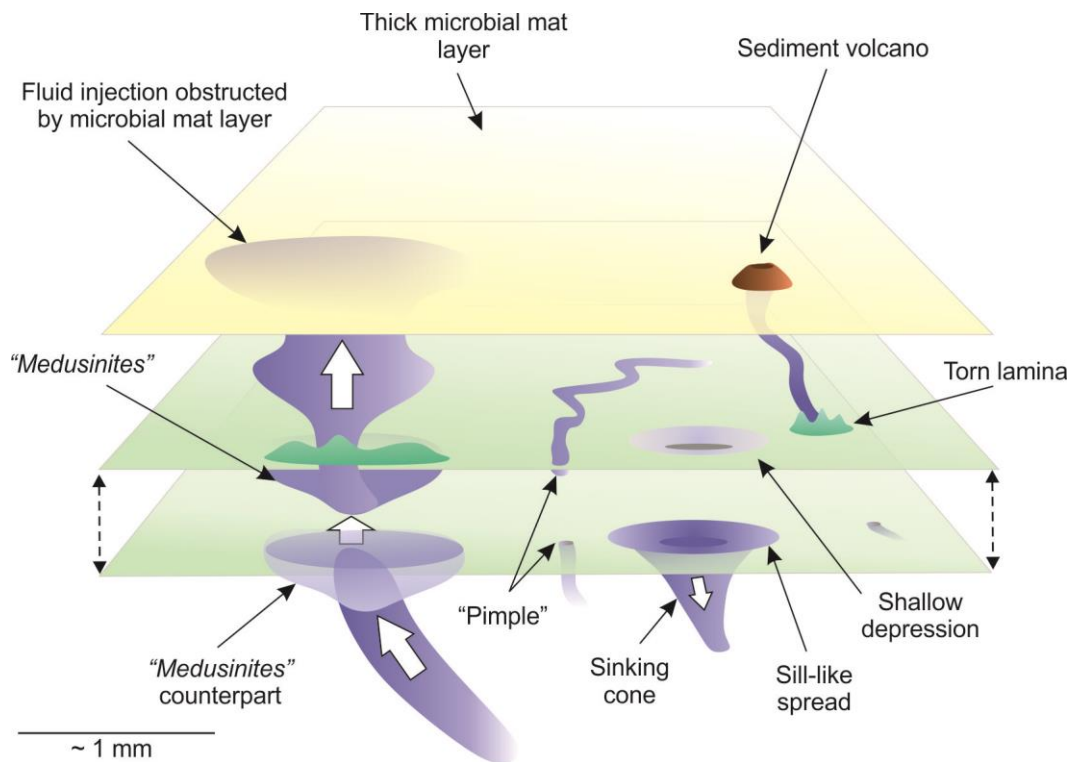


Fig. 2.11. Schematic 3D representation of proposed model for formation of *Medusinites*-like forms and shallow depressions in the upper Burway Formation. Exploded view of two contiguous surfaces at the bottom of the diagram (dashed arrows) shows markings on sole of bed and counterparts on top of lamina below. To left, “*Medusinites*” feature is formed by injection and spread of sand slurry, resulting in displacement and loading of sediment. The injected slurry rises until obstructed by a thick microbial mat layer. To right, shallow, *B. brunsa*-like depression is produced by sinking, through loading, of a conical sand body in lamina directly below. Formation of smaller scale “pimple” (“*B. minutae*”) and sediment volcano are also shown.

a small horizontal spread of sand slurry between laminae (Fig. 2.8C). This additional sand concentrated around the injection pipe is inferred to cause loading into the underlying unconsolidated pore-water-rich muds to produce an inverted cone with a central depression, causing distortion of laminae in the mudstone (Fig. 2.8A, B; Fig. 9). The presence of a sinking cone in a lamina just below the bedding surface causes the surface layer to drop (Fig. 2.8B), thereby producing the characteristic rimless depression of Longmyndian *B. brunsa* (Fig. 2.11).

This interpretation of the Long Mynd sediments explains many of the conical, columnar, and discoidal features seen in the Burway Formation as fluid injection structures rather than trace or body fossils (cf. McIlroy et al., 2005). The Longmyndian form of *Medusinites*, “*Beltanelliformis minutae*”, and the rimless depressions in the Burway Formation previously called *Beltanelliformis brunsa* can now confidently be regarded as pseudofossils. Since *B. minutae* was introduced based on this material it should now be considered to be an invalid name.

2.2.4 Conclusions

This study widens the range and scale of the dynamic influence exerted by microbial mats on Ediacaran sediments. Microbial mats are already understood to play a key role in capturing and promoting the rapid lithification of moulds of Ediacaran organisms, leading to their being cast by unconsolidated sandy sediment from above or below (the “death mask” scenario; Gehling, 1999). In that case, the movement of sediment is passive, filling the void resulting from the decay of the organism. In the model proposed here, the microbial matgrounds are considered to have had a dynamic effect on the underlying sediment, the sealing effect of matgrounds driving small-scale fluid escape and remobilization of unconsolidated sediment during sediment compaction.

As a consequence, at least some of the distinctive discoidal markings of the Long Mynd, markings whose biogenicity has been debated for over a century, are hereby shown to be pseudofossils: the mat-influenced surface expression of mat-sealing-

driven fluid escape. That several of the markings occur as positive impressions on sole surfaces is of particular relevance, as fluid-escape-related features are generally expected on bed tops, as sand volcanoes, so that positive hyporelief impressions are generally considered more likely to be biogenic.

The study also highlights the critical importance of examining ancient structures in cross-section. The small-scale mat-sealing-driven fluid injection features described here, summarized in Fig. 2.11, should now be sought in other matground-dominated palaeoenvironments. While such features may arise in any unconsolidated, fine sediments with microbial mat layers, Recent or ancient, their potential for producing abiogenic discoidal structures is particularly significant for interpreting Precambrian palaeobiology, palaeoecology, and taphonomy. In the light of this work, the biogenicity of some of the simple circular bedding plane impressions claimed as very old fossils, such as the “Twitya discs” (Hofmann et al., 1990), requires careful reassessment.

The association of a range of small discoidal impressions with the dynamic impact of microbial mats helps to explain their widespread occurrence in Ediacaran successions. With the restriction of microbial mats to areas of low metazoan activity following the onset of bioturbation (see e.g. Seilacher and Pflüger, 1994), equivalent textures and markings are uncommon after the early Palaeozoic. These discoidal markings reflect the unique conditions of the mat-dominated world before the Cambrian Explosion.

2.3 MICROBIAL MATS OF THE BURWAY FORMATION

2.3.1 A closer look at the white laminae

Examination of hand specimens from the upper Burway Formation in cross-section, combined with serial grinding, has revealed a variety of unusual sedimentary and microbial-mat-associated structures in addition to those described above. One specimen shows areas in which the grey-green mudstone is broken up into small blocks by fine dark channels which cut through the laminae, including one of the intermittent white layers (Fig. 2.12). These sedimentary fabrics may be related to local variations in the texture and softness of the unconsolidated mud combined with fluid escape. The white crinkly layer (two closely spaced layers in this case), initially thought to be a microbially colonized fine tuff, shows a cohesiveness in its broken pieces. In one part of the same specimen, a composite white layer comprising two close crinkly laminae is distorted upwards and broken, with the isolated pieces, which are forked at their ends, scattered along the mudstone lamina (Fig. 2.13). Cutting the block orthogonally confirms that this is a white lamina that has disintegrated in parts, and shows a stringy character (Appendix 2.4, Fig. A2.11).

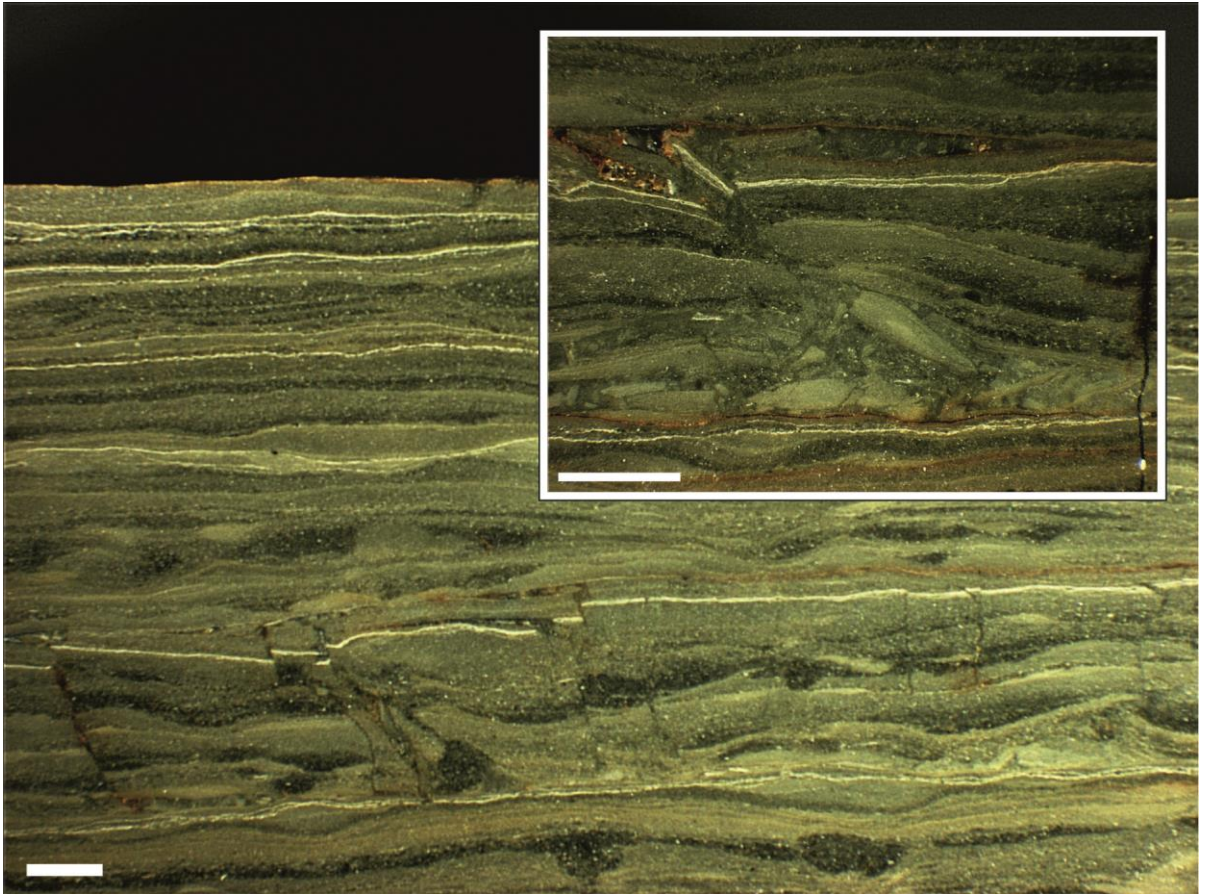


Fig. 2.12. Cross-section showing sediment disruption in upper Burway Formation rocks. Note dark channels and break-up of white layer in lower part of image. Inset shows detail of disruption from another part of same block. RCL-AH/7. Scale bars: 1 mm.

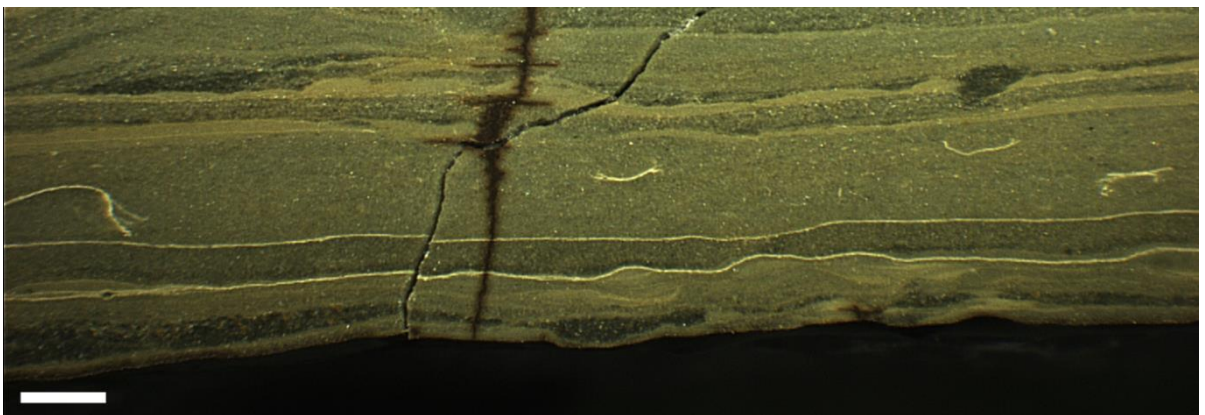


Fig. 2.13. Torn white layer, with fragments, in cross-section. RCL-AH/7. Scale bar: 1 mm.

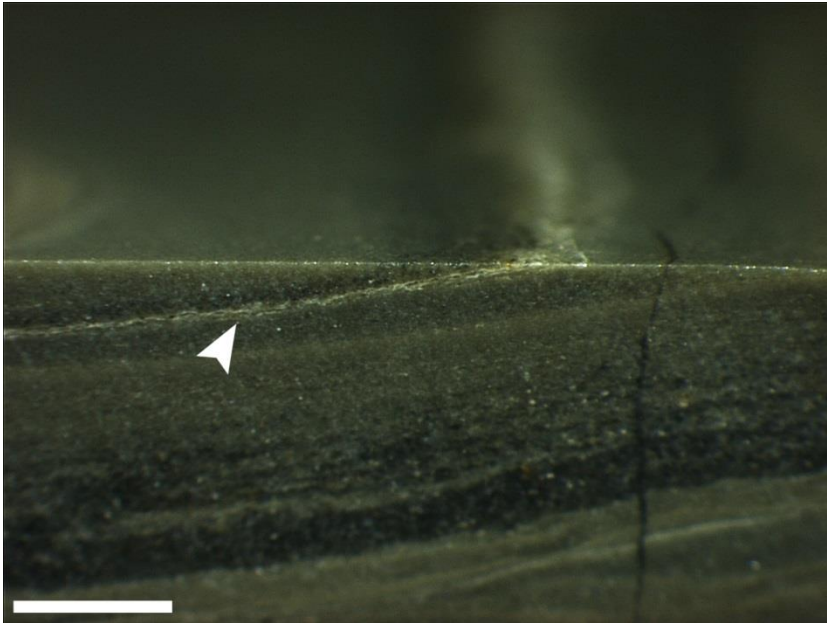


Fig. 2.14. Top of specimen ground to reveal top edge of crinkly white layer, arrowed in cross-section. L-AH/13. Scale bar: 1 mm.

To examine the nature of the white layers in more detail, specimens with a white lamina close to the top surface were hand ground at a slight angle to bedding so that part of the top of the white lamina was revealed (Fig. 2.14). Under the microscope, the thin crinkly white laminae are found to consist of intermeshed white microbial filaments (Fig. 2.15), together with black, carbonaceous material.

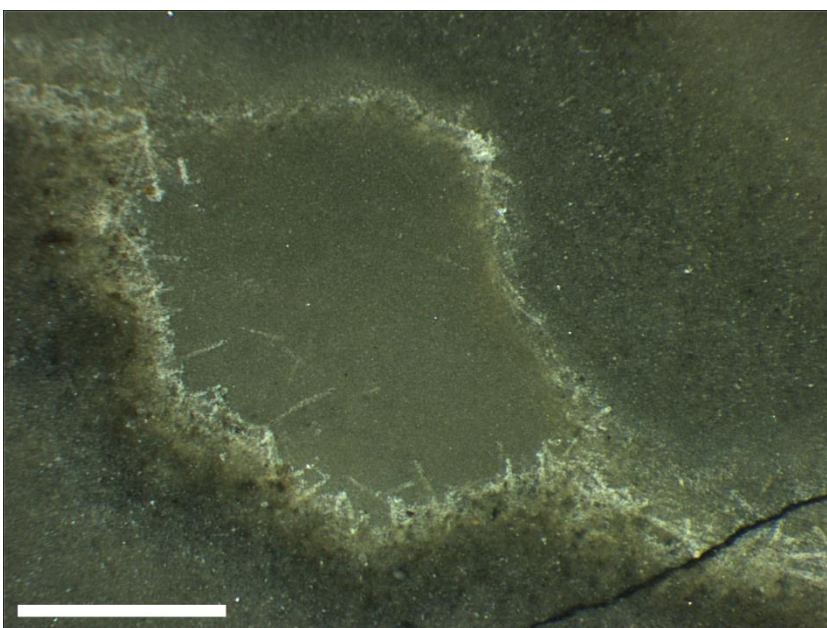


Fig. 2.15. Top edge of white crinkly layer shown in Fig. 2.14, viewed from above. L-AH/13. Scale bar: 1 mm.

White filaments and sphaeromorphs had been reported from tops of bedding planes in the Burway Formation by Peat (1984). Dense networks of white filaments preserved as an aluminosilicate, and making up a microbial matground, have been described by Callow and Brasier from within thin sedimentary laminae (Callow and Brasier, 2009). The white laminae are as a result of this study considered to consist entirely of the mineralized remains of microbial mats.

2.3.2 Longmyndian microbial communities

Close examination of the microbial filaments reveals several different morphologies. The tops of microbial mat layers are composed of straight to slightly curved, non-septate, unbranched white filaments of 20-25 μm width, some reaching over 1.5 mm in length. Possible sphaeromorphs, about 100 μm in diameter, are also observed, similar to those described by Callow and Brasier, although they may be large filaments at an angle to bedding seen in cross-section (Fig. 2.16; Callow and Brasier, 2009).

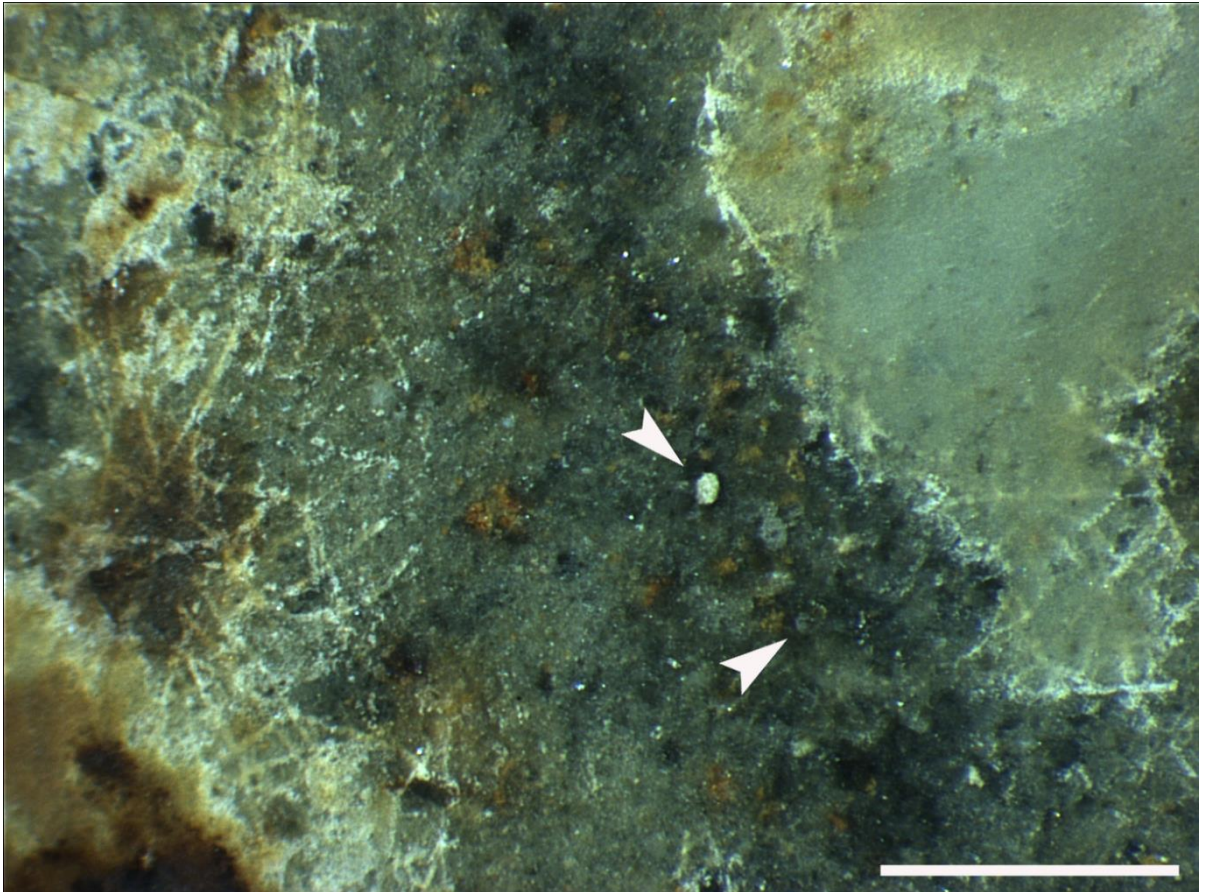


Fig. 2.16. Filaments and possible sphaeromorphs (arrowed) forming top of a white microbial mat layer, viewed from above. L-AH/10a. Scale bar: 1 mm.

A layer of more delicate filaments of ~6-10 μm diameter is revealed below the intermeshed straight filaments in some specimens, visible by grinding down the top surface at a slight angle to bedding, and in thin section (Fig. 2.17). The straight filaments reach several hundred micrometres in length. Among the finer filaments are occasional corkscrew-shaped forms (Fig. 2.18A), and others with club-shaped termini (Fig. 2.18B). Note that in thin section, the white filaments are opaque in transmitted light (e.g. Fig. 2.17B). At least some of Peat's "carbonaceous" filaments may in fact be the white filaments under transmitted light (Peat, 1984).

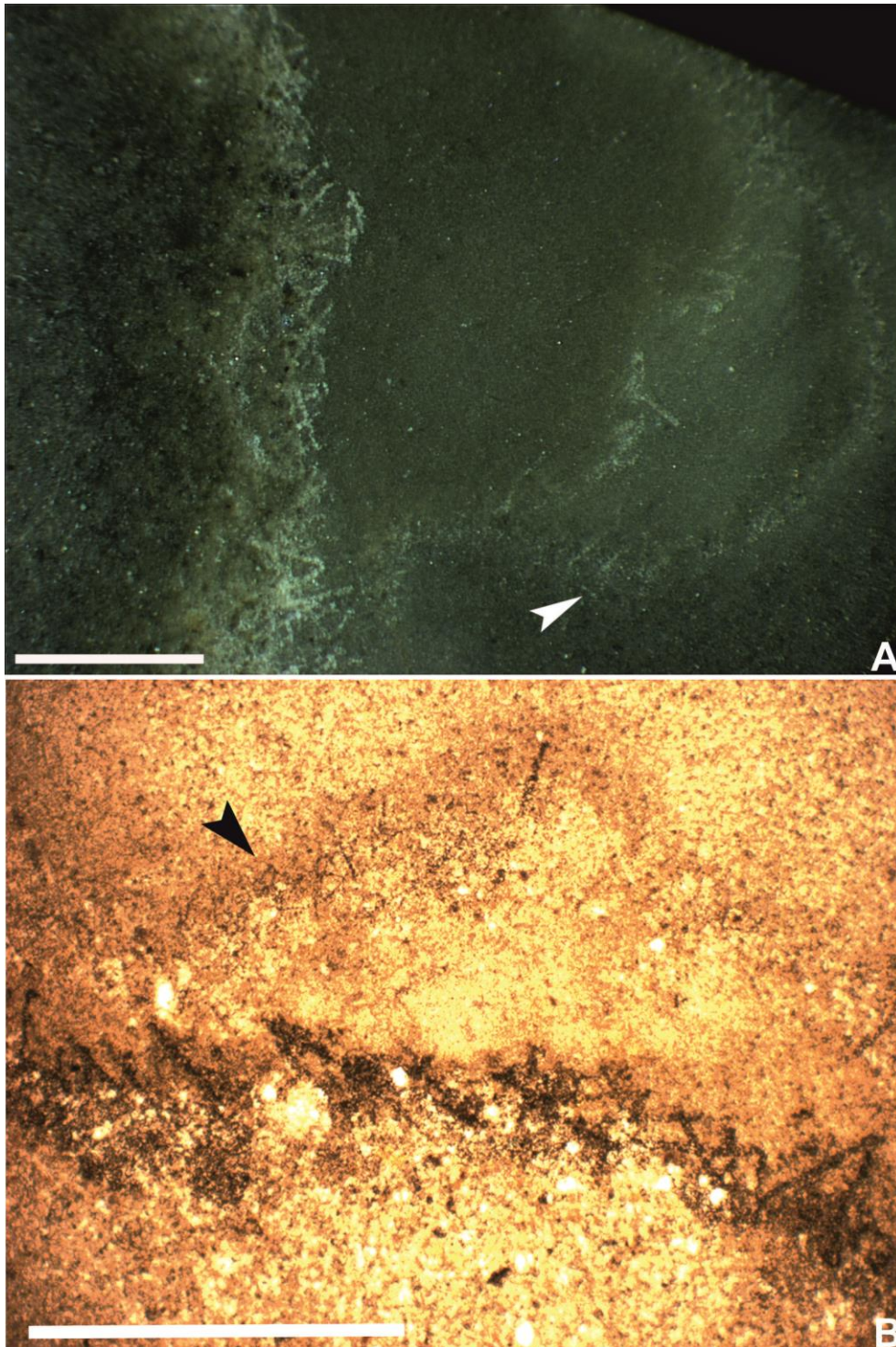


Fig. 2.17. Layering of microbial mats. **A:** A layer of fine filaments (arrowed) is visible below the straight intermeshed filaments of 20-25 μm diameter at far right of picture. View from above of top surface ground at a slight angle to bedding. **B:** The layer of fine filaments (arrowed) observed in thin section at slight angle to bedding. L-AH/13. Scale bars: 1 mm.

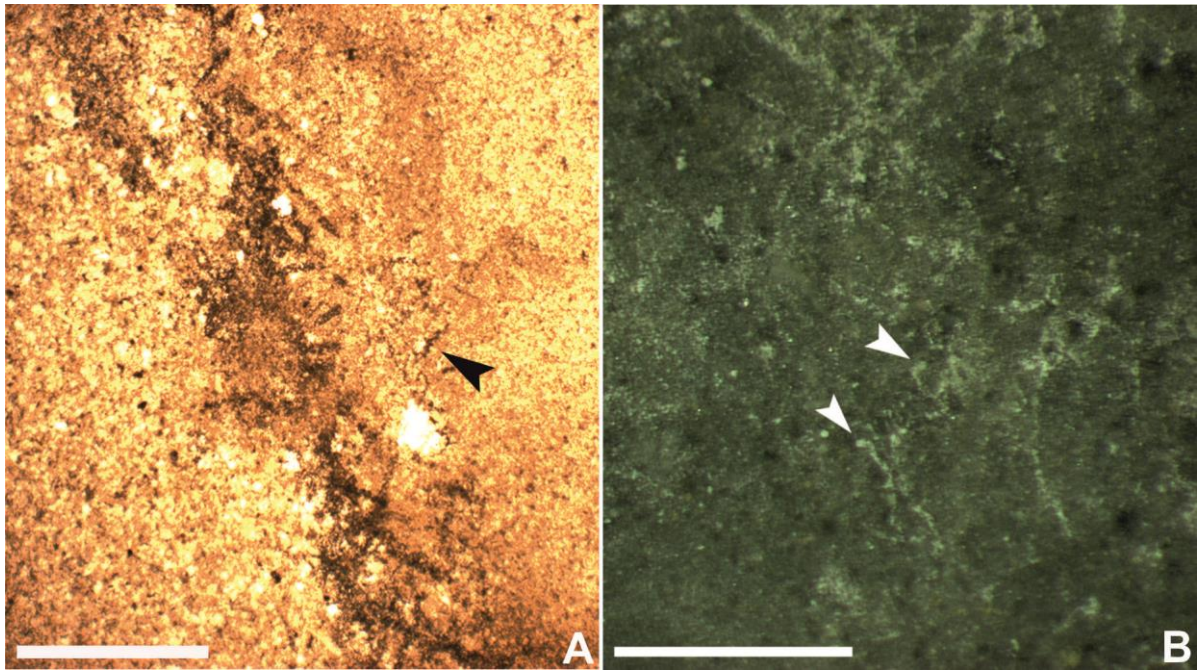


Fig. 2.18. **A:** Corkscrew-shaped form (arrowed) among the finer filaments, longitudinal thin section. L-AH/13. **B:** Fine filaments with club-shaped terminus. View from above. L-AH/2. Scale bars: 500 μm .

Isolated white filamentous forms are also observed on bedding planes, while others penetrate into the rock. The filaments may be sinuous, twisted, and folded, and can be tangled into knots (Fig. 2.19A). These are also generally $\sim 20\text{-}30\ \mu\text{m}$ diameter, matching the typical main mat-forming filaments seen in Fig. 2.15. Unlike the straight mat-forming filaments, however, one filament shows Y-branching, similar to an example described by Callow and Brasier (Fig. 2.19B; Callow and Brasier, 2009). Others apparently have T-branching (Fig. 2.19C), but this may be due to crossing filaments, one of which is partially out of the plane of section. Occasional wide filaments apparently composed of fused, fine threads are also observed (Fig. 2.19D). A final unusual filamentous form occasionally observed in both transverse and longitudinal thin section consists of a short or partially preserved filament of $\sim 14\ \mu\text{m}$ diameter extending from a wider, rounded terminus (Fig. 2.19E,F).

The more rigid filaments may be acicular crystals. However, examples captured end-on reveal that all these filaments were originally hollow (Fig. 2.20). In addition to the ~20-25 μm main mat-forming filaments, portions of much larger tubular filaments, some with diameters of ~ 40-50 μm , others of 80-100 μm , are observed to protrude from the surface, at a range of angles including perpendicular to the plane of the microbial mat (e.g. Fig. 2.20A-D). Some of the tubular filaments have a star-shaped central cavity of three to five narrow points (Fig. 2.20F).

Fig. 2.19. **A:** Twisted, folded, and other unusual filaments on top surface, seen from above. **B:** Example of Y-branching, top surface. **C:** Possible example of T-branching, top surface. **D:** Wide, "frayed" thread which appears to consist of fused fine filaments. Top surface. **E, F:** Short filaments of ~ 14 μm with larger, rounded terminus in thin section. **E:** Isolated example in longitudinal thin section, made at slight angle to bedding. **F:** Several such forms and rounded structures below a mat layer, seen as a dark band to top left. Transverse thin section. A-D, RCL-AH/4; E,F, L-AH/13. Scale bars: A-C: 1 mm; D: 500 μm ; E, F: 100 μm . ►

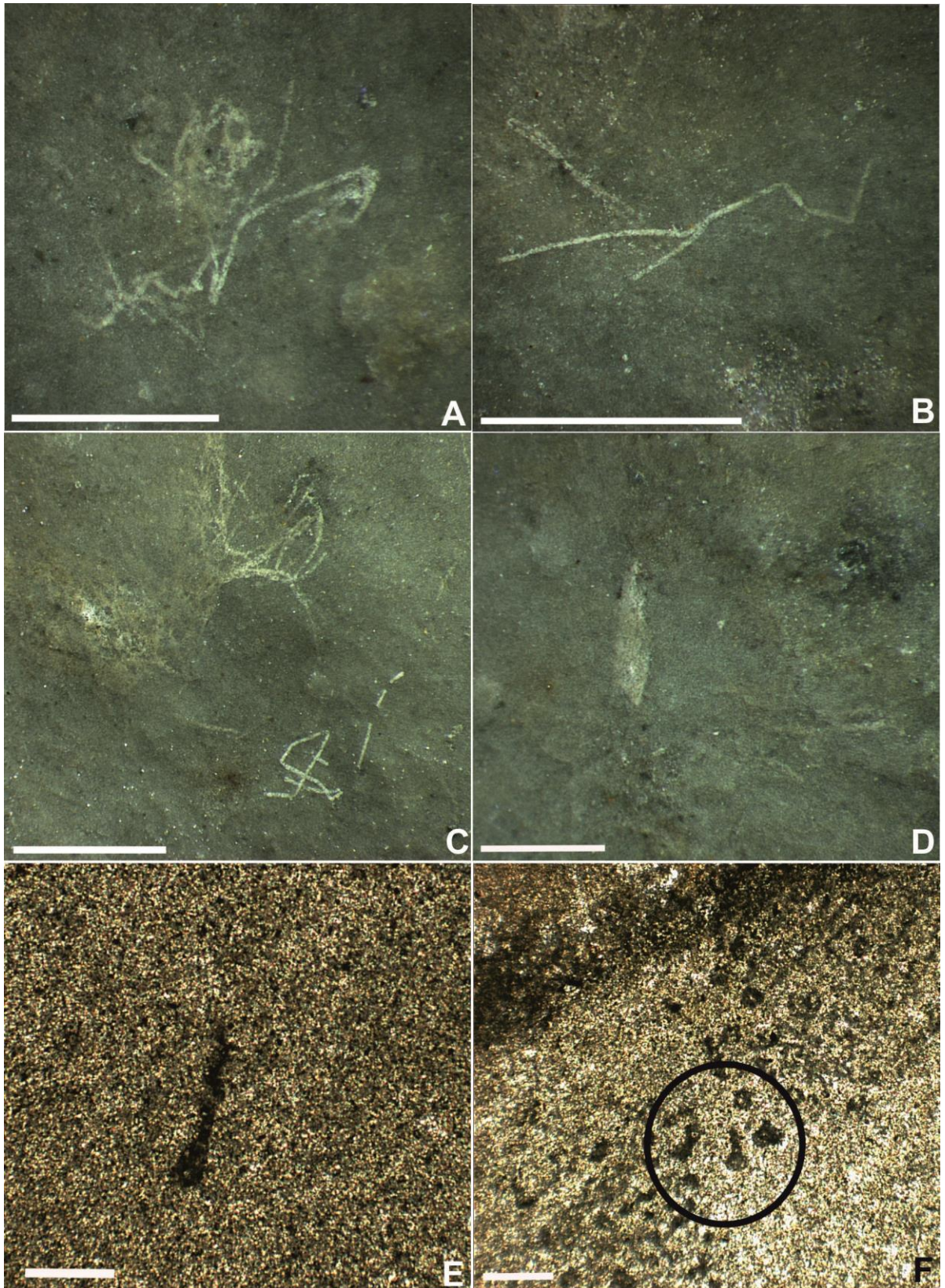


Fig. 2.19.

Element mapping using energy-dispersive X-ray analysis (SEM-EDX; Figs 2.21–2.24) reveals that some of the filaments are preserved not as an aluminosilicate (cf. Callow and Brasier, 2009) but as calcium carbonate (Figs 2.22–2.24; Appendix A2.5). In transverse thin section, bands of rutile grains are observed along the plane of some microbial mats, and an iron-rich band is also visible in some cases (Fig. 2.21; Appendix A2.5). In thin sections parallel to bedding, individual filaments of ~20–25 μm diameter are picked out in Ca and Ti (Fig. 2.22, 2.23). There are also suggestions of other structures rich in iron (Figs 2.22, 2.23) and the top of what appears to be a large Fe-rich tubular filament is observed in one case (Fig. 2.24).

Fig. 2.20. Evidence for tubular filaments. **A:** Large filament of 89 μm diameter (arrowed), distinctly tubular in cross-section, emerges at an angle from below a layer of ~20–25 μm filaments. Another large filament (also arrowed) can be faintly seen nearby. **B:** Top of filament of 89 μm diameter (left-hand arrow), with narrow central cavity, emerges at steep angle to the surrounding mat-forming ~20–25 μm filaments. Note the rounded terminus, with indication of a ridge at the start of the main tube. A smaller tubular filament with a simple open terminus is seen to right (right arrow). **C:** Another example of a filament of 89 μm diameter with terminus identical to that in B (arrowed). **D:** Cluster of tightly packed tubular filaments of ~40 μm diameter seen end-on (circled). A larger tubular filament, of 78- μm diameter is arrowed, and several others are visible. **E, F:** Examples of tubular filaments of the ~20–25 μm , mostly straight, mat-forming type. The arrowed filament in E shows an oblique, extended central cavity. Several filaments with star-shaped centres with three or four points are seen in F (arrowed). Fine tubular filaments seen at bottom left are ~10 μm in diameter. A–D, L-AH/10; E, L-AH/13; F, L-AH/2. Scale bars: A, E, F: 500 μm ; B, C, D: 1 mm. ►

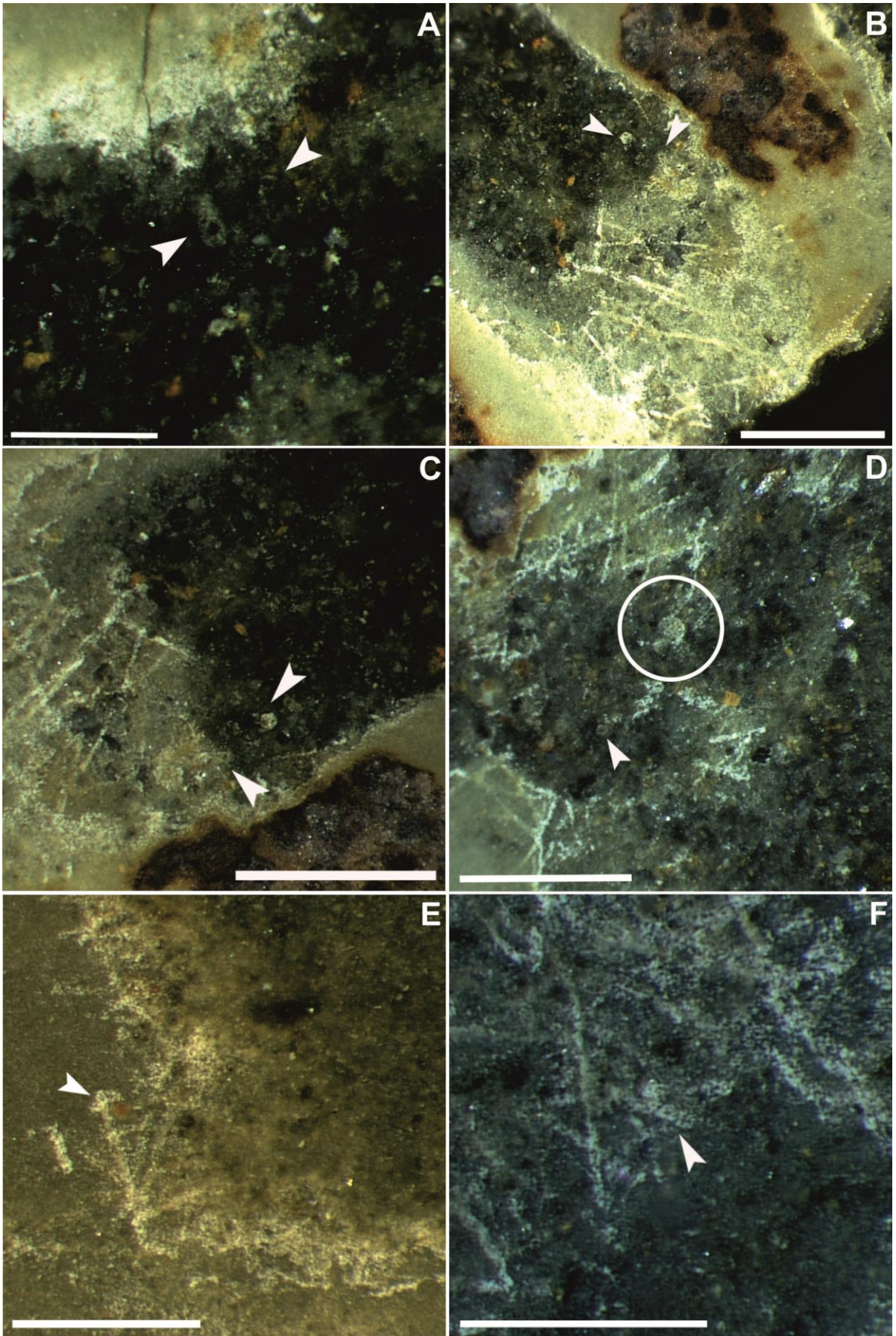


Fig. 2.20.

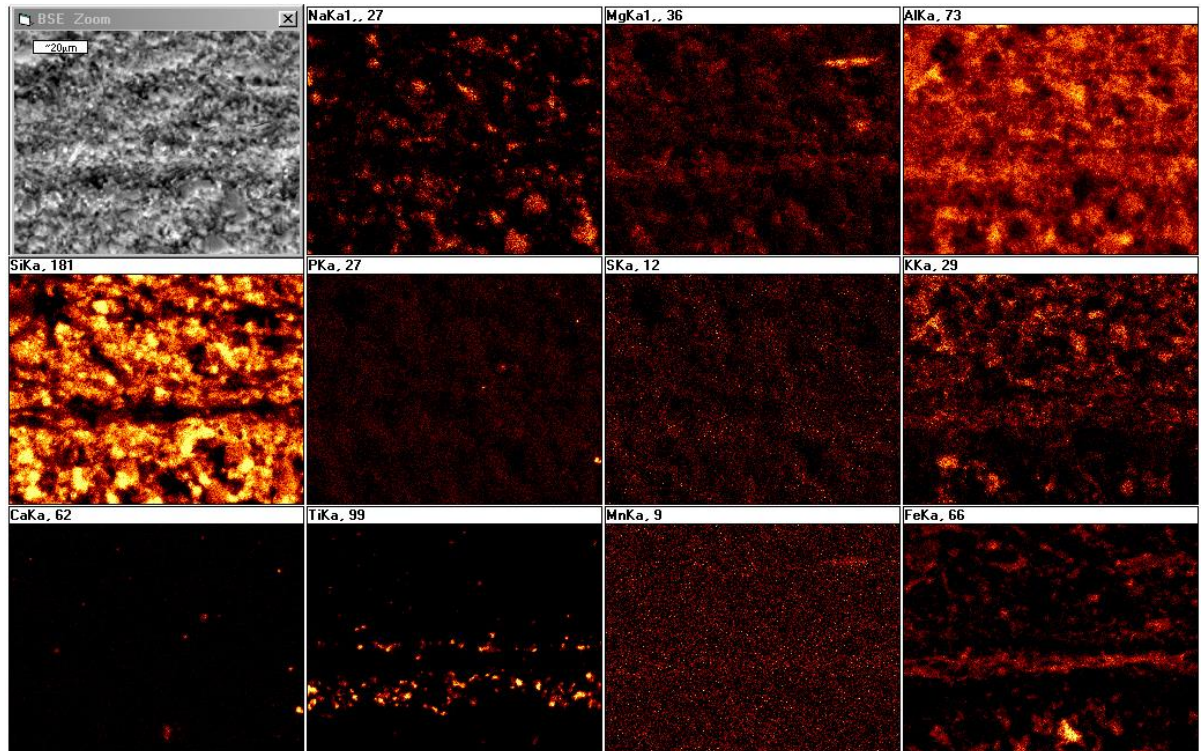


Fig. 2.21. SEM-EDX mapping of portion of transverse thin section through a microbial mat layer. Two lines of small, bright rutile crystals may be made out in the backscattered electron (BSE) image at top left. The titanium alignment along the mat plane is visible in the Ti element mapping in the bottom row. Note also the band of Fe-rich material that appears between the two Ti-rich layers. The calcium signal is also high, but the element distribution is not clearly visible in this image. L-AH/10a. Acceleration voltage 20 kV, probe current 10 nA.

2.3.2 Preliminary conclusions

The microbial mats of the upper Burway Formation contain microbial forms similar to those described also from the overlying Lightspout Formation and the underlying Stretton Shale by Peat, and Callow and Brasier (Peat, 1984; Callow and Brasier, 2009), with branched and unbranched forms alongside possible sphaeromorphs. Detailed examination has revealed several further morphologies and provided clues concerning their relative arrangement (Table 2.2).

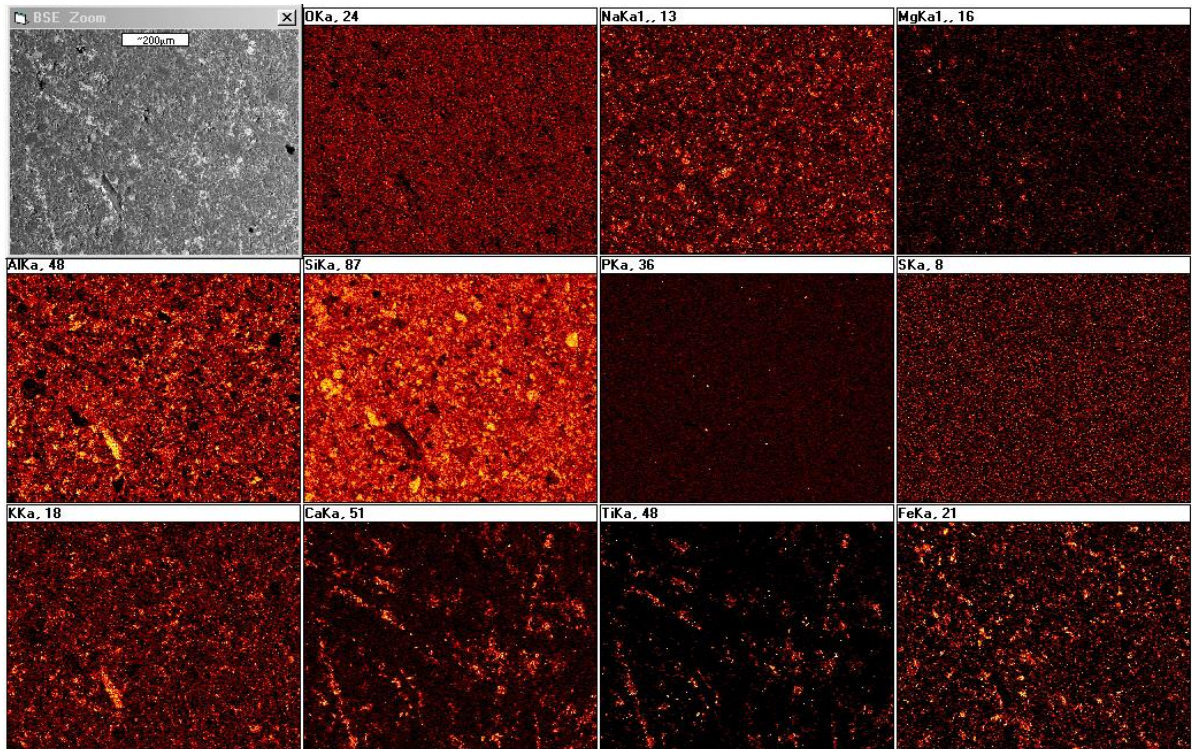


Fig. 2.22. SEM-EDX element mapping of longitudinal thin section made at slight angle to bedding. Filaments of $\sim 20\text{-}25\ \mu\text{m}$ are picked out in the Ca and Ti maps. There are suggestions of other, Fe-rich structures too. (Al- and K-rich feature to lower left may be a foreign object on the slide.) L-AH/2b. Accelerating voltage 20 kV, probe current 10 nA.

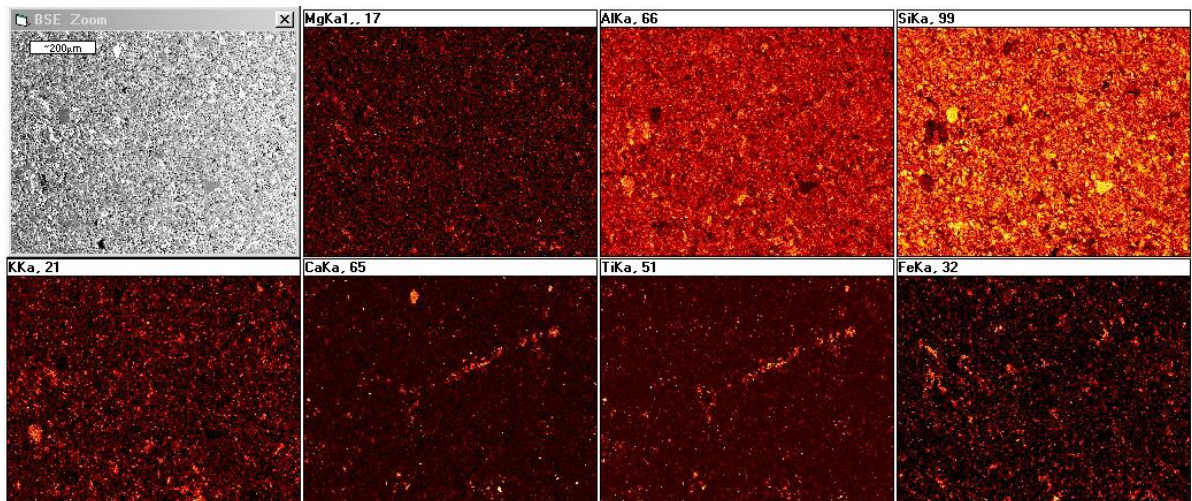


Fig. 2.23. SEM-EDX element mapping of longitudinal thin section. A single filament of $\sim 23\ \mu\text{m}$ is picked out in Ca and Ti. Again, there are suggestions of filaments in the Fe mapping. L-AH/2b. Accelerating voltage 20 kV, probe current 10 nA.

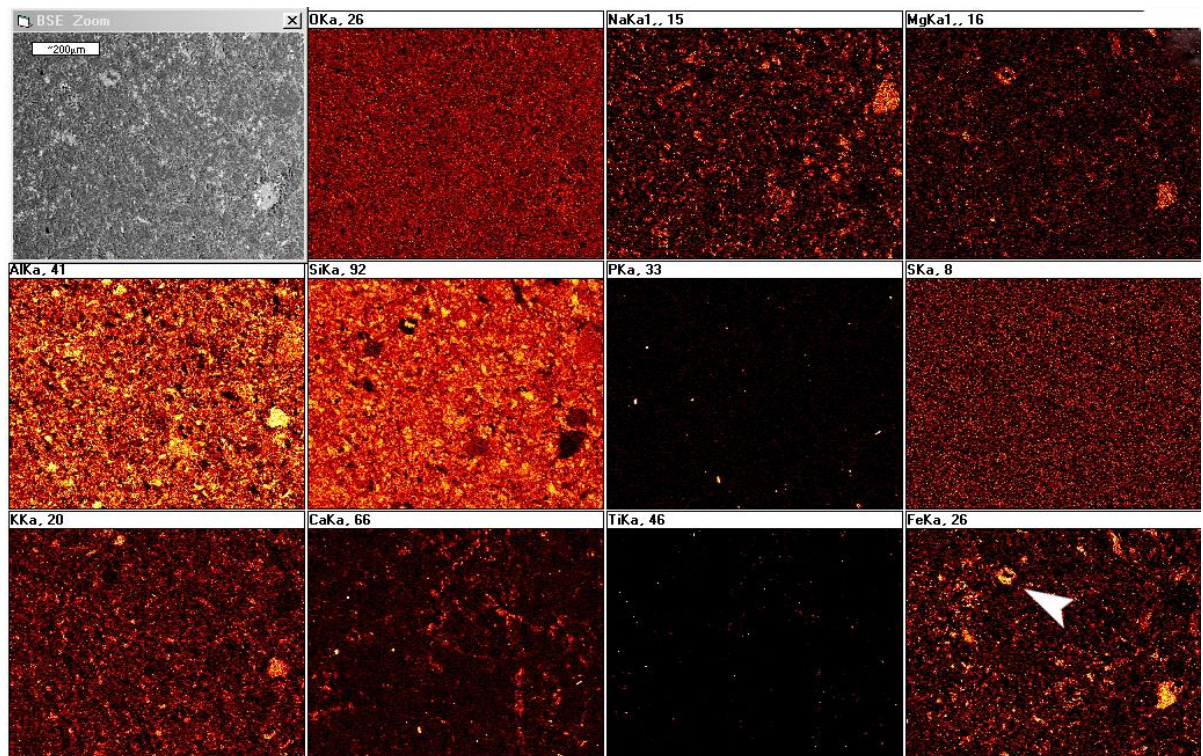


Fig. 2.24. SEM-EDX element mapping of longitudinal thin section. In addition to filaments of $\sim 20\text{-}25\ \mu\text{m}$ diameter picked out in Ca (Ti count is also high but mapping is not clearly visible here), what appears to be a large tubular filament of $\sim 60\ \mu\text{m}$ diameter, aligned almost orthogonal to the mat plane, is clearly picked out in the Fe mapping (arrowed). Note dearth of sulfur in all these mappings. L-AH/2b. Accelerating voltage 20 kV, probe current 10 nA.

Importantly, two distinct layers can be identified in the mat, an upper layer with generally straight filaments of $\sim 20\text{-}25\ \mu\text{m}$ diameter, and a lower layer with less rigid filaments of $\sim 6\text{-}10\ \mu\text{m}$ diameter. A separate component consists of larger filaments, reaching up to $\sim 100\ \mu\text{m}$ in diameter, cutting the mat plane at angles up to 90° . All these filaments appear to have been hollow, and therefore clearly biological.

Elemental analysis with SEM-EDX indicates that some of the main mat-forming filaments of $20\text{-}25\ \mu\text{m}$ diameter are probably preserved as calcite (since there is virtually no apatite or other likely Ca compound). Their dark appearance in thin section in transmitted light suggests that the calcite is in the form of micrite.

	Filament type	Diameter (approx. μm)
1	Straight to slightly curved, square terminus, unbranching, in mat plane, length up to at least 1.65 mm measured	20–25
2	Fine, straight to curved, unbranched, square terminus, in mat plane, 200-400 μm length	6–10
3	Fine, flexible, with club-shaped terminus, in mat plane	6–10
4	Fine, corkscrew-shaped, square terminus (?), in mat plane	6–10
5	Larger filaments, unbranched, at angles up to orthogonal to mat plane	40–60
6	Large, unbranched filaments, at angles up to orthogonal to mat plane, two examples show rounded, ridged terminus	85–100
7	Twisted, folded filaments, occasionally branched, isolated from main mat, varying angles to bedding	20–25
8	Possible sphaeromorphs	100

Table 2.2. A summary of microbe morphologies observed in the Burway Formation in this study. Categories 5 and 6 may form a single broad range for the large filaments. Lengths of filaments in categories 3–8 are uncertain as they disappear into the rock.

(There may also be carbonaceous matter, as suggested by Peat (1984).) Given their size, and the fact that they were hollow, a plausible interpretation would be that this component consists, at least in part, of the calcified sheaths of cyanobacteria.

Sheath-calcified cyanobacteria are rarely found in the Proterozoic (Knoll et al., 1993; Riding, 2006). One of the earliest reports of calcified cyanobacterial sheaths is from the stromatolites of the ~750-Ma Draken Formation, Spitzbergen, Greenland (Swett and Knoll, 1985; Knoll et al., 1993). Reports are then scarce until the Precambrian-Cambrian boundary (Riding, 2006). The precipitation of CaCO_3 on cyanobacterial sheaths may be stimulated *in vivo* by the fixing of carbon by photosynthesis (see e.g. Arp et al., 2001). Calcification of sheaths occurs only in certain conditions. It is dependent on: 1) the CaCO_3 saturation state of the seawater; 2) the dissolved inorganic carbon (DIC), associated with the atmospheric partial pressure of CO_2

($p\text{CO}_2$); and 3) the presence of sufficient Ca^{2+} in the waters surrounding the cyanobacteria (Arp et al., 2001; Riding, 2006). The scarcity of calcified cyanobacteria until close to the beginning of the Cambrian has been widely debated, but may be associated with changes in seawater chemistry and development of CO_2 -concentrating mechanisms by cyanobacteria (Knoll et al., 1993; Riding, 2006). The presence of calcified cyanobacteria in 560-Ma rocks is therefore of wider significance in understanding palaeoenvironmental changes in the Earth system at the end of the Neoproterozoic.

The close association of titanium to these calcified filaments remains puzzling. It may be a diagenetic effect, or may possibly represent enrichment of Ti by the microbes. The question merits further investigation.

Element mapping by SEM-EDX shows iron-coated tubular structures $\sim 60 \mu\text{m}$ in diameter, which is consistent with the observations of large filaments orientated at an angle to the plane of the microbial mat (Fig. 2.20). Some cyanobacteria are known to concentrate iron on their sheaths (Stal, 1994), so it is possible that these filaments represent a different form of cyanobacterium. The reason for their arrangement at an angle to the plane of the main microbial mat layers is presently unclear. It may be possibly be due to accretion of the sediment-water interface.

Any microbial components preserved in an aluminosilicate mineral, as described by Callow and Brasier (2009), would be difficult to discern in X-ray mapping against

the strong Al and Si signals of the surrounding clay matrix. At least some of the white filaments reported by them to be preserved as an aluminosilicate are shown here to be calcified. Carbonaceous material is also difficult to detect by SEM-EDX and may well be present. Carbon is indicated in spot spectra of dark patches in thin sections.

The isolated, branched filaments are suggestive of fungal hyphae (Callow and Brasier, 2009; Fig. 2.19B). However, those described by Callow and Brasier (2009) were on tops of beds, and the examples described here were found close to a parting, although grinding parallel to bedding indicated that they penetrated at least 2 mm into the rock. Caution is necessary to rule out contamination by modern fungi that may have penetrated partings at any time following exposure of the rock. Further work will be necessary to confirm that these are original structures. However, their penetration of the rock and comparable size to filaments observed in the mineralized mat suggest that they are authentic components of the Ediacaran mat community of the Burway Formation. The partial filaments with a rounded terminus seen in thin section, sometimes in isolation (Fig. 2.19E,F), offer an intriguing possibility in this regard: at a width of 32 μm , these round forms are within the range of fungal spores that, given the presence of short extensions, may have been captured in the process of germination. These forms are significantly larger than the 17- μm -diameter club-shaped heads of 10- μm filaments seen within the microbial mat layer, which are part of the consortia of fine filaments that make up the matground fabric (Fig. 2.18B).

The Burway Formation rocks evidently host a complex microbial community with several components. The three-dimensional architecture of the mat remains to be explored, and may be approached using micro-CT and other tomographic techniques. Further work will hopefully lead to the characterization of several of the microbial components. That list of components to the microbiota is likely to include fungi as well as calcified cyanobacterial sheaths.

A curious aspect is the apparent lack of pyrite in these rocks. The sulfur signal in SEM-EDX is low. Yet in shallow marine sediments with plenty of iron and cyanobacterial mats, sulfate-reducing bacteria and methanogenic bacteria would be expected. The dearth of sulfur requires sedimentological investigation and may force a re-interpretation of the palaeoenvironment in which these rocks were laid down, perhaps as freshwater (D. McIlroy, pers. comm.).

A final point of interest regarding the Burway Formation is the similarity of its suite of features, microbial mat and MISS, with those of the 1-Ga Diabaig Formation, Torridon Group, Scotland. The latter, interpreted as lacustrine, and deposited in very shallow water, also has microbial textures, Arumberia (the ridges formerly known as "*Arumberia banksi* Glaessner and Walter 1975", now interpreted as a form of MISS; see McIlroy and Walter, 1997), "pimples" on top surfaces interpreted as small gas domes, and discs described as *Beltanelliformis* (Callow et al., 2011a). The Diabaig sediments also have laminae of mudstone and fine-grained sandstone that contain structures that are likely to be mat-driven fluid escape features akin to those

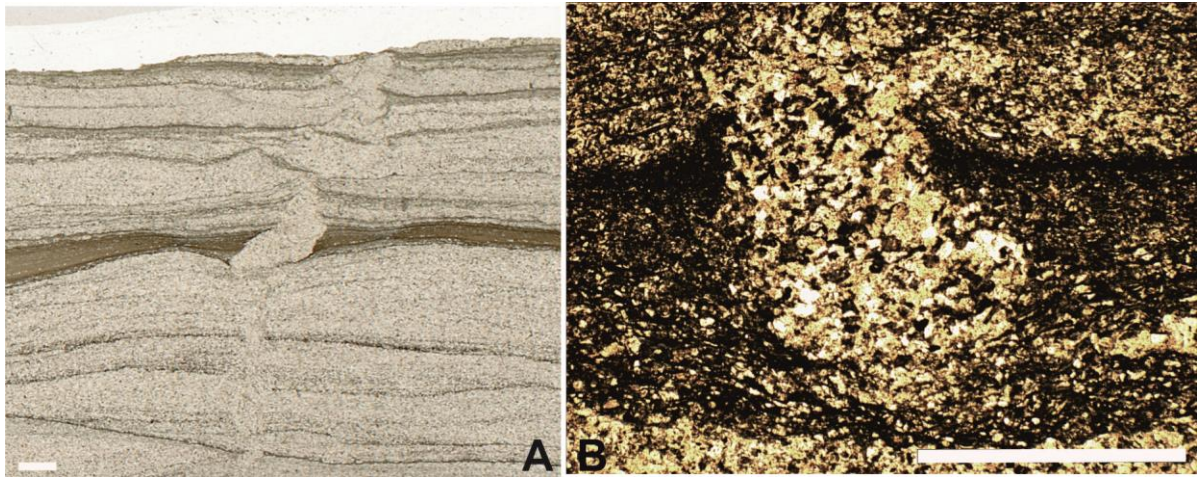


Fig. 2.25. A: Petrographic thin section from 1-Ga Diabaig Formation, Torridon Group, Achiltibuie, north-west Scotland, showing fluid escape structure of pale sandstone cutting through siltstone laminae. OUMNH Á.2596/p6. **B:** Detail of another small fluid escape feature from same locality. Dark layers show 45°-angled filaments and trapped grains suggestive of a microbial mat. OUMNH Á.2596/p7. Scale bars: 1 mm. Pustules are seen on tops of beds in this formation, as well as widespread microbial mat fabrics (Callow et al., 2011a; fig. 11c). Thin sections from the Martin Brasier Collection, Oxford Museum of Natural History. Scale bars: 1 mm.

described above (see Callow et al., 2011a, fig. 6D; Fig. 2.25). Systematic comparison of the Longmyndian rocks and their microbes with those of the Torridon - far older and freshwater - may shed further light on the nature of Precambrian matgrounds, their composition, and their involvement in the formation of a variety of discoidal markings.

2.4 THE NATURE OF LONGMYNDIAN *INTRITES*

The first section of this chapter explained several types of discs observed in the upper Burway Formation - “Longmyndian *Medusinites*”, “Longmyndian *Beltanelliformis brunsaе*”, and “*B. minutae*” - as pseudofossils resulting from microbial-mat-influenced fluid injection and loading. One other type of discoidal impression also seen in these rocks has so far been omitted from the discussion: the

Longmyndian disc described as a form of *Intrites punctatus* Fedonkin (McIlroy et al., 2005; Fedonkin et al., 1980). This discoidal taxon is somewhat different from the others, and new observations of its structure and an interpretation are given below. It should be emphasized that this discussion refers purely to the Longmyndian form described as *Intrites* and not the type material.

2.4.1 The morphologies of Longmyndian *Intrites*

The discoidal *Intrites*-like form described from the Long Mynd is unusual in having the same morphology on the soles and tops of beds – as both positive epirelief and positive hyporelief (Fig. 2.26). There is little size variation within the *Intrites*-like material, which is generally 2–3 mm in diameter, with rare examples reaching 4 mm. This morphotype appears in a continuum of forms, from a raised mound with a small central depression to broad, low-relief ridges forming an incomplete ring around a wide central flat area (Fig. 2.27). In some cases instead of arcs forming an incomplete ring, Longmyndian *Intrites* can be found as paired, almost straight

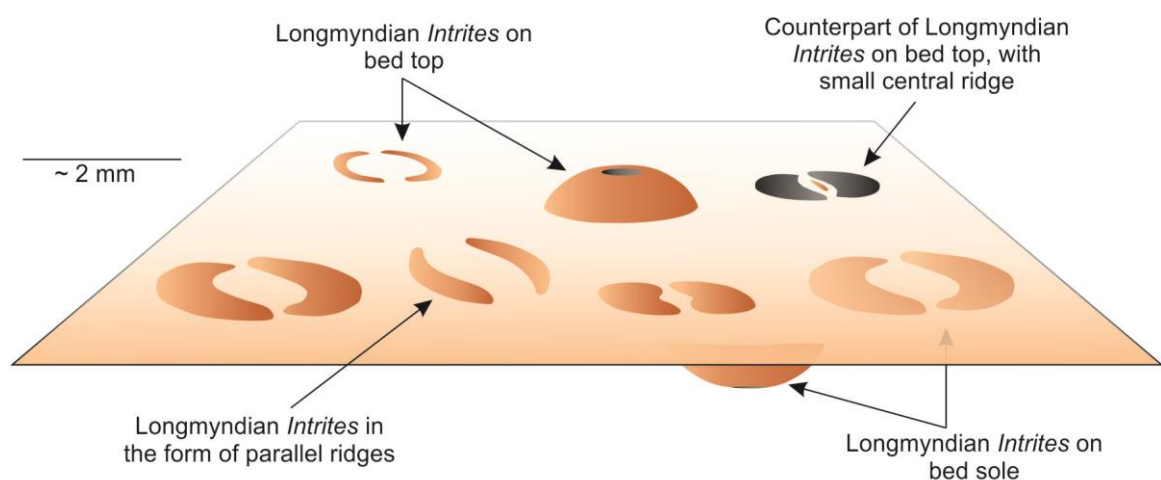


Fig. 2.26. Summary of different morphologies of Longmyndian *Intrites*. See also Fig. 2.27.

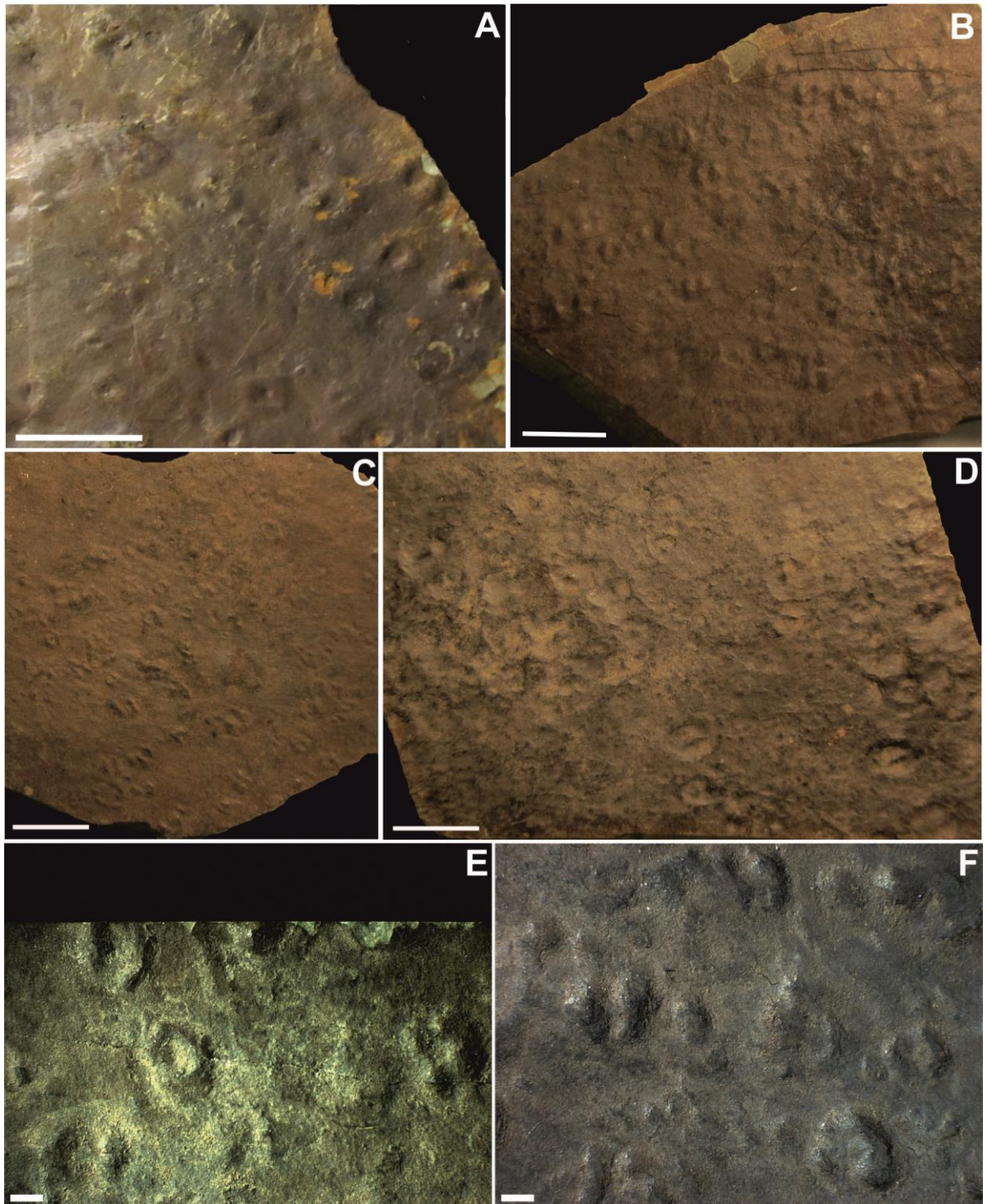


Fig. 2.27. Various forms of Longmyndian *Intrites*. **A:** On bed sole, both as raised rings with flat centre, and as mounds with central depression. OUMNH Á.2544. **B:** On bed top, as raised mound with central depression or two slightly curved parallel ridges. RCL-AH/3. **C:** On bed sole as relatively narrow rings and parallel ridges. RCL-AH/5. **D:** Counterparts on top surface as gentle negative impressions with central peaks or ridges. RCL-AH/4. **E, F:** Close ups of portions of specimen in C, sole surface, with complete and near-complete ring-like forms (E) and approximately aligned ridges and pairs of arcs (F). RCL-AH/5. Scale bars: A–D, 1 cm; E, F, 1 mm.

ridges (Fig. 2.27C, F). Counterparts of the *Intrites*-like form typically appear on bed tops as negative impressions with a central peak or ridge (Fig. 2.27D). *Intrites*-like discs are usually found in clusters on bedding planes. Interestingly, they are not found alongside the ridges of *Arumberia* (McIlroy and Walter, 1997; McIlroy et al., 2005). They are sometimes seen in association with “Longmyndian *Medusinites*”, but generally occur without other taxa in dense aggregations on bedding planes.

2.4.2 Longmyndian *Intrites* in cross-section

To gain insight into its nature, this subtle and variable feature needs to be examined in cross-section. A number of hand specimens from the upper Burway Formation with *Intrites*-like forms on top or sole surfaces were sectioned and serially ground. On top surfaces, Longmyndian *Intrites* can look similar to collapsed gas domes or sediment volcanoes in being raised structures with central depressions, although the crater flanks are more rounded than the conical shape typical for either of these explanations. Given the small-scale fluid escape that characterizes these rocks (see Section 2.2), Longmyndian *Intrites* might be expected to be a typical sediment volcano. Examination in cross-section suggests a more complex interpretation, since in cross-section, Longmyndian *Intrites*, whether on the top or sole of beds, typically consists of two lobes formed from the pinching and swelling of laminae (Fig. 2.28). The symmetry of the lobes above and below the horizontal plane explains the identical appearance of *Intrites*-like forms on sole and top surfaces. Some examples however only have upper lobes (e.g. Fig. 2.28E). Rarely, additional laminae overarch the upper lobes, forming a dome-like structure (Fig. 2.28G).

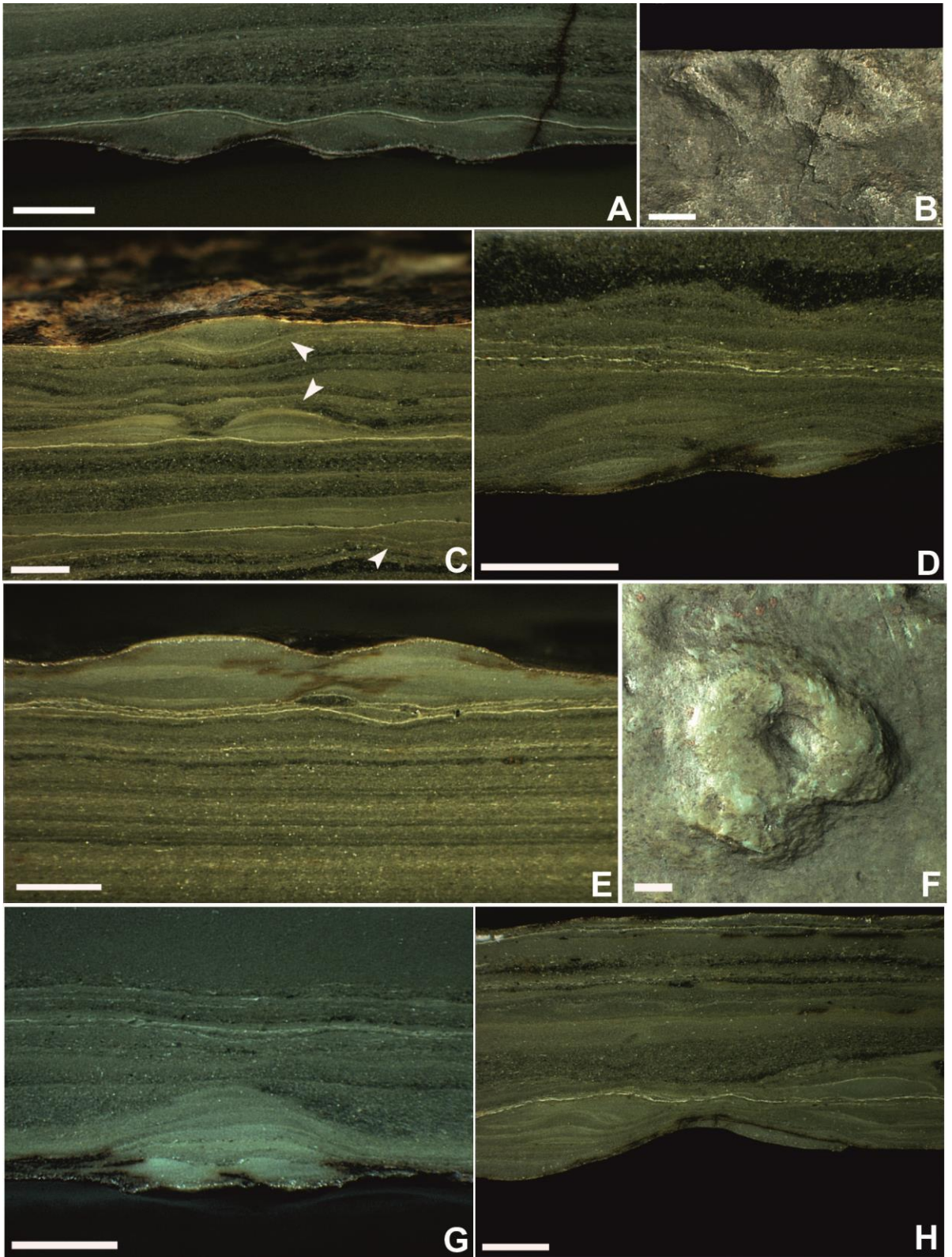


Fig. 2.28.

◀ **Fig. 2.28.** Longmyndian *Intrites* in cross-section. **A:** Cross-section through a double Longmyndian *Intrites* on bed sole. RCL-AH/1a. **B:** Plan view of double Longmyndian *Intrites* shown in cross-section in A. **C:** Several *Intrites*-like forms, including edge of one on the top surface showing a single lobe, a full *Intrites*-like form within the rock, and at bottom of picture a very shallow *Intrites*-like form. RCL-AH/3b. **D:** Longmyndian *Intrites* on bed sole clearly showing layering. Note whitish colour of layers. RCL-AH/10. **E, F:** An unusually large and well-formed *Intrites*-like form on bed top shown in cross-section (E) and plan view (F). Note the paler colour and different texture within the Longmyndian *Intrites*. L-AH/18. **G:** *Intrites*-like form on bed sole, with dome-like laminae above the lobes. L-AH/4b. **H:** Simple indentation on bed sole, compressing overlying laminae, with some Longmyndian *Intrites*-like build-up of laminae within the gentle lobes on either side of the indentation. A white matground overlies the structure. RCL-AH/10. Scale bars: 1 mm.

In three dimensions, Longmyndian *Intrites* is a complete or partially open torus that is sometimes so open as to form extended, almost parallel lobes. Longmyndian *Intrites* has such a characteristic appearance that it is clearly identifiable when entirely within cross-sections, allowing both its upper and lower bounds to be examined (Figs 2.28C, 2.29).

In the Longmyndian succession, *Intrites* occur only in association with mudstone laminae, and almost all are juxtaposed against a white microbial mat lamina (see Section 2.3), which may be either above or below, or sometimes both above and below the *Intrites*-like form (Fig. 2.28A). Longmyndian *Intrites* with only upper lobes invariably have a thick white microbial mat as the base (Fig. 2.28C, E; Fig. 2.29A). In some cases, an indentation compresses overlying laminae but formation of upper lobes seems constrained by an overlying white matground (Fig. 2.28H).

Longmyndian *Intrites* are sometimes found to approximately overlies other *Intrites*-like forms at lower stratigraphic levels (e.g. Figs 2.28C, 2.29B). Within the lobes, the

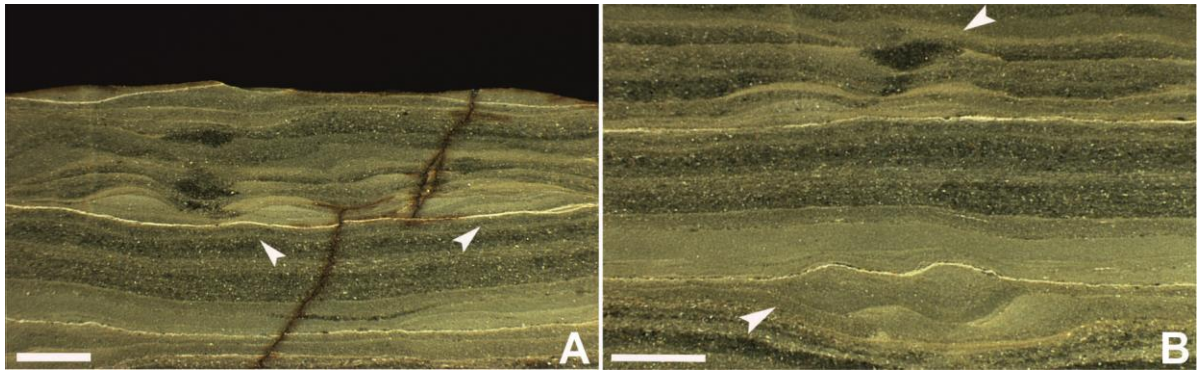


Fig. 2.29. A: Longmyndian *Intrites* above white microbial mat layer (left, arrowed), showing internal layering and dark sandstone in the dip between lobes. The edge of a further, shallow *Intrites*-like form is seen to the right (arrowed). **B:** Two *Intrites*-like forms, arrowed, in approximate vertical alignment. Upper specimen has associated sandstone feature; lower specimen is unusual in having a thick white microbial layer above rather than below, although a thin white layer forms the lower bound. RCL-AH/3a. Scale bars: 1 mm.

sediment is fine-grained and commonly paler in colour, and sometimes contains whitish laminae (Figs 2.28D, G; 2.29A). Sandstone structures are often found in the central dip of the torus (Fig. 2.29) in examples in which the *Intrites*-like form is seen to be underlain by a white microbial matground lamina.

2.4.3 Interpretation

Examination of Longmyndian *Intrites* in cross-section confirms that the structures develop above or occasionally between white microbial matgrounds and would appear therefore to be associated with microbial activity. (In specimens found on the soles of beds, the white layer below is inferred.) Interpretation of these *Intrites*-like forms as a microbially mediated structure appears plausible in the context of the Long Mynd. While some examples of Longmyndian *Intrites* in negative counterpart (e.g. Fig. 2.27D) superficially resemble negative impressions of *Aspidella terranovica* Billings (see Chapter 5), they lack the radial ornamentation of *Aspidella*, and no “Billings-type” *Aspidella* have been found on sole surfaces in the Long Mynd

despite extensive searching. There is currently therefore no evidence for any authentic Ediacaran macrofossils in these rocks. On the other hand, the presence of various types of microbially induced sedimentary structure (MISS), including *Arumberia*, in the Longmyndian rocks has already been noted (McIlroy et al., 2005, and discussion above).

The common occurrence of sandstone fluid escape structures between the lobes of Longmyndian *Intrites*, just above a white microbial matground lamina (Fig. 2.29), may provide the key to understanding the *Intrites* structure. It has already been noted that microbial mat activity may result in gas effusions which escape upwards, with fluidized sand subsequently exploiting the same path (Section 2.2). Fluid escape columns and disturbances often originate at matground laminae. Gas, and pore fluid, may seep through tears in the matgrounds without leaving any indication of a feeder column below. The *Intrites* structure may thus have been centred on a small sediment volcano. A striking example is shown in Fig. 2.28F. Here, the surface expression of the *Intrites*-like form is similar to a volcano crater, but with rounded rather than conical flanks. The indentations on sole surfaces, with local compression of laminae (e.g. Fig. 2.28H), suggest failed injections or narrow seepage of fluid through the structure, with the indentation itself resulting in gentle lobes of displaced muddy sediment on either side. Fluid escape structures with entrained dark sand are sometimes observed to have disrupted the tops of lobes (Fig. 2.30).

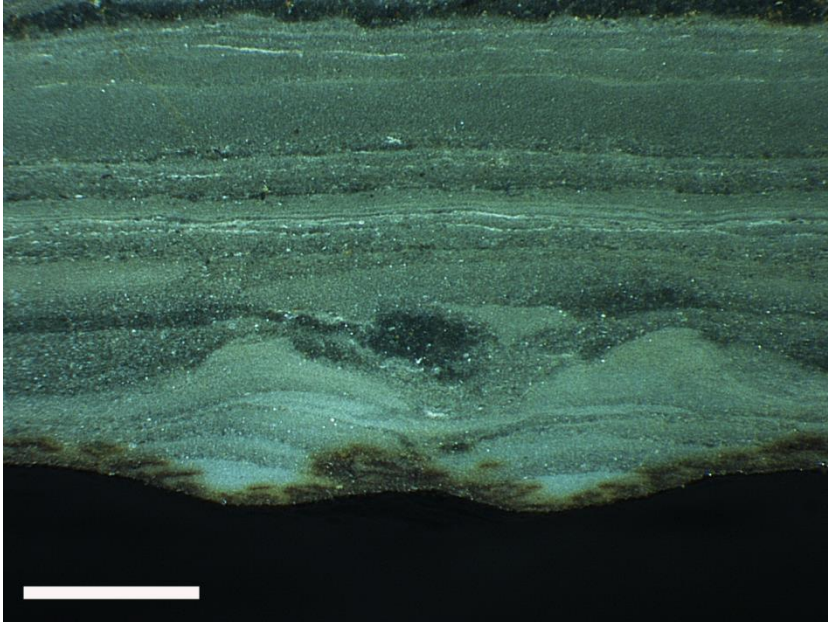


Fig. 2.30. Example of Longmyndian *Intrites* on bed sole, showing pale layers in the lobes and disruption by fluid escape above, resulting in distortion of the still soft and unconsolidated mud laminae at the top of the lobes. L-AH/4a. Scale bar: 1 mm.

The lobes of Longmyndian *Intrites*, with their pale internal laminae, were probably the result of microbial activity. Features resulting from the trapping and binding of sediment by microbes can be expected in these rocks. In addition, the evidence for calcified cyanobacterial sheaths discussed in Section 2.3 above demonstrates that precipitation of carbonate also occurred. In thin section, the whitish laminae within the lobes of the *Intrites*-like form are dark in transmitted light, probably due to the presence of micrite (Fig. 2.31).

The homogeneous mudstone within the lobes may have accumulated from baffling and trapping by microbes, and may also have involved some microbially mediated authigenic clay-mineral precipitation – a process that has been implicated in the

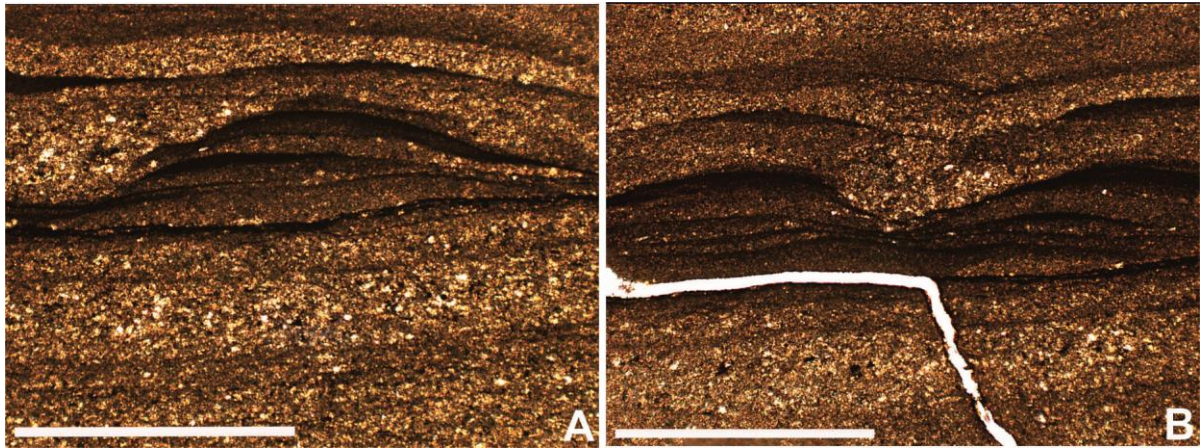


Fig. 2.31. Thin sections through *Intrites*-like forms in plane polarized light. Note dark laminae in transmitted light resulting from carbonate precipitation as micrite. (White band in B is a crack in the original rock.) RCL-AH/3a. Scale bars: 1 mm.

exceptional preservation of fossils in lagerstätten such as the Burgess Shale (see e.g. Orr et al., 1998; Butterfield et al., 2007; Gabbott et al., 2001; Wacey et al., 2014) and has already been proposed to explain aluminosilicate preservation of Longmyndian microbes (Callow and Brasier, 2009).

Trapping and binding, together with the precipitation of carbonate on to the extracellular polymeric substances (EPS) of the microbial mats, may cause the build-up of laminae (Dupraz et al., 2009; Noffke and Awramik, 2013). On a much bigger scale, the resultant domes and other structures would be called stromatolites. At the scale of build-up of several laminae, the *Intrites*-like form is far smaller, and appears to lie on the boundary between the primarily two-dimensional structures of MISS and the mainly three-dimensional stromatolites (see Noffke and Awramik, 2013).

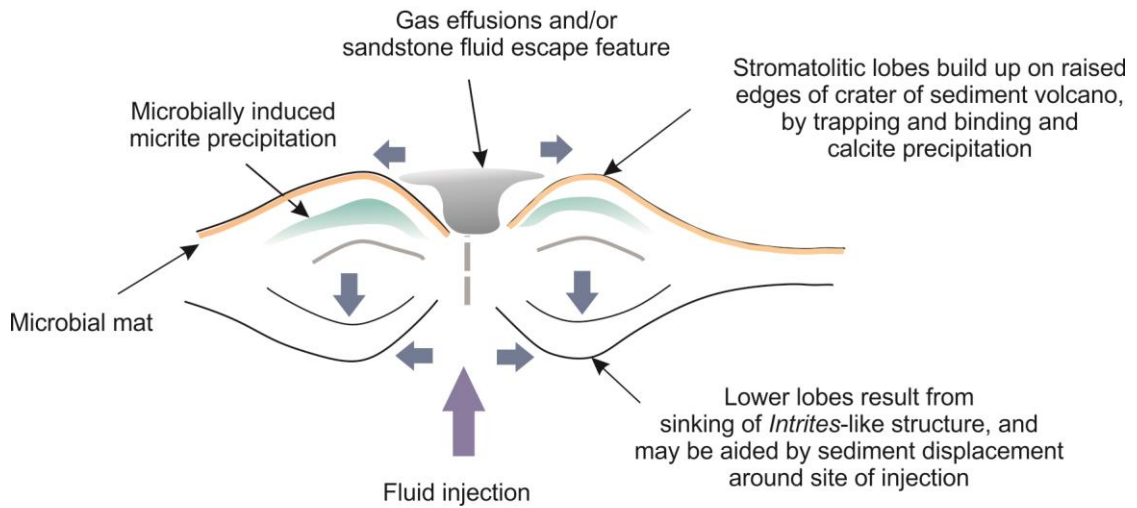
Combining this stromatolitic build-up with indications of fluid effusions at the centre of many *Intrites*-like forms now suggests an explanation for the (usually

incomplete) torus shape of Longmyndian *Intrites*. The effusions may have produced a surrounding small raised ring of sediment, in the form of a shallow sediment volcano. The raised topography of the ring would draw the build-up of cyanobacteria competing for light (Gerdes et al., 1994). Trapping and binding of sediment by the cyanobacteria, together with carbonate precipitation, would result in the build-up of internal laminae, resulting in the growth of a ring-shaped microstromatolite built up around a small sediment volcano (Fig. 2.32).

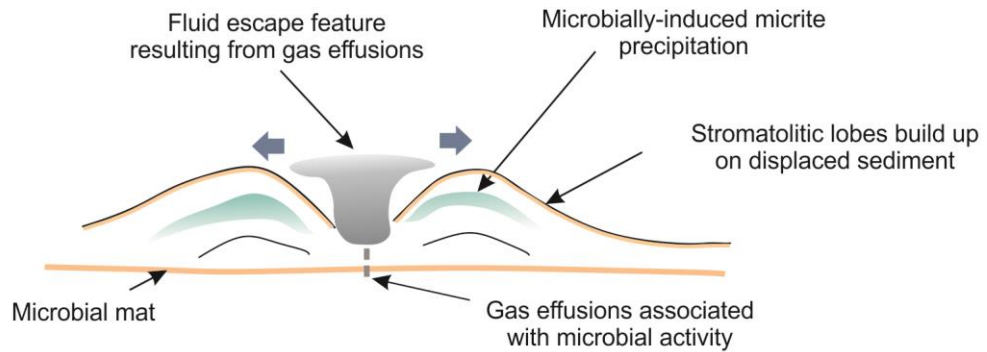
Sinking of the built-up laminae into the soft muddy sediment beneath produces an equivalent ring-like feature on the sole of beds. Displacement of muddy sediment around the injection site may also play a role in the formation of the lower lobes. In some cases, the build-up of laminae by trapping and binding may grow into a more typical stromatolitic dome shape, overarching the original lobes (Figs 2.28G, 2.32C).

Trapping and binding by cyanobacteria tends preferentially to build up laminae parallel to a current (Logan et al., 1964; Garlick, 1988; Schieber, 1998, 1999). Thus the sides of the ring broadly parallel to the current are more likely to have been built up, resulting in incomplete rings and, where the current is stronger, in parallel ridges (Fig. 2.33). This may explain the alignment of the double-ridge form of Longmyndian *Intrites* observed on some bedding planes (e.g. Fig. 2.27C). Preserved as a negative counterpart on the top of a lower bedding plane, the resulting double grooves may provide the explanation for Salter's paired pits (Salter, 1856; Callow et

A. Double-lobed Longmyndian *Intrites*



B. Longmyndian *Intrites* with upper lobes only



C. Dome construction

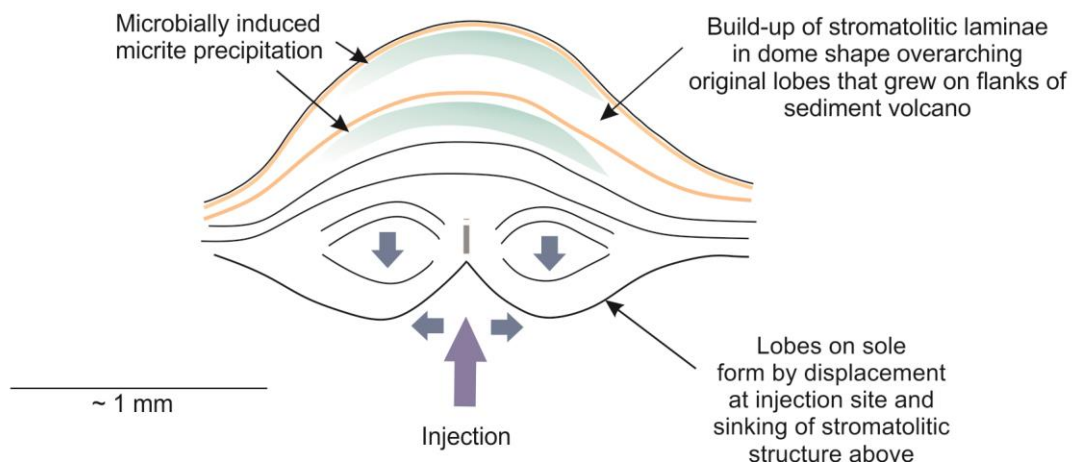


Fig. 2.32. A model for the formation of Longmyndian *Intrites* by the build-up of stromatolitic laminae on the raised topography of a small sediment volcano produced by injection from below with seepage of fluid through compressed laminae (A,C), or effusions of gas through tears in the matground (B).

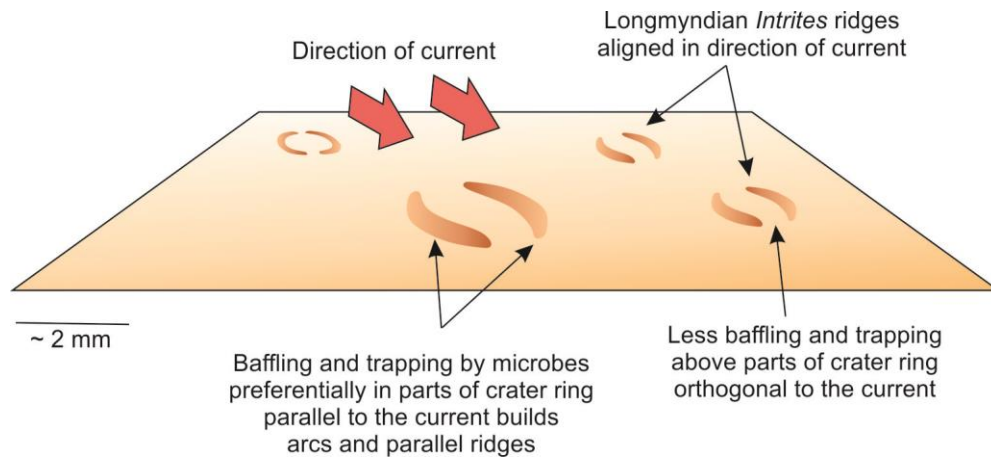


Fig. 2.33. Preferential build-up of current-parallel sides of a low-relief sediment volcano crater due to trapping and binding by cyanobacteria produces two arcs or parallel ridges on the bedding surface. Equivalent structures on sole surfaces result from the sinking of the stromatolitic structure into soft, muddy sediment below. See also Fig. 2.27C, F.

al., 2011a; see Appendix A2.5 for a re-assessment of Salter's original specimens in the light of the interpretations in this chapter). Thus "Longmyndian *Intrites*" can now be understood as a form of torus-shaped microstromatolite that grows from the slightly raised sides of a small-scale sediment volcano. It can be regarded as a new form of MISS.

2.5 CONCLUDING REMARKS

Detailed examination has demonstrated that all the discoidal impressions of the upper Burway Formation rocks can be explained by a combination of microbial activity and physical processes. The Longmyndian example highlights the importance of microbial mats in the interpretation of Ediacaran rocks. This study has widened the recognized range of their influence, and has added to the variety of MISS through the identification of "Longmyndian *Intrites*" as a form of microstromatolite built up around sediment volcanoes.

Although apparently lacking in Ediacaran macrofossils, the rocks of the upper Burway Formation are proving important for their rich fossilized microbial communities. Building on work by Peat (1984), and Callow et al. (2011b), the presence of several types of permineralized microbial forms has been established. Element mapping by SEM-EDX indicates that at least some filaments represent the calcified sheaths of cyanobacteria – uncommon in the Ediacaran Period until close to the Cambrian boundary. More general microbially mediated calcite precipitation is supported by the suggestions of micrite in the *Intrites*-like structures.

The larger hollow tubes may include other forms of cyanobacteria or similar microbes that precipitated iron on their sheaths. Indications of T- and H-branching in other filaments, supported also by re-examination of the surfaces of Salter's original specimens (Appendix A2.6), add support to the possibility of fungi in the Longmyndian matgrounds, as first suggested by Callow and Brasier (2009). These preliminary results open up several avenues of enquiry. Detailed study involving high-resolution element mapping and X-ray tomography are now required to characterize the microbes of this Ediacaran microbial assemblage, the nature of their preservation, and the three-dimensional architecture of the microbial mats. At the same time, through identification of the apparent lack of pyrite in these sediments, this work should provoke a sedimentological re-assessment of the palaeoenvironment of the Burway Formation, and the Longmyndian Supergroup as a whole.

The discs of the Long Mynd have provided a cautionary tale: even discs on bed soles with simple morphological elements used as taxobases in describing discoidal fossils, such as bosses and lobes, need not be biogenic. Nevertheless, many other Ediacaran discoidal impressions are undoubtedly of biological origin. It is to these that I now turn.

CHAPTER 3

DISCS AS HOLDFASTS

3.1 INTRODUCTION

The most obvious examples of undoubtedly biological Ediacaran discs are those with attached fronds. It has hitherto largely been assumed that the discoidal part of the organism functioned as a holdfast to anchor benthic frondose taxa to the sea bed. Given the present lack of firm evidence regarding the affinities, functional morphology, and lifestyle of Ediacaran forms such as *Charniodiscus*, and since the associated discs appear to have been partially buried in the sediment, the inference that the discs functioned, at least partly, as holdfasts seems reasonable. Alternative functions of Ediacaran discs are also considered in this chapter and the next, including the possibility that they may have been the main functional part of the organism, with the frond being a subsidiary, even temporary, growth.

This chapter draws on observations of discs attached to fronds from several Newfoundland localities (Fig. 3.1) - Mistaken Point, Little Catalina, and Spaniard's Bay, and possible holdfast discs in the disc-dominated Fermeuse Formation at Ferryland on the Avalon Peninsula (discussed in detail in Chapter 5). Rather than seek differences in disc morphology between frondose taxa, my approach has been to come to a general model, based on the premise that the discs of the frondose taxa share a basic architecture related to a common function. The rayed disc *Hiemalora*,

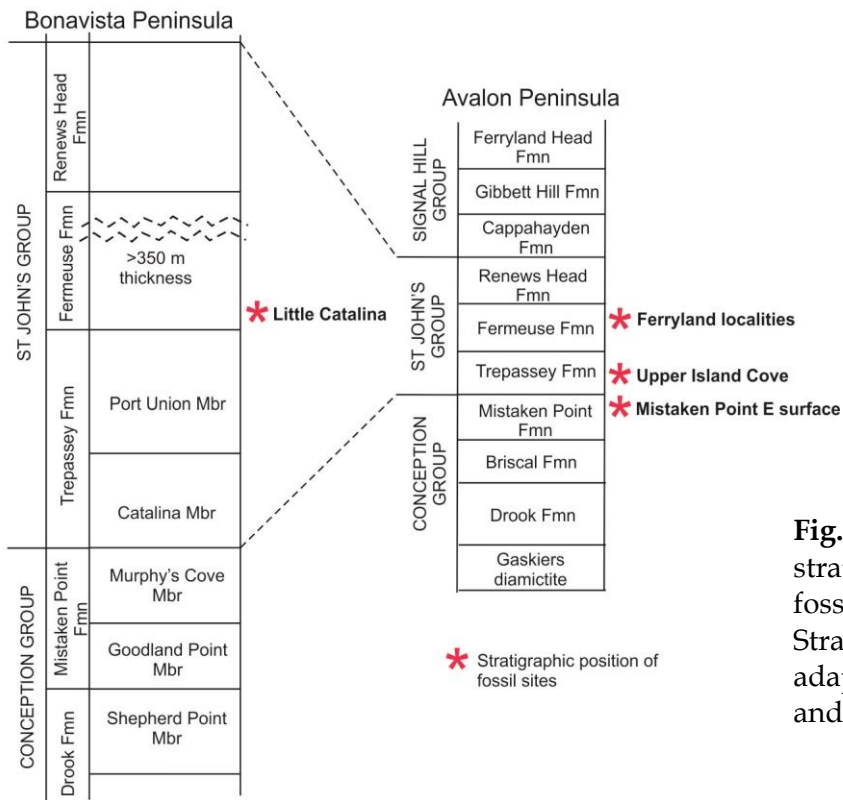
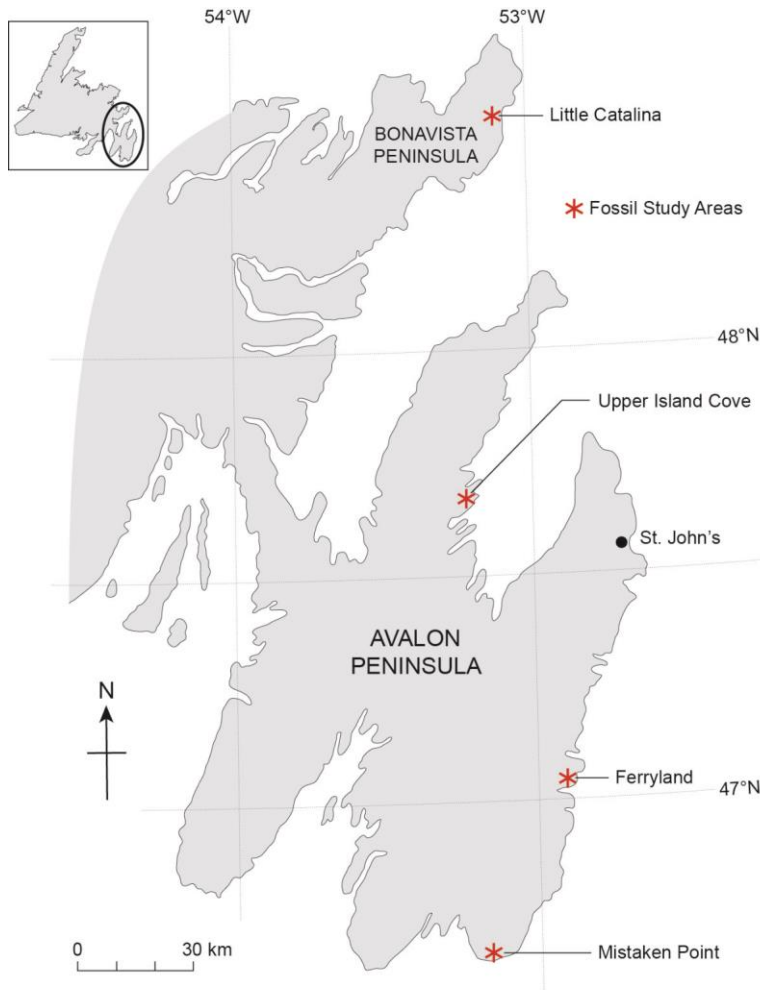


Fig.3.1. Location and stratigraphic position of fossil sites discussed. Stratigraphic columns adapted from O'Brien and King (2005).

associated with the frond *Primocandelabrum* (Hofmann et al., 2008), is an exception, and will be discussed separately in the next chapter.

There are two fundamental difficulties in examining the nature of holdfast discs:

- 1) Only a small minority of discs are preserved with attached fronds, probably because the holdfast discs were partially buried in the sediment, and therefore more likely to be preserved. They are the only forms, along with trace fossils, that would be captured by Fermeuse-style preservation (casting of external moulds of partially buried discs by collapse of sand from above; see Gehling et al., 2000; Narbonne, 2005). The interpretation of isolated discs as holdfasts relies on similarity of appearance and/or close association with discs bearing fronds. Yet, some use has to be made of isolated discs in building a model due to the small set of frond-linked discs. I have used some isolated discs on the basis of close spatial association and morphological similarity, but such extrapolations must necessarily be tentative.
- 2) Given the need to protect well-preserved frond-bearing discs, it has not been possible to section any such specimens. In the absence of information from grinding through cross-sections, it has been necessary to rely on observations of surfaces alone.

These are serious drawbacks. Nevertheless, observations from several sites allow progress towards a tentative model.

3.2 HOLDFAST DISC MORPHOLOGIES

3.2.1 The tops of holdfasts: Mistaken Point

The frond-bearing discs of the classic Mistaken Point assemblage (Fig. 3.2) form an obvious starting point for examining holdfast disc morphology. These fossils show Conception-style preservation, in which the tops of the organisms were moulded by an ash flow which lithified rapidly and, on their decay, the moulds were cast by sediment pushed up from below (Narbonne, 2005; Liu et al., 2011). The ash has subsequently eroded, leaving positive casts on upper bedding surfaces. The palaeoenvironment in which the Mistaken Point biota lived is interpreted to have been a deep marine slope (Wood et al., 2003). The deep marine interpretation of the Mistaken Point assemblages has recently been questioned by Retallack (2014), who argues for a terrestrial to marginal marine setting for the upper part of the Conception Group. However, the types of arguments used to infer terrestrial and intertidal settings for the Ediacaran biota have been widely refuted by sedimentologists and palaeontologists (e.g. Callow et al., 2013; Xiao et al., 2013).

Frond-bearing discs from the Mistaken Point E surface (Fig. 3.2A, B) typically form gently sloping mounds with a relief of 1–5 mm from the top of the bed, and a wide central boss which rises steeply a further 1–5 mm above the base. The associated frond lies directly next to the disc, with the stem often merging with the side of the

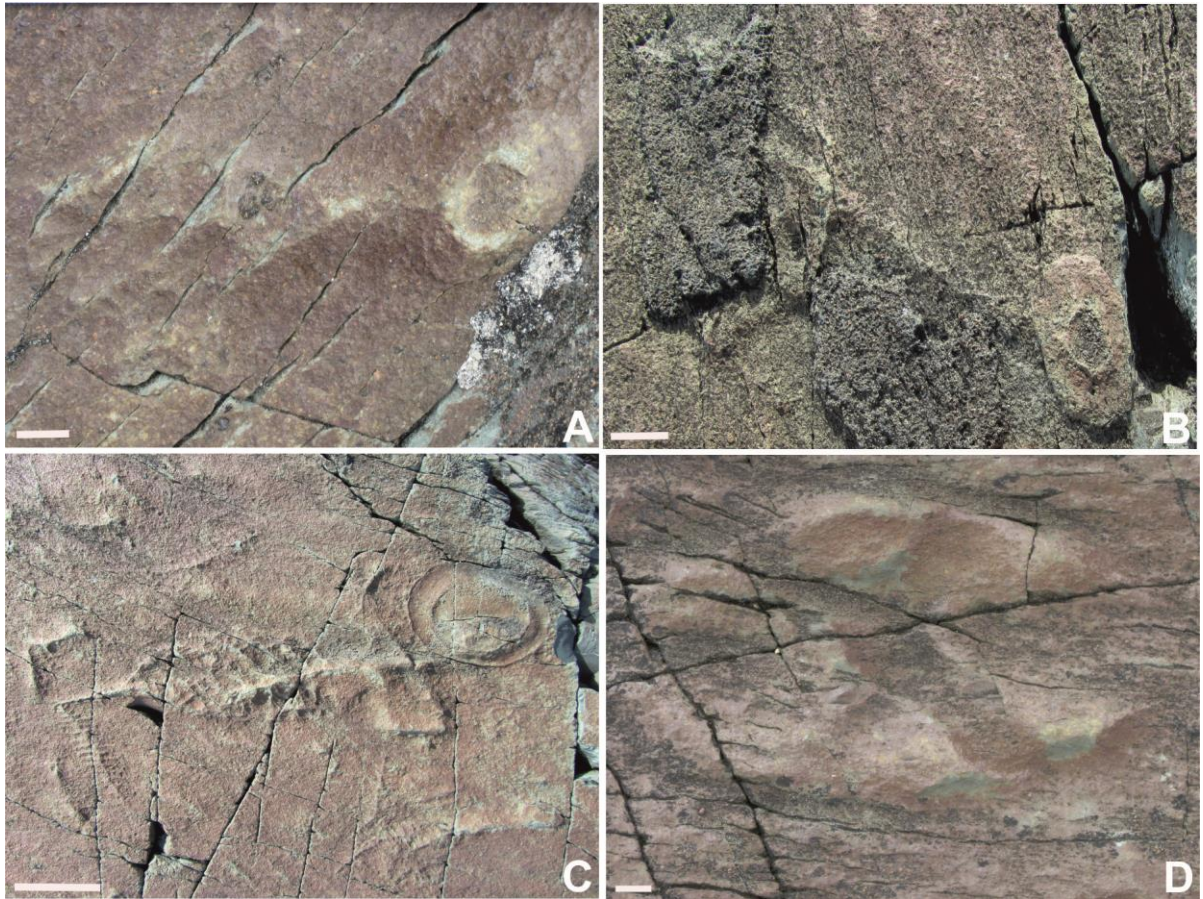


Fig. 3.2. **A, B:** Typical preservation of discoidal holdfasts (*Charniodiscus* specimens) under ash layer in Conception style on the E surface, Mistaken Point, as raised mounds with central wide boss and stems to side. **C:** *Charniodiscus spinosus* with base preserved as negative moat-like furrow surrounding wide positive central boss. **D:** Probable decayed holdfast. Scale bars: A, B, D: 1 cm; C: 5 cm.

holdfast due to taphonomic processes (e.g. Fig. 3.2A-C; Narbonne, 2005; Burzynski and Narbonne, 2014). There are rare exceptions to this pattern of holdfast preservation: the disc of a well-preserved *Charniodiscus spinosus* has a base consisting of a deep furrow surrounding the wide central boss (Fig. 3.2C). The E surface also contains poorly preserved effaced discs, inferred to be partially decomposed and sediment-draped discs that are no longer identifiable (Liu et al.,

2011; Fig. 3.2D). These effaced discs do not have associated identifiable fronds preserved, in contrast to most other discs on the E surface.

From observations of the upper surfaces of discs at Mistaken Point, it is evident that the discoidal holdfasts were partially raised above the sea bed, and may have had a stepped appearance, with a raised central portion from within which the frond presumably emerged. The Mistaken Point discs provide little clue, however, to the internal structure of the holdfast.

3.2.2 Ringed discs: Little Catalina

Striking evidence for the internal structure of the holdfast comes from an example of *Charniodiscus* at Little Catalina, on the Bonavista Peninsula (Fig. 3.3). The stratigraphic relationships and fossil localities of the Bonavista Peninsula were first identified by O'Brien and King (2004, 2005) and later discussed in detail by Hofmann et al. (2008). The Bonavista fossils are preserved in deep-water turbiditic siliciclastics overlain by thin tuffs, similar to fossil preservation at Mistaken Point (Hofmann et al., 2008). Little Catalina is Locality 21 Hofmann et al. (2008, fig. 1). The dark grey shales and fine-grained sandstones are interpreted by Hofmann et al. to be equivalent to the Fermeuse Formation of the St John's Group. Unlike the full positive relief shown by the discs on Mistaken Point E surface, the discs at Little



Fig. 3.3. Specimen of *Charniodiscus* from Little Catalina, showing eroded top surface of holdfast revealing raised concentric rings, and a central anchoring boss for the stem. Detail in inset. A faint ring between the outer and middle rings may be the base of the shallow slope of the middle ring. Scale bar: 1 cm.

Catalina are partially eroded, to reveal some internal structure. One partial *Charniodiscus* shows three distinct concentric rings, and the stem of the frond clearly arising from a boss at the centre (Fig. 3.3). Each of the three rings is raised, and the space between rings is flat. The outer side of each ring slopes at a shallow angle, while the inner side is steep and slightly concave, producing a small overhang at the top of the ring (Fig.3.3, inset detail). Similar, though less well preserved, examples of the same type of disc can be found in the same locality (Fig. 3.4).

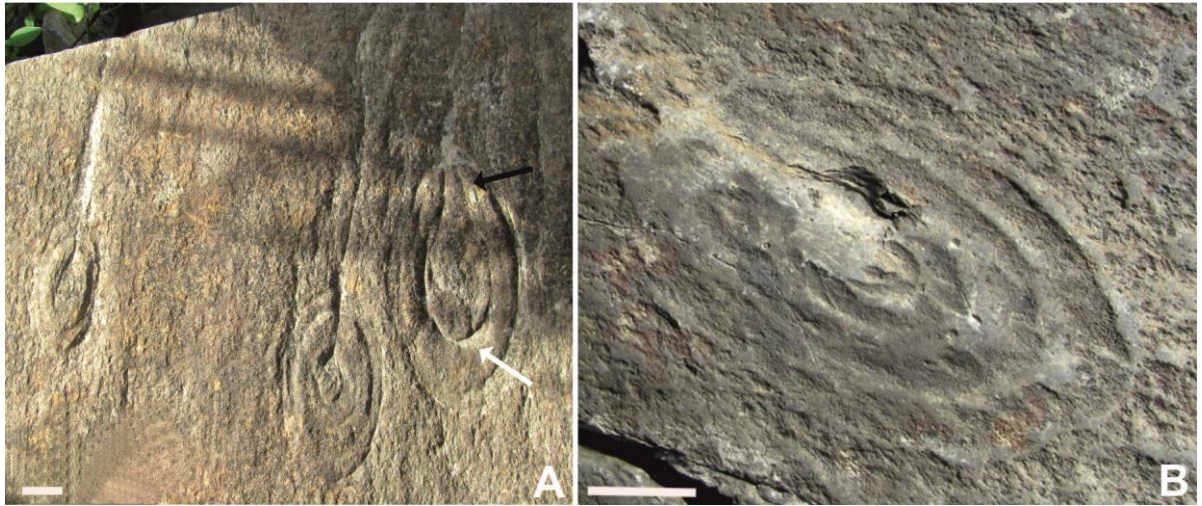


Fig. 3.4. A: Three holdfasts with several distinct rings, one showing protruding inner ring (white arrow). Stems are preserved positive and arise from central ring (black arrow). **B:** Weathered disc showing four distinct rings and anchoring point of the stem. (Close up of disc associated with a *Charniodiscus* frond, see Appendix A3.1B.) Little Catalina. Scale: 1 cm.

3.2.3 Dome-like structures: small discs of Spaniard's Bay

A single bedding plane in the Trepassey Formation at Upper Island Cove, Spaniard's Bay, in the northern part of the Avalon Peninsula, preserves small, high-relief, presumed juvenile fronds about 2–3 cm in length, with holdfasts discs (Narbonne, 2004; Narbonne et al., 2009). The inferred mode of preservation was originally entrainment in fine-grained, distal turbidites followed by encasement in concretions (Narbonne, 2004; Narbonne et al., 2009). Subsequent work demonstrated that the fossils were neither in concretions nor within a turbidite bed, but preserved in flutes and scours on a bedding surface (Brasier et al., 2013b). The new interpretation of the Spaniard's Bay fossils explains the remarkable preservation in terms of felling of the fronds in a high-velocity erosive current, and the impression of the soft body tissues in the relative shelter of their own erosional

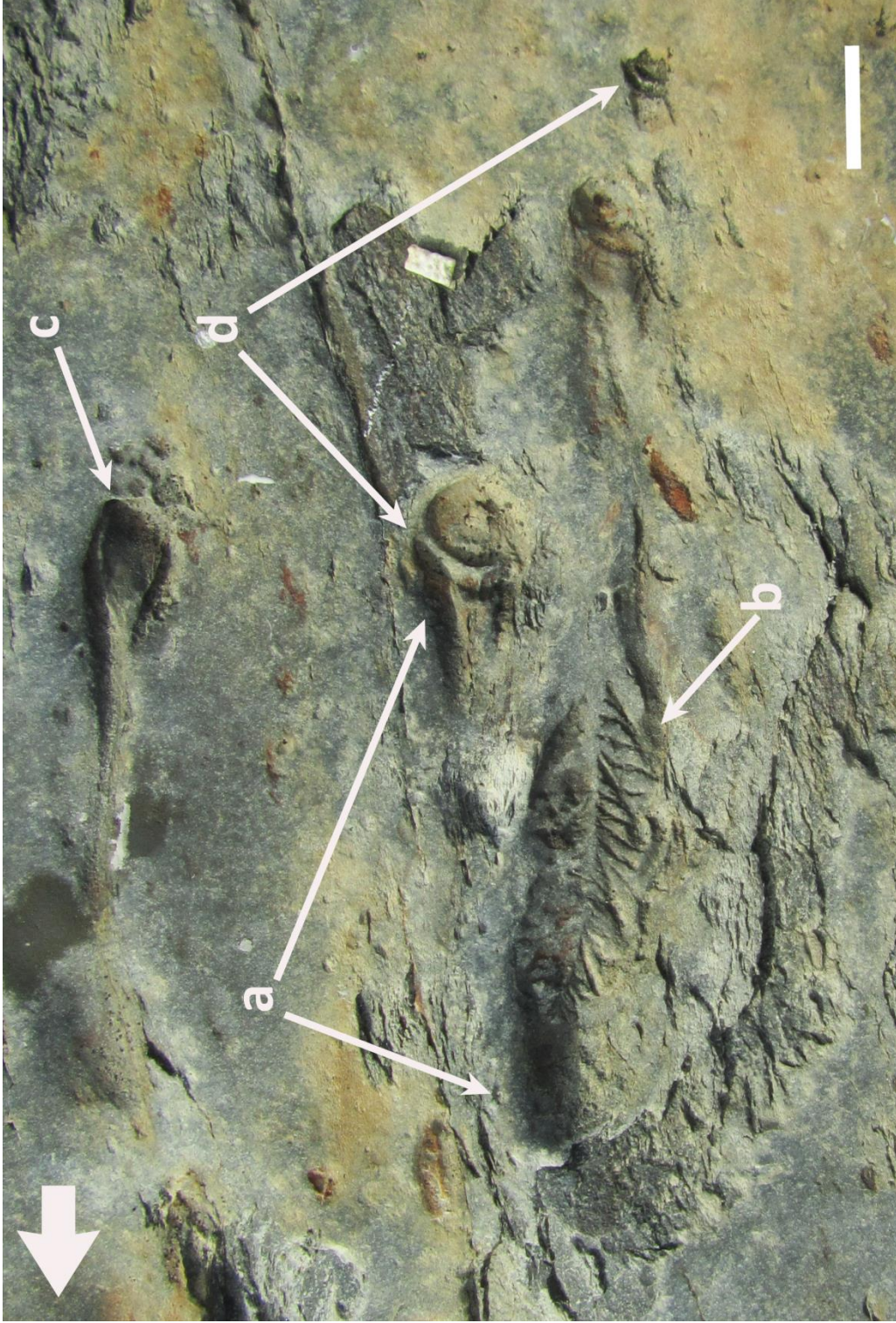


Fig. 3.5. Scours (a) preserve frond (b) and discs (c, d) on top of bedding plane at Upper Island Cove. Note the overhang on the up-current side of discs (c), and partial dome-like structures around central boss of discs, preserved on the down-current side (d). Arrow at top left marks palaeocurrent direction. Scale bar: 1 cm.

scours. The whole assemblage was subsequently covered and cast by a rippled, fine-grained sandstone, now weathered, revealing the fossils. The holdfasts lie in steep-walled hollows that commonly overhang on the up-current side, and extend down-current into a long shallow flute (Fig. 3.5).

The majority of fronds on this surface (mostly *Beothukis* sp.) are associated with holdfast discs. In some cases only a deep pit is left where the holdfast would have been (Fig. 3.5c). Other specimens reveal morphological detail of the top of the holdfast, where it was protected by the scour. The top of the holdfasts commonly have a central pit or boss, possibly the anchorage point of the stem, and often the cast of a surrounding partial dome-like enveloping structure, evident in several examples at the centre and lower right of Fig. 3.5, and most obviously in Fig. 3.6.

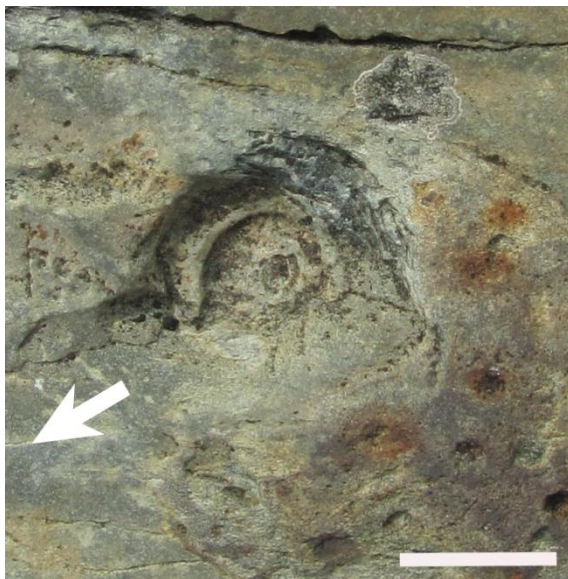


Fig. 3.6. Holdfast disc on top of bedding plane, Upper Island Cove. Exceptional morphological detail of the disc top is preserved on the sheltered down-current side of the scour, with a curved dome-like structure, and a central rimmed pit, probably the anchor of the stem. Arrow marks probable palaeocurrent direction, based on protected side of disc, although the disc overhang and extension of scour are here eroded. Scale bar: 1 cm.

3.2.4 Isolated holdfast discs

Most discs in the Conception Group and St John's Group of the Avalon and Bonavista Peninsulas are isolated, as is common for discs that are demonstrably holdfasts. However, caution must still be applied in inferring that such isolated discs are holdfasts, as other types of biological discoidal impression may also occur, as well as pseudofossils. In the lower Fermeuse Formation of Bonavista, at the Back Cove locality (Liu et al., 2014), a disc with large numbers of rings ≤ 1 mm apart was observed (Fig. 3.7). This is unlikely to be a holdfast disc, since those tend to show far fewer and more distinct rings. It may be an example of a microbially induced structure, for example a "fairy ring" such as can be formed by cyanobacteria (Gerdes et al., 1994; Grazhdankin and Gerdes, 2007), or of fungal origin (Peterson et al., 2003). The frondless discs of the Fermeuse Formation in Avalon are gregarious



Fig. 3.7. A possible microbial colony, lower part of Fermeuse Formation, Back Cove, near Melrose, Bonavista Peninsula. Note similarity to densely ringed discs observed in the "Outwoods" locality, Charnwood Forest, UK (Ford, 2000). Scale bar: 1 cm.

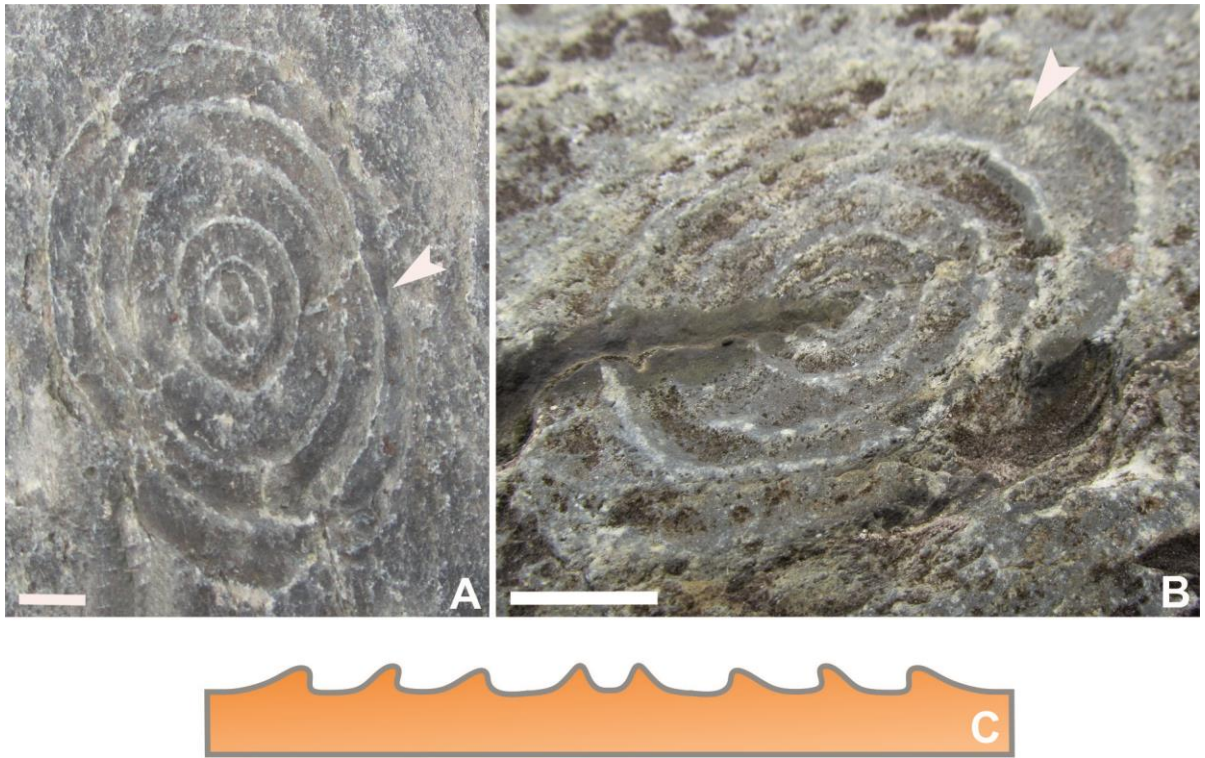


Fig. 3.8. Discs with curved, raised ridges at Upper Island Cove. **A:** Note the curved gentle rise of the ridge and steep, concave drop on inner side (arrowed). **B:** Partially eroded disc. Note the dip between outer ridges, arrowed. **C:** Schematic profile of discs such as those shown in A and B, illustrating shallow outer slope and steep, sometimes slightly overhanging, inner slope (fewer rings shown for clarity). Scale bars: 1 cm.

and have a variety of morphologies, so that the assumption that a disc is a holdfast can no longer be made with confidence (see Chapter 5; Menon et al., 2013).

Isolated discs, showing patterns of several broad concentric rings, are reported here from slightly above the well-preserved fossil bed at Upper Island Cove (Brasier et al., 2013b; Fig. 3.8). These fossils show raised rings with a curved, rising slope on the outside and a steeply sloping inside, similar to the frond-related discs from Little Catalina (Figs 3.3, 3.4). The preserved discs are almost flat, with only a shallow concave drop of a few millimetres in the base between the outermost and innermost ridges. One example (Fig. 3.8B) shows a marked dip between the

ridges formed by two outer rings that is reminiscent of the wide furrow in the base of the *Charniodiscus spinosus* on the E surface at Mistaken Point shown in Fig. 3.2C. Many other isolated discs, such as the example shown in Fig. 3.9, are heavily eroded and show no high-relief ridges but instead paired rings which can be interpreted as the eroded bases of typically 3–5 spaced concentric raised rings surrounding a central boss or depression - a pattern regularly observed in *Charniodiscus* holdfasts (see e.g. Fig. 3.3). These discs vary considerably in size, ranging from about 2 cm to 10 cm and more.

A large disc on a bed stratigraphically about 1 cm below the main Upper Island Cove fossil level (Brasier et al., 2013b; Fig. 3.10) is inferred here to be the cast of the top of a large collapsed disc. The specimen has a partially recessed inner raised lip, which may be a collapsed version of the dome-like envelope inferred for other fossils from this locality, and demonstrates their flexible, organic nature. This



Fig. 3.9. A: Eroded disc, typical of isolated discs found in localities near Melrose, Bonavista Peninsula. Note the close-double pattern of the rings. **B:** Schematic profile of heavily eroded discs in Conception-style preservation. Scale bar: 1 cm.



Fig. 3.10. Impression of a large, partially collapsed and decayed holdfast, Upper Island Cove, on a bed stratigraphically below the scoured surface bearing juvenile fronds. Note raised lip of an inner ring, and fine, positively preserved filaments, linear (white arrow), and forming a fine fringe (red arrow) on parts of surface. Scale bar: 1 cm.

envelope surrounds a central pit from which the frond presumably emanated. The fine <0.5 mm wide ridges on portions of the disc are spatially variable; some are parallel and linear, but in other parts of the disc they resemble a frayed fringe. It is considered that the irregular margin is more likely to result from the growth of microbial mat over the decaying organism, rather than ornamentation intrinsic to the disc. The linear marks are positive and unlikely to be tool marks resulting from the partial dragging of the disc in a scouring current (cf. Tarhan et al., 2010).

3.2.5 The underside of holdfasts: discs preserved in Fermeuse style

Conception-style preservation, involving smothering of a fossil assemblage by an ash layer, preserves impressions of the tops of anything on the seafloor, including discs. Any indications of the shape of the underside of a holdfast disc is most likely to be found under Fermeuse-style preservation (Narbonne, 2005), in which the external mould of the underside of partially buried forms is cast by sediment from above. Unfortunately, this style of preservation tends to capture the lower external surface of discs but not fronds. The resulting frondless discs are not easy to recognize as holdfasts, and it is difficult to differentiate them from other possible types of discoidal impressions. Occasional, more resistant disc specimens in which the upper surface has been captured (Fig. 3.11) reveal morphologies very similar to that observed in the large collapsed disc at Spaniard's Bay (Fig. 3.10) and the discs of Little Catalina (e.g. Fig. 3.3). This suggests that at least some of the Ferryland discs were holdfasts (see Chapter 5 for a more detailed discussion of the discs of the Fermeuse Formation).



Fig. 3.11. Probable collapsed top of holdfast disc, upper bedding surface, Fermeuse Formation, Ferryland, Avalon Peninsula. Note the three concentric collapsed levels. Scale bar: 0.5 cm.



Fig. 3.12. Discs preserved on sole of bed, Fermeuse Formation, Ferryland, showing compressional folds and protruding boss, in some cases recessed by compaction. (Note *Palaeopascichnus* visible below disc at right-hand edge of photo.) FR-H/18. Scale bar: 1 cm.

If we accept that the stepped appearance of *Ediacaria*-type discs in the Fermeuse Formation of Avalon is caused by differential compression of sand and mud (see Gehling et al., 2000), the underside of holdfasts may be considered to be bulbous, with a protruding central boss. It is not always necessary to invoke differential compression. Remarkably preserved discs on bed soles display simple compression folding resulting from compaction, and confirm such forms as the undersides of circular bulbous structures, most likely holdfast discs (Fig. 3.12).

3.3 HOLDFAST TAPHONOMY

The disc morphologies described above have resulted from the capture of impressions of different parts of holdfasts under ash and sand, with casting occurring by pushing up of sediment from below the bedding plane (“Conception-style” preservation) or from above the bedding plane (“Fermeuse-style” preservation; Narbonne, 2005). These different regimes have been described as preserving the tops and undersides of holdfast discs respectively (Gehling et al., 2000; Narbonne, 2005), but the story is often more complex (e.g. Tarhan et al., 2015a).

Covering by ash captures the tops of benthic organisms, some of which may already be in varying states of decay (Liu et al., 2011), resulting in impressions of effaced discs and partially collapsed holdfasts with microbial overgrowth (Figs 3.1D, 3.10).

Following exposure on weathering of the overlying tuff, the top impression will have suffered erosion, and delicate structures will have been lost, although in sheltered locations, such as within the lee of scours, some structure may be retained (Fig. 3.5). The ringed discs observed in Little Catalina can be interpreted as eroded impressions of the tops of holdfasts (Fig. 3.13). Even in heavily weathered examples in which the disc has a gently stepped profile (Fig. 3.9), twinned rings indicate that the impression is of the eroded top of a disc rather than the underside. The differential compaction model of Gehling et al. (2000) is not applicable here: it is intended to explain preservation of the undersides of discs in Fermeuse style.

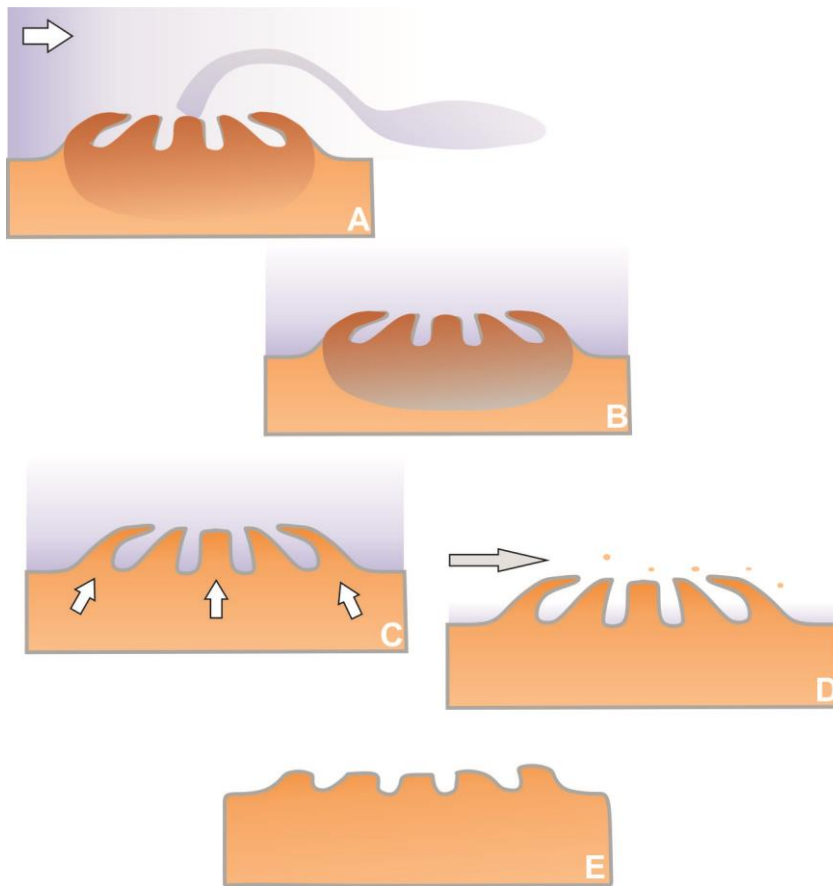


Fig. 3.13. Model for formation of ringed discs, such as those seen in Little Catalina, by Conception-style preservation and subsequent erosion. Smothering by ash (A) fells fronds, leaving the partially buried holdfast in place. The upper impression of the holdfast is captured as a mould on the underside of the rapidly lithifying ash, while the remains of the organism below decays (B). With the disintegration of the organism, sediment from below pushes up to form a cast of the ash mould (C). Weathering of the soft ash layer exposes the cast of the impression of the original disc top, but erosion gradually degrades the impression (D). The eroded stumps of raised structures remain in the form of rings (E).

Fermeuse-style preservation can however sometimes preserve disc tops too (Fig. 3.11). (The relevance to disc interpretation of the previously unrecognized preservation of occasional disc tops in the Fermeuse Formation will be discussed in Chapter 5.) Indeed, the preservation of the bases of rings in heavily eroded discs even some depth below the bedding plane suggests that the recesses between the

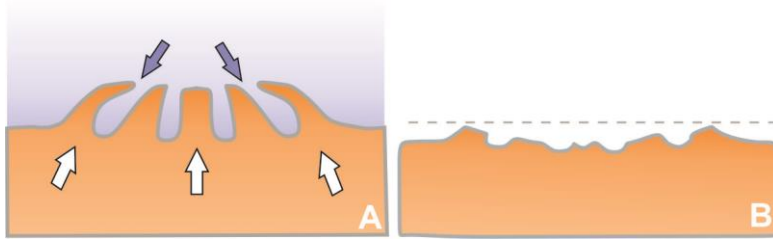


Fig. 3.14. Preservation of stumps of rings in heavily eroded discs with a stepped, gently concave profile in cross-section is interpreted here to imply deep recesses in the top of the disc that would have been at least partially filled by ash (A), with surrounding structures cast from below after decay of the organism. The heavily eroded profile retains indication of rings below the level of the outer margin of the disc (B).

domes of the disc top, captured by the penetrating ash, extended some distance into the disc body (Fig. 3.14, and discussion below).

3.4 A MODEL FOR HOLDFAST DISC STRUCTURE

From the observations from various localities and different modes of preservation discussed above, we may infer a tentative general structure for the holdfasts of fronds. The tops of discs preserved at Mistaken Point indicate that the holdfast was not a simple partially buried bulb but had some internal architecture. There appears to have been a central portion, from which the stem emerged, and which was raised above a surrounding mound on the surface (e.g. Fig. 3A, B). The rimmed, negatively preserved moat-like surround to the raised centre of the *Charniodiscus spinosus* holdfast in Fig. 3C suggests that the central portion was separated from, rather than an extension of, the surrounding mound.

The eroded tops of holdfasts of *Charniodiscus* demonstrate that the frond was anchored at the centre of the holdfast and also indicate that the holdfast consisted of

several concentric chambers separated by envelopes. This is evinced by the inclination of the raised remnants of the envelopes (see e.g. Fig. 3.3). The envelopes are presumed to have been spherical, although domes arising from a flat base cannot be ruled out from the ringed top impressions.

The internal geometry of the holdfasts can at this stage only be inferred, since the Conception style of preservation captures only a mould of the upper surface of the organism (Gehling, 1999; Narbonne, 2005; Fig. 3.13), although collapsed holdfasts (e.g. Fig. 3.10) provide some clues. The lack of fully three-dimensional preservation suggests that sectioning of holdfasts is unlikely to reveal any evidence of concentric envelope architecture if, as seems likely, it was composed of non-mineralized organic tissues.

Examples of small holdfasts sheltered within their scours on the Upper Island Cove surface, Spaniard's Bay, clearly show a preserved, partially enclosing outer dome (Fig. 3.6). Such structures would have been captured as a mould by the filling by ash of recesses between raised envelopes, with the shape of enclosing envelopes subsequently cast from below, but they rarely survive erosion on exposure (Fig. 3.13).

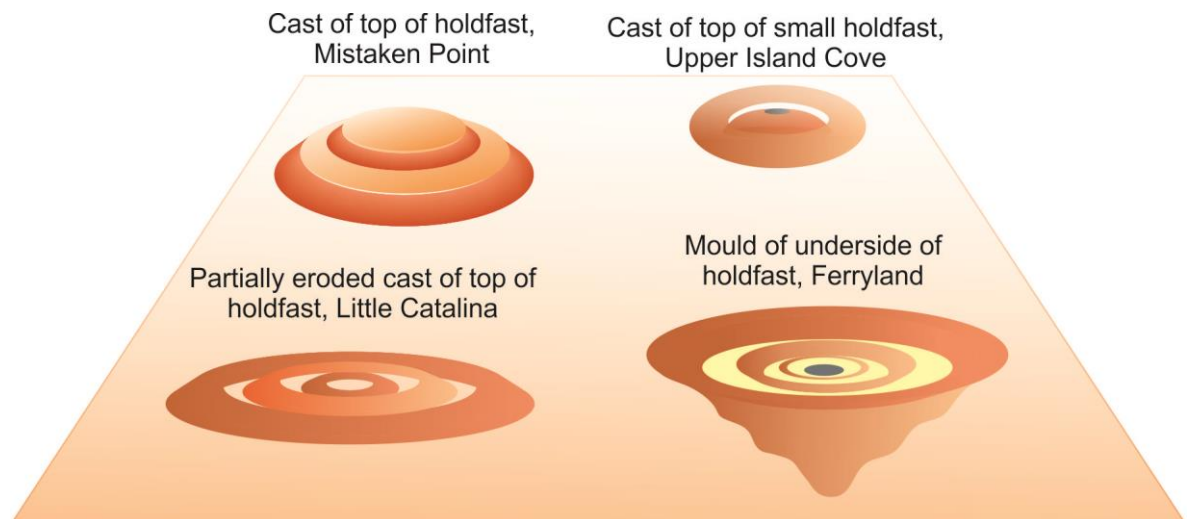


Fig. 3.15. Summary of clues to holdfast architecture from disc impressions preserved at different localities. The diameter can vary from ~ 2 ->200 mm.

The central portions of the top impression tend to be preserved either as a small boss or depression, where the stem is inferred to have been torn out by the scouring current that elsewhere on the same bed preserves fronds in scours (Brasier et al., 2013b). Isolated presumed holdfasts also support these observations, and, where the underside of the disc is preserved, as in the Fermeuse Formation in Avalon, it appears to have been rounded with a protruding central boss (Fig. 3.12; Gehling et al., 2000; Burzynski and Narbonne, 2015). (Further examples of discoidal impressions from the various localities are given in Appendix 3.)

Drawing together these observations (Fig. 3.15), it is inferred that the holdfast may have consisted of several concentric chambers separated by envelopes, with the stem of the frond probably attached at the centre of the holdfast, and extending from a robust central anchoring structure. The combined evidence from the many examples here discussed allows consideration of an idealized model of possible holdfast construction (Fig. 3.16).

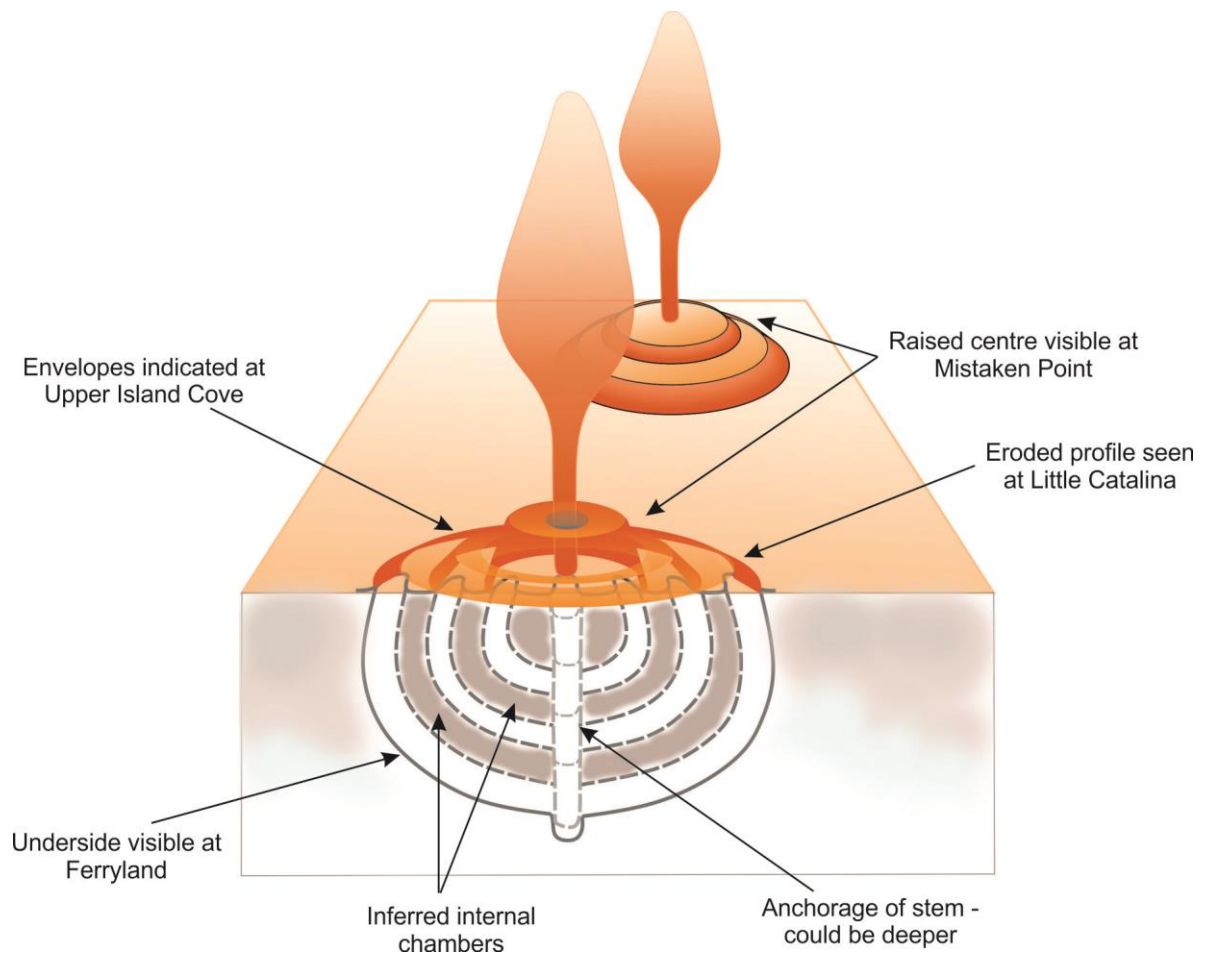


Fig. 3.16. A tentative model for the general structure of frond holdfasts. The internal architecture is inferred from the several inclined raised rings observed at Little Catalina. The gaps between the rings indicate space between the concentric envelopes (coloured dark brown here), which may have been filled by fluid, possibly containing symbionts. It is presumed that the positive hyporelief discs observed in the Fermeuse Formation at Ferryland represent the lower surfaces of holdfasts. The lower surface is shown as smoothly convex, based on the assumption that probable holdfast lower surfaces observed in Fermeuse-style preservation have undergone compressional folding (see also smooth convex surface suggested by specimens in Chapter 5, Fig. 5.10). It may have been a flatter spheroid (cf. Steiner and Reitner, 2001). The central boss may have extended further into the sediment. The diameters of holdfast discs cover a wide range, from ~ 2-→200 mm.

While the model developed here is based on observations of specimens in several localities from Newfoundland, it is consistent with the morphologies of frond holdfast impressions described from other assemblages. The several raised rings observed in *Charniodiscus concentricus* (Ford, 1958) and other probable holdfast discs preserved on upper bedding surfaces in Charnwood (Boynton, 2008; Wilby et al.,

2011), are similar to the disc morphologies observed at Little Catalina and interpreted here as the eroded tops of holdfasts, displaying their inner architecture. Examples from South Australia commonly capture lower surfaces of presumed holdfasts, with a central boss and several stepped or compression rings (e.g. *Cyclomedusa davidi* Sprigg 1947) and sometimes upper surfaces in the form of composite moulds, often with a stem attached (e.g. Tarhan et al., 2015b, fig. 5f). Similar discoidal impressions, of *Cyclomedusa* form, are observed in the White Sea assemblage, Russia (see e.g. Sokolov and Iwanowsky, 1985). (For further discussion of preservational variants of holdfasts, see Chapter 5.)

3.5 DISCUSSION

The proposed holdfast architecture (Fig. 3.16) is based on the inference of several discrete concentric envelopes. This layering may be simply for strength. The possibility that sandy sediment may have been taken in between the envelopes as a form of ballast, in the manner of *Psammocorallia* (Seilacher, 1992) is ruled out by the examples of collapsed discs (e.g. Figs 3.10, 3.11A, and 3.12). A sand-filled form would necessarily leave a more robust impression, similar to *Spatangopsis* and *Nemiana* (see Seilacher, 1992), although filling by silt or mud would allow for greater compaction. The structure would be consistent with fluid-filled, quilted pneu (Seilacher, 1989), with loss of fluid post-mortem resulting in collapse.

Intriguingly, the inferred internal architecture hints at functions for the disc beyond that of a simple holdfast. While compartmentalization may have added strength, it

is most efficient as a means of conferring strength when lightness is also required, as for example in the air-filled cancellous bone of birds (see e.g. Kaiser, 2007). For the mechanical needs of a holdfast, a simple fleshy basal extension would suffice. Additional surface area would benefit osmotrophy, but this would be more efficiently achieved by external appendages that can spread into the surrounding microbial mat, a morphology suggestive of the rayed disc *Hiemalora* (see Chapter 4). Another possibility is that the apparently enclosed fluid-filled chambers may have harboured symbionts.

Lenticular Eocene *Nummulites*, although single-celled Foraminifera, grew to sizes of several centimetres through compartmentalization, with chambers that are thought to have housed algal photosymbionts, rather as extant benthic Foraminifera such as the Nummulitidae do today (see e.g. Racey, 2001; Hallock, 1999). The idea that Ediacaran forms living in shallow waters may have harboured photosymbionts has been proposed previously (Hedgpeth, 1964; Seilacher, 1984; Conway Morris, 1985; McMenamin, 1986). The Ediacaran assemblages in Newfoundland lived in deep water, probably below the photic zone (Wood et al., 2003), thus ruling out photosymbionts, but the organisms could have exploited sulfide-oxidizing bacteria in the host sediment for energy. The positioning of holdfasts, partially embedded within microbial mats (Steiner and Reitner, 2001), would potentially allow the organism to tap such an energy resource, perhaps via the protruding boss at the base of the holdfast. Modern organisms exploiting chemosymbiosis, such as the Lucinidae and other families of bivalves, have evolved sophisticated mechanisms

for chemosymbiosis, involving a probing foot and the housing of sulfide-oxidizing bacteria intracellularly, in bacteriocytes in their gills (e.g. Taylor and Glover, 2000, 2010). Ediacaran organisms are likely to have been much simpler. Even a flattened spheroidal form partially embedded in the sediment does not however appear ideal for the purpose, unless the shape represents a trade off with its holdfast role.

The inferred architecture presented here indicates a hitherto overlooked complexity for the construction of frond holdfasts, the function of which is as yet unclear. The discs of Newfoundland offer further scope for investigation of this question, and with it, insights into the mode of life of the whole frondose organism.

CHAPTER 4

THE RAYED DISC *HIEMALORA*

4.1 INTRODUCTION

The rayed disc *Hiemalora* Fedonkin 1982 is a cosmopolitan Ediacaran genus (Narbonne, 1994) first recognized from the White Sea coast of Russia (Fedonkin 1980, 1982, 1985) and northern Siberia (Vodanjuk, 1989). It occurs for example in Podolia (Fedonkin, 1983); the Flinders Ranges, Australia (Jenkins, 1995); Finnmark, Norway (Farmer et al., 1992); northwestern Canada (Narbonne, 1994; Narbonne et al., 2014); Charnwood, England (Wilby et al., 2011); and the Dengying Formation in China (Chen et al., 2014). A single specimen has also been found in the disc-dominated assemblage of Carmarthen, South Wales (Cope, 2000). A possible report of *Hiemalora* from the Vindhyan Hills, India (De, 2003), remains uncertain.

In Newfoundland, *Hiemalora* occurs in the Mistaken Point, Trepassey, and Fermeuse Formations of the Avalon Peninsula (Anderson and Conway Morris, 1982; Gehling et al., 2000; Narbonne et al., 2001) and equivalent units in the Bonavista Peninsula (O'Brien and King, 2004; Hofmann et al., 2008). Re-examining Vodanjuk's specimens from the Khatyspyt Formation, Bykova (2010) proposed that discs with non-branching rays should be described under the genus *Mawsonites*; a number of the Newfoundland examples show branching, and are thus considered to be *Hiemalora*. No examples of the other well-known Ediacaran rayed disc, *Eoporpita*

medusa Wade 1972, which has a dense fringe of rays, have been documented from Newfoundland.

Two species of *Hiemalora* have been described: *H. stellaris* (Fedonkin 1980, 1982) first found on the White Sea Coast of Russia, and *H. pleiomorpha*, identified from the Khatyspyt Formation, northern Siberia (Vodanjuk, 1989; see also Serezhnikova, 2007). However, the distinction between them, primarily based on fine linear markings on the disc of *H. pleiomorpha*, is by no means clear cut, since the markings are not always visible and may be a taphonomic or strain-related feature rather than a valid morphological character (Hofmann et al., 2008). As none of the *Hiemalora* specimens observed so far in Newfoundland preserve such linear markings on the disc, and these are in any case of uncertain taxonomic value, I will describe the rayed discs by the genus name alone.

Hiemalora appendages have previously been interpreted as the tentacles of a polyp (Fedonkin, 1980, 1982), and trails of protoplasm from xenophyophores (Seilacher et al., 2003). Anderson and Conway Morris considered and rejected the possibility that *Hiemalora* represents a trace fossil (Anderson and Conway Morris, 1982), and considered that the smoothness of the disc precluded the existence of an attached frond. They proposed that *Hiemalora* represents the remains of “a unique type of organism”. More recently, the rays have been interpreted as root-like structures or algal rhizoids of a holdfast (Runnegar, 1995; Narbonne, 1998; Dzik, 2003; Serezhnikova, 2007), and as possible fungal hyphae (Hofmann et al., 2008). The

associated frond proved elusive until, in 2008, Hofmann et al. identified a new frond, *Primocandelabrum*, from the Bonavista Peninsula, three examples of which have a rayed basal disc (Hofmann et al., 2008). They named the organism *Primocandelabrum hiemaloranum*. Grazhdankin et al. also reported indications of a stem associated with *Hiemalora* from the Khatyspyt Formation, Siberia (Grazhdankin et al., 2008). However, no examples of *Primocandelabrum* other than the three described by Hofmann et al. from the Bonavista Peninsula, Newfoundland, have so far been reported with a holdfast showing *Hiemalora*-like rays, either in Newfoundland localities or in other Ediacaran successions (cf. Wilby et al., 2011; Narbonne et al., 2014). Association with a frond brought *Hiemalora* into the group of holdfast-bearing Ediacaran rangeomorphs (see e.g. Narbonne, 2005) and comparison with co-occurring holdfasts of *Charniodiscus* and other fronds, commonly referred to as “*Aspidella*”, has led to the view that *Hiemalora* forms a continuum with such holdfasts (Hofmann et al., 2008; Burzynski and Narbonne, 2014). For reasons that will become clear in Chapter 5, I will refer here to “typical holdfasts”, rather than the form taxon *Aspidella*, to describe basal discs of *Charniodiscus* and other frondose forms excepting *Primocandelabrum*.

In this chapter, I examine *Hiemalora* specimens from several localities in Newfoundland, noting characteristics of preservation, comparison with co-occurring *Charniodiscus* holdfasts, details of ray morphology, and relationship with the frond *Primocandelabrum*. These considerations lead to a new interpretation of the nature and lifestyle of this enigmatic Ediacaran discoidal impression.

4.2 HIEMALORA IN NEWFOUNDLAND: OCCURRENCE AND PRESERVATION

The first examples of *Hiemalora* from Newfoundland were described from the Mistaken Point Formation, Conception Group, at Mistaken Point in the Avalon Peninsula (Anderson and Conway Morris, 1982), and rare examples were noted in the Fermeuse Formation, St John's Group, at Ferryland (Gehling et al., 2000).

However, the majority of *Hiemalora* specimens in Newfoundland have been found in correlative strata of the Mistaken Point and Fermeuse Formations in the Catalina Dome outcrops of the Bonavista Peninsula (Fig. 4.1). In both sets of localities, on Avalon and Bonavista Peninsulas, the depositional environments have been interpreted as deep water slope (Conception Group) to pro-delta slope for the lower part of the St John's Group (Williams and King, 1979; O'Brien and King, 2004, 2005).

First described from this region by O'Brien and King (2004), a detailed discussion of *Hiemalora* specimens from Bonavista fossil localities, with (retrodeformed) photographs of some of the finest examples, appeared in Hofmann et al. (2008). A remarkable concentration of *Hiemalora* occurs in one small locality in the equivalent of the Mistaken Point Formation at Murphy's Cove (Fossil Locality 3 Hofmann et al. 2008), on rocky ledges on the shoreline. Here, in the thick to medium-bedded turbidites of the Goodland Point and Murphy's Cove Members (Mason et al., 2013; Fig. 4.1) I noted over 50 specimens, the majority accessible only at low tide

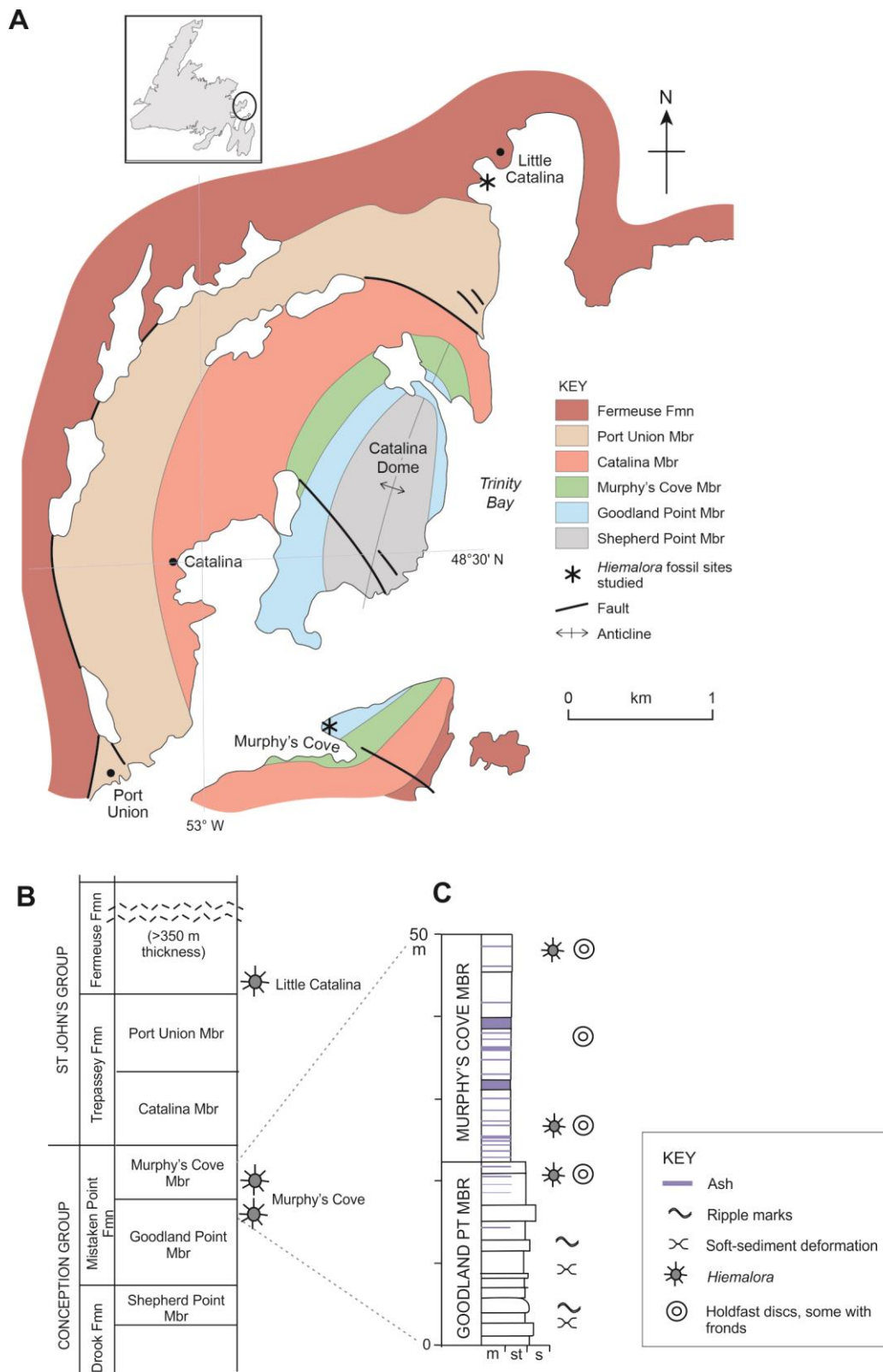


Fig. 4.1. A: Simplified geological map of the Catalina area, Bonavista Peninsula, Newfoundland, with *Hiemalora* fossil sites discussed in chapter indicated. Inset: Location of Bonavista Peninsula within Newfoundland. **B:** Stratigraphic position of *Hiemalora* sites studied. **C:** Schematic log of Murphy's Cove locality. Map and log adapted from Hofmann et al. (2008) and Mason et al. (2013), supported by field observations.

(Appendix 4, Fig. A4.1). Proximity to the sea has taken its toll, and over the past few years, some portions of the fossiliferous surface, including some examples illustrated here, have been washed away, while the quality of detail of the remaining specimens has visibly deteriorated through weathering. Another clustering of *Hiemalora* occurs at Little Catalina (Locality 21 Hofmann et al. 2008), though less well preserved than the Murphy's Cove examples (Appendix 4, Fig. A4.3).

The *Hiemalora* specimens described here come from Ediacaran assemblages showing two distinct modes of preservation. The Ediacaran fossils of the Bonavista Peninsula and from Mistaken Point in the Avalon Peninsula are preserved in Conception style, with the impression of the upper surface of the organism captured under a layer of ash, in contrast to the typical preservation of the undersides of discs cast by sand from above (Fermeuse-style preservation) in the Fermeuse Formation of the Avalon Peninsula (Narbonne, 2005; see Chapter 3). As demonstrated below, under both types of preservation, *Hiemalora* shows unique characters.

4.3 THE DISTINCTIVENESS OF *HIEMALORA*

Descriptions of *Hiemalora* have tended to focus on their obvious distinguishing character – the rays. Previous workers have sought to extract possible patterns and taxonomic value from measurements of the relative diameter of disc to lengths of rays, and from number of rays for discs of different diameters (see Hofmann et al., 2008, for Bonavista specimens; and Serezhnikova, 2007, for Khatyspyt examples of

H. pleiomorpha). However, at least in the case of the Newfoundland examples, such statistics must be treated with caution: the rays vary in quality of preservation, some rays seem to extend as filaments over considerable distances, and many peter out into the substrate without a clear endpoint. A potential complication can be confusion between *Hiemalora* rays and microbial filaments that may have extended to, around, and over the organisms after death. The bedding planes particularly in Murphy's Cove show many examples of extended filaments which are probably of microbial origin (see Liu et al., 2011, and discussion below).

4.3.1 *Hiemalora* preserved in Conception style

Hiemalora discs in the Bonavista and Mistaken Point localities, where they are preserved in Conception style under a layer of tuff, have a distinctive appearance. They mostly occur as flat, smooth, low-positive-relief discs, the majority preserving a layer of the smothering tuff on top of the disc, sometimes weathered grey; a clear, sometimes raised rim; and positive epirelief rays, commonly flat with raised margins, extending from the edge of the disc (Fig. 4.2A, B). In some cases the ash covering is partially eroded away, and occasionally most of the raised disc is weathered out, leaving a narrow raised rim (Fig. 4.2C, D). Many discs have only one or two discernible rays (Fig. 4.2E, F). Rare examples have a small central pit on the raised disc, evident if the tuff covering has been lost (Fig. 4.2G). The characteristic low-positive-relief, flat disc, usually retaining a tuff covering, makes *Hiemalora* discs sufficiently distinctive to be recognizable in many cases even when they occur without rays.

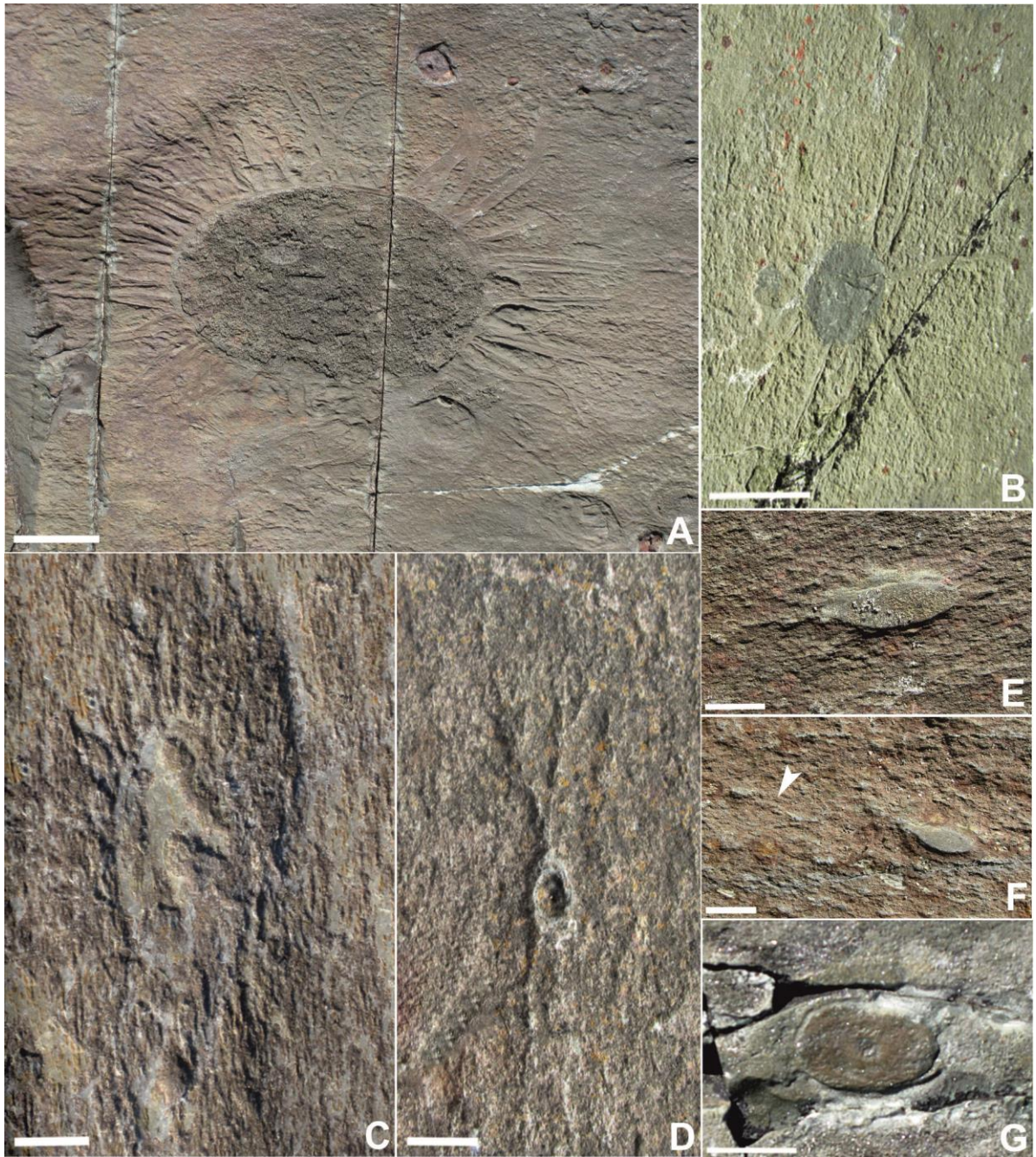


Fig. 4.2. *Hiemalora* specimens from Murphy's Cove (A, B, G) and Little Catalina (C-F). **A,B:** *Hiemalora* specimens from Murphy's Cove, first figured by Hofmann et al. (2008), with central disc retaining covering of tuff, weathered dark grey. **C:** Specimen with partially eroded tuff covering. **D:** Eroded *Hiemalora* disc with double-branched frond and long ray. **E, F:** Specimens with typical flat, smooth discs covered by tuff. A faintly visible branched ray is arrowed in F. **G:** Specimen which appears to have lost its tuffaceous covering, showing small central depression on a smooth disc. Scale bars: 1 cm.

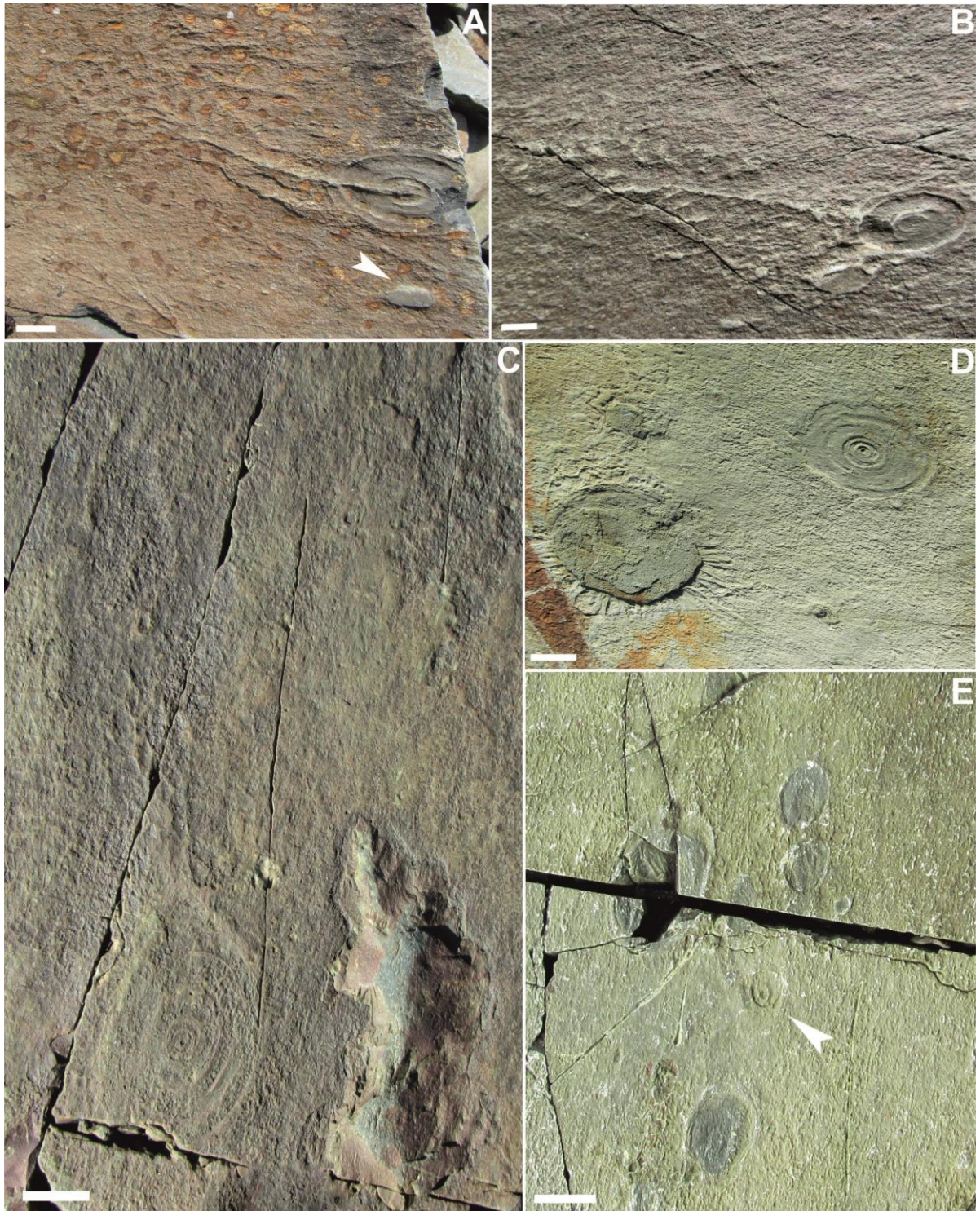


Fig. 4.3. Comparison of *Hiemalora* and *Charniodiscus* holdfast disc preservation. **A, B:** *Charniodiscus* specimens from Little Catalina, with typical eroded form of several distinct concentric rings surrounding central boss from which the stem of the frond emerges (Chapter 3), alongside *Hiemalora* preserved as smooth raised discs covered by tuff. **C:** *Charniodiscus* and *P. hiemaloranum* side by side at Murphy's Cove, with *P. hiemaloranum* retaining thick layer of tuff. **D:** *Hiemalora* with rays alongside annulate disc attributed to *Charniodiscus*, Murphy's Cove. **E:** Presumed typical holdfast with several distinct rings (arrowed) amid *Hiemalora* specimens showing typical preservation as smooth discs covered with tuff, Murphy's Cove. Scale bars: 1 cm.

Hiemalora co-occurs with other forms, in particular *Charniodiscus*, in all the localities examined. The holdfast discs of *Charniodiscus* at Little Catalina and Murphy's Cove are preserved flat to slightly concave, with several distinct, raised concentric rings. They do not generally preserve the overlying tuff, unlike *Hiemalora* specimens (Fig. 4.3). The difference in preservation between the two types of disc is evident when they occur adjacent to each other, especially when the presence of attached fronds allows clear identification (Fig. 4.3A-C). No examples have been observed of frond-bearing or presumed holdfast discs preserved with raised concentric rings that show clear *Hiemalora*-like rays. The presence of fine filaments that form part of the texture of the surrounding microbial mat, or may be related to microbial activity following decay of the organism, can be a misleading factor.

Hiemalora may occasionally show faint compression rings, unlike the distinct raised rings of typical holdfasts, and some weathered-out *Hiemalora* discs show indications of structure within that have led to their being regarded as intermediate forms between *Hiemalora* and typical holdfasts (see Burzynski and Narbonne, 2015, fig. 12). The markings within these discs do not show the systematic concentric raised rims of typical holdfasts, and may arise from microbial filaments wrapped around and within the area occupied by the original disc. The one example described by Burzynski and Narbonne (2014) of what appears to be a *Charniodiscus*-type holdfast with raised concentric rings associated with a *Primocandelabrum* (their fig. 9) is, I propose, an accidental juxtaposition of a torn frond with an unassociated disc. The stem crosses to the side of the disc and extends beyond it, and a wider

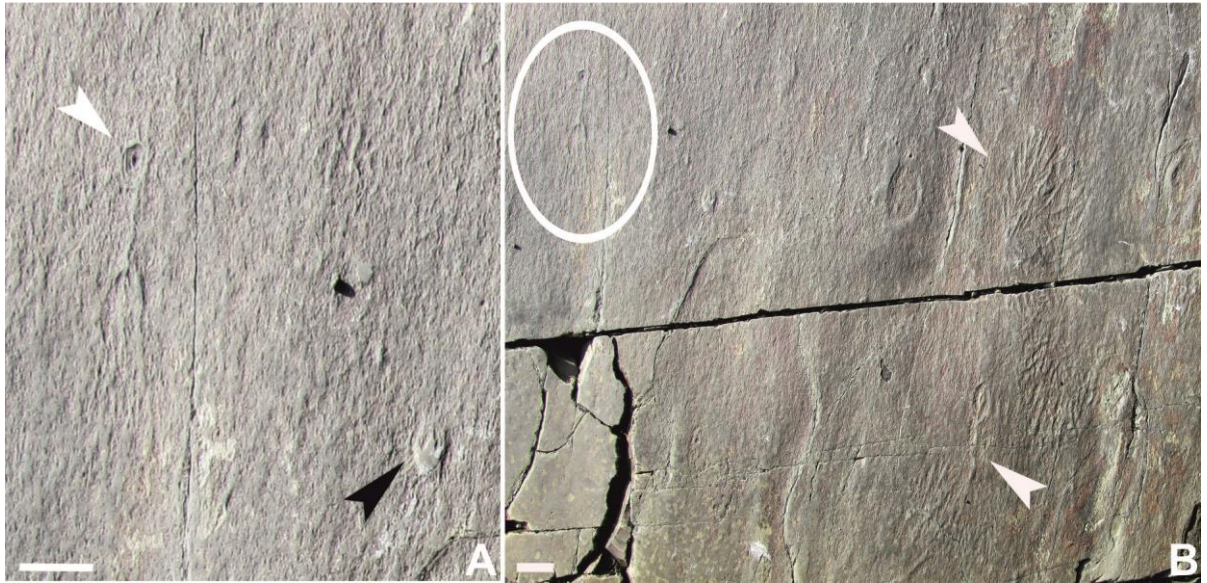


Fig. 4.4. A: *Primocandelabrum* lying close to an annulate typical holdfast (white arrow). Note that the frond stem passes to one edge of the disc and extends beyond it. A *Hiemalora* with partially eroded tuff covering is seen nearby (black arrow). **B:** Wider view of bed, with *Primocandelabrum* in A indicated with white ellipse. Note torn frond pointing in opposite direction, and another disc with frond stem intact (arrows). Scale bars: 5 cm.

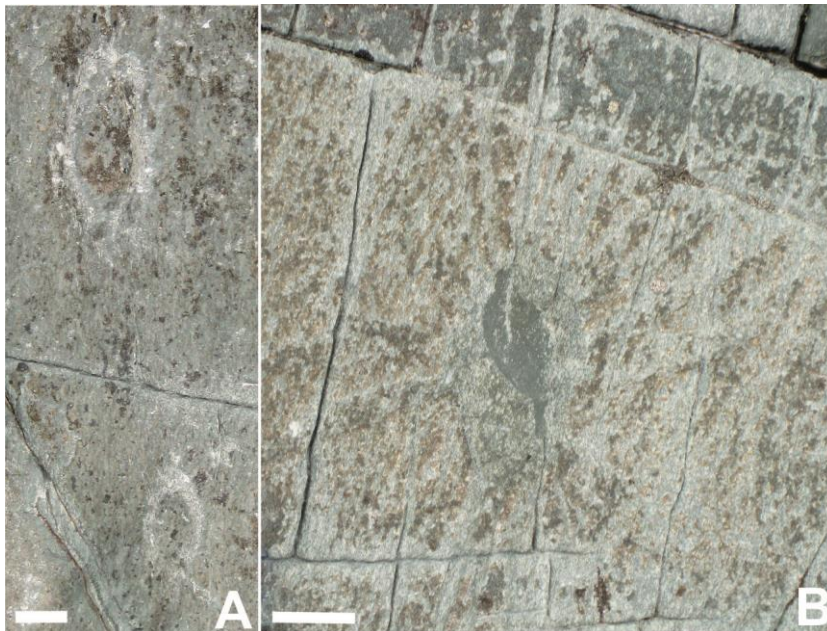


Fig. 4.5. Hiemalora from a surface close to Mistaken Point. **A:** Two eroded discs retaining rims. **B:** *Hiemalora* with grey tuff covering and poorly preserved rays. Scale bars: 1 cm.

view of the surface indicates other torn fronds, including one pointing in the opposite direction (Fig. 4.4).

Examples of *Hiemalora* from the Mistaken Point Formation at Mistaken Point, on the Avalon Peninsula, though less well preserved, show similar characteristics to those from the Bonavista Peninsula (Fig. 4.5).

4.3.2 *Hiemalora* preserved in Fermeuse style

The distinctiveness of *Hiemalora* discs from other holdfasts is underlined by occasional examples preserved in Fermeuse style in the rocks around Ferryland, in the Avalon Peninsula. As noted in Chapter 3, Fermeuse-style preservation typically preserves external moulds of the undersurface of holdfast discs, in negative epirelief and positive hyporelief (Narbonne, 2005). Impressions of discs of one to several centimetres diameter are presumed to have been holdfasts of fronds, though the fronds have not been preserved (Gehling et al., 2000). On upper bedding surfaces, these impressions show the concertina effect of compaction, and have a deep central depression reflecting a protruding boss at the centre of the lower surface of the originally bulbous disc (Gehling et al., 2000; Burzynski and Narbonne, 2014).

Occasional examples of *Hiemalora* found on these bedding surfaces among such negatively preserved discs are virtually identical in appearance to those observed under Conception-style preservation, except that they lack the covering of tuff: the Ferryland *Hiemalora* specimens are smooth, low-positive-relief discs, with a minute

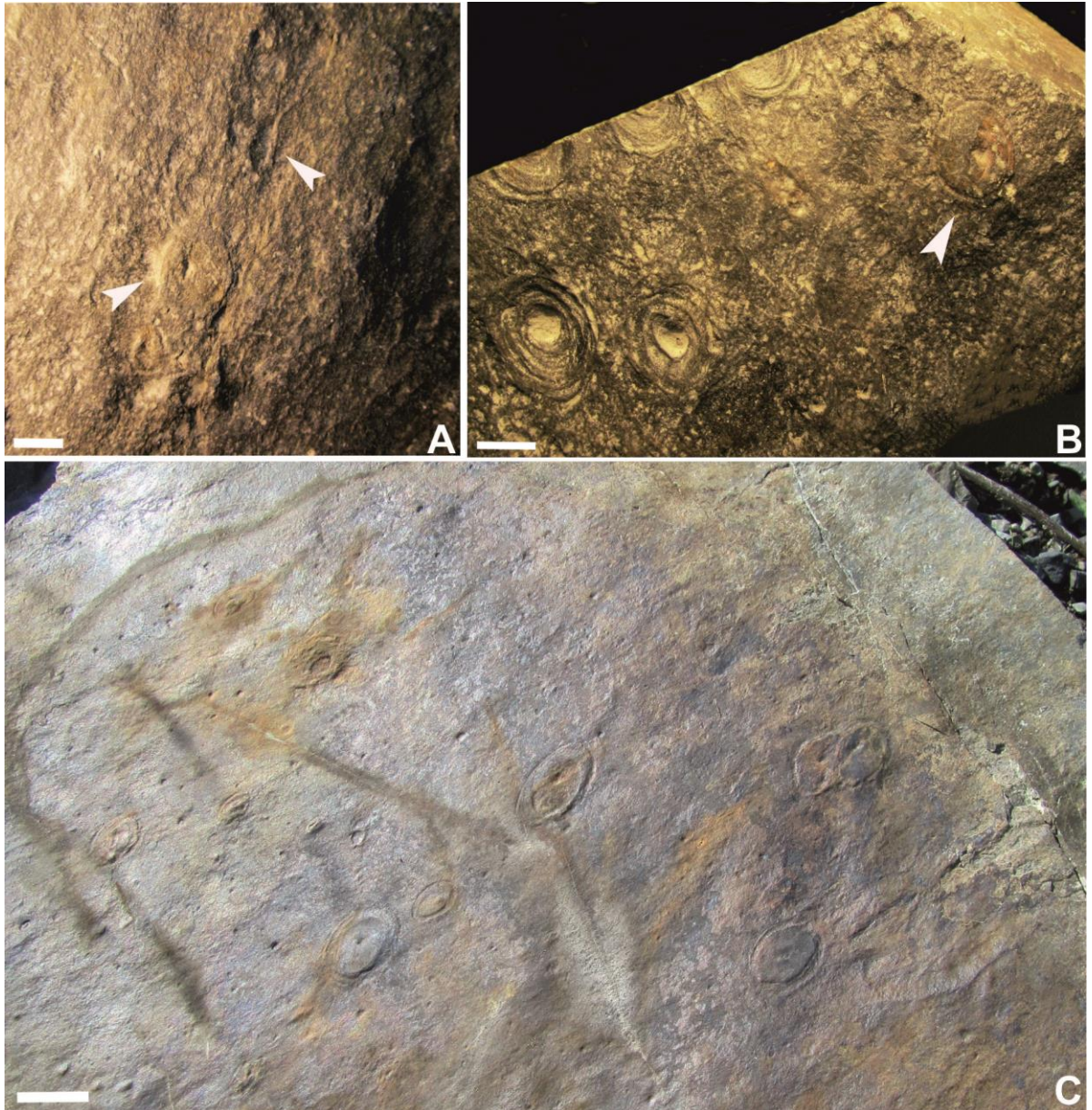


Fig. 4.6. *Hiemalora* specimens from Ferryland, preserved in Fermeuse style. **A, B:** *Hiemalora* preserved as positive discs with small central depression and faint rays, alongside negative typical holdfast discs on upper bedding surfaces. **C:** A group of presumed *Hiemalora* specimens, showing characteristic smooth discs with small central depression but with no rays preserved. Note a double disc towards centre right. Scale bars: 1 cm.

central depression of ~1 mm diameter, and faint impressions of positive rays (Fig. 4.6). The difference with the surrounding high-negative-relief impressions of the undersides of presumed holdfast discs is striking (Fig. 4.6A, B). As was the case for localities with Conception-style preservation, their distinctive appearance under

Fermeuse-style preservation at Ferryland allows *Hiemalora* specimens to be recognized and differentiated from other discs even when rays are barely visible or even lacking (Fig. 4.6C; cf. Fig. 4.2G; see also Appendix 4, Fig. A4.4).

4.4 PRIMOCANDELABRUM HIEMALORANUM

The discs of the holotype and two paratypes of *Primocandelabrum hiemaloranum* described by Hofmann et al. (2008) from the Bonavista Peninsula and reexamined here, reflect the morphological distinctness of *Hiemalora* described above.

The paratype at Little Catalina (Fossil site 21 Hofmann et al.) has a disc preserved as a high-positive-relief smooth mound, with a wide central depression, presumably the result of partial weathering of the covering tuff (Fig. 4.7A). A number of faint rays are visible around the disc. The ratio of frond length L to disc diameter D , L/D , is nearly 6, compared to the more typical value of ~ 3 for *Charniodiscus* (see e.g. examples in Fig. 4.3; Hofmann et al., 2008, fig. 17(3)), illustrating an unusually small disc for the length of frond. Anomalous relative sizes of discs to fronds have been noted in other examples of *P. hiemaloranum* (Wilby et al., 2011).

A short, thick ray extends from the disc edge parallel to the stem, and divides into three equal branches (Fig. 4.7B). While some *Hiemalora* rays do branch, the width of the ray and branching node, and the equal width and parallel alignment of the branches in this example is quite different from that of typical branching rays. The three-branched “trident” shape reflects the branching pattern of some

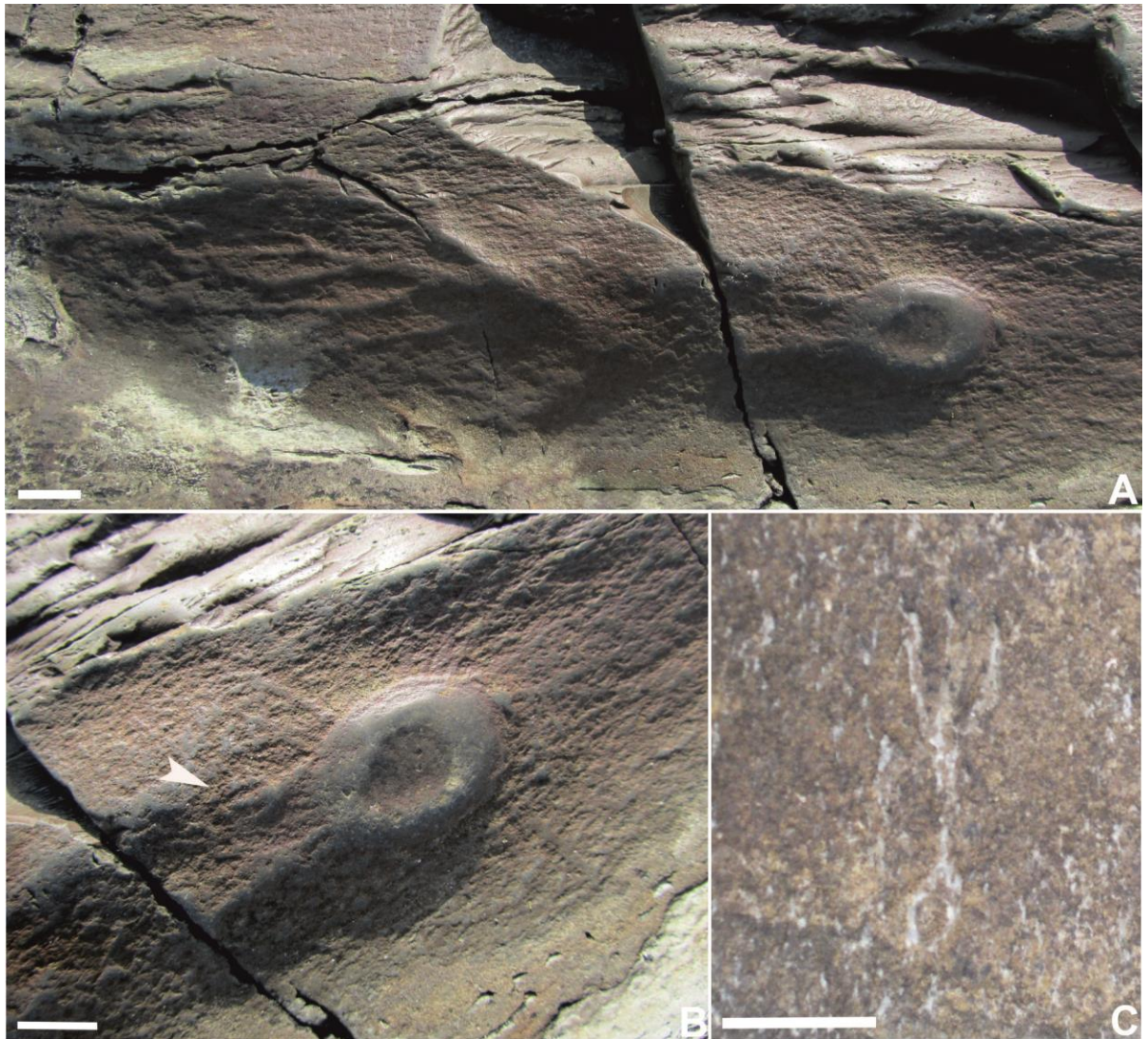


Fig. 4.7. **A:** *P. hiemalorum* Hofmann et al. 2008 paratype, Fossil Locality 21 Hofmann et al., Little Catalina. **B:** Close up of *Hiemalora* base of paratype in A, with unusual three-branched extension arrowed. **C:** Small three-branched *Primocandelabrum* frond with (non-rayed) *Hiemalora* disc, locality near Melrose, Bonavista Peninsula. Note similarity with the three-branched “ray” in the paratype (B). Scale bars: 1 cm.

Primocandelabrum fronds, such as the example shown in Fig. 4.7C, raising the intriguing possibility that the three-branched “ray” on the *P. hiemalorum* paratype might be a small, new stem that had begun to grow from the *Hiemalora* disc.

The examples of *P. hiemalorum* described by Hofmann et al. (2008) do not preserve details of the connection between stem and holdfast. The connection can however

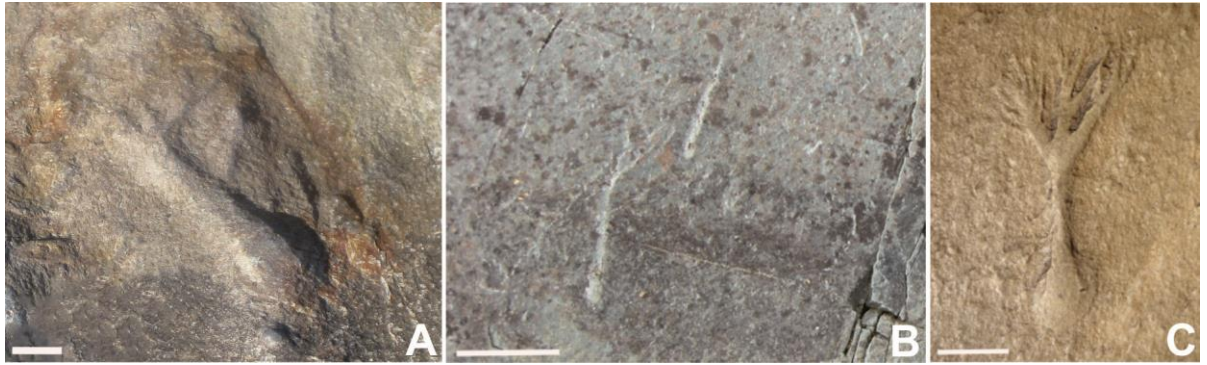


Fig. 4.8. Examples of *P. hiemaloranum* with disc–frond connection preserved, showing widening trunk and bulbous base enveloping top of disc. **A:** Well-preserved lower part of specimen, Little Catalina. **B:** Poorly preserved examples, Watern Cove, near Mistaken Point. **C:** Well-preserved specimen, near Melrose, Bonavista Peninsula. Photo C taken by Alexander Liu, and originally published in Liu et al. (2015). Note the lack of rays in all these examples. Scale bars: A, C: 1 cm; B: 5 cm.

be glimpsed in some specimens preserved in Conception style, and here a further distinction may be observed between *P. hiemaloranum* and other frondose forms. In *P. hiemaloranum*, the stem widens out to encompass the whole of the top of the disc at the base, giving a thicker stem and a bulbous base. This is observed in examples from Little Catalina and surfaces around Mistaken Point (Fig. 4.8). By contrast, *Charniodiscus* specimens on these surfaces tend to show a narrower stem, clearly arising, as evident in Little Catalina examples, from the centre of a disc with several concentric rings (see e.g. Fig. 4.3A, B).

4.5 HIEMALORA RAYS AND MICROBIAL MATS

Remarkably preserved *Hiemalora*-bearing surfaces at Murphy’s Cove reveal a surface criss-crossed by extended filaments, knobbly filamentous bundles, and other indications of a rich microbial mat covering (Fig. 4.9A, C). One filament has a widened portion suggestive of the impression of a “pool” in a viscous trail (Fig.

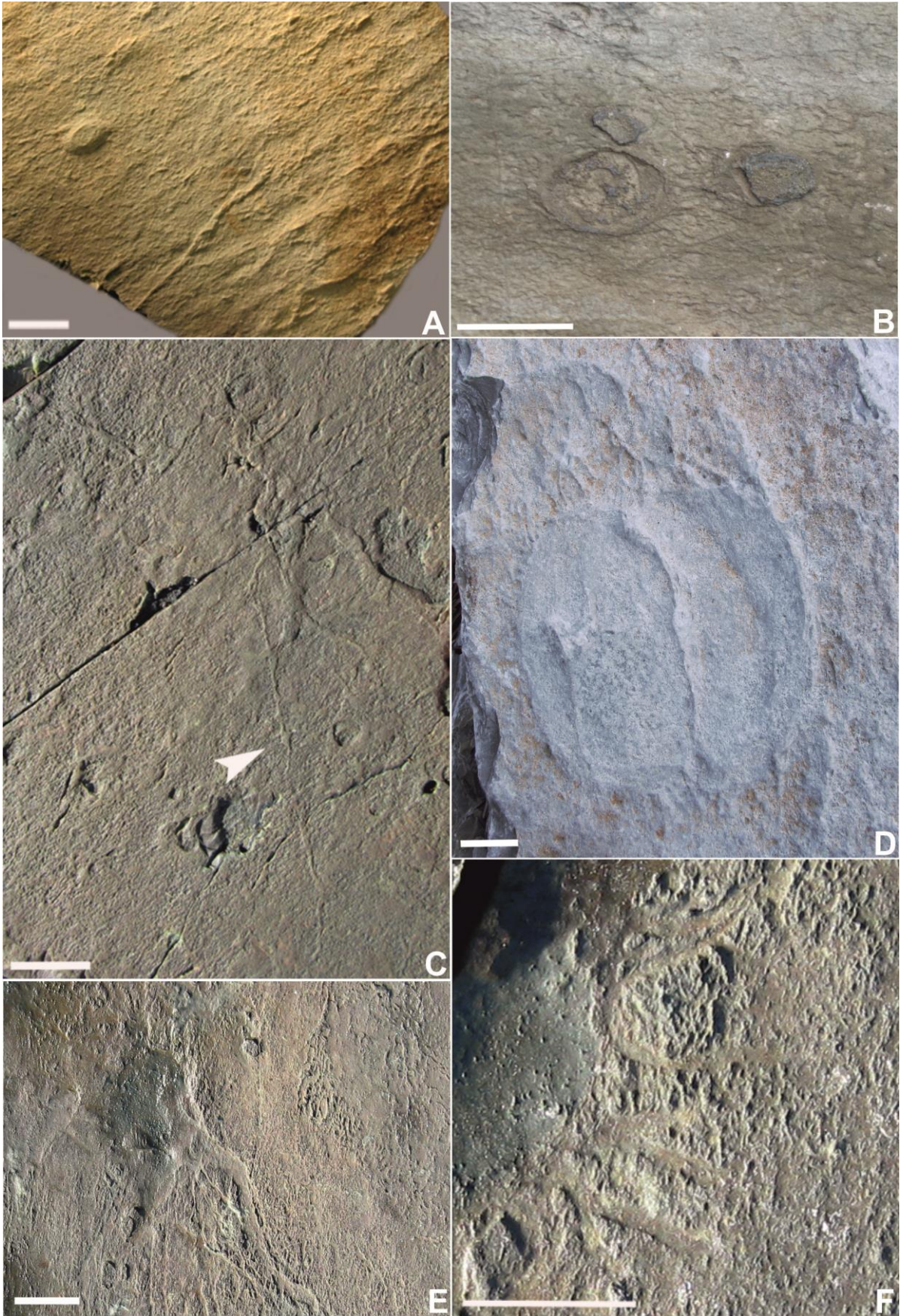


Fig. 4.9.

◀ **Fig. 4.9.** Examples of *Hiemalora* and microbial mat filaments from Murphy's Cove and surrounding areas. **A:** Raised, knotted and cord-like filaments form part of complex microbial mat-related structures on top surfaces bearing *Hiemalora* discs. **B:** *Hiemalora* specimens with partially eroded tuff covering surrounded by microbial textures. **C:** Long microbial filament showing "pooling" (arrowed) suggestive of mucous trail, among weathered *Hiemalora* discs and possible collapsed frond. **D, E:** Partially decayed *Hiemalora* discs, E with probable collapsed frond. Microbial filaments stretch across the decaying form and it is unclear in D whether the fine markings around the disc are rays or microbial filaments. **F:** Close up of *Hiemalora* rays, with microbial mat textures below. Scale bars: 1 cm.

4.9C, arrowed). The *Hiemalora* discs with their sometimes branching rays appear to be intimately associated with this mat (Fig. 4.9D-F). Some *Hiemalora* specimens are captured in a state of partial decay, with stringy microbial fibres extending and wrapping over the collapsing forms (Fig. 4.9D, E). Long filaments also extend over 15 cm, as far as can be followed. Rays extending from the edge of the *Hiemalora* discs branch and disappear into the complex mat texture. This interaction with the microbial filaments covering the substrate complicates assessment of the morphology of *Hiemalora* rays.

A preserved portion of the rays of a *Hiemalora* disc now lost from the block (Fig. 4.10A) illustrates the variation in length of the rays, which divide into fine branches at the tips. The rays are seen to cross-cut each other. Further characters are illustrated by the rays of the *Hiemalora* specimen in Fig. 4.2A, shown in close up in Fig. 4.10B. Hofmann et al. (2008) noted the fusing of two rays, and their apparent association with a small, weathered disc. Two other rays also show division into fine branches towards their tips, while a possible further fusion of rays, poorly preserved, is suggested (Fig. 4.10B). The variable width and irregularity of rays is particularly noticeable in the second paratype of *P. hiemaloranum*, a rare

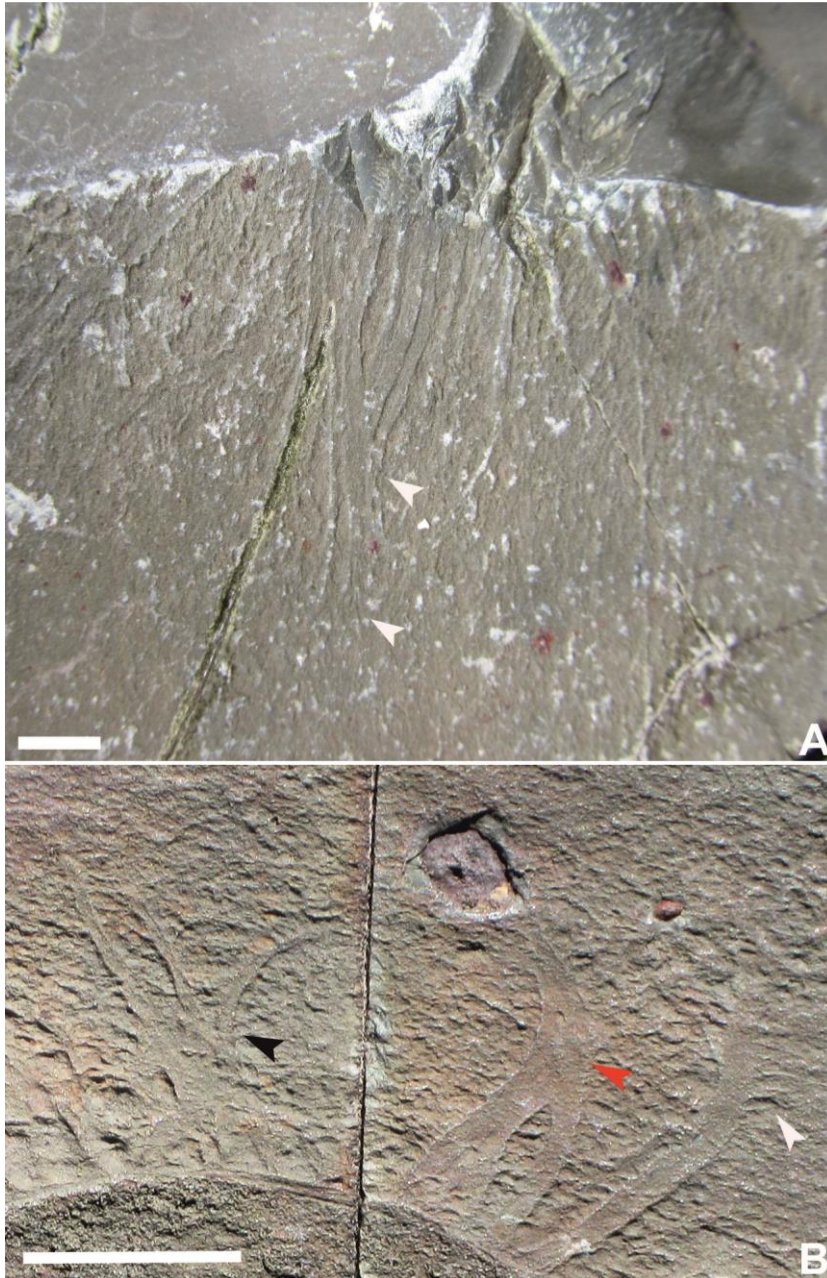


Fig. 4.10. Close ups of *Hiemalora* rays. **A:** Rays preserved from a lost disc, showing cross-cutting, and fine branching at tips (arrowed). **B:** Portion of *Hiemalora* specimen shown in Fig. 4.2A. Ray on far right shows branching at distal end (white arrow). To left of that, two rays merge (one may already have merged with another close to the disc), and appear to extend to a weathered out *Hiemalora* disc, which may or may not be associated (red arrow). Towards left, a group of three rays, the central one showing branching at tip, emerge from an apparently single wide fused ray (black arrow). Note variation in width of rays, and apparent folded rim on this part of the disc. Scale bars: A, 5 mm; B, 10 mm.

example of a full-rayed *Hiemalora* with a presumed associated *Primocandelabrum* nearby (Fig. 4.11).

Examination of a resin cast of the specimen shown in Figs 4.2A and 4.11B under a microscope reveals further detail (Fig. 4.12). The well-developed rays are mostly flat with edges curved upwards to form ridges, and the merging of two rays is confirmed as a full fusion. The flat rays lie over a network of filaments forming the microbial mat texture of the substrate, and some filaments are seen to cross over the rays. Close ups of the point of emergence of the rays from the disc edge, parts of which can be glimpsed beneath the covering of tuff, show no sign of any joining structure – the transition from disc to ray is wholly smooth (Fig. 4.12B, C). Rays often branch distally (Fig. 4.12D; see also Fig. 4.10B), and most peter out, though rare examples end in a rounded tip (Fig. 4.12E). A detailed view of the group of close and possibly fusing rays towards the left of Fig. 4.10B shows a bulging outward extension of the disc edge, from which several rays emerge (Fig. 4.12F). Given the lack of a sharp edge to the disc, the appearance of narrow folds and furrows in some parts of the circumference would seem to be the result of compression (Figs 4.2A, 4.10B, and 4.12A, F).



Fig. 4.11. **A:** Paratype of *P. hiemaloranum* Hofmann et al. 2008, Fossil Locality 26 Hofmann et al. The frond's connection to the disc is missing, and this "specimen" may represent a chance association of the *Primocandelabrum* with the *Hiemalora*. Scale bar: 5 cm. **B:** Cast of disc from A. Note variability in width of rays, and a thick ray at bottom left of disc. A region at the top of the disc may represent fused rays or may be obscured by part of the felled stem of the frond. **C:** Sketch from cast, underlining the irregularity of the rays.

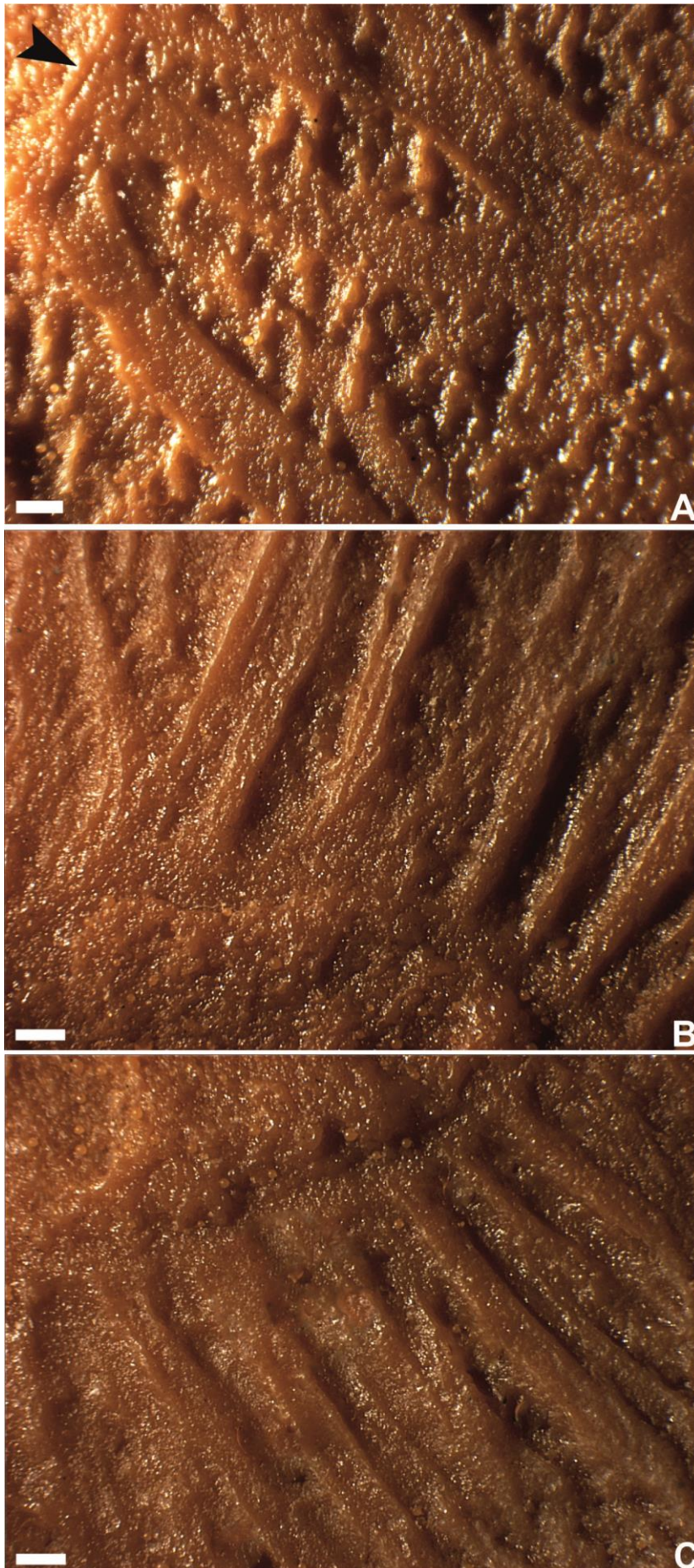


Fig. 4.12 (A-C). Details of rays, from positive resin cast of *Hiemalora* specimen shown in Figs 4.2A and 4.10B. **A:** Merging rays (centre right in Fig. 4.10B), with microbial filaments of underlying mat, some of which encroach over the rays. Note the flat, smooth nature of the rays, with raised margin, and their smooth fusion towards right of picture. Edge of disc to left (black arrow). **B, C:** Areas of disc margin appearing below grainy tuffaceous covering (lower part of B, upper part of C) showing emergence of rays. Note smooth extension into rays and lack of a clear disc edge. Rays in B appear in places as fused filaments, though this may be a taphonomic effect. Scale bars: 1 mm. (Fig. 4.12, D-F overleaf.)

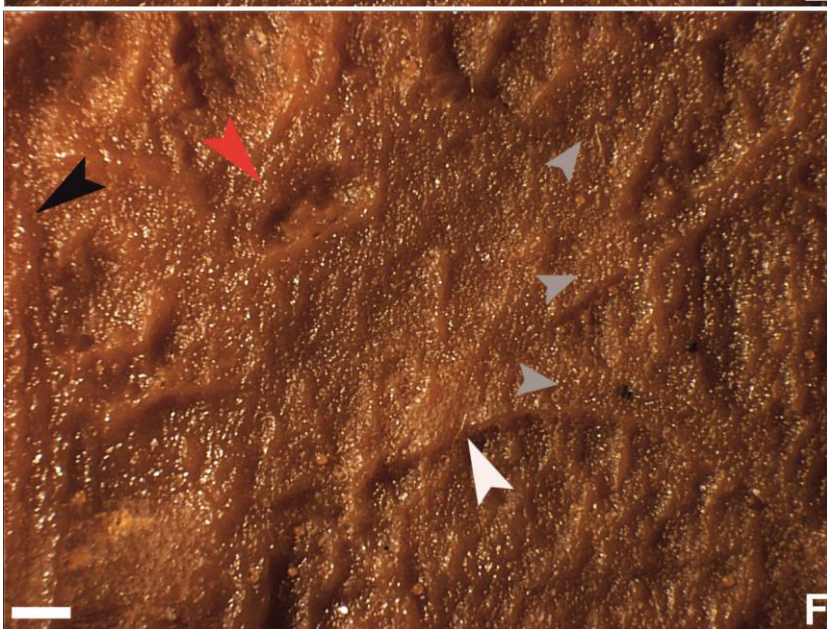
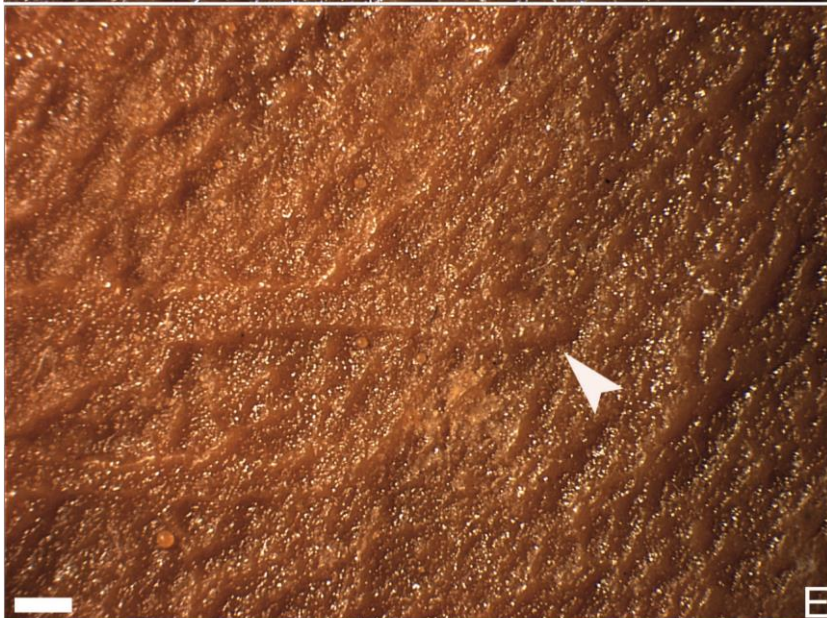
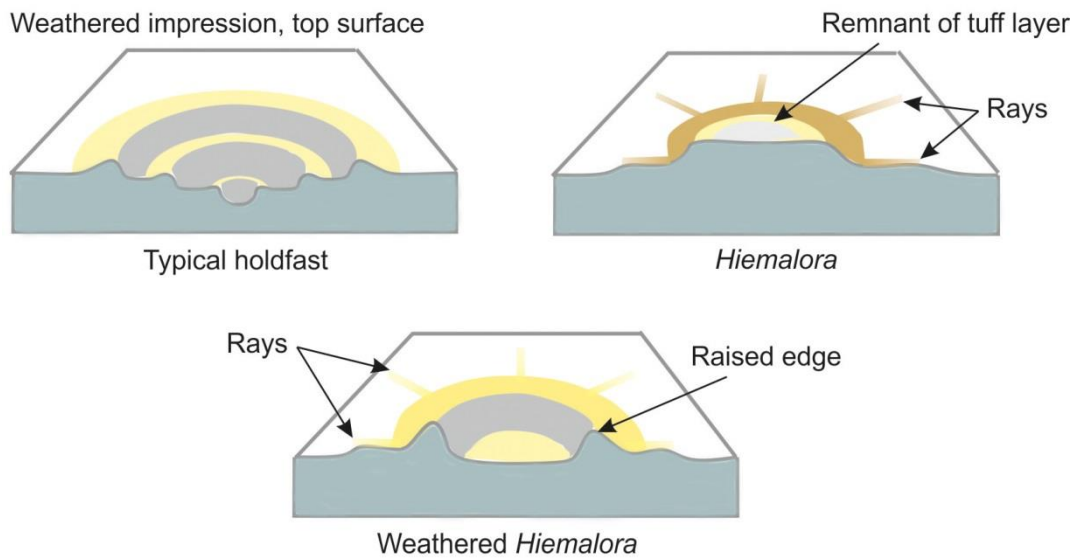


Fig. 4.12 (D-F). D: Branching tip of ray (right side of Fig. 4.10B). E: Unusual rounded, unbranching tip of ray (arrowed). F: Bulge (white arrow) extending from disc margin (black arrow), which divides asymmetrically into three rays (grey arrows). A rounded gap or hole can be observed within the bulge (red arrow). Scale bars: 1 mm.

A. Conception-style preservation at Murphy's Cove, Little Catalina



B. Fermeuse-style preservation at Ferryland

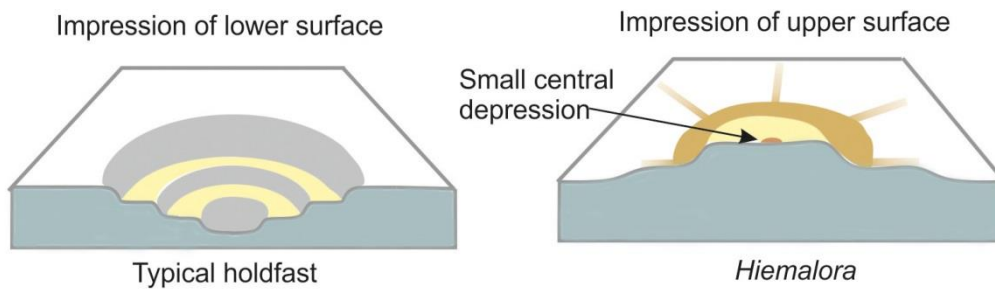


Fig. 4.13. Comparison of *Hiemalora* and typical holdfast profiles as preserved in Conception and Fermeuse styles. Disc diameters of *Hiemalora* vary from ~ 3–30 mm, while typical holdfasts range from ~ 2–>200 mm.

4.6 DISCUSSION

The systematic difference in preservation between *Hiemalora* and other holdfast discs observed in all these Newfoundland localities and under two different preservation regimes suggests a real morphological and, by implication, taxonomic, distinction (Fig. 4.13).

Several tentative conclusions may be inferred from the differences in disc form between *Hiemalora* and typical holdfasts (here primarily referring to the holdfast of *Charniodiscus*):

- 1) The tendency of *Hiemalora* to preserve as slightly raised flat discs retaining some of the overlying ash suggests that the disc was more resistant than typical holdfasts, and/or the disc surface may have bonded in some way with the overlying ash. Even in Fermeuse-style preservation, in which generally the under-surfaces of buried holdfast discs were cast, the *Hiemalora* organism was resistant enough to produce a positive impression, similar to the Flinders-style preservation of *Dickinsonia* (Fig. 4.13; Gehling, 1999; Narbonne, 2005).
- 2) The difference in preserved disc form between the smooth discs, sometimes with a small central depression which may be the anchorage point for the stem, and the usual concentric rings of typical holdfasts (Fig. 4.3) points to intrinsic differences in internal architecture between the associated organisms. This is further supported by the differences observed in stem-holdfast connections between *Primocandelabrum*, with its widening stem and bulbous base, and the thin stem of typical holdfasts (Fig. 4.8, cf. Fig. 4.3A,B). Combined, these observations indicate that *P. hiemaloranum* represents an organism very different to *Charniodiscus*.
- 3) If *Hiemalora* and typical holdfasts do not represent a continuum but two distinct organisms, then rays are not extensions that arise at a particular life stage of *any* discoidal organism but are genuinely confined to *Hiemalora*,

although whether they only arose at particular stages in the life cycle of *Hiemalora* remains uncertain. Rays are not always seen in isolated discs that otherwise display typical characteristics of *Hiemalora* (e.g. Fig. 4.2G, Fig. 4.6C).

The detailed observations of *Hiemalora* rays presented here help to constrain the possibilities regarding their nature and function. The probable fusion of two rays in the specimen shown in Fig. 4.2A, which has been used to argue against the interpretation that they are roots and to suggest a possible fungal affinity (Hofmann et al., 2008), is confirmed as a full fusion by close-up images (Fig. 4.12A). The rays vary in width (Fig. 4.11B, C). Hints of construction of rays from fused filaments, suggestive of rhizomorphs (e.g. Fig. 4.12B), may be a taphonomic artefact. The lack of evident side or cross-branching between the rays, or a reticulate network of finer filaments, argues against a fungal interpretation. In the closely studied specimen (Fig. 4.2A), the outward extension of the disc perimeter, which shows a hole in coverage and divides unevenly into several rays (Fig. 4.12F), as well as the full fusion between rays and their smooth emergence from the central discoidal region (Fig. 4.12A-C), suggest the possibility of cytoplasmic flow (cf. Seilacher et al., 2003). The regular and close association between *Hiemalora* and thick microbial mat textures further suggests a lifestyle dependent on the surrounding mat, either through osmotrophy or phagocytosis.

The smoothness of the *Hiemalora* disc first noted by Anderson and Conway Morris (1982), who argued that this implied the lack of an associated frond, may be related to the quite different connection between disc and frond in *P. hiemaloranum* compared to other frondose forms. It is also curious that most examples of *P. hiemaloranum* have discs that show no sign of *Hiemalora* rays. In the one example of *P. hiemaloranum* with a richly rayed disc – the paratype from Fossil Locality 26 Hofmann et al. 2008 (Fig. 4.11) – the connection between the *Hiemalora* and the *Primocandelabrum* frond is only presumed. This may be a chance association between a frond and a disc.

While the lack of a rayed disc in most examples of *P. hiemaloranum* may be due to preservational biases, an alternative possibility is that the *Hiemalora* organism only produced a frond at particular times in its life cycle, and rays tended to form at other times. The appearance of a small *Primocandelabrum*-like triple-branched extension from the disc of the paratype of *P. hiemaloranum* at Fossil Locality 21 Hofmann et al. 2008 (Fig. 4.7B) hints at the possibility that new fronds may have grown from the *Hiemalora* disc. This implies a different relationship between *Hiemalora* and its frond to that of a basal holdfast disc. The difference may also be reflected in the ratio of frond length to disc diameter, L/D . A basal holdfast disc would be expected to grow proportionally with the frond, as observed in the case of *Charniodiscus* (e.g. Hofmann et al., 2008; fig. 17(3); see also Liu et al., 2012, fig. 5b, an example of a possible juvenile *Charniodiscus*, with a holdfast of ~ 2.5 mm diameter, also with an L/D ratio of ~ 3). By contrast, if *Primocandelabrum* grows from a

Hiemalora disc, examples with a relatively large disc and small, still-growing frond may be expected. As noted above, a wide variation in L/D has been observed in *P. hiemaloranum* (Wilby et al., 2011; Section 4.4). If correct, this interpretation makes the lifestyle of *Hiemalora* likely to have been different from that of *Charniodiscus*, and perhaps other Ediacaran frondose organisms. The possibility that *Primocandelabrum* may have been a growth associated with reproduction, broadly analogous to a fruiting body (cf. Steiner and Reitner, 2001), cannot be ruled out.

The resistance of the *Hiemalora* disc may further hint at some form of tough and possibly adhesive amoeboidal, or plasmodial construction, perhaps associated with times of stress for the organism. The difference in surface properties indicated by the adhesion of tuff to the tops of the impressions preserved in Conception style is also suggestive of the characters of a variety of extant amoeboidal forms (e.g. Foraminifera, Rhizamoeba) which have sticky surfaces and acquire a covering of debris. These observations would appear to point towards the interpretation of *Hiemalora* by Seilacher et al. (2003) as a possible xenophyophore, with the rays as the marks left by pseudopodia. But in addition to problematic points such as the uncertain age of origin of Xenophyophoria, and the complex agglutinated test architecture of modern forms, such an interpretation importantly fails to explain the associated frond.

Another possibility, drawing together all these observations, is that *Hiemalora* reflects an aggregate form of multicellularity, involving an amoeboidal or plasmodial lifestyle in which, perhaps under conditions of environmental stress, streams of cells converge to form a mass, from which a reproductive structure may emerge, to broadcast spore-like forms to potentially more promising territories. Such lifestyles are today most commonly found in terrestrial environments, sharing aspects with Myxobacteria, Mycetozoa (slime moulds within the Amoebozoa), and fungi. Marine conditions would require different adaptations and mechanisms for aggregation and the broadcasting of spore-like forms. However such a lifestyle would be generally consistent with the observations of converging rays (paths left by the aggregating streams or, more probably, given the variations in ray cross-sections, impressions of viscous mucus trails), a central sticky mass (resistant, and bonding with fine tuff), the bulbous base of *P. hiemaloranum* (typical of the growing stalk of a reproductive body such as those produced Myxobacteria on a far smaller scale), the variation in L/D ratio, and the lack of rays in the majority of examples of *P. hiemaloranum* and in some examples of isolated *Hiemalora*-like discs, which may represent resting stages.

This discussion has been based on studies of *Hiemalora* and *P. hiemaloranum* from Newfoundland, but the main observations would appear to be consistent with accounts of *Hiemalora* from other successions. Examples of *Hiemalora* from the White Sea coast of Russia have been noted in some cases to have rays that extend partially into the disc margin and grooves on the top of the disc (Vodanjuk, 1989;

Serezhnikova, 2007). These features can be explained within the model given above by the compression and partial collapse of a three-dimensional rounded plasmodial form and creasing of a surface of thick, mucus-like material. No examples of discs with fine extensions described as "*Mawsonites reticulatus*" (cf. *Palaeophragmodictya reticulata* Gehling and Rigby 1996) and "*Mawsonites pleiomorphus*" (cf. *Hiemalora pleiomorpha* Vodanjuk 1989) by Grazhdankin (2014; see also Bykova, 2010), have been observed in Newfoundland. The possible relationship between *Hiemalora* and *Mawsonites* awaits a comparative study of specimens from Newfoundland with those from Siberia and the White Sea.

As noted above, only a few examples of *Primocandelabrum* attached to rayed *Hiemalora* discs have so far been reported, these confined to the Bonavista Peninsula, Newfoundland (and described in Hofmann et al., 2008). Further, given the occurrence of *Hiemalora* in both Avalon and White Sea clusters of assemblages (Waggoner, 2003; Fig. 1.1), it is curious that *Primocandelabrum* has as yet only been reported from Avalonian assemblages – Newfoundland (Hofmann et al., 2008), Charnwood, England (Wilby et al., 2011), and Sekwi Brook (Narbonne et al., 2014). This is in marked contrast to observations of forms such as *Charniodiscus* and *Charnia* across all these assemblages, and further points to a difference between *P. hiemaloranum* and typical rangeomorphs.

4.7 CONCLUDING REMARKS

The possibilities concerning *Hiemalora* lifestyle given above must remain speculative. But the evidence presented in this chapter nevertheless points strongly to the conclusion that *Hiemalora*, and its frond *Primocandelabrum*, was a different type of organism from typical Ediacaran rangeomorphs, which have no rays and appear to have proportionally sized basal discs. Fungal and slime mould interpretations of Proterozoic organisms have been proposed before (e.g. Steiner and Reitner, 2001; Peterson et al., 2003; Bengtson et al., 2007), as has the possibility of xenophyophores (Seilacher et al., 2003). The observations described above indicate the shortcomings of all these explanations in the case of *Hiemalora*, namely: a) the apparent lack of fine side branching with T- and H-junctions in otherwise well preserved specimens argues against a fungal interpretation; b) the presence of a frond arising from a few rayed *Hiemalora* discs precludes xenophyophores; and c) although showing distinct similarities with slime moulds, the latter are adapted almost entirely to terrestrial habitats. However, the documented characteristics would be consistent with an amoeboidal or plasmodial lifestyle. (The suggestion of an amoeboid lifestyle for *Hiemalora* does not amount to a claim for any specific phylogenetic affinity for either *Hiemalora* or *Charniodiscus* and other Ediacaran forms. However, it indicates that more than one group may be represented among discs with associated fronds.)

The possibility that the rays may represent aggregating streams or slime trails that draw together to form a disc, rather than outwardly extending rhizomorphs or

pseudopodia, with the *Primocandelabrum* stalk as a temporary growth perhaps functioning as a reproductive structure, represents a radically different way in which to view *Hiemalora*. Such an interpretation implies that the “organism” producing *Hiemalora* would only be preserved during certain phases of its life cycle. If aggregation is prompted by particular environmental conditions, then one may predict that *Hiemalora* would tend to be found only on certain bedding planes and search for clues to common environmental conditions, particularly signs of environmental stress. Further studies are needed to test such a hypothesis.

The early Ediacaran assemblages of Newfoundland represent the emergence of large-scale forms after the Cryogenian glaciations. According to molecular clock estimates, these assemblages should include simple animals (e.g. Erwin et al., 2011; Chapter 1). While there are indications that some of the Ediacaran forms may well have been animals (e.g. Liu et al., 2010, 2014; Menon et al., 2013), the possibility that others represent early explorations of aggregate multicellularity in the oceans, reaching large scales in the absence of major predation, seems plausible. Further, while Ediacaran discs have been divided into many different taxa, some of which are very probably synonyms resulting from taphonomic differences, and others not even biogenic, the observations in this chapter suggest that there may be very real differences lurking behind these morphologically simple impressions.

CHAPTER 5

THE LIMITS AND NATURE OF *ASPIDELLA TERRANOVICA* BILLINGS 1872

Section 5.5.2 is adapted from a paper published in Geology, Menon et al. (2013), co-authored by DMC and MDB. The paper was written by me; I discovered the structures and conducted the experimental work, under the guidance of MDB and DMC.

5.1 INTRODUCTION

The discoidal impression *Aspidella terranovica* Billings 1872 was the first-named Ediacaran body fossil (Gehling et al., 2000). Described from outcrops of the Fermeuse Formation in St John's, Newfoundland, it has a characteristic morphology. On bed soles in the Fermeuse Formation it appears as a positive impression, with a central furrow or invagination from which extend fine radial grooves (Fig. 5.1A).

Counterparts on bed tops appear as negative discoidal impressions with a central ridge and fine radial ridges (Fig. 5.1B). The idiomorphic form (that described by Billings) is found in large numbers on bedding planes towards the top of the Fermeuse Formation on the Avalon Peninsula of Newfoundland. *Aspidella*-rich outcrops are common in a road cut and around the harbour of Ferryland, as well as several nearby coves, together known locally as the "Silos Cove" locality (Fig. 5.2).

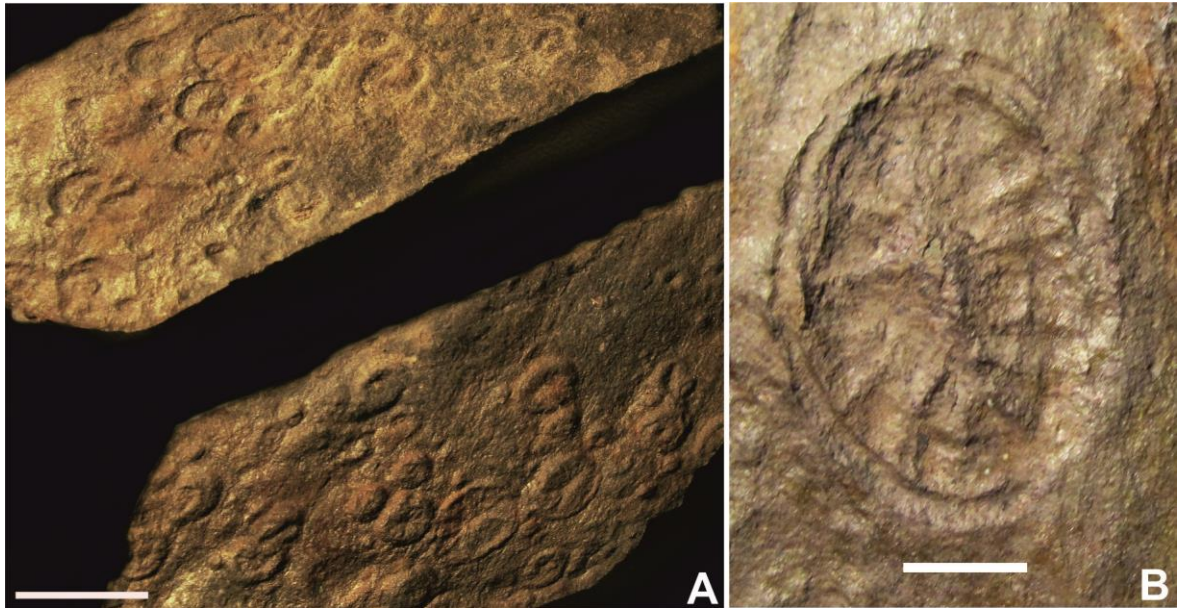


Fig. 5.1. A: Part and counterpart *Aspidella terranovica* Billings. Note occasional circular forms amid the elliptical examples. Specimen no. FR-R/35. (See Appendix A7 for specimen list.) **B:** Close-up of *Aspidella* on top of bed. FR-H/7. Scale bars: A: 1 cm; B: 0.5 cm.

Aspidella is not documented below the Fermeuse Formation in Newfoundland, and appears to be rare or absent in Ediacaran successions elsewhere, a notable exception being the disc assemblage of the Llangynog inlier near Carmarthen, South Wales (Cope, 1977). Two other forms named as species of *Aspidella* – *A. costata* and *A. hatyspytia* – have been described from the Olenek Uplift, Siberia (Vodanjuk, 1989), but these are not recorded from Avalonia.

A detailed study of *Aspidella* in the Ferryland localities was undertaken by Gehling et al. (2000), who argued for the biogenicity of *Aspidella*, and synonymized the Billings holotypic form with two other forms observed in these localities, described by Gehling et al. as: 1) *Ediacaria*, a high-relief convex disc as preserved on bed soles, with a prominent central boss and typically several concentric convex zones

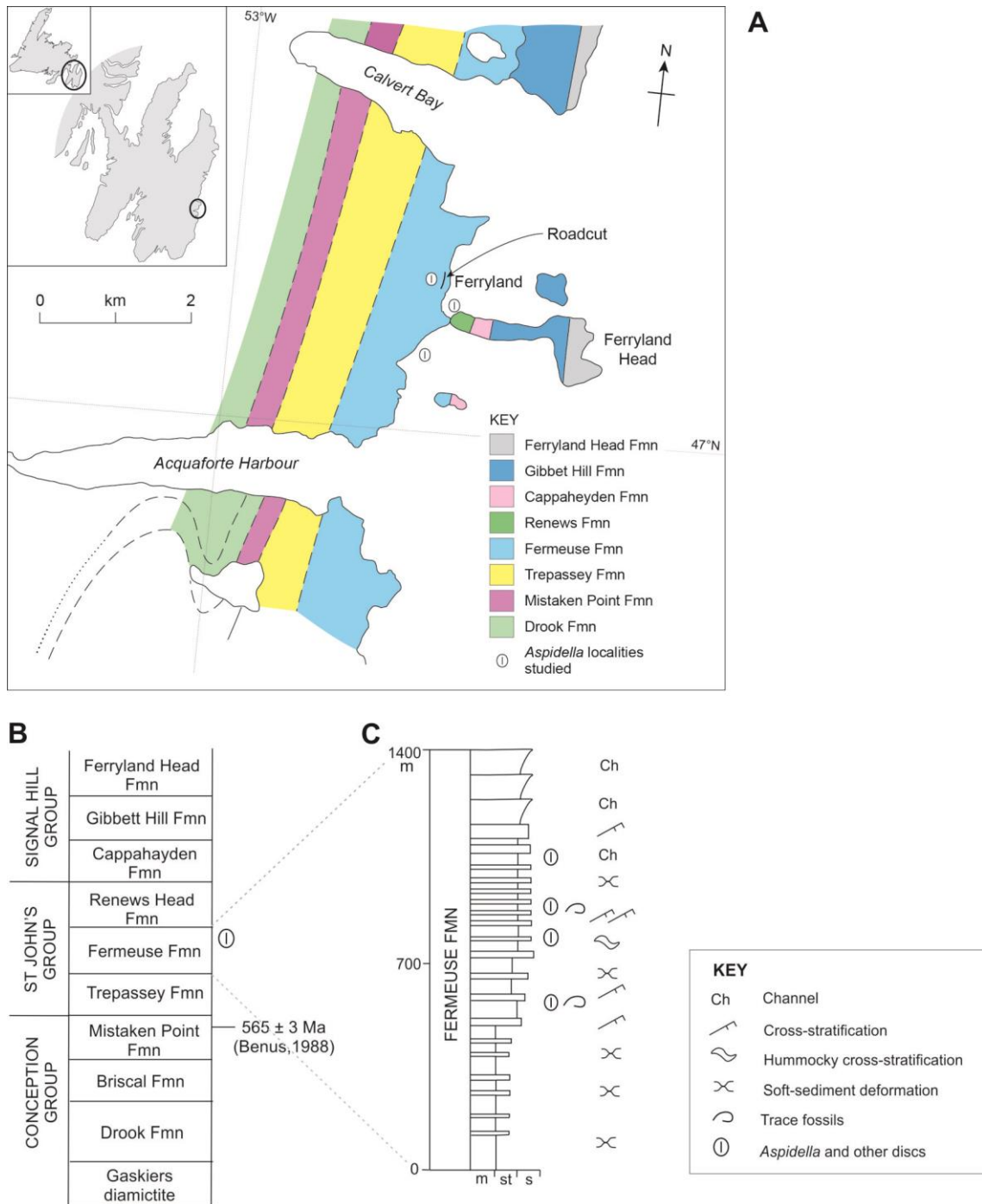


Fig. 5.2. A: Simplified geological map of Ferryland and surroundings, with *Aspidella* study localities indicated. Insets: Location of Avalon Peninsula within Newfoundland, and Ferryland within the Avalon Peninsula. **B:** Stratigraphic column showing position of Fermeuse Formation and occurrence of *Aspidella*. **C:** Schematic log of Fermeuse Formation. Map and stratigraphy adapted from King (1988); log based on Wood et al. (2003), Gehling et al. (2000), and my field observations.

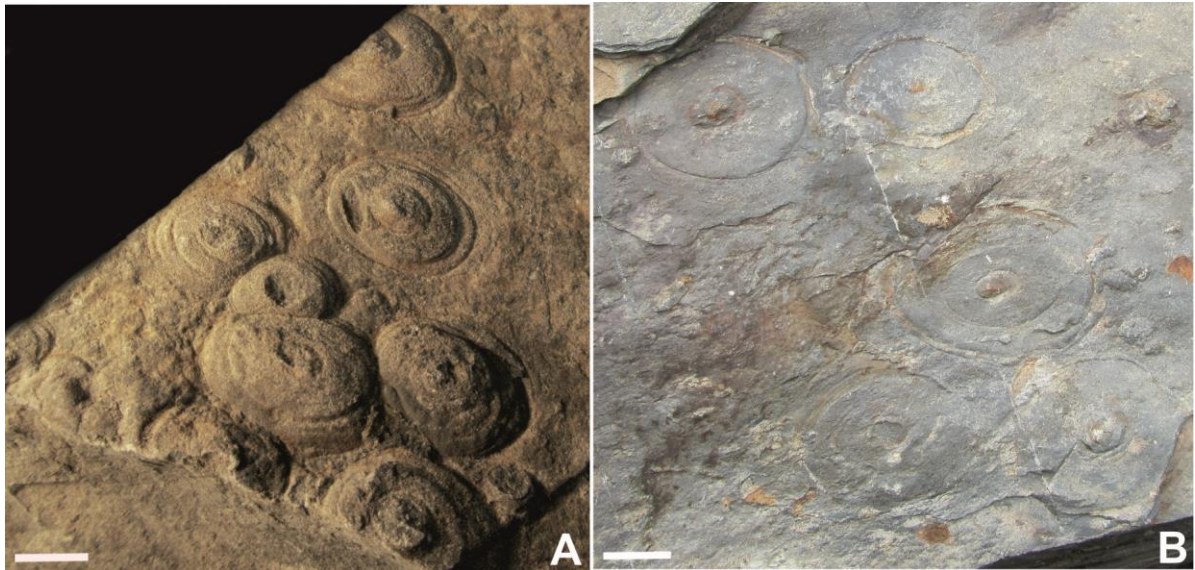


Fig. 5.3. *Ediacaria* (A) and *Spriggia* (B) on bed soles. Note distorted boundaries of abutting discs in A. A, FR-H/18. Scale bar: 1 cm.

(Fig. 5.3A; although *Cyclomedusa davidi* Sprigg 1947 may be a closer description); and *Spriggia*, an almost flat annulated form (Fig. 5.3B). These were explained as “taphomorphs” of the idiomorphic Billings form or “typemorph” (Gehling et al., 2000). The three synonymized taxa were considered to form an “*Aspidella* plexus” that was used to simplify a plethora of named discoidal forms from other Ediacaran successions, including *Cyclomedusa* spp., *Medusinites patellaris* Sokolov, and *Tirasiana* spp., all of which were synonymized with *Aspidella terranovica* Billings in a case of “taxonomic lumping”. This wide-ranging synonymization under *Aspidella* has not been accepted by all researchers (notably Serezhnikova, in Fedonkin et al., 2007). Although no definitively identified fronds are preserved in association with *Aspidella* anywhere in the world, Gehling et al. (2000) proposed that all the discs synonymized as *Aspidella* were probably holdfasts of fronds.

In this chapter, the biogenicity of the discoidal forms of the upper Fermeuse Formation is assessed; the relationship between Billings-type *Aspidella* and other discoidal forms in the Fermeuse Formation is reconsidered; a possible relationship between *Aspidella* and the three-lobed form *Triforillonia costellae* Gehling et al. 2000 is proposed; new morphological evidence that demonstrates that the *Aspidella* organism was mobile is presented; and the findings are synthesized into an understanding of the probable nature and biological affinity of *Aspidella*.

5.2 THE BIOGENICITY OF THE UPPER FERMEUSE FORMATION DISCS

The c. 1400-m-thick Fermeuse Formation, St John's Group, crops out in the southeastern part of the Avalon Peninsula, Newfoundland, as part of a coarsening upward succession which shallows from delta slope mudstones to fluvial and alluvial sediments in the overlying Signal Hill Group (Williams and King, 1979).

The upper part of the Fermeuse Formation contains the highest stratigraphic occurrences of Ediacaran macrofossils in the Avalon Peninsula (Fig. 5.2). The upper Fermeuse Formation consists of heterolithic siltstones and sandstone beds, along with slumps, soft-sediment deformation, and evidence of storm-worked sediments (Fig. 5.4) that are inferred to have been deposited in a pro-deltaic setting (Gehling et al., 2000; Wood et al., 2003). (See also Appendix 5, A5.1, A5.2.)

The Fermeuse Formation currently lacks dated tuffs but, based on the age constraints provided by dates from the Mistaken Point Formation below (dated as

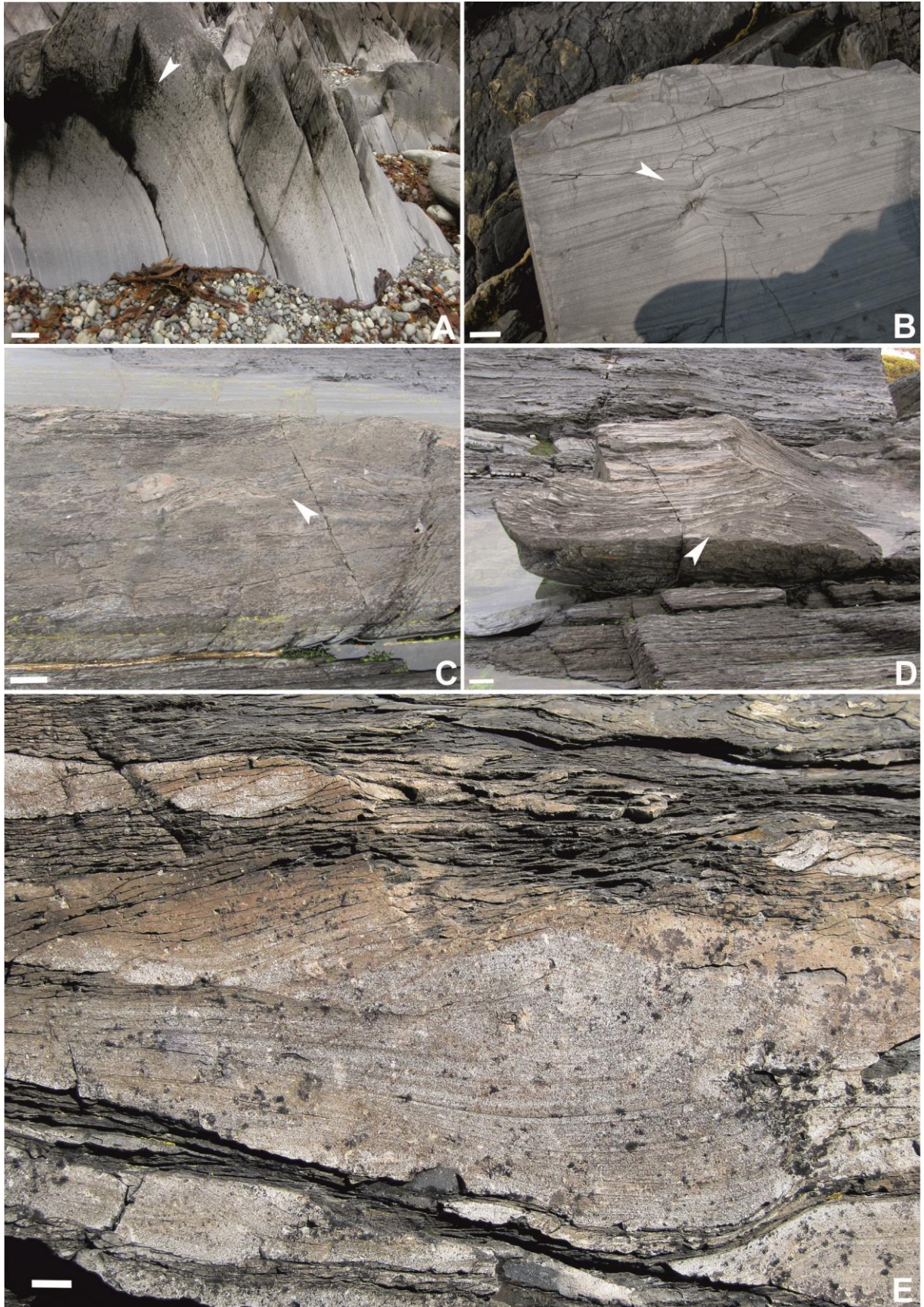


Fig. 5.4. Soft-sediment deformation structures (A,B), slump deposits (C,D), and hummocky cross-stratification (E) in the upper Fermeuse Formation. Scale bars: A-D, 5 cm; E, 1 cm.

565 Ma \pm 3 Ma; Benus, 1988), and the correlation of the top of the Signal Hill Group with formations in the nearby Burin Peninsula that underlie the stratotype of the Precambrian–Cambrian boundary (King, 1980; Landing, 1994), the age of the Fermeuse Formation is generally estimated as *c.* 560 Ma.

The Fermeuse Formation of the Avalon Peninsula is one of the most challenging successions in terms of disc interpretation. Bedding planes are covered in thousands of discoidal impressions that show a wide range of sizes and morphotypes.

Discoidal fossils have been considered to be preserved in the Fermeuse style of Narbonne (2005; see Chapter 3). The fossils have previously been considered to be casts of the lower surface of holdfasts, typically on the soles of sandstone and siltstone beds (Gehling et al., 2000; Narbonne, 2005). Given the presence of slumping and soft-sediment deformation in the Fermeuse Formation, the possibility of fluid escape structures and the abiogenic discs it can produce must be borne in mind. Additionally, microbial mat textures are observed on surfaces (Fig. 5.5A), and

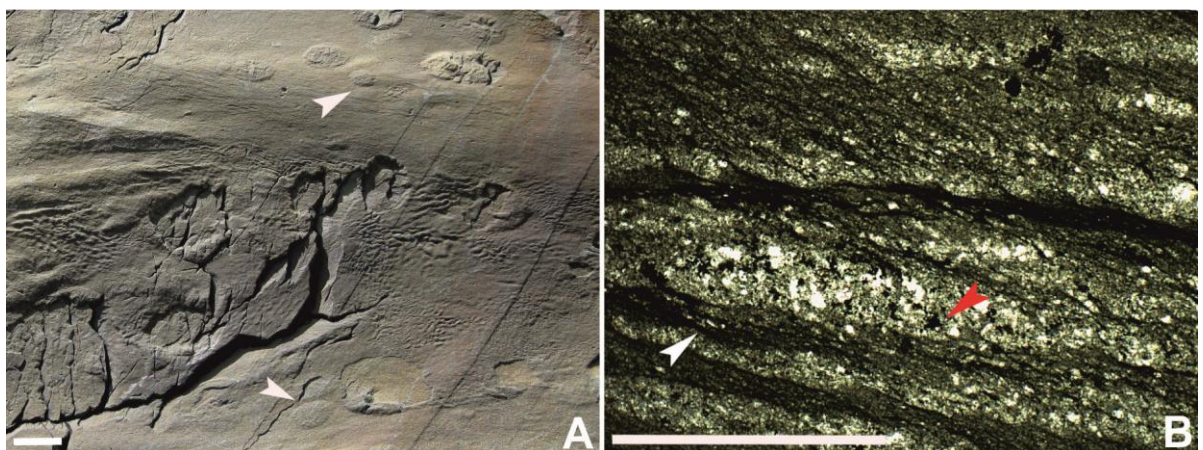


Fig. 5.5. **A:** Microbial textures and round markings (arrowed). **B:** Thin section with microbial mat layers (white arrow) and framboidal pyrite (red arrow). FR-H/21. Scale bars: A, 1 cm; B, 1 mm.

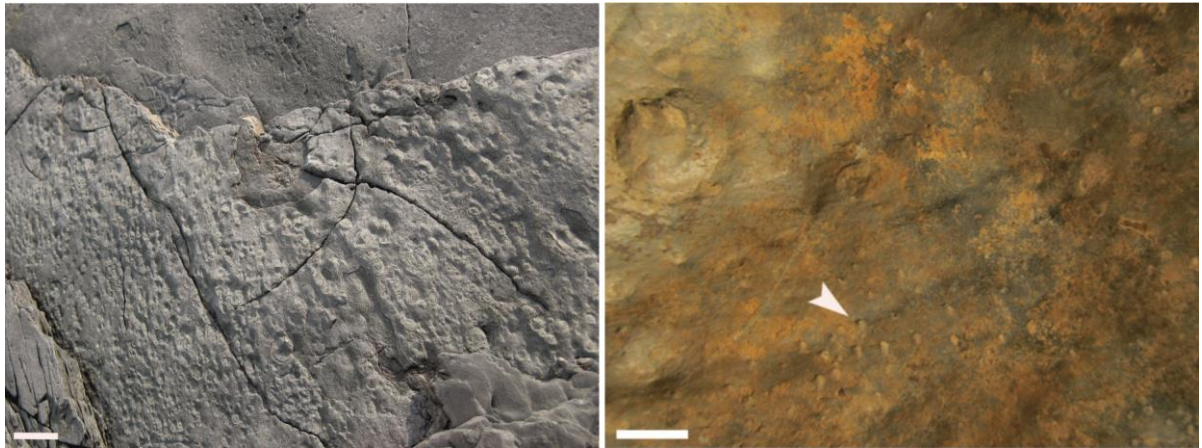


Fig. 5.6. Small pits on bed tops which may be abiogenic – resulting from small-scale fluid escape. **A:** Heavily pitted surface, Silos Cove. **B:** Pits (arrowed) on bed with disc impressions. FR-H/9. Scale bars: A: 1 cm; B: 5 mm.

mat layers are seen in thin section for the first time (Fig. 5.5B), so that the influence of microbial mats on the dynamics of pore fluid should be integrated into the understanding of the complete organism-sediment-microbiota system in terms of palaeobiology and taphonomy (see Chapter 2). The biogenicity of all the Fermeuse discs cannot therefore simply be assumed.

Some bedding surfaces show small pits (Fig. 5.6) that are probably the result of small-scale fluid escape processes. Rarely, examples of fluid escape are captured in cross-section (Fig. 5.7). Some low-relief discoidal markings associated with microbial mat textures may also be the result of gas domes and bubble bursts,

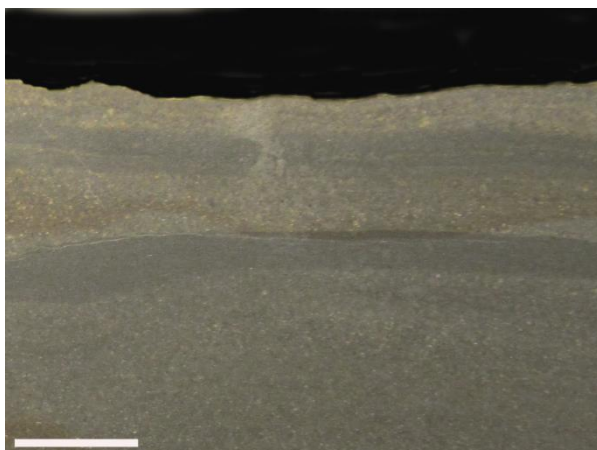


Fig. 5.7. Fluid escape column captured in cross-section. Such examples are rare. FR-J/6. Scale bar: 1 cm.

resulting from microbial activity (Fig. 5.5A). In spite of these indications of some abiogenic discoidal forms, however, many Fermeuse discs appear to be biogenic. Biogenic discs are recognized by:

- 1) distorted boundaries between contiguous discs (e.g. Fig. 5.3A; Gehling et al., 2000);
- 2) pyritic cements in the sandstone bed overlying discoidal impressions that are inferred to result from the decay of an organic form (Fig. 5.8);
- 3) the presence of distinct rims (Fig. 5.1B; cf. “Longmyndian *Medusinites*”, Fig. 2.2);
- 4) the absence of any sign of fluid movement directly below the discoidal impressions (Fig. 5.9);
- 5) the lack of spreading columns of sandy sediment in cross-section (Chapter 2), which also argues against fluid-escape structures (Fig. 5.9; cf. “Longmyndian *Medusinites*”, Fig. 2.2).

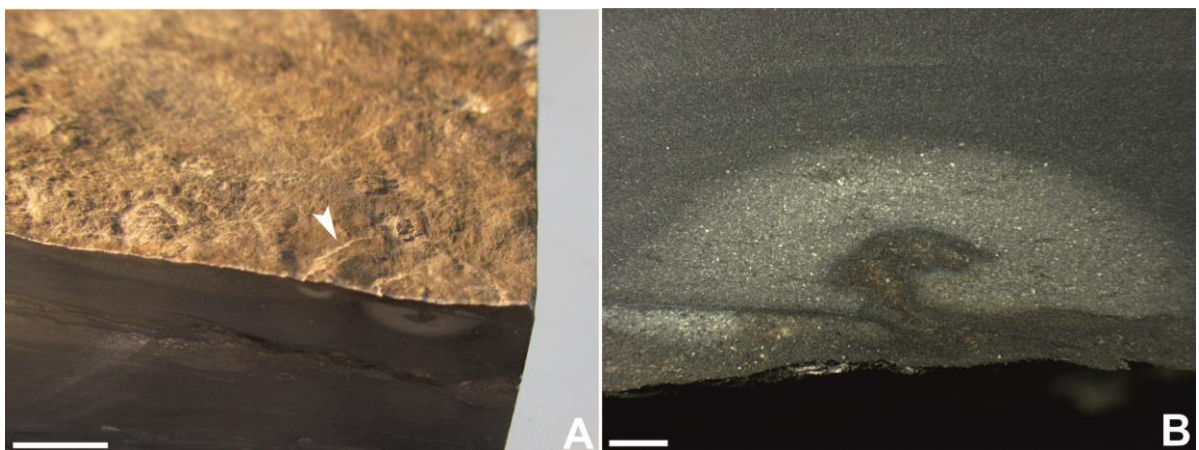


Fig. 5.8. Pyritic cement in overlying sandstone, probably due to migrating sulfidic fluids from decay of the disc-making organism. **A:** Low-positive-relief disc with inner and outer rings on bed sole (arrowed), showing fluid migration just above disc centre and edge of outer disc. **B:** Close up of pyritic cement. FR-H/13. Scale bars: A, 1 cm; B, 1 mm.

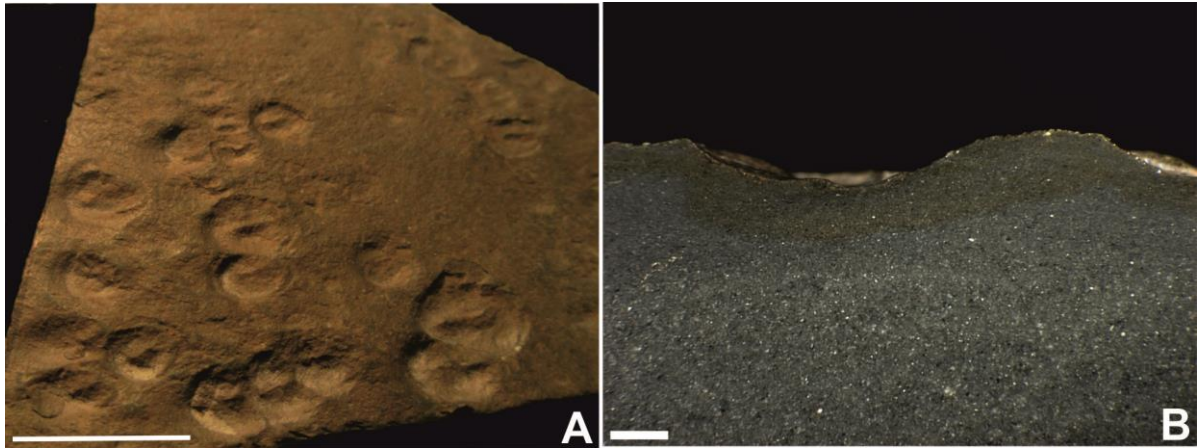


Fig. 5.9. A: Simple Billings-type *Aspidella* with prominent central ridge on top surface. There are clear rims in some specimens, but also cross-cutting of rims of overlapping discs, e.g. two discs at bottom right. This may suggest a fluid-escape origin, or may result from overprinting of impressions from an overlying lamina. **B:** In cross-section, no indication of fluid column or disturbance below, unlike Long Mynd examples of fluid escape discussed in Chapter 2. FR-R/33. Scale bars: A, 1 cm; B, 1mm.

Fermeuse-style preservation, with casting of underside of discs by sand from above, can sometimes be difficult to distinguish from simple load casts, and judgement of biogenicity may rely on context and subtle ornamentation. Two highly convex *Ediacaria* discs on a sole surface were found on cutting to be filled with sand from a higher layer (Fig. 5.10A, B). Although in cross-section the *Ediacaria* discs resemble simple loading structures (Fig. 5.10B), the rounded forms with a slight boss, and their isolation, suggest that the sand cast the external moulds left by biological forms.

On the same hand specimen, close to the two convex *Ediacaria*, a flat *Spriggia* disc with several concentric rings and a depressed centre was found in cross-section to

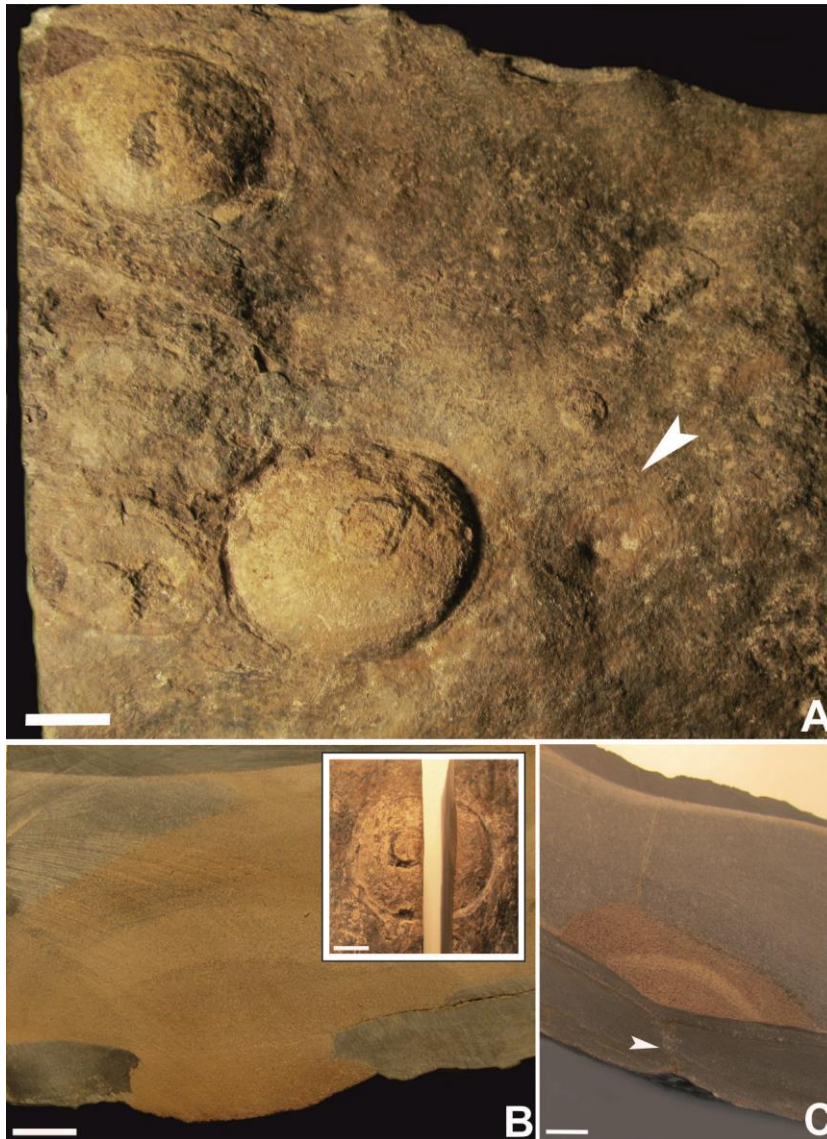


Fig. 5.10. A: Portion of sole surface of hand specimen, with two strongly convex *Ediacaria* discs, lower example with a small boss, and flat, annulated *Spriggia* disc (arrowed) with central depression. **B:** Cross-section through lower *Ediacaria* in A, reveals a sand fill from a higher layer. The wide, pale stripes in the sand body are probably liesegang rings. Inset: plan view of cut disc. **C:** Cross-section through centre of *Spriggia* shown in A reveals large sand body in higher bed and probable fluid escape structure (arrowed) rising from centre of discoidal impression on sole surface. FR-J/1. Scale bars: 1 cm.

be associated with a fine sub-vertical column of sand and pyritic cement, with the column base directly above the depressed centre of the disc (Fig. 5.10C). Above the rising column is a large sand nodule. The column may be interpreted as fluid escape resulting from localized loading by the sand nodule. However, the pyritic cement suggests the possibility that the basal disc was biogenic, and the loading drove escape of fluids from the decaying organism. (For a discussion of the interpretation of *Spriggia* compared to *Ediacaria*, see Section 5.3.)

The majority of discoidal impressions on the bedding planes of the Fermeuse Formation of Avalon are therefore considered here to be biogenic. However, are they all taphomorphs of *Aspidella*? And are they all necessarily holdfasts?

5.3 DELIMITING *ASPIDELLA*

The fossiliferous bedding planes of the upper Fermeuse Formation in the Ferryland localities typically either have dense populations of small discs (0.3–1.5 cm diameter), or relatively small numbers of large discs (3–7 cm and more), either isolated individuals or gregarious, with distorted boundaries where they are contiguous with one another (Fig. 5.11; Figs 3.12, 5.1A, 5.3; Gehling et al., 2000). All these discs have been synonymized as *Aspidella* (Gehling et al., 2000).



Fig. 5.11. Successive upper bedding planes showing changes in the dominant size and relative abundance of discoidal Ediacaran body fossils. Scale bar: 1 cm.

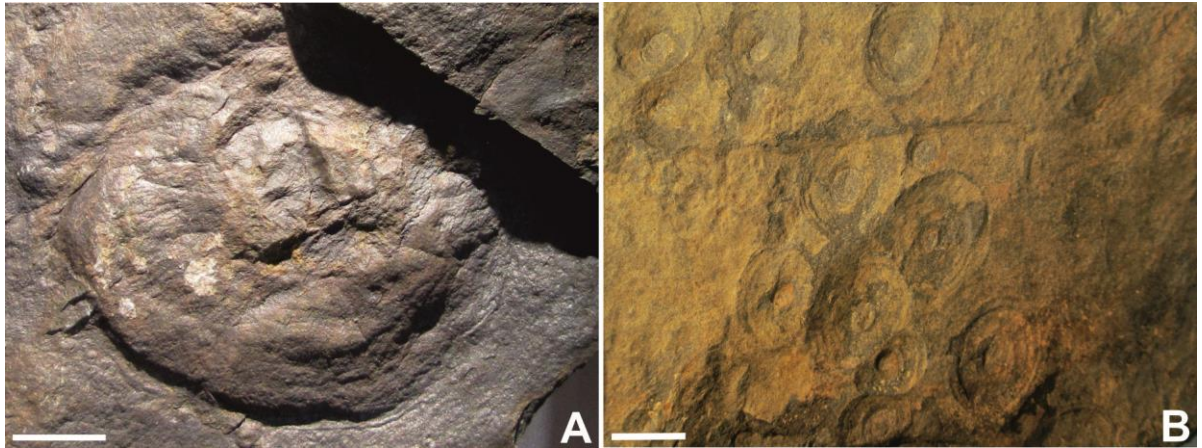


Fig. 5.12. A: *Ediacaria* on bed sole with fine folds from compaction. The compaction may be due to the collapse of the disc or casting in shale rather than less compressible sand. Compare with Fig. 5.10A. SC-2/1. **B:** Negative impressions of *Ediacaria* on bed top. FR-H/17. Scale bar: 1 cm.

5.3.1 *Ediacaria* and *Spriggia* reconsidered

Ediacaria discs larger than ~2.5 cm diameter preserved on the soles of beds usually have a series of folds indicating concertina-type compression of what was once a bulbous structure (Fig. 5.12A; see also Fig. 3.12). The amount of compaction varies in part according to whether the disc is primarily cast in sand or shale (Fig. 5.12A, cf. Fig. 5.10A). No unambiguous examples of the stepped profile from differential compaction described by Gehling et al. (2000) were however observed in this study. *Ediacaria* specimens have previously been described from these localities preserved as positive hyporelief (Gehling et al., 2000), with negative counterparts seen on the tops of beds (Fig. 5.12B). However, *Ediacaria*-type discs are also reported here in positive epirelief on top surfaces (Fig. 5.13).

Flat annulated discoidal impressions that would be described as *Spriggia*, the “flat morph” of *Aspidella* according to Gehling et al. (2000; cf. Southcott, 1958;



Fig. 5.13. Positively preserved *Ediacaria* on bed tops. **A:** disc showing some compression, with central raised ring. **B:** Unusual examples, especially large disc at bottom centre, showing what may be the envelope surrounding a frond stem, based on the model presented in Chapter 3. Scale bars: 1 cm.

Sun, 1986), occur on both bed tops and soles, either singly or gregariously (Fig. 5.14). Most *Spriggia* forms in this locality have several widely spaced rings, sometimes as raised ridges that are asymmetrical in radial cross-section (Fig. 5.14A).

Following the model of holdfast architecture proposed in Chapter 3, it is evident that these *Spriggia*-type discs are comparable to the holdfast discs from Little Catalina and Spaniard's Bay (Chapter 3, Figs 3.2, 3.8). Those *Spriggia* with raised annular rings are considered here to be the eroded tops of holdfast discs that retain only remnants of the original dome-like envelopes (Chapter 3, Fig. 3.6; Fig. 5.14A). In some cases the upper surface of *Spriggia* discs are somewhat flattened but otherwise remarkably well preserved, with rare examples showing the base of a stem (Fig. 5.14B). Fine radial ridges are suggestive of the deflation of a taut skin-like integument, or may possibly be septa (Fig. 5.14C). Similarly the positive-relief *Ediacaria*-type discs on bed tops (e.g. Fig. 5.13) are consistent with partially collapsed or well preserved tops of discs, such as the large disc specimen at Upper

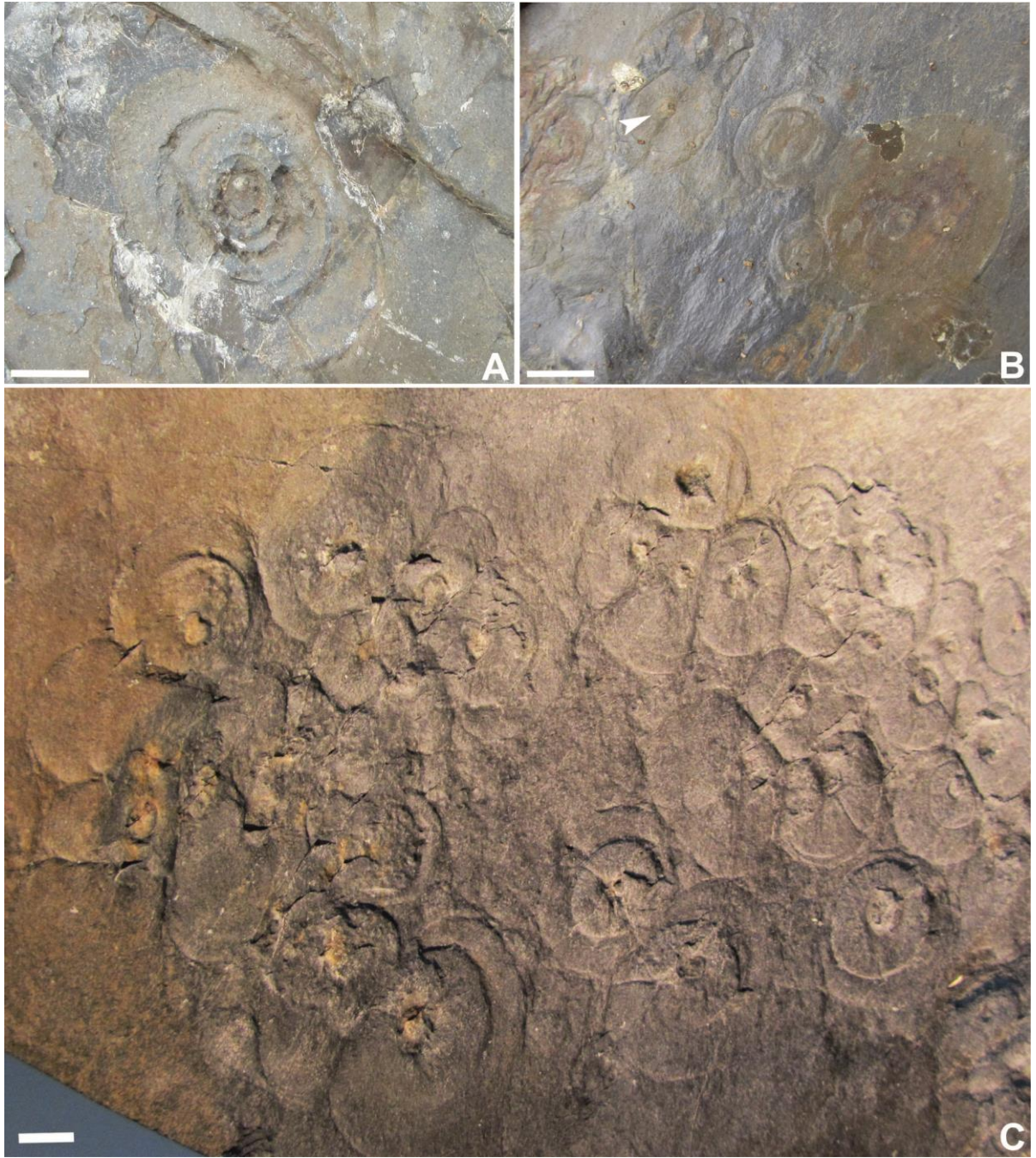


Fig. 5.14. *Spriggia*-type discs (Gehling et al., 2000) on upper bedding surfaces of sandstone. **A:** Disc with several distinct raised asymmetrical ridges. **B:** Group of medium and large *Spriggia*, one (arrowed) with the base of a stem preserved. **C:** Mass of *Spriggia* with distorted, impinged boundaries and fine radial ridges. FR-H/24. Scale bars: 1 cm.

Island Cove (Fig. 3.12). By contrast, the high-positive-relief *Ediacaria*-type discs on bed *soles*, and their negative counterparts on bed tops (Fig. 5.12B), can reasonably be taken to represent the undersides of holdfasts (Gehling et al., 2000; see Chapter 3).

It is not necessary to invoke differential compaction to produce both flat and convex taphomorphs (*Ediacaria* and *Spriggia*) of the same (*Aspidella*) discoidal organism (*contra* Gehling et al., 2000). While some variability in relief is indeed taphonomic, the main differences in morphology between *Ediacaria* and *Spriggia* are explained here by consideration of whether the eroded top or the underside of the organism is preserved. This interpretation suggests that preservation in the Fermeuse Formation does not only retain external moulds of the undersides of discs but also captures impressions of disc tops in a number of cases (“Conception-style” preservation of Narbonne, 2005).

Given that some upper surfaces of discoidal forms assumed to be holdfasts are preserved as *Ediacaria* and *Spriggia*, and some specimens retain the probable base of a stalk (e.g. Fig. 5.14B), the absence of any obvious fronds becomes more surprising. The gregariousness observed in *Spriggia* disc clusters (e.g. Fig. 5.14C) is also puzzling. While environmental conditions may be the first-order cause of higher population density of discoidal taxa in the upper Fermeuse Formation, the gregariousness of *Spriggia* suggests a different mode of life to the other frondose organisms in the Ediacaran of Newfoundland, which are generally isolated and not

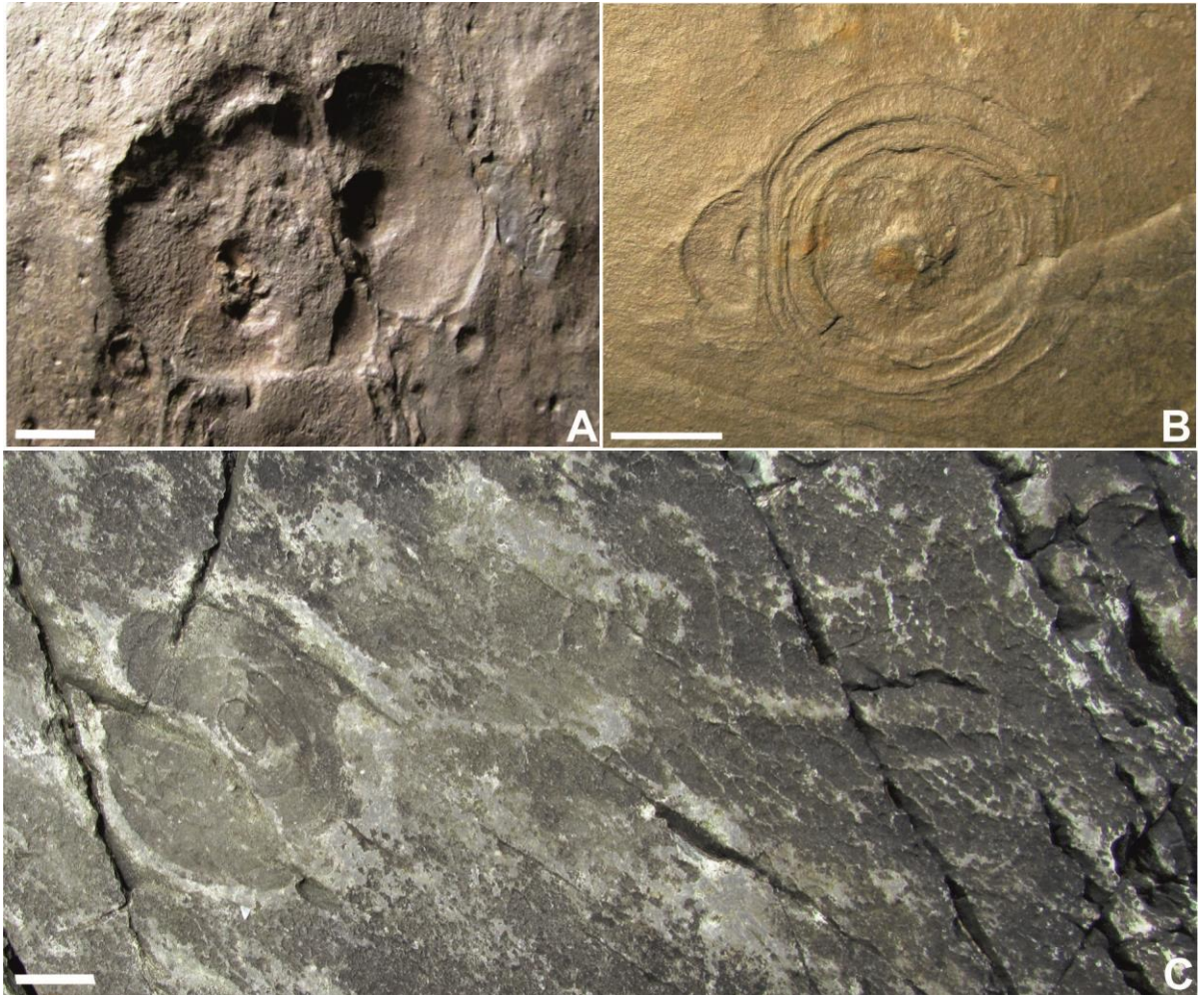


Fig. 5.15. **A:** Two interacting *Ediacaria* discs, a possible example of asexual fission. SC-1/4. **B:** *Spriggia* with associated lobe, highly suggestive of budding. FR-H/24. **C:** *Charniodiscus* with double disc, near Melrose, Bonavista Peninsula. All specimens, A-C, on bed tops. Scale bars: 1 cm.

contiguous with one another. On the other hand, examples of double discs and discs with side lobes (Fig. 5.15A, B) have been observed elsewhere among typical Ediacaran holdfasts (Fig. 5.16C; Tarhan et al., 2015b) and may hint at asexual reproduction (Xiao et al., 2009). Given also the similarities in disc structure of some *Ediacaria* and *Spriggia* discs with *Charniodiscus* holdfasts, *Ediacaria* and *Spriggia* are therefore considered here to be impressions of undersides and tops of holdfast discs, probably associated with unknown/unpreserved fronds, although they may represent or include another type of organism.

5.3.2 The distinctiveness of *Aspidella*

In contrast to the annulated *Ediacaria* and *Spriggia*, which have a central boss, idiomorphic *Aspidella terranovica* have a central furrow and radial grooves, features not seen in discs that are demonstrably holdfasts of frondose organisms.

Synonymization of *Aspidella* with *Ediacaria* was based on the inference that the central extended groove of *Aspidella* is the preservational expression of a completely recessed boss, resulting from variations in sand-to-clay ratio. Elongation of the central furrow is considered to be the result of tectonic deformation of the otherwise sub-circular recessed boss, aligning with a radial groove (Gehling et al., 2000).

The idiomorphic *Aspidella* morphology, with its elongated central ridge or furrow, is only seen in small discs (<2 cm diameter; Gehling et al., 2000). If simple recession of the boss of an *Ediacaria*-type disc were the cause of the central furrow in *Aspidella*, then examples of larger discs with such furrows should occur. While partially recessed bosses are seen in some larger *Spriggia* and *Ediacaria* (>2 cm diameter; Fig. 5.3A), complete retraction to produce a slit is not seen, unlike the idiomorphic Billings-type form. Further, if the elongated furrow or ridge results from tectonic deformation, then a progressive change from round central bosses to extended ridges should be observed in proportion to the ellipticity of the disc.

To test this, all discs showing ornamentation sufficiently distinct to identify as having either a rounded boss or central ridge/furrow were examined in three large densely populated hand specimens, with combined total number of discs measured,

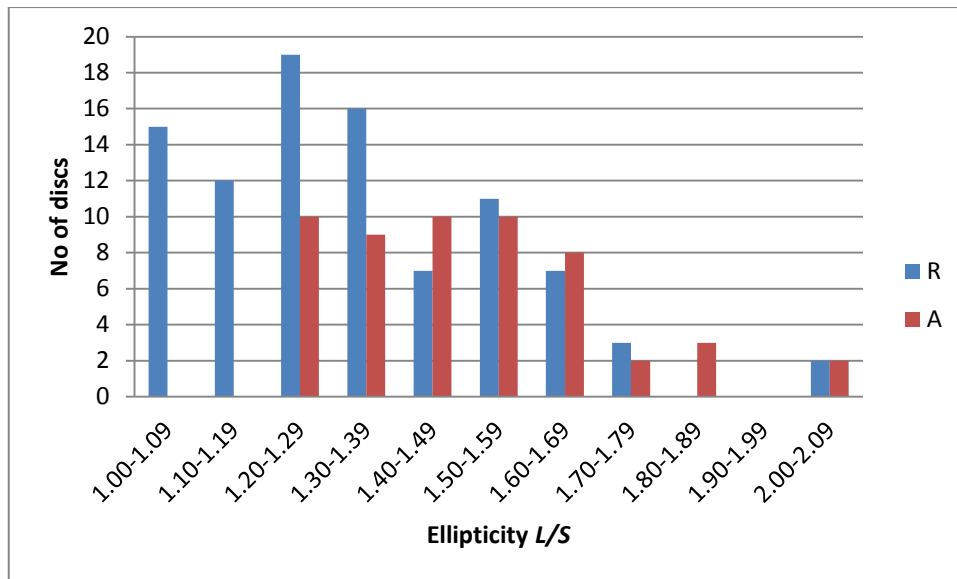


Fig. 5.16. Ellipticity, L/S , of discs with round bosses (R) compared to those with elongated ridges/furrows (A). $N = 149$.

$N = 149$. The short and long axes, S and L , of each (non-retrodeformed) disc was measured, so that the ellipticities, L/S , of discs with round bosses and those with Billings-type ridges could be compared (Fig. 5.16).

The results indicate that while the idiomorphic *Aspidella* form tends to appear only in discs with ellipticity of 1.1 or more, and round bosses are observed mostly from discs of ellipticity close to 1, round bosses are nevertheless observed in discs with comparable ellipticity to those with the central ridge. It is therefore evident that the ridges are not simply the result of tectonic deformation. This is further supported by the fact that the ridge in Billings-type *Aspidella* often extends, unbroken, almost all the way across the disc (e.g. Fig. 5.1B), which would be unexpected from simple retraction of a central circular boss, even if aligned with a radial furrow. In addition,



Fig. 5.17. Near-circular *Aspidella*, some with a central round boss (black arrows), while neighbouring round impressions have a central groove (white arrow) and a central ridge (red arrow). Such a grouping of circular *Aspidella* is unusual, but note that smaller discs, e.g. to top left of picture, are ellipsoidal. Note the alignment of the two discs with ridge/groove. Round-centred *Aspidella* only ever exhibits a single central ring or boss, unlike holdfast-type discs. Scale bar: 1 cm.

round *Aspidella* with ridges may be found alongside others with round central bosses or depressions (Fig. 5.17). It would seem therefore that the ridge or furrow is intrinsic to Billings-type *Aspidella*.

The general alignment of the long axes of discs, together with their central ridges/furrows, on bedding planes would seem to support tectonic deformation as the entire cause of ellipticity (Gehling et al., 2000), in spite of the arguments given above. However, there is significant variation of angle (up to 25°) as well as ellipticity ($L/S \sim 1.0-1.8$) between *Aspidella* discs within even 10 cm² of bedding surface (Fig. 5.18), so that retrodeformation fails to produce uniformly circular discs

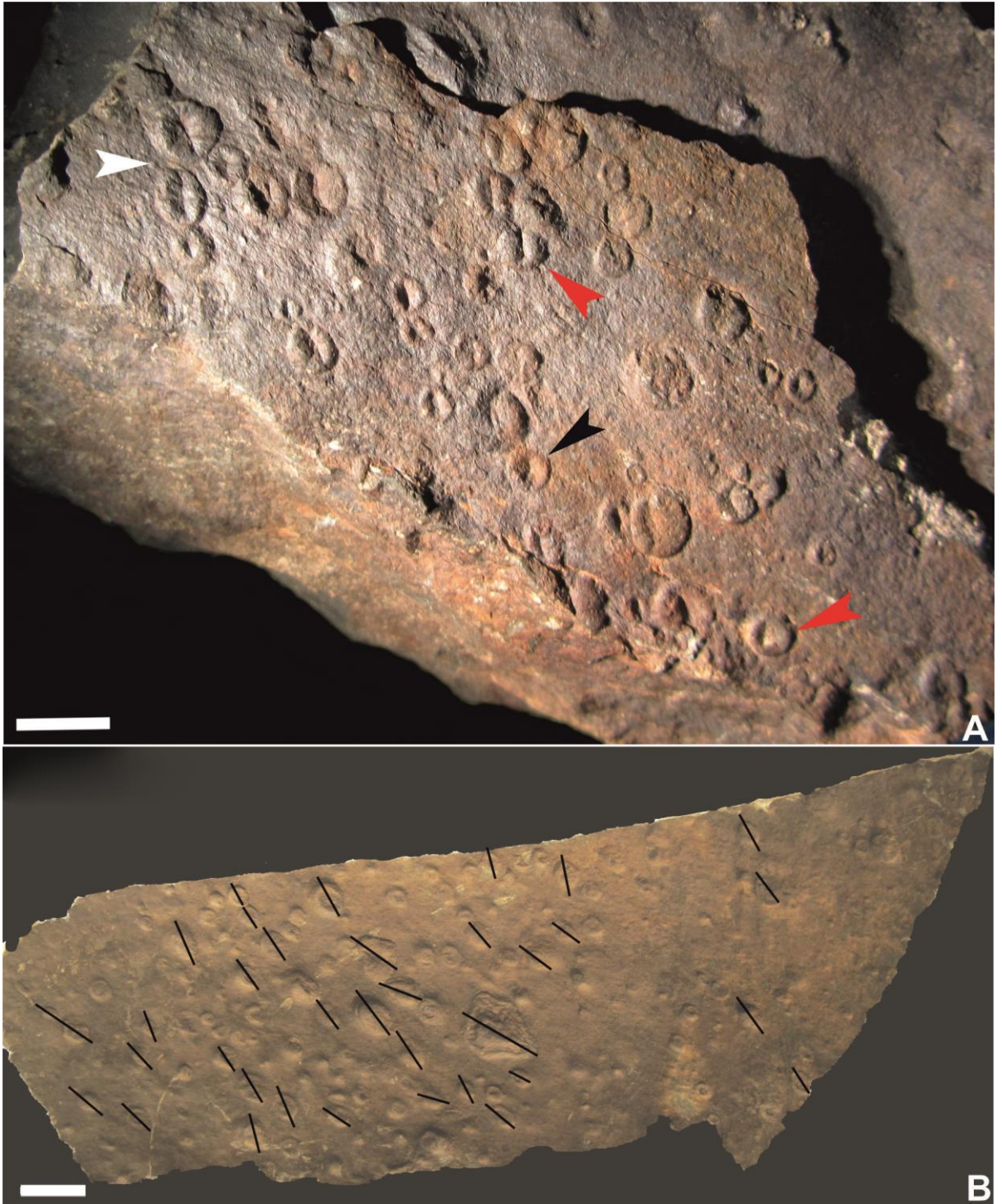


Fig. 5.18. A: Idiomorphic *Aspidella* on bed sole. To left, two neighbouring well-preserved specimens differ in angle by 20° (white arrow). Note that the central furrow extends across the whole disc. Circular forms are also seen nearby (black arrow). In two examples (red arrows), the furrow stretches across the shorter axis of slightly ellipsoidal discs. FR-J/3. **B:** Small hand specimen with *Aspidella* and a poorly formed *Triforillonia* and two distorted discs (see Section 5.4). Angles of long axes of ellipsoidal discs are picked out with black lines. *Aspidella* disc axes vary in angle by $\sim 25^\circ$ (the *Triforillonia* and two distorted discs are at greater angles, but have not been included in this assessment). A number of circular discs are also visible. FR-H/6. Scale bars: 1 cm.

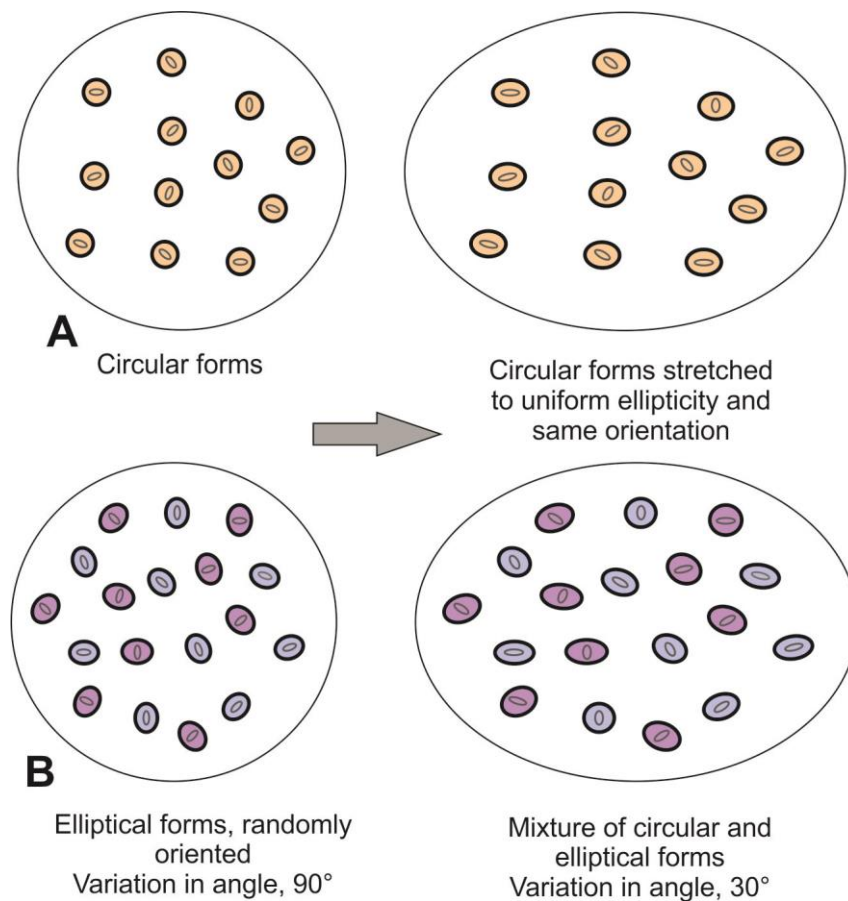


Fig. 5.19. Schematic figure demonstrating the impact of extensional stress (diagrams to right) on originally circular and elliptical forms (left). **A:** Deformation of a group of circular forms results in uniform ellipticity, with the long axis in the direction of the stress (i.e. the strike of the cleavage on the bedding plane). **B:** A group of randomly oriented elliptical forms is deformed into elliptical and circular forms. The range of ellipticity has increased, but the range of angles from horizontal has decreased, as the deformation effectively rotates angled specimens towards alignment with the direction of the stress. Central furrows are shown in random orientations within the circular forms in A, and parallel or orthogonal to the long axis of the elliptical forms in B, as the most likely configurations. Circular forms with a central furrow, such as those marked with red and white arrows in Fig. 5.17, only arise in case B, and only if the original furrow is very narrow.

(Liu et al., 2011). Given some tectonic deformation on these bedding planes, the presence of almost circular *Aspidella* specimens alongside strongly elliptical examples, and the modest variation in angle, suggests rather that at least *some* of the original forms were not circular prior to tectonic deformation and that they probably varied randomly in angle (Fig. 5.19).



Fig. 5.20. *Aspidella* specimen revealing a narrow margin (arrowed) surrounding the central invagination, in this case an ellipse rather than a furrow. A partial specimen to right is deeply invaginated, with a narrow central groove and sharper radial grooves. FR-R/15. Scale bar: 1 cm.

A further indication that the central furrow of Billings-type discs does not arise from the retraction of the central boss of an *Ediacaria*-type disc comes from a particularly well-preserved Billings-type *Aspidella* which shows a marked margin surrounding the central furrow (Fig. 5.20). This suggests that the structure at the centre of the base of the *Aspidella* organism was invaginated in life, rather than being a protruding boss pushed inwards by post-mortem compression.

The above observations suggest that *Aspidella terranovica* Billings is distinct from the holdfasts of rangeomorph taxa. Its most characteristic form suggests that it was, at least for some of the time, a naturally elongate disc with a central furrow on its lower surface with surrounding radial grooves. It is difficult to ascertain whether

neighbouring discs with round central bosses also represent the same form, but given their frequent appearance alongside each other, and examples in which there is a central small boss rather than a ridge but with surrounding fine radial ridges identical to that in the holotype Billings discs (see e.g. Fig. 5.1A), it may reasonably be assumed that at least some of the round forms of discs are also *A. terranovica* Billings, with the base of the organism preserved in varying original life-positions.

According to the interpretation given here, the discs of the upper Fermeuse Formation are of at least two kinds: a) probable holdfast discs, with upper or lower surface captured (*Spriggia* and *Ediacaria*); and b) a separate form, *A. terranovica* Billings, which is absent from the Mistaken Point and Drook Formations in the Avalon Peninsula (and correlative units in the Bonavista Peninsula). *Aspidella terranovica* may have been confined to slightly shallower palaeoenvironments rather than the deep-water assemblages of the Mistaken Point Formation (Wood et al., 2003). This discussion emphasizes that not all discs described as *Aspidella* were necessarily holdfasts of fronds.

5.4 ASPIDELLA AND TRIFORILLONIA

In their study of *Aspidella*-bearing beds of the upper Fermeuse Formation, Gehling et al. identified a new, three-lobed impression from the Ferryland locality which they named *Triforillonia costellae* (Gehling et al., 2000). To investigate this form further, disc-covered bedding planes from the Ferryland road-cut, the three adjacent coves about 1 km south of the settlement of Ferryland collectively called Silos Cove,

and outcrops by Ferryland Harbour (the *Aspidella* study localities marked on the map in Fig. 5.2), were examined for examples of *Triforillonia*. Remarkably, among the hundreds of discs in these localities, specimens of *Triforillonia* were only found in a fresh rock fall of several blocks representing just a few bedding planes in the central portion of the Harbour outcrop. These fallen blocks contained some 30 examples of *Triforillonia*, including a couple in part and counterpart, alongside *Aspidella* and simple high-relief convex discs without bosses (Fig. 5.20). Examination of the same area in subsequent years revealed no further examples. Only two isolated specimens of *Triforillonia*-like forms have been found beyond this narrow region, in one of the Silos Cove localities (Fig. 5.22).

The holotype material of *Triforillonia* all consists of three lobes, but these are not usually equal in size and spacing. There are often two rounded lobes and a more extended, sometimes more pointed, third lobe, forming an approximate isosceles triangle (see e.g. Fig. 5.21A). The directionality of this elongation remains even if tectonic deformation is taken into account (see Appendix A5.10). This long axis may be emphasized by a ridge or furrow that extends from one lobe roughly along the centre of the fossil to the more elongated lobe. Faint radial ridges or grooves are sometimes present, centred upon the main ridge and within the lobes (Fig. 5.21). The *Triforillonia* specimens appear among well-preserved *Aspidella* discs but are commonly of lower relief than *Aspidella* impressions.



Fig. 5.21. A: *Triforillonia* (white arrow) and a large Billings-type *Aspidella* with long central ridge, alongside small discs on bed top. The distorted centre of a large disc from an overlying level, with a faint, wide margin, is visible (red arrow) above the *Aspidella*. Note the two sets of paired small discs at top of picture, the right-hand pair sharing an outer boundary. FR-H/12. **B:** Two small examples of *Triforillonia* (arrowed) alongside a well-preserved large *Aspidella* (counterpart of the specimen in Fig. 5.1B) on a bed sole. FR-H/8. Scale bars: 1 cm.

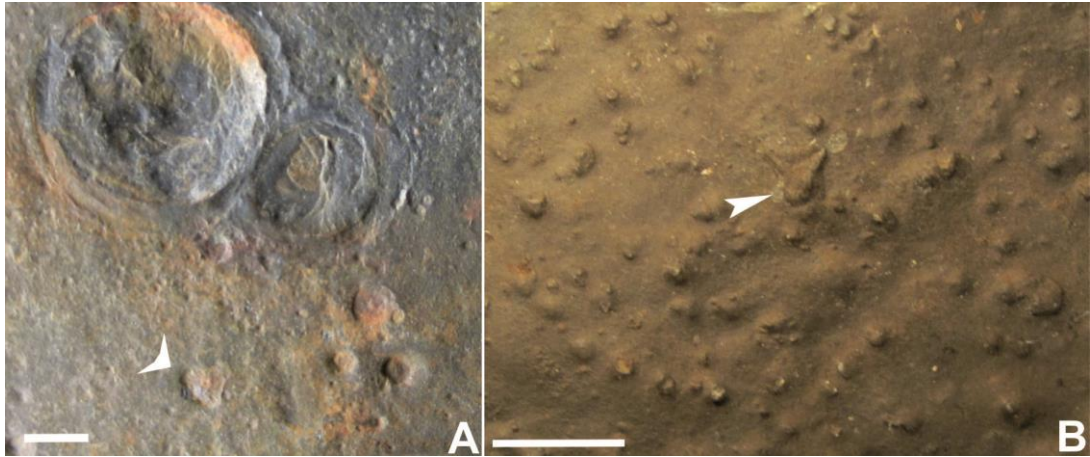


Fig. 5.22. Two small, isolated examples of *Triforillonia*-like discs, arrowed, Silos Cove. **A:** This form, on an upper bedding surface, exhibits a small, curved central groove to the apex of the triangular shape, as expected for *Triforillonia*. **B:** This form, on a bed sole, does not fit the typical pattern, having a groove extending from one lobe to the next, and may not be a *Triforillonia* at all. B, SC-2/6. Scale bar: 1 cm.

While some *Triforillonia* specimens display the characteristic, approximately symmetrical shape, others have distorted lobes. In one or two examples, two *Triforillonia* specimens appear in contact and distorted (Fig. 5.23).

Some morphotypes preserved alongside *Triforillonia* have more than three lobes, and others are little more than large, effaced low-relief features that are approximately *Triforillonia*-like in shape, sometimes with irregularly oriented shallow ridges (Fig. 5.24; cf. Liu et al., 2011).

A wider examination of the *Triforillonia*-bearing blocks also reveals a number of distorted discs ranging from Billings-type *Aspidella* discs with curved central ridges, a pointed, broadly triangular-shaped morphology, to asymmetrical forms that have a bulge to one side (Fig. 5.25). While distorted discs are occasionally seen on other



Fig. 5.23. *Triforillonia* with another indistinct example (or two?) alongside. The clear specimen of *Triforillonia* (arrowed) has a main ridge towards the right-hand side, and fine side ridges. Two *Aspidella* specimens with ornamentation can be seen just above, one clearly showing a central ridge. FR-H/14. Scale bar: 5 mm.

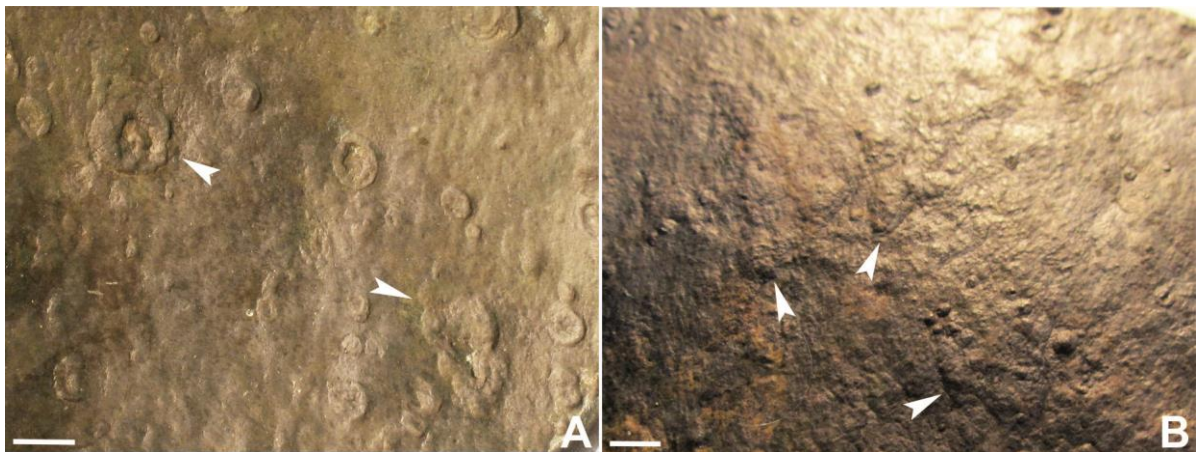


Fig. 5.24. Irregular and faint examples of aff. *Triforillonia*. **A:** Two amorphous, ivesheadiomorph-like examples on bed top (arrowed). The right-hand example may consist of two joined specimens. FR-H/4. **B:** Three very faint, low-relief specimens on bed sole (arrowed), the rightmost example points upward. FR-H/1. Scale bars: 5 mm.

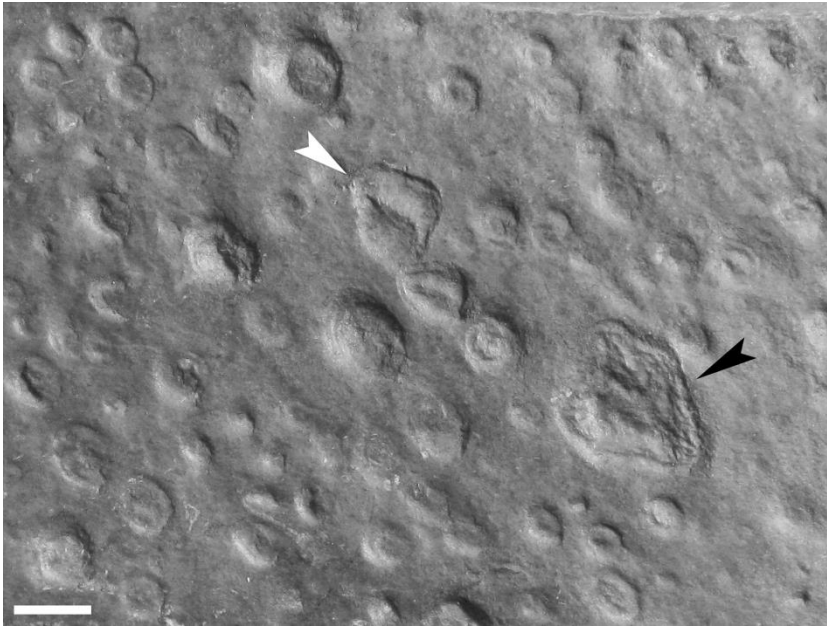


Fig. 5.25. An irregular aff. *Triforillonia* (black arrow) associated with distorted *Aspidella* discs. Note the curved central ridge of the *Aspidella* specimen just above centre (white arrow), and the haphazard ornamentation within the irregular *Triforillonia*. FR-H/6. Scale bar: 5 mm.

disc-covered bedding planes, they are common on the *Triforillonia*-containing blocks and show a wider range of morphologies.

Taken together, these observations point to a possible continuum between Billings-type *Aspidella* discs, through various distorted forms to *Triforillonia*, and extending into a variety of *Triforillonia*-like forms of increasingly disordered shape and internal structure (Fig. 5.26). Taxonomic similarities between *Aspidella* and *Triforillonia* are suggested by the central ridge that is common to both taxa but not known from other Ediacaran fossils (Fig. 5.27).

Well-formed *Triforillonia* fits within the size range of *Aspidella* (Fig. 5.28). The more effaced forms may be of larger sizes, but their very low relief and disorganized

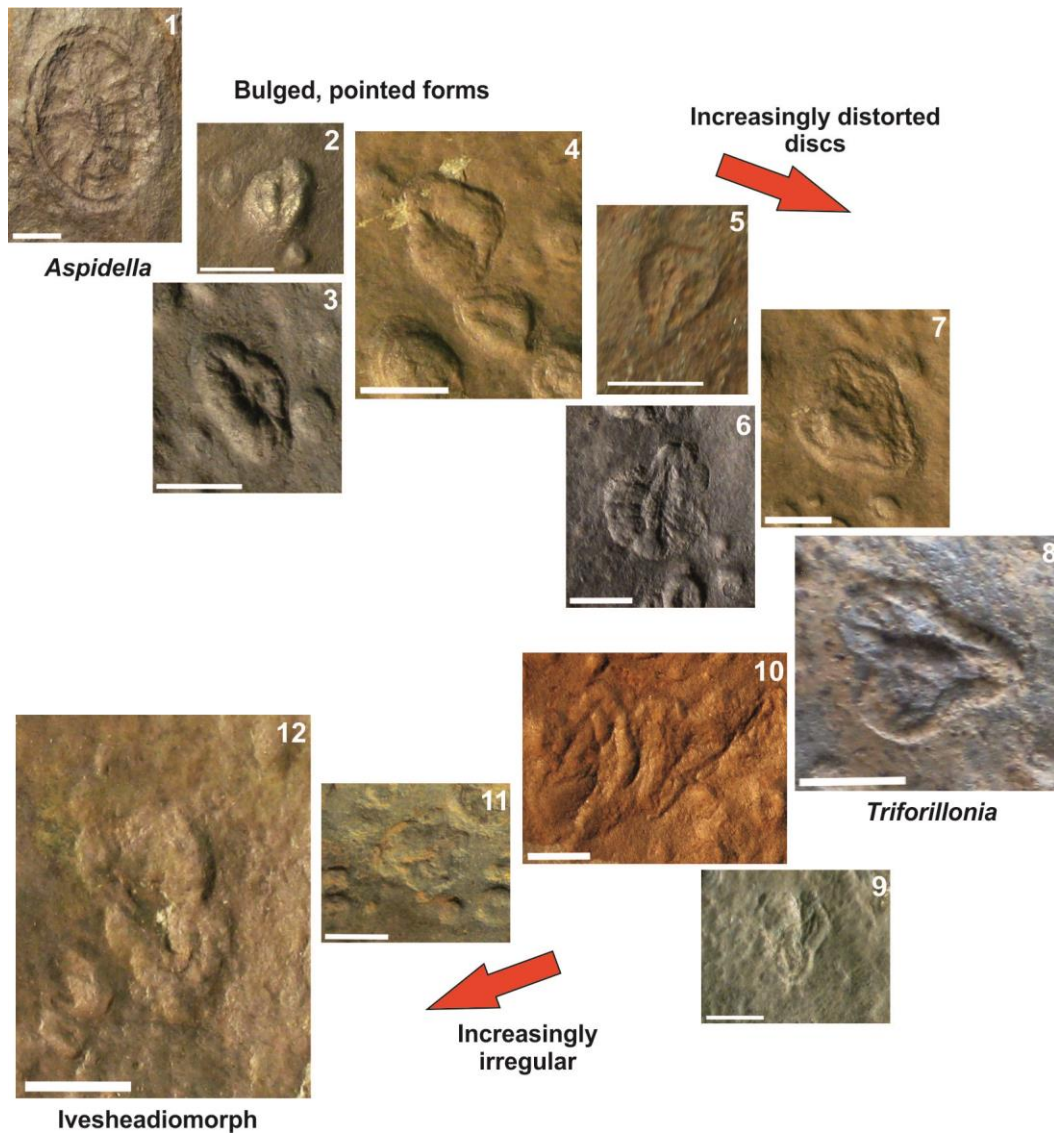


Fig. 5.26. Pictorial representation of the possible morphological continuum between *Aspidella*, *Triforillonia*, and aff. *Triforillonia* ivesheadiomorph forms. 1: FR-H/7; 2,3,6: FR-H/1; 4,7: FR-H/6; 5,8: FR-H/12; 9,10: FR-H/14; 11,12: FR-H/4. Scale bars: 5 mm.

shape makes an assessment of maximum size difficult (cf. Liu et al., 2011).

Nevertheless, the size ranges of the two forms are consistent with a possible relationship between them.

The range of *Triforillonia*, stratigraphically within the Fermeuse Formation, and in geographical terms, is extremely restricted. Not only have no examples been

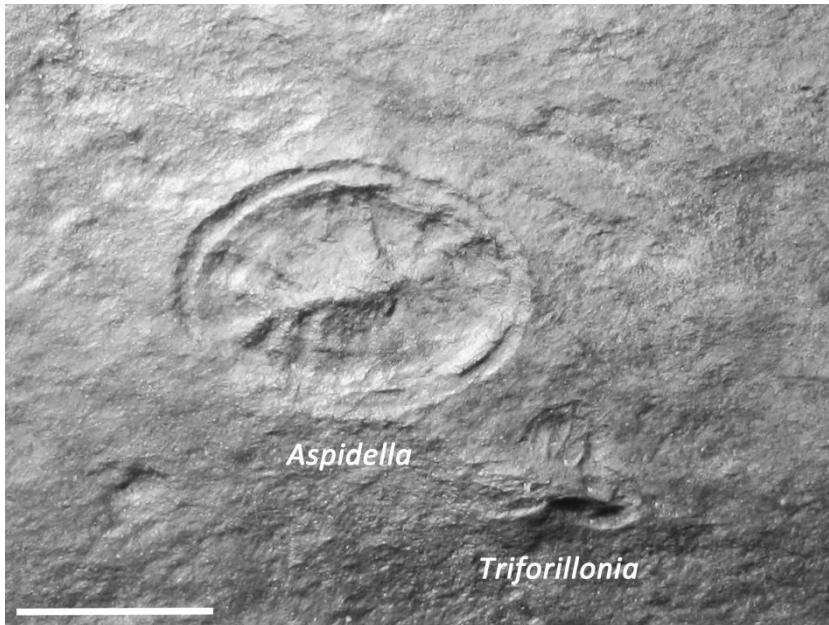


Fig. 5.27. Close up of *Aspidella* and *Triforillonia* on upper bedding surface, showing central ridge and faint radial ridges of both. This is the counterpart of the specimen shown in Fig. 5.20. FR-H/7. Scale bar: 1 cm.

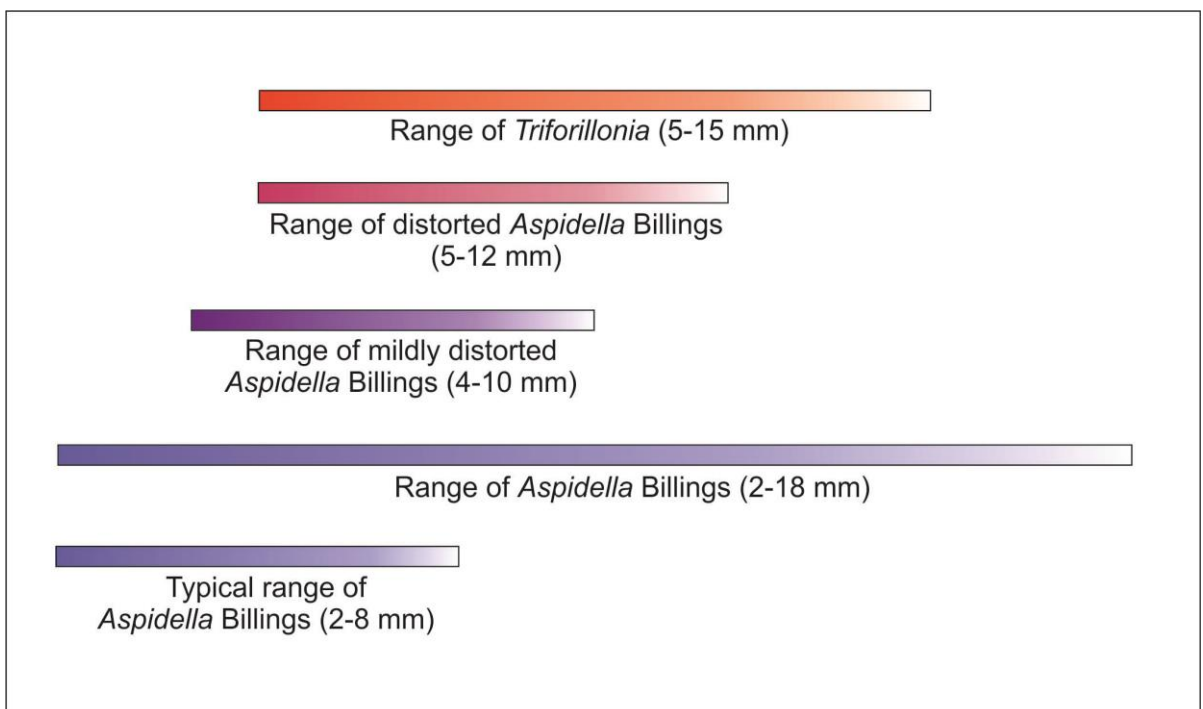


Fig. 5.28. The size range of *Triforillonia* relative to *Aspidella*. Ranges of distorted discs and *Triforillonia* based on 79 specimens.

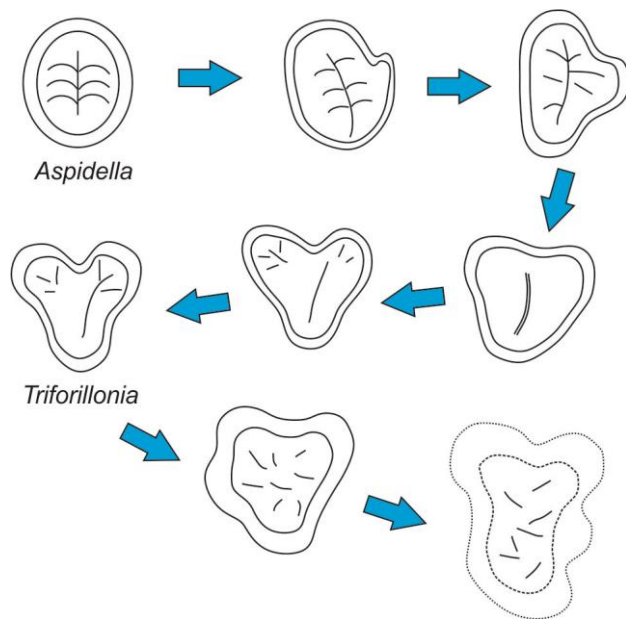


Fig. 5.29. Schematic figure showing one possible route of development from *Aspidella* to *Triforillonia*, to increasingly irregular forms and ivesheadiomorphs, based on the observed variants.

observed from the surrounding disc-rich beds of the upper Fermeuse Formation (with the exception of two isolated specimens from Silos Cove, Fig. 5.22), but no examples of *Triforillonia* have been described from other Ediacaran successions, including the otherwise similar assemblage of discoidal taxa from the Llangynog Inlier, Carmarthen, South Wales (Cope, 1977). The highly localized occurrence, combined with the presence of a continuum of distorted discs alongside *Triforillonia*, suggests that rather than being a separate taxon, *Triforillonia* is more likely to have been a transient, variant form of *Aspidella*. It may even represent a diseased form, in which a latent tri-radial morphology becomes manifest by changes to the developmental programme or integrity of the epithelium of an *Aspidella* (Fig. 5.29). The existence of several tri-radial forms such as *Tribrachidium* among the Ediacaran biota makes such a possibility seem plausible. Alternatively, the form may have arisen due to errors in a process of asexual reproduction such as fission. Another

possibility is that the appearance of a number of distorted discs and *Triforillonia* on these several bedding planes may have been due to some form of environmental stress, although there are no obvious indications of an environmental change. No difference in sedimentology is evident in the *Triforillonia*-bearing beds.

5.5 THE NATURE OF *ASPIDELLA*

5.5.1 Polyp-like features

The impressions of characteristic Billings-type *Aspidella*, with its central invagination or ridge and fine surrounding radial ornamentation, frequently occurs alongside other similar discs with a more rounded boss or central depression, retaining the surrounding ornamentation (Figs 5.1A, 5.30D). Others still have raised central areas, or have a small compressed bulbous base (Fig. 5.30A). It would be difficult to tell this latter form apart from a small specimen of a holdfast disc as described above. However, allowing for the possibility that some of these impressions may also represent Billings-type *Aspidella*, taken together, these variant impressions suggest that the organism responsible had a flexible base. The invaginated and gently protruding forms further suggest the possibility of a muscular structure that may have been captured in everted or introverted form in neighbouring individuals (Fig. 5.30).

The range of impressions is consistent with the varying appearance of the flexible basal physa of modern burrowing actinians such as *Peachia hastata* Gosse (Ansell

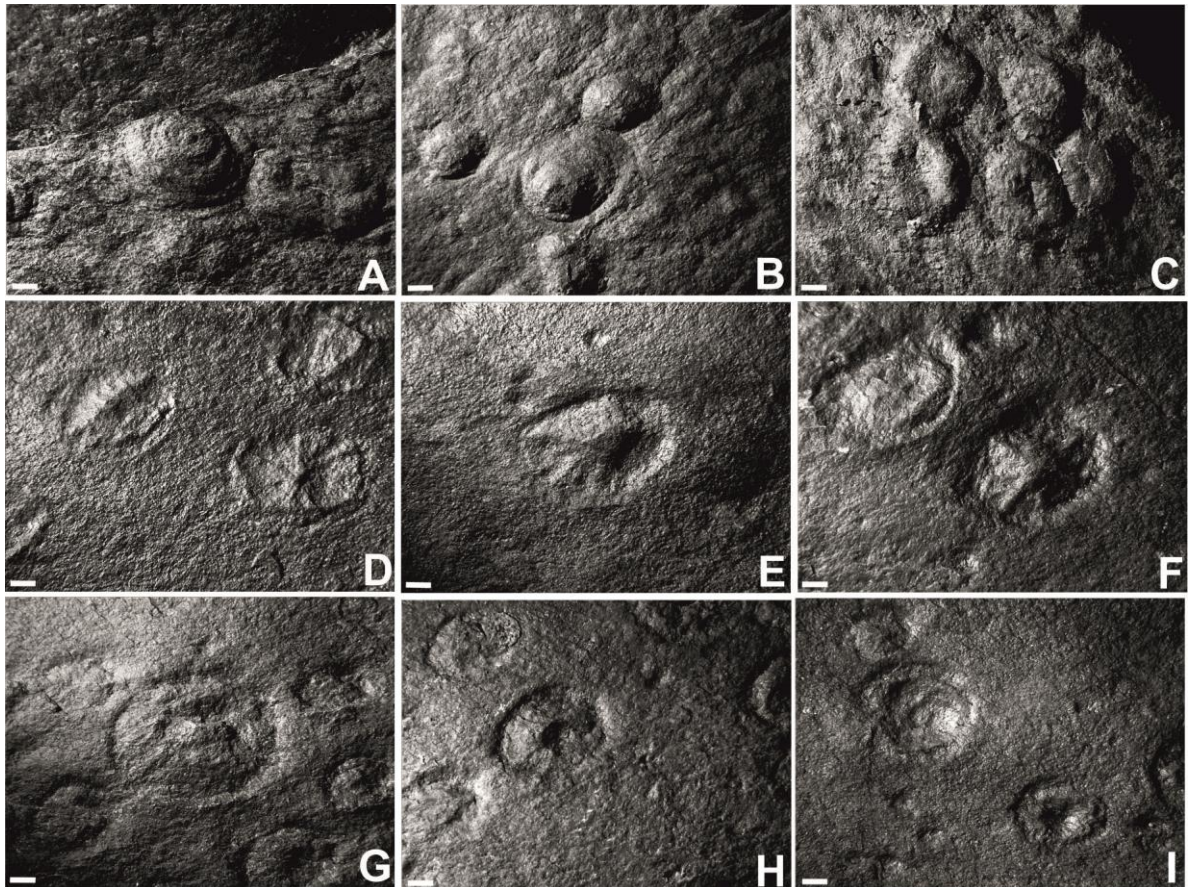


Fig. 5.30. Varying in form of Billings-type *Aspidella*. **A-C:** positive hyporelief impressions. **D-I:** negative epirelief impressions. Note the directly neighbouring elongated and round forms with radial ornamentation in D. FR-H/14, FR-H/28. Scale bars: 1 mm.

and Trueman, 1968; Figs 5.31, 5.32), or the pedal disc of *Phyllactis concinnata* (Mangum, 1970). In the case of *Peachia*, the physa is normally introverted but peristaltic movements result in rapid eversion during the process of burrowing. In *Phyllactis* the pedal disc constricts as muscle contractions pass through. Both modern examples involve phases in which the base appears invaginated, with the contraction of longitudinal muscles, and others in which it is filled with fluid and forms an anchor in the sediment. Unlike the burrows of modern cerianthids, the burrows of actinians are simple and unlined, and reflect the morphology of the organism (Frey, 1970). Actinians are also known to burrow upwards in order to

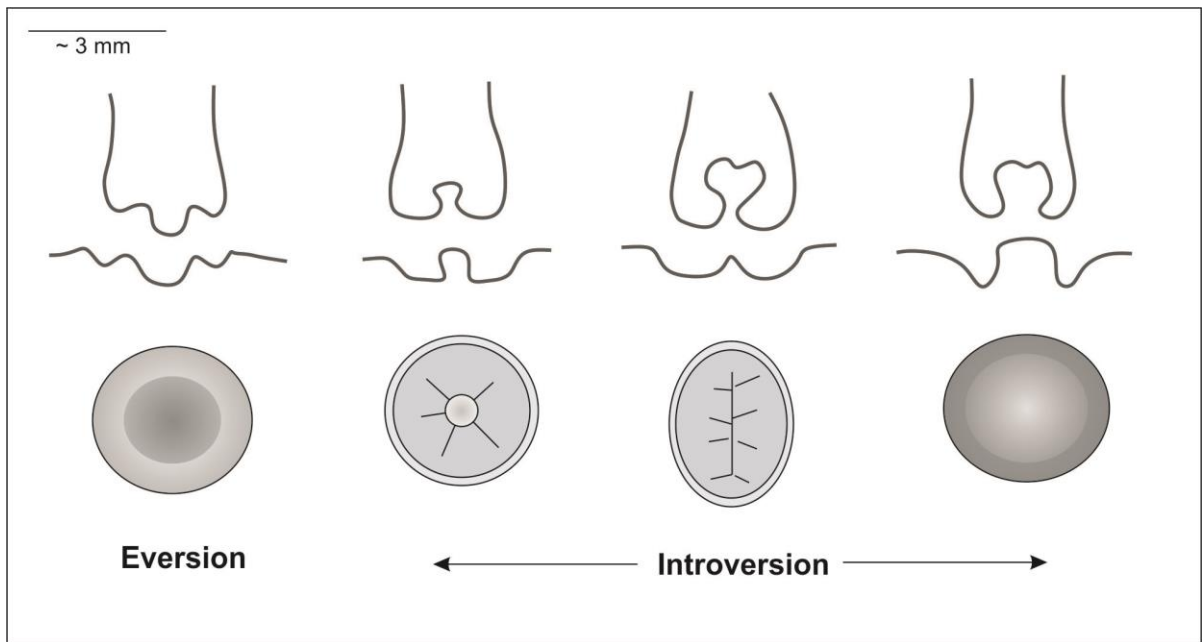


Fig. 5.31. Schematic illustration of the possible formation of different basal impressions of *Aspidella* modelled on the eversion and introversion of the flexible basal physa of modern burrowing Actiniaria. Compare with Fig. 5.30.



Fig. 5.32. Specimens of the modern burrowing actinian, *Peachia hastata* Gosse, showing the flexible basal physa. Note the radial pattern extending to the base. © The Natural History Museum, London.

avoid smothering by small pulses of sediment (Schäfer, 1956; Elders, 1975; Shinn, 1968). These are modern examples, but molecular clock estimates currently locate the origin of the Metazoa deep in the Cryogenian, at *c.* 800 Ma or even earlier (Erwin et al., 2011), such that the presence of simple cnidarians in the Ediacaran



Fig 5.33. Wider view of sole surface in Fig. 5.21B, showing simple mounds (red arrow) surrounding the *Aspidella* (white arrow) and *Triforillonia* (black arrow) specimens. FR-H/8. Scale bar: 1 cm.

Period is a reasonable possibility (cf. Liu et al., 2014). If the variable morphology of Billings-type *Aspidella* does reflect varying positions of a flexible basal physa-type structure, the obvious implication is that the impression-making organism may have been a polyp-like form capable of limited movement. The simple convex bulges observed alongside *Aspidella* on some bedding planes (Fig. 5.33) may be associated with burrowing activity (see Section 5.5.2; Menon et al., 2013), although not forming a substantial, *Bergaueria*-type structure. The presence of an organism capable of raising its lateral margins is also suggested by a single remarkable specimen which, although *Ediacaria*-like, lacks any kind of boss and appears with several large *Aspidella*-type invaginated discs on a bed sole (Fig. 5.34). Although the lack of predation in the Ediacaran Period might suggest that ability to burrow into the sediment would be an unlikely adaptation at this time, burrowing would have had some value in protecting the organism from minor sedimentation events.



Fig. 5.34. Unusual specimen on bed sole, showing compression creases and a slightly folded margin on the left, indicating the delicate nature of the organism. Sediment that has penetrated underneath the organism blots out part of the right-hand side, suggesting that this side was lifted slightly off the bed. FR-H/7. Scale bar: 1 cm.

Likewise the ability to burrow upwards to escape obrution would greatly improve survival, and may well have evolved by this time (Menon et al., 2013).

5.5.2 Evidence of locomotion in *Aspidella*

Although probable bilaterian traces such as *Archaeonassa* and, more questionably, putative radular feeding traces of a possible primitive mollusc, *Kimberella*, have been described from the latest Ediacaran rocks, mostly from Russia and Australia (Fedonkin and Waggoner, 1997; Jensen et al., 2003, 2006; Seilacher and Hagadorn, 2010; Rogov et al., 2012, though see also Brasier et al., 2013a), the apparent lack of

evidence for animal activity prior to *c.* 555 Ma among the characteristic frondose and discoidal Ediacaran macrobiota is at odds with the molecular clock evidence, that predicts that the evolution of Metazoa occurred far earlier, at nearly 800 Ma, than the earliest well-authenticated Ediacaran fossils (Erwin et al., 2011).

The report by Liu et al. (2010) of an assemblage of horizontal trails in the Mistaken Point Formation, Newfoundland, dated at 565 ± 3 Ma (Benus, 1988), raised the possibility of motile metazoans amid the sessile fronds and holdfasts of this oldest Ediacaran assemblage. The evidence presented here, from the *c.* 560 Ma rocks of the upper Fermeuse Formation, directly links similar horizontal traces to *Aspidella terranovica* Billings as well as being the earliest evidence to date of vertical equilibration traces, also associated with Billings-type *Aspidella*.

5.5.2.1 Sedimentary structures associated with Aspidella

Examination of portions of the Ferryland road cut and associated float revealed a number of short horizontal trails in association with small *Aspidella* discs (Fig. 5.35). Such trails are uncommon, and the most striking examples have been observed in an exceptionally heavily colonized portion of a bed. Some trails show radiating sculpture characteristic of the holotype of Billings *Aspidella* (Fig. 5.35A), confirming that these traces were made by Billings-type *Aspidella*. Their crescentic ridges and raised marginal rims are consistent with movement of *Aspidella* along a soft substrate. Adjacent trails vary in direction (Fig. 5.35B), with some pushing into the substrate, which is inconsistent with their formation by simple gravitational sliding

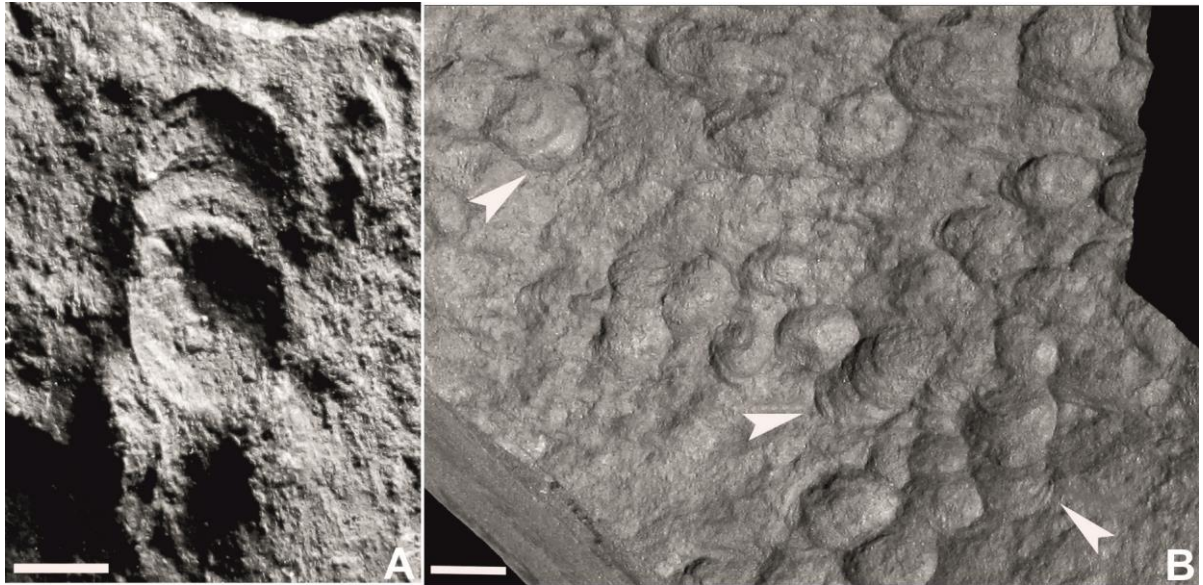


Fig. 5.35. **A:** Short horizontal trail. Note faint radial sculpture associated with *Aspidella* visible on the crescentic ridges. FR-R/13. **B:** Short trails in differing directions on a densely populated bed top. FR-R/6. Scale bars: A: 3 mm; B: 1 cm. (See also Appendix 5.)

or current-driven “tilting marks” (Wetzel, 2013). Moreover, the restriction of trails to a few individuals among otherwise static neighbours (Fig. 5.36) makes movement through the action of currents unlikely. Crescentic marks associated with specimens of *Bergaueria* from younger Ediacaran rocks may represent similar short trails (Fedonkin, 1983; Seilacher, 1990).

Blocks of several centimetres thickness were sectioned in parallel cuts 1 cm apart. The polished sections reveal rounded profiles with sand or silt infill of the kind typically observed for *Aspidella* impressions at colonized surfaces (Gehling et al., 2000; Laflamme et al., 2011), set amid undisturbed thin sandstone and siltstone laminae interbedded with mudstone. Importantly, polished vertical sections through slabs at two localities reveal rare, vertically stacked meniscate structures a few millimetres wide below rounded profiles taken to be *Aspidella* in cross-section



Fig. 5.36. Oblique view of horizontal trail in Fig. 5.35A, showing characteristic *Aspidella* ornamentation in crescentic trail (arrow), and the horizontal movement of one organism among static neighbours. FR-R/13. Scale bar: 3 mm.

(Fig. 5.37A-E). Where these structures arise from the base of the block they lie directly above simple rounded, rimmed disc impressions of similar scale on the sole of the block (Fig. 5.37G). The stacked meniscate structures arise only from certain beds and all terminate at the same sand layer. They are broadly vertical, though some are oblique.

In thin section under the microscope, the rounded profiles topping the structures, and to a lesser extent the menisci below, are observed to have concentrations of coarser grains (primarily quartz and some feldspar) of the kind typically found associated with *Aspidella* - as confirmed by SEM-EDX elemental mapping (Fig. 5.38).

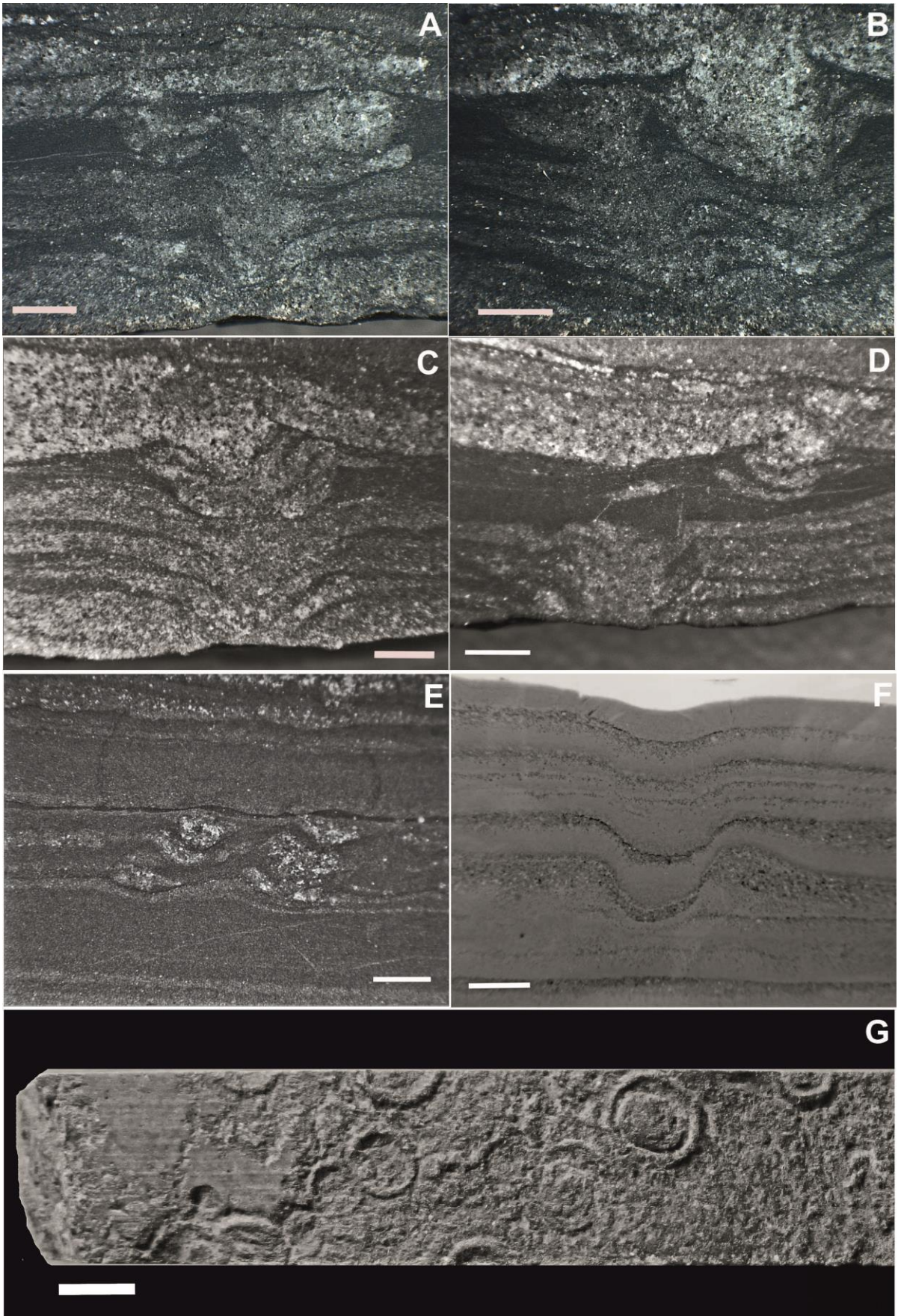


Fig. 5.37.

◀**Fig. 5.37.** Vertical structures associated with *Aspidella*, with experimental structure for comparison. **A-E:** Examples of structures in sectioned slabs from two Ferryland localities, here interpreted as equilibrium traces. (Horizontal line in E is a crack in the sectioned rock.) Scale bars: 2 mm. **F:** Experimentally produced structure resulting from gravitational collapse of sand and mud layers into an artificially induced void. (See Appendix A5.5.) Scale bar: 1 cm. **G:** Associated round impressions with positive rims on sole of sectioned slab. A-D, G, SC-3/1; E, FR-R/1. Scale bar: 5 mm.

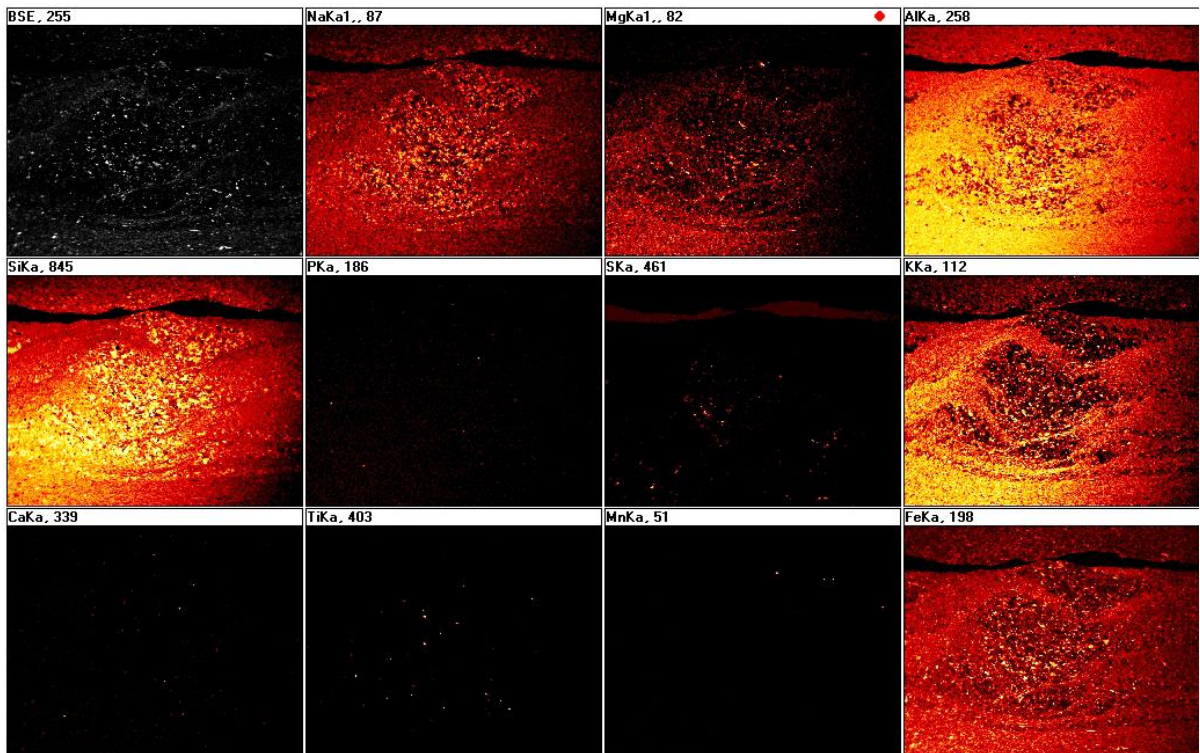


Fig. 5.38. SEM-EDX element mappings of the right-hand trace shown in Fig. 5.37E (FR-R/1). Maps illustrate quartz and some feldspar concentrated in trace (Si, Na maps), and spilling out to sides, with clay minerals (picked up in Al, K maps) dominating surrounding matrix and forming fine, fragmented mud drapes between menisci of equilibrium trace. Acceleration voltage: 20 kV; probe current 6 nA; magnification x20.

Fine-grained, dark layers rich in clay minerals extend from the host sediment to beneath the menisci. These mud layers do not encase the menisci and are discontinuous in the manner of simple mud drapes. Diagnostic features for microbial mats (e.g. Noffke, 2010), such as trapped grains, are not apparent here, though microbially generated framboidal pyrite grains are observed.

5.5.2.2 Interpretation of sedimentary structures

In interpreting such unusual structures, abiogenic processes must first be considered. The variety of structures that can arise from fluid escape, even at millimetre scale, where microbial mats are present, are demonstrated by the Long Mynd examples discussed in Chapter 2. Even simple meniscus-like forms are sometimes seen in those rocks.

The structures observed in cross-section in the Fermeuse Formation however differ markedly from the Long Mynd examples of fluid escape and loading. Two key differences in the rising structures are:

- a) that the Fermeuse structures are far more regular, and do not vary greatly in width unlike the Long Mynd structures; and
- b) that a number of the examples observed (Fig. 5.37A-D) clearly show matching depressions in consecutive sandstone laminae, whereas in the Long Mynd case, the sandstone structures are generally seen to be vertically continuous and to cut through mudstone laminae. Sinuous sandstone structures can appear isolated by being partially out of the plane of the cross-section studied (e.g. Fig. 2.3B; Appendix 2, Fig. A2.6F, H). However, these occur within a wider context of continuous, irregular, usually widening fluid escape structures, rarely observed in the Fermeuse Formation.

Moreover, simple ring-like structures are associated with the traces on the sole surface, rather than the mounds observed in the Long Mynd example, and no

evidence is seen of sediment injection below negative *Aspidella* on bed tops (Fig. 5.9B), so that no equivalent regime of sediment injection and loading appears to be operating. Where small-scale fluid escape does occur, it is quite distinct, forming a vertically continuous, irregular rising structure (Fig. 5.7; Appendix 5, Fig. A5.13). A final distinction between the Longmyndian example and that of the Fermeuse Formation is the widespread evidence for body fossils of Ediacaran macrobiota in the latter, making the possibility of associated trace fossils rather more likely. No such evidence has so far been found in the Long Mynd. Examples of small-scale fluid escape observed in the Fermeuse Formation often contain pyrite and are occasionally found above fossil impressions (Figs 5.8B, 5.39).

Another possible abiogenic explanation for the vertical structures follows from the presence of benthic organisms and invokes gravitational sediment collapse into a void. Such voids might have been created by decomposition of the body tissues of the *Aspidella*-making organism. Gravitational collapse has previously been observed typically to produce a flame-like, downward-pointing profile, plus increasingly shallow dips in overlying strata (Buck and Goldring, 2003). To test this further, experiments were conducted in small aquaria, in which mud and sand layers were built up over buried dissolving fluid-filled capsules (see Appendix A5.5). The dissolution of the capsules produced voids into which the overlying sediment layers collapsed. The resultant sedimentary fabrics show increasingly shallow dips upwards through the sediment pile overlying the position of the dissolved (void-producing) structure (Fig. 5.37F). This is contrary to observations of the Fermeuse

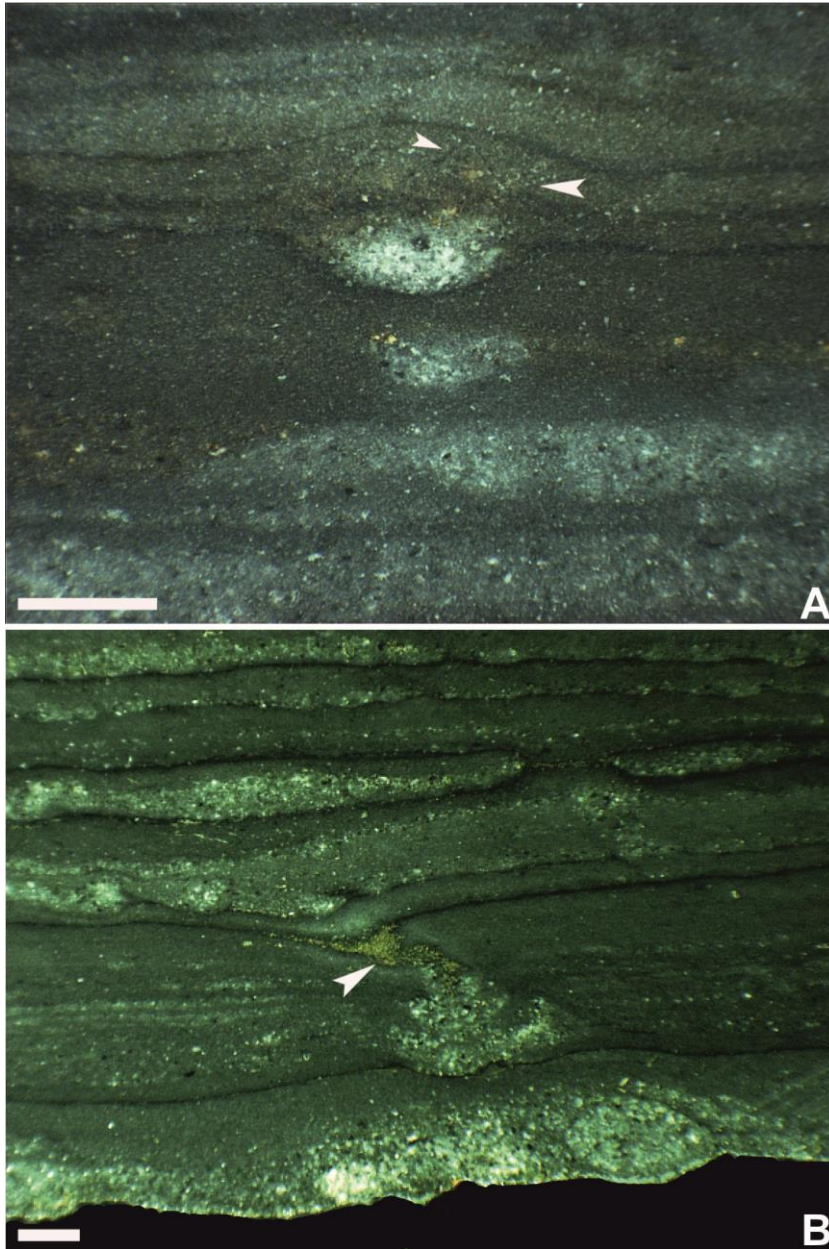


Fig. 5.39. Two examples supporting the likely biogenicity of meniscus-like structures within cross-sections, Fermeuse Formation. **A:** Example of probable *Aspidella* exhibiting characteristic fill of sand grains (dense white meniscus). A fainter meniscus of sand grains is seen below. A thick, dark lamina, perhaps microbially colonized, surrounds the lower part of the upper meniscus. Above the upper meniscus, some disruption to the overlying dark lamina can be seen, with a faint trail of sand grains (large arrow) and small fragments of the dark overlying lamina (small arrow) seen above, together with a pale orange colour which may be suggestive of sulfidic fluids resulting from decay. The dark lamina above the disturbance is distorted upwards into a slight dome. These features may be interpreted as capturing an earlier position of the organism (lower, faint meniscus), which then settled at a higher level (upper meniscus), with a microbial mat developing to surround the base. It subsequently died, and was covered by a thin, probably microbially colonized mud lamina and a silt layer. As the organism decayed, the small-scale escape of sulfidic fluids entraining some sand grains produced the disturbances arrowed, and doming of the overlying lamina. FR-J/5. **B:** Two menisci reducing in size are seen above a meniscus of sand grains with a

central rise, suggestive of the shape of an invaginated *Aspidella*. Above the upper, small meniscus is a sinuous, widening pyritic structure (arrowed). This structure may be interpreted as resulting from the migration of sulfidic fluids following the decay of the organism, following an initial rise. The narrowing of the trace may indicate the flexibility of a polyp-like form. Note that by contrast fluid escape structures tend to widen on rising. FR-H/21. Scale bars: 1 mm.

structures, which show broadly parallel inwardly dipping laminae, often slightly thickened with coarser grains, and usually culminating in a rounded form with coarse sediment infill. Such vertically stacked meniscate structures are unlikely to have formed by gravitational collapse above a decayed *Aspidella* body.

The observed structures are therefore interpreted here as resulting from vertical movement, and it is proposed that they are equilibrium traces created by marine organisms that were partially buried in normal life position. Such traces arise from intermittent vertical movement, and are characterized by recurring meniscus-shaped sedimentary structures of approximately equal width, produced as the animal moves up to maintain its position at the sediment-water interface, in response to new pulses of sediment (Fig. 5.40).

The resultant menisci then simply represent consecutive resting positions of the partially buried organism, though they do not always correlate with layers of bedding; extra menisci may be produced. Unlike traces produced by rapid escape of a buried form through sediment, equilibration involves only small vertical adjustments, with gaps in time in between, so bedding layers are usually unbroken, and there may be mud drapes (and biofilms may form) between the menisci (see Buck and Goldring, 2003 and Bromley, 1990 for Phanerozoic examples of

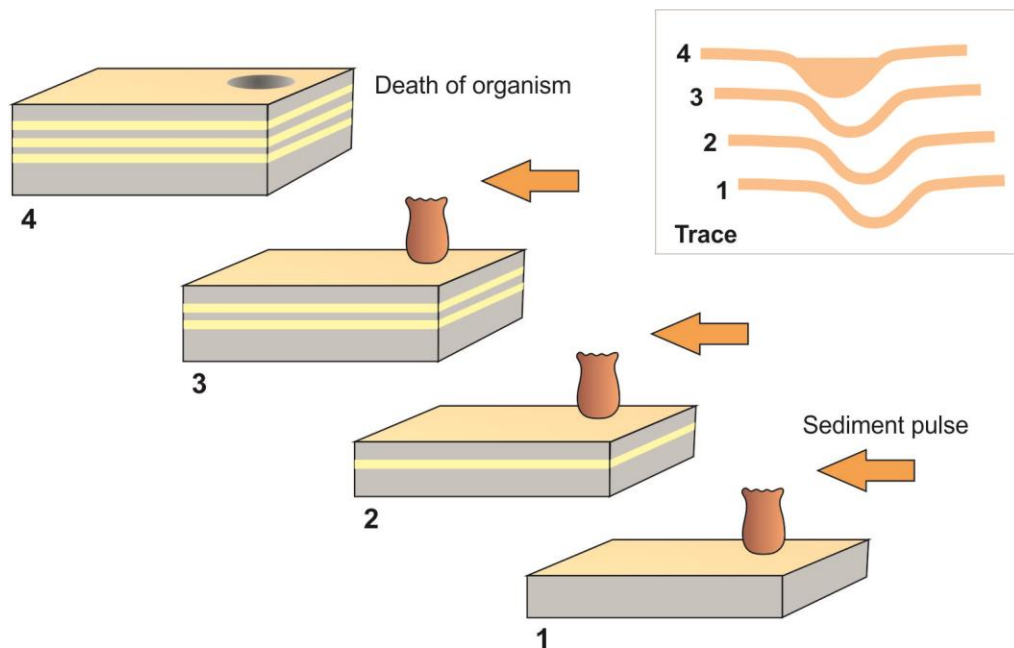


Fig. 5.40. Schematic diagram showing interpretation of traces. (1) In response to each pulse of sediment from the right, the organism adjusts its position vertically to maintain itself at the sediment–water interface (2, 3), producing an equilibrium trace. The organism is eventually smothered by a substantive pulse, and sand fills from above as it decays (4). The organism is represented here as a simple polyp, based on the discussion in Section 5.5.1.

equilibrium traces). All these features are observed here. The association of the traces with simple round, rimmed impressions on bed soles (Fig. 5.37G) rather than with ornamented high-relief *Aspidella* specimens may be explained if the round structure represents the lower surface expression of a trace fossil, while the type *Aspidella* replicates a taphonomically influenced body impression.

The concentration of coarse grains at the top of the traces, representing the final resting position of the organism, but also found to some extent in menisci below, and frequently observed to extend a short distance on either side, is hard to explain by sand ingestion during life, as proposed by Laflamme et al. (2011). The vertical alignment is especially conspicuous at levels having few individuals, and observed in over 10 examples, so that coincidental stacking of separate individuals seems

very unlikely. *Aspidella* may have been loosely coated with grains, shed on moving upwards (perhaps in addition to sand incorporation). External adhesion of a layer of size-selected sediment grains is commonly observed in modern actinians (Hyman, 1940).

5.5.2.3 Discussion

While giant deep sea protists are known to agglutinate and have been observed to move horizontally (Matz et al., 2008), they have never been observed to create crescentic horizontal trails (Liu et al., 2010). The appearance of the characteristic ornamentation of *Aspidella* on crescentic trails is also inconsistent with impressions of giant protists. Likewise, trails made by slug-aggregating phases of slime moulds lack crescentic markings (Bengtson et al., 2007; Retallack, 2013).

More significantly, no large protist has ever been observed to adjust its vertical position in this way. Although a living infaunal xenophyophoran protist is known, it is associated with regular, horizontal, *Paleodictyon*-like hexagonal tests (Levin, 1994). In contrast, equilibrium traces typically result from life at – or with continuous access to – the sediment–water interface. Equilibration therefore implies complex behaviour, involving life in the boundary layer, and the ability to respond rapidly to mild environmental stress induced by sedimentation. Further, since sponges cannot move vertically through sediment, such behaviour indicates a eumetazoan trace-maker, able to propel itself through small pulses of fine sediment by muscular contraction. These findings support the view first tentatively suggested

above from the varied forms of Billings-type *Aspidella* impressions, that the *Aspidella*-forming organism was a polyp-like form capable of limited movement. The simplest explanation is that *Aspidella* was a burrowing or facultatively vagile epifaunal animal of cnidarian grade.

5.6 CONCLUDING REMARKS

5.6.1 Separating the Fermeuse discs

These observations force consideration of *Aspidella terranovica* Billings, a key Ediacaran taxon, as a eumetazoan displaying characteristically animal behaviour (cf. Retallack, 2013). If so, these represent the earliest vertical animal traces described so far and demonstrate that such behaviour existed *c.* 20 Myr before the Ediacaran–Cambrian boundary. The recent discovery of *Haootia quadriformis* Liu et al. 2014 (Liu et al., 2014), a body fossil interpreted as showing evidence of metazoan musculature, lends further support to such a possibility.

It is conceivable that Billings-type *Aspidella* may represent a mobile, juvenile form of the apparently sessile holdfast discs, one that is not preserved in other facies of the Ediacaran succession in Newfoundland, although, given the quality of preservation on the bedding surfaces of e.g. Murphy's Cove on the Bonavista Peninsula, this seems surprising. In addition, holdfast-disc morphologies are observed down to within the size range of Billings-type *Aspidella* (within 2 cm diameter, e.g. the small discs at Upper Island Cove, and the even smaller juvenile rangeomorphs in the Drook Formation; Liu et al., 2012), which argues against such an explanation. A

simpler interpretation would be that *Aspidella terranovica* Billings was an early cnidarian-grade form that co-existed with the enigmatic frondose Ediacaran forms, with their possibly symbiont-containing basal discs.

The aim of this chapter has been to seek to discriminate between the disc morphologies in the Fermeuse Formation through systematic observation, inference, and comparison with other types of discs, including holdfasts and the abiogenic forms discussed earlier, in order to establish the limits of the currently widely applied genus *Aspidella*. Without an understanding of the possible types of discs represented, statistical analyses are misleading, as they are likely to be based on false precepts. Previous studies such as that of Peterson et al. (2003), which explored the possibility that *Aspidella* may have been of fungal grade, counted all forms of disc as *Aspidella* in assessing population structure, resulting in a strongly right-skewed graph, indicating a superabundance of juveniles. The interpretation offered here radically alters the perspective. Given the difficulties of interpreting the disc-dominated outcrops of the Fermeuse in the absence of fronds, considerable further work is needed before rigorous statistical modelling can be effectively applied. Nevertheless, this new interpretation of *Aspidella* offers hope that such approaches may eventually become feasible.

The removal of *Aspidella* from a synonymized plexus of discoidal impressions representing holdfasts as proposed by Gehling et al. (2000), and its re-interpretation herein as a small polyp-like form, greatly reduces its range. No discoidal

impressions of the Billings-type form have yet been reported from the White Sea cluster of assemblages (see Fig. 1.1; Waggoner, 2003). Discs described as "*Aspidella*" from the Flinders Ranges, Australia, are evidently holdfasts, commonly showing evidence of attached stems (e.g. Tarhan et al., 2010, 2015b). Discoidal fossils from Charnwood Forest localities, preserved in negative epirelief, are likewise associated with fronds or stem attachments, and/or display the pattern of several raised concentric rings described here as *Spriggia* and interpreted as the tops of holdfasts (e.g. Ford, 1958; Boynton, 2008; Wilby, 2011; see also Chapter 3); no examples of *Aspidella* are evident. Beyond the Fermeuse Formation of Newfoundland, and possible examples in one locality in the Renew's Formation, Bonavista Peninsula (Hofmann et al., 2008, fig. 7(3)), the only examples of discs with the Billings-type morphology are those in the Ediacaran Avalonian assemblage of the Llangynog Inlier near Carmarthen, Wales (described as "*Medusinites*", Cope, 1977, 1982). As noted earlier, this assemblage bears a remarkable similarity to that of the Fermeuse Formation in Newfoundland.

The limited range of *Aspidella* contrasts with the ubiquity of frondose forms and holdfasts among Ediacaran assemblages (see e.g. Waggoner, 2003). This limitation, even within Avalonian assemblages, may reflect palaeoenvironmental factors such as water depth, currents, and wave energy, as well as endemism.

A systematic palaeontology is given below to reflect the new interpretation of *Aspidella terranovica* Billings. A formal synonymy with emended diagnosis of the

forms described by Gehling et al. (2000) as *Spriggia* and *Ediacaria* from the Fermeuse Formation, as representing impressions of the upper and lower surfaces of holdfasts respectively, is not attempted here. As Gehling et al. (2000) explained, in not attempting to formalize their synonymy of discs in the “*Aspidella* plexus”, the relationships between the many isolated discoidal forms named and described from Ediacaran assemblages worldwide (e.g. *Cyclomedusa*, *Tateana*, *Tirasiana*, *Medusinites*, etc.) – a number of which may be impressions of holdfasts – are currently too uncertain to allow formal classification. Indeed, no such classification has been attempted since the late 1980s, when discs became regarded as form taxa rather than medusae (Sun, 1986, may represent the last effort). Various character differences, such as the presence or absence of fine radial markings on convex discs, may be taphonomic in origin. Further, while many of the discoidal forms may be holdfasts, some relatively flat examples with lobe-like segments and many closely spaced fine annulations, may be microbial colonies (Grazhdankin and Gerdes, 2007). A detailed comparative study will be required to bring taxonomic order to the multiplicity of names under which frond holdfasts, preserved in different ways, and reflecting biostratigraphic and other taphonomic differences, have been described. Meanwhile, a tentative list of the form taxa probably representing holdfasts, reflecting the conclusions presented herein, is given in Table 5.1 as probable junior synonyms of *Cyclomedusa davidi* Sprigg 1947 (cf. Gehling et al., table 1). The *Cyclomedusa* form is preferred here to *Ediacaria* due to its more prominent boss, similar to those found in many convex discs in the Fermeuse Formation, although the size range of *Ediacaria* is greater (Sprigg, 1947, 1949), but the choice is moot.

Discoidal form	Assemblage	Remarks
1947 <i>Ediacaria flindersi</i> Sprigg	S. Australia	Probable lower surface of holdfast (but can also appear as positive epirelief in the Fermeuse Formation, Newfoundland, probably capturing the partially collapsed tops of holdfasts)
1949 <i>Cyclomedusa gigantea</i> Sprigg	S. Australia	Probable lower surface of holdfast
1949 [?] <i>Cyclomedusa radiata</i> Sprigg	S. Australia	Possible lower surface of variant holdfast form (or radial lines may be taphonomic)
1949 [?] <i>Protoniobia wadea</i> Sprigg	S. Australia	Possible upper surface of holdfast
1949 <i>Tateana inflata</i> Sprigg	S. Australia	Lower surface of holdfast
1949 <i>Madigania annulata</i> Sprigg [partim?]	S. Australia	Sprigg, 1949, Plate XVI, fig. 2 [?non fig. 1]. Possible upper surface of holdfast (fig. 2), while fig. 1 (later Spriggia, Southcott, 1958) may be lower surface of holdfast, or microbial colony
1958 <i>Charniodiscus concentricus</i> Ford	Charnwood, UK	Upper surface of holdfast of <i>Charniodiscus</i>
1976 <i>Tirasiana coniformis</i> Palij	White Sea, Russia	Probable lower surface of holdfast
1976 <i>Tirasiana disciformis</i> Palij	White Sea, Russia	Possible lower surface of holdfast, or could be a form of <i>Nemiana</i>
1985 <i>Tirasiana centralis</i> Becker	Ural Mountains, Russia	Probable lower surface of holdfast
1981 <i>Cyclomedusa delicata</i> Fedonkin	White Sea, Russia	Probable lower surface of holdfast
1986 <i>Spriggia wadeae</i> Sun	S. Australia	Possible upper surface of holdfast
1995 <i>Cyclomedusa cliffi</i> Boynton and Ford	Charnwood, UK	Probable upper surface of holdfast
2000 “ <i>Ediacaria</i> ”/“convex morph” (Gehling et al.)	Newfoundland	Probable lower surface of holdfast
2000 “ <i>Spriggia</i> ”/“flat morph” (Gehling et al.)	Newfoundland	Probable upper surface of holdfast
2008 “ <i>Aspidella terranovica</i> ” (Hofmann et al., following Gehling et al. synonymization)	Newfoundland	Probable upper surface of holdfast [?non fig. 7(3)]
2010 “ <i>Aspidella</i> ” (Tarhan et al., following Gehling et al. synonymization)	S. Australia	Upper and lower surfaces of holdfasts

Table 5.1. Probable junior synonyms of *Cyclomedusa davidi* Sprigg 1947, interpreted as the impression of a holdfast.

5.6.2 Systematic palaeontology

Genus *ASPIDELLA* Billings 1872

Type species. Aspidella terranovica Billings 1872

Aspidella terranovica Billings 1872

Fig. 5.1B

- 1872 *Aspidella terranovica*; Billings, p. 478, Fig. 14
- 1899 *Aspidella terranovica* Billings, "probably of organic origin"; Walcott, pp. 230-231, plate 27(7), (8)
- 1962 *Aspidella* Billings, "probably of inorganic origin"; Häntzschel, p. W232, fig. 145 (3a, b)
- 1962 *Aspidella terranovica* Billings, "concretion"; Glaessner (quotes Matthew in Walcott, 1899, "a slickensided mud concretion"), p. 471
- 1971 *Aspidella*, "of mechanical origin"; Hofmann, pp. 14-17, plate 5(1), (2), (3), (5), ([?]6)
- 1977 *Medusinites* sp.; Cope, fig. 1b
- 1982 *Medusinites*; Cope, p. 13, plate 1([?]2), (3); plate 2(1)
- 1989 *Aspidella terranovica*, "more likely to be inorganic"; Conway Morris, p. 12
- 1992 *Aspidella terranovica* Billings, "possibly organic"; Jenkins, p. 142
- 2000 *Medusinites*; Cope, p. 198, fig. 8.10(g)
- [partim]2000 *Aspidella terranovica* Billings, "type morph"; Gehling et al., pp. 427-450,

- text-figs 4, 5 [partim], 6 [partim], 7 [partim], 8 (A-D, H), 9
- 2000 *Triforillonia costellae*; Gehling et al., pp. 451–452, text-fig 17
- 2003 *Aspidella*; Peterson et al., p. 127
- 2007 *Aspidella terranovica* Billings; Fedonkin et al., pp. 54, 64–65, figs 70 [partim], 71
- 2007 *Triforillonia costellae*, “[t]hree lobed organism”; Fedonkin et al., pp. 55, 65, 289
- [partim]2007 *Aspidella terranovica*; MacGhabhann, pp. 301–303, fig. 1 [partim], fig. 2 [partim]
- 2008 *Aspidella terranovica* Billings; Boyce and Reynolds, plate 1F; plate 4A,B; plate 6B[?]
- [?]2008 *Aspidella terranovica* Billings; Hofmann et al., pp. 5–6, [?]fig. 7(3)
- [?]2011 *Aspidella*; Laflamme et al., Fig. 1A
- 2013 *Aspidella terranovica* Billings; Serezhnikova, p. 234
- 2013 *Aspidella terranovica* Billings; Menon et al., p. 895, fig. 2
- 2014 *Triforillonia costellae* Gehling et al., “tribrachiomorph”; Grazhdankin, p. 272
- 2015 *Aspidella terranovica*; Liu and McIlroy, pp. 143–144
- 2015 *Aspidella terranovica*; Liu et al., p. 1365, table 1
- 2015 *Triforillonia costellae*; Liu et al., p. 1365, fig. 5c
- 2015 *Aspidella terranovica* Billings; present work, Table 1.2, pp. 132, 148–181, Figs 5.1, 5.2, 5.9, 5.17, 5.18, 5.20, 5.21, 5.23, 5.25, 5.26, 5.27, 5.29, 5.30, 5.33, ?5.34, 5.35–5.39

2015 *Triforillonia costellae*; present work, pp. 155–163, Figs 5.21, 5.22, 5.23,
5.24, 5.25, 5.26, 5.27, 5.29

Emended diagnosis. Small discoidal form, ranging ~2–20 mm in diameter, consisting of an ovate disc with sharp boundary, a central furrow, and fine radial grooves extending to inner margin, as preserved in positive hyporelief. May also be circular, and preserved in negative epirelief/positive hyporelief, commonly with radial grooves extending from a small circular central boss/depression. Rare, localized occurrences of a three-lobed variant with central ridge/furrow and fine, short, approximately radial ridges/grooves extending to inner margin. Common taphomorphs include concentric compression features.

Emended interpretation. *Aspidella terranovica* Billings is here interpreted (*contra* Gehling et al., 2000) as a small discoidal form distinct from holdfast discs variously described as *Ediacaria*, *Spriggia*, *Cyclomedusa*, etc. (see synonymization in Gehling et al., 2000). Indications, in the varied morphologies of basal impressions, of a flexible base, perhaps capable of muscular contraction, combined with evidence of limited horizontal and vertical movement, lead to the interpretation proposed here, that *Aspidella* was a polyp-like animal of cnidarian grade.

Three-lobed forms with a central furrow have been described as “*Triforillonia costellae*” (Gehling et al., 2000), but have been reinterpreted here as a distorted (in life) variant of *Aspidella terranovica* Billings.

CHAPTER 6

CONCLUSION

If anything is evident from this study, it is that all discs are not the same. The simplicity of the discoidal impression belies the great variety of potential causes. Consequently, discs are surprisingly rich in possibilities. For what may initially appear to be a limited line of enquiry involving refractory and ambiguous fossils, the exploration of discs has proved to touch on many interesting aspects of evolution and Earth history – microbial influence in the Neoproterozoic; the dawn of multicellularity; symbiosis; early animal evolution. For all the challenges of interpreting discs, enumerated in the Introduction, they have been shown to hold important insights into the nature of Ediacaran life. Abiogenic discoidal impressions too are valuable, as they are surface expressions of physical processes, often influenced by microbial activity, that are indicative of the environmental conditions in which the sediments were laid down.

In terms of the aims for this study set out in the Introduction, the following conclusions may now be drawn.

- a) The first described Precambrian impressions, Longmyndian examples of *Medusinites* aff. *asteroides*, *Beltanelliformis brunsaе*, as well as the type material of “*B. minutae*” (McIlroy et al., 2005), have been found to be the surface expression of small-scale sediment injection and loading, inferred to result

from microbial mat sealing. The identification of this suite of sub-millimetric fluid escape features as a mat-driven phenomenon enlarges the range of dynamic influence of microbial mats on Ediacaran sediments. The remaining discoidal form in the Longmyndian, previously described as *Intrites* (cf. McIlroy et al., 2005), is now interpreted as a new form of MISS: effectively a form of microstromatolite, resulting from trapping and binding of sediment by microbial mats, together with microbially induced precipitation of calcite, on the raised topography of a small sediment volcano. A closer look at the Longmyndian microbial mats has led to a more detailed characterization of the microbial assemblage, considerably extending the observations of Peat (1984) and Callow and Brasier (2009). Importantly, SEM-EDX element mapping has indicated that at least some of the white filamentous forms are calcified cyanobacterial sheaths. Other, larger filaments at steep angles to the mat plane may be of fungal origin, pointing to a possible fungal association with cyanobacteria.

- b) Drawing on observations of evidently biogenic discs under different forms of preservation from various Newfoundland localities, a tentative model has been proposed here for the structure of the holdfast discs of fronds.

According to this model, the frond holdfast consists of several envelopes that are robust but not rigid or sand-filled, as they collapse on decay. There are signs of possible septa further dividing the resulting chambers. This architecture may have merely provided strength, but given no requirement for lightness in a holdfast, the complex structure suggests that the basal discs

of rangeomorphs had a function beyond that of simple holdfast, perhaps involving housing symbionts.

- c) Observations of the preservation of the rayed disc *Hiemalora* compared to typical holdfast discs, and its relationship to the frond *Primocandelabrum*, lead to the conclusion that *Hiemalora* was probably a different type of organism to *Charniodiscus* and other discoidal fossils in the Ediacaran of Avalonia. Based on examination of the rays, and indications that the “frond” may have been a branched stalk that grew from the base at certain times in its life cycle, it is proposed that *Hiemalora* may have had an amoeboid lifestyle, with the stalk a type of temporary reproductive structure.
- d) In spite of the slumping and sediment deformation in the upper Fermeuse Formation, resulting in some fluid escape features, most of the discoidal impressions found in these sediments are assessed to be biogenic. Several conclusions have been reached with regard to the first-named Ediacaran body fossil, *Aspidella terranovica* Billings:
 - a. A re-evaluation of *Aspidella* alongside *Ediacaria* and *Spriggia*, other discoidal forms found in the Fermeuse Formation that have been synonymized with *Aspidella* by Gehling et al. (2000), has led to a rejection of that synonymy. *Ediacaria* appears to have captured partially collapsed tops as well as undersides of holdfast discs, while *Spriggia* is here interpreted as the impression of the partially eroded tops of holdfasts, revealing their internal architecture of chambers. *Ediacaria* and *Spriggia* as observed in Newfoundland are regarded as

two examples of a variety of discoidal impressions under different names that probably captured impressions of the surfaces of holdfasts. These names are listed here as probable junior synonyms of *Cyclomedusa davidi* Sprigg 1947. Billings-type *Aspidella*, it is argued, is a separate form, with a size range limited to ~ 2–20 mm diameter.

- b. The three-lobed form *Triforillonia costellae* may not be a separate taxon but a transient variant of *Aspidella*, occurring in a very limited spatial and temporal range, and possibly representing a diseased population.
- c. The range of morphological expressions of the base of the *Aspidella*-making organism is consistent with that of a simple polyp with a flexible basal disc or physa.
- d. Evidence is presented for short horizontal trails and vertical equilibration traces directly associated with *Aspidella* (Menon et al., 2013; see also Liu et al., 2010a). These observations lead to the conclusion that *Aspidella* may have been a simple animal of cnidarian grade, capable of limited burrowing upwards to escape small pulses of sediment. A systematic palaeontology of *Aspidella terranovica* Billings is given here to reflect this new interpretation.

The emerging picture is that a variety of organisms and lifestyles are represented by Ediacaran discs, including 1) basal structures of rangeomorphs that were more than holdfasts and may have played a role in energy acquisition; 2) large forms with an amoeboid lifestyle that may have represented an early, aggregate form of

multicellularity; and 3) small, simple polyp-like animals that co-existed alongside the enigmatic Ediacaran organisms. These insights underline the transitional nature of the Ediacaran Period, a time in which the earliest ancestors of modern animals were beginning to emerge, while amoeboid forms and predominantly sessile organisms exploiting the symbiotic possibilities of the widespread microbial mats may have reached giant sizes. Discoidal forms hold much promise for further elucidation of this vanished world.

This thesis also emphasizes the importance of critical assessment of biogenicity in the case of discs without evidently biological features such as fronds or rays. The value of cross-sectioning is in particular underlined. Blisters and much larger discoidal forms occurring on upper bedding surfaces are generally suspect, even when they have radial ornamentation, as probable fluid escape structures and gas domes. Careful sedimentary assessment has previously been used to separate sedimentary structures (*Astropolithon*) from expected fossil medusae in the Middle Cambrian (Hagadorn and Miller, 2011; cf. examples of established Cambrian fossil medusae, e.g. Cartwright et al., 2007; Hagadorn and Belt, 2008). Such reassessment becomes even more important for earlier discs. Discoidal impressions on upper bedding surfaces have been used to extend the biogeographical range of Ediacaran assemblages and for biostratigraphic purposes (Bertrand-Sarfati et al., 1995; Cruse and Harris, 1994). This study shows that discs may be abiogenic even when they appear on bed soles and have some simple ornament, such as central bosses and lobes (Chapter 2).

Discoidal forms have been interpreted as fossil evidence for the presence of metazoans as far back as the Mesoproterozoic or even earlier (Cruse and Harris, 1994; Rasmussen et al., 2002). The interpretation of discs, their nature and biogenicity, is not only central to efforts to decode the Ediacaran biota, but to our whole understanding of the evolution of complex life. They should remain neglected no longer.

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