Of time and taphonomy: preservation in the Ediacaran

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OF TIME AND TAPHONOMY: PRESERVATION IN THE EDIACARAN

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ABSTRACT.—The late Neoproterozoic witnessed a revolution in the history of life: the transition from a microbial world to the one known today. The enigmatic organisms of the Ediacaran hold the key to understanding the early evolution of metazoans and their ecology, and thus the basis of Phanerozoic life. Crucial to interpreting the information they divulge is a thorough understanding of their taphonomy: what is preserved, how it is preserved, and also what is not preserved. Fortunately, this Period is also recognized for its abundance of soft-tissue preservation, which is viewed through a wide variety of taphonomic windows. Some of these, such as pyritization and carbonaceous compression, are also present throughout the Phanerozoic, but the abundance and variety of moldic preservation of body fossils in siliciclastic settings is unique to the Ediacaran. In rare cases, one organism is preserved in several preservational styles which, in conjunction with an increased understanding of the taphonomic processes involved in each style, allow confident interpretations of aspects of the biology and ecology of the organisms preserved. Several groundbreaking advances in this field have been made since the 1990s, and have paved the way for increasingly thorough analyses and elegant interpretations.

INTRODUCTION: THE IMPORTANCE OF TAPHONOMY

Taphonomic analyses can provide valuable insights into a spectrum of paleobiological questions, including biology, tissue composition, and paleoecology, as well aspects of the paleoenvironment such as sediment pore-water composition and ocean water geochemistry. In celebrated examples, unique taphonomic windows and exceptional preservation have allowed fundamental questions about a group to be resolved. Ediacaran macrofossils are amongst the least-well understood of any macrobiotic assemblage in terms of their biology, paleoecology, and phylogenetic affinity. A thorough understanding of the processes involved in their preservation is required to distinguish between taphonomic artifact and genuine morphological features. Accordingly, there is a long history of actualistic taphonomic analyses undertaken on this biota, combining field-based observations with petrographic and experimental data. Furthermore, recent research has demonstrated that the coincidence of multiple taphonomic windows operating on the same organisms allow resolution of fundamental questions regarding the taphonomic processes themselves; each window provides a test against which the others can be compared. Of all Ediacaran macrofossil assemblages, those traditionally referred to as the 'Ediacara biota' (e.g., Gehling, 1999; Narbonne, 2005) have been the most intensively scrutinized, and thus form the focus of this discussion.

The most notable difference between the Ediacaran and the Phanerozoic is the abundance of moldic preservation of soft parts, particularly in coarse-grained sediments, but the differences in geochemistry and taphonomic processes between the two are not yet fully understood. There remain fundamental questions regarding life and its preservation in the Ediacaran, including composition of the soft parts of the organisms, taphonomic biases imparted by the various paleoenvironments in which the organisms lived, and the relationship between organisms, microbial mats, and sediment. Only by understanding the taphonomy of these organisms can other aspects of their biology be elucidated. Herein, Ediacaran diversity and paleobiology are reviewed, and the dominant preservational styles, the importance of microbial mats, and a few intriguing oddities are discussed. We explore the limitations to our

current knowledge, and suggest future directions for research in this fascinating Period.

Ediacaran macrofossils—it's life, but not as we know it!

The earliest macrofossils currently known from the rock record date from the Ediacaran Period (635–541 Ma; Knoll et al., 2004). These include the ~600 Ma Lantian biota (Yuan et al., 2011), and the much more widely studied assemblages commonly and collectively referred to as the 'Ediacara biota' (e.g., Gehling, 1999; Narbonne, 2005; see MacGabhann, 2014 for a discussion). Assemblages included in the latter biota span some 40 Ma of Earth history, from immediately after the Gaskiers glaciation to the base of the Cambrian (Fedonkin et al., 2007; Narbonne et al., 2012), and shape our ideas of early metazoan evolution and the development of Phanerozoic ecosystem structure. They also provide a means of calibrating molecular clocks and thus the origination of metazoan clades (Erwin et al., 2011). These assemblages are thought by many to include some of the earliest metazoans (e.g., Narbonne, 2005), but interpretations regarding their phylogenetic affinity are as varied as the organisms themselves. They have been interpreted as, or allied to, stem- or crown-group metazoans (e.g., Glaessner, 1979; Clapham et al., 2003; Sperling and Vinther, 2010; Sperling et al., 2011), algae (Ford, 1958), xenophyophores (large benthic foraminifera; Seilacher et al., 2003), fungal-grade organisms (Peterson et al., 2003), an extinct Kingdom (the Vendobionta; Seilacher, 1984, 1992) and even lichens (Retallack, 1994). Part of this confusion is, at least in part, attributable to the historic treatment of the biota as one phylogenetic group when it almost certainly includes representatives from many disparate clades (Xiao and Laflamme, 2009; Erwin et al., 2011). Treatment of the organisms on a case by case basis will, no doubt, lead to a clearer understanding of the diversity and biology of the organisms present.

Most workers now recognize several distinct groups (Fedonkin et al., 2007; Laflamme et al., 2013), including: 1) rangeomorphs, characterized by repeated branching that creates a pseudo-fractal, 'modular' architecture (Narbonne, 2004; Brasier et al., 2012); 2) arboreomorphs, which are similar in gross appearance to rangeomorphs but have a different (non-fractal) branching pattern; 3) kimberellomorphs, which are bilaterally symmetrical, display clearly defined anterior-posterior differentiation, and have at least three concentric zones; 4) erniettomorphs, which are modular and consist of tubular units, and 5) dickinsoniomorphs, which are also modular but show anterior-posterior differentiation. Four additional groups are defined based purely on their symmetry: bilateralomorphs (which are likely polyphyletic; Laflamme et al., 2013), triradialomorphs, tetraradialomoprhs, and pentaradialomorphs (Laflamme et al., 2013). Although considered phylogenetically distinct, individuals of all described groups comprise serially repeated units.

Three assemblages have been proposed: the Avalon, White Sea, and Nama assemblages (Waggoner, 2003). While these correlate broadly with current understanding of paleogeography and age, debate as to the extent of the influence of depositional environment on biotic composition of any given site persists (Grazhdankin, 2004; Droser et al., 2006; Gehling and Droser, 2013). Understanding the paleoenvironment of a site, and thus the biases imposed on taphonomic processes, is of critical importance in assessing the fidelity of the fossil assemblage to the life assemblage (e.g., Grazhdankin et al., 2008).

Many sites record diverse subaqueous communities (e.g., Xiao et al., 2013), comprising upright and flat-lying forms as well as some thought to be wholly or partially buried in the sediment; the majority were benthic, sessile, and epifaunal (Narbonne, 2005; Laflamme and Narbonne, 2008). While scant evidence for motility has been documented from the oldest of these sites (Liu et al., 2010), it is not until the latest Ediacaran that bioturbation (e.g., Chen et al., 2013; Meyer et al., 2014c) and macrobenthic predation (e.g., Hua et al., 2003) become obvious. Microbial mats are widespread and well-documented from these assemblages, and have been implicated in their paleoecology (e.g., Seilacher, 1999).

Peeking through the taphonomic windows at a soft-bodied world

Ediacaran-age rocks are notable for the sheer abundance of soft-tissue preservation they contain. Dozens of sites are known from across five continents, and include representatives from multiple paleoenvironmental settings, hosting abundant and diverse communities. They allow glimpses onto a world populated almost entirely by soft-bodied organisms. Without such abundant preservation of these soft parts, little would be

known of macrobenthic life during most of this critical interval of Earth history; mineralization in macro-organisms only evolves in the terminal Ediacaran (e.g., Grant, 1990; Grotzinger et al., 2000; Penny et al., 2014), and the makers of trace fossils from this time remain largely unknown.

Many aspects of the Ediacaran paleoenvironment differed from the Phanerozoic, and different taphonomic biases held sway: sediment surfaces were sealed by microbial mats, scavenging and deep bioturbation were absent, and organisms were largely sessile and immotile. Consequently, there was a lack of disturbance and an attendant lack of significant time-averaging. Microbes are often cited as key to preservation (e.g., Briggs, 2003; Raff and Raff, 2014), and they formed ubiquitous mats in the Ediacaran (see below). This Period also had very different sedimentary and oceanic chemistry, with lower seawater sulfate concentrations (Canfield et al., 2008), abundant labile dissolved organic carbon in the deep oceans (Sperling et al., 2011), and a condensed sediment-water geochemical profile (Callow and Brasier, 2009b), all of which have been proposed as favoring early diagenetic mineralization.

The multiple views provided onto the community by the different taphonomic windows, coupled with the lack of significant time-averaging, give us greater confidence in the relative completeness of ecosystems. This has allowed inferences about community successions (Clapham et al., 2003), evolutionary progressions (Xiao and Laflamme, 2009), and ecological interactions to be made (Clapham and Narbonne, 2002; Clapham et al., 2003; Droser et al., 2006; Darroch et al., 2013). Nevertheless, details of the anatomy of many Ediacaran organisms are largely unknown: only external and, rarely, internal surfaces are preserved (Meyer et al., 2014a, b). In marked contrast to the Phanerozoic, convincing evidence of preserved internal structures is virtually absent (although see Dzik, 2002, 2003; Narbonne, 2004).

VARIETY IS THE SPICE OF LIFE

The taphonomic windows through which the biota can be viewed are many and varied, each giving a different perspective on their biology. Crucially, some organisms are preserved in more than one taphonomic mode, allowing biases introduced by each mode to be ascertained (e.g., Grazhdankin et al., 2008). Ediacaran preservation is dominated by three major taphonomic modes: 1) moldic; 2) replication by early diagenetic minerals; and 3) carbonaceous compression, each of which are detailed below. Two or more modes sometimes combine in an individual specimen (Fig. 1; Cai et al., 2012). The mode in which a fossil is preserved depends on a variety of factors, many of which are still incompletely understood, but which include the nature of the burial sediment, depositional environment (Narbonne, 2005), microbial community (Gehling, 1999; Gehling et al., 2005), and the chemistry of the pore waters (Mapstone and McIlroy, 2006; Callow and Brasier, 2009b).

Upsides and downsides: moldic preservation

Moldic preservation is the most abundant and typical preservational style of the Ediacaran (Figs. 2–4; Gehling, 1999; Steiner and Reitner, 2001; Narbonne, 2005; Grazhdankin et al., 2008; Cai et al., 2012) but, barring a few exceptional examples (e.g., MacGabhann et al., 2007), is largely unknown outside of this Period. Terms used to describe the nature of the molds and their relationship to the beds preserving the fossils were introduced by Glaessner and Wade (1966). Features observed on the top surface of a bed are termed epirelief (Fig. 2), and those seen on the base of a bed are hyporelief (Fig. 3). Features that form hollows or depressions have negative relief (Figs. 2A, C–D, F, 3A–C), and those that protrude above the substrate surface have positive relief (Figs. 2B, E; 3E).

The sense of relief is thought to involve an interplay between the relative resistance of the soft parts to collapse, and the timing of substrate lithification (Gehling, 1999; Narbonne, 2005): more robust or recalcitrant parts collapse or decay more slowly, and so are cast by still-soft material from the underlying bed being injected upwards (creating negative hyporelief impressions, Fig. 3A–C; or positive epirelief impressions, Fig. 2B, E), while more fragile, fluid-filled, or labile parts collapse or decay quickly, creating impressions that are filled and presumably cast by material from the overlying bed subsiding into the void (resulting in positive hyporelief impressions, Fig. 3E; or negative epirelief impressions, Figs. 2A, C–E, 4). The latter process likely requires stabilization of the lower surface of the organism prior to complete decay in order to retain the observed level of morphological detail (Darroch et al., 2012). Both senses of relief may be seen within a single specimen, and in different
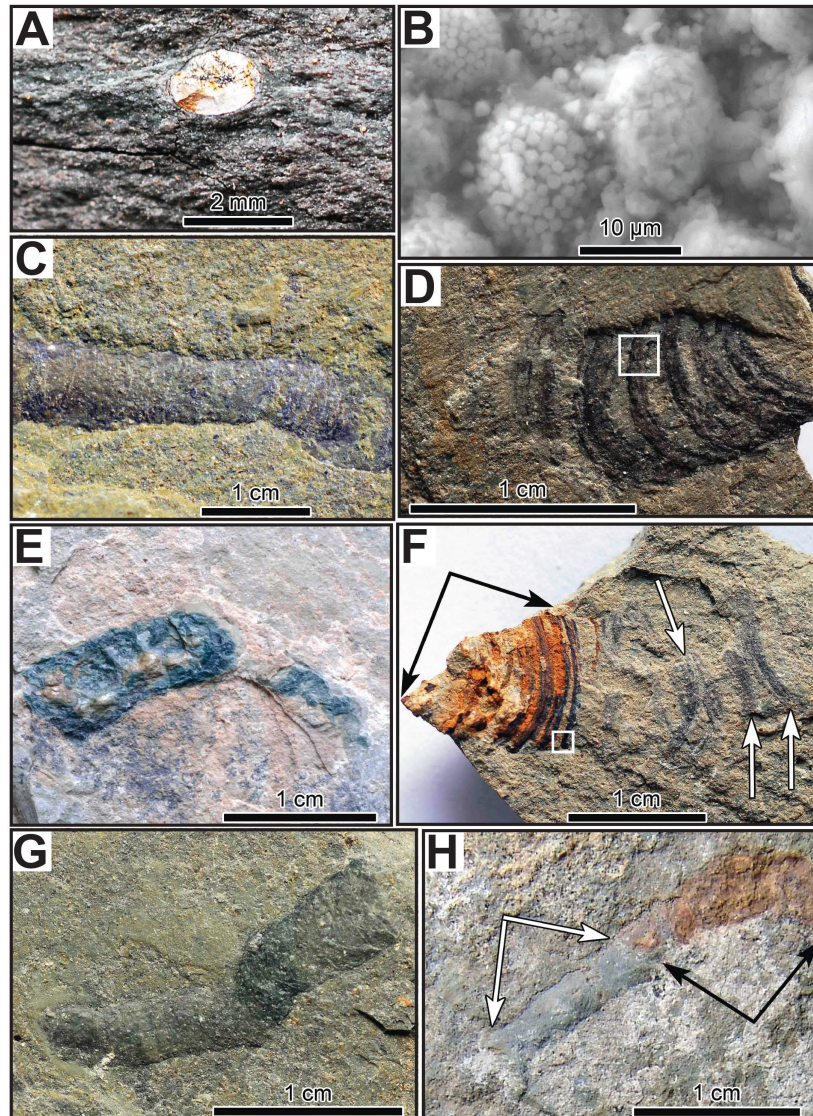
FIGURE *1*.—Preservation of single fossils from the Gaojiashan biota in multiple taphonomic styles; all reflected light photographs except B. A) Cross-section through a pyritized *Conotubus hemiannulatus* specimen; B) SEM photomicrograph of (A) showing pyrite framboids on exterior of specimen. C, D) Carbonaceous compression fossils. E) Replication by green aluminosilicate minerals. F) Specimen exhibiting both pyritization (rust-colored area, black arrows) and carbonaceous compression (grey parts, white arrows). G) Specimen preserved in both carbonaceous compression and greenish aluminosilicate minerals (central part of the tube). H) Specimen exhibiting all three preservational styles: pyritization (between black arrows), carbonaceous compression, and aluminosilicate mineral replication (between white arrows). Rectangles in C, D, and F indicate areas analyzed using ESEM EDS. Reproduced from Cai et al. (2012) with permission from Elsevier.

specimens of the same taxon from different localities (Fig. 2B–E). In the Avalon Assemblage sites of Newfoundland and Charnwood Forest, fossils are only preserved as epirelief impressions (Figs. 2, 4); the counterparts are, as of yet, unknown.

The influence of the nature of the surrounding sediment and depositional environment on the taphonomy of an organism is apparent from the four styles of moldic preservation proposed by Narbonne (2005), but is not yet completely understood. He considered 'Conception-style' preservation to be attributable to early diagenesis of reactive minerals in a smothering volcanic ash. In contrast, the classic White Sea Assemblage sites of Australia preserve their fossils on the bases of event beds (hyporelief), for which Narbonne (2005) coined the term 'Flinders-style'
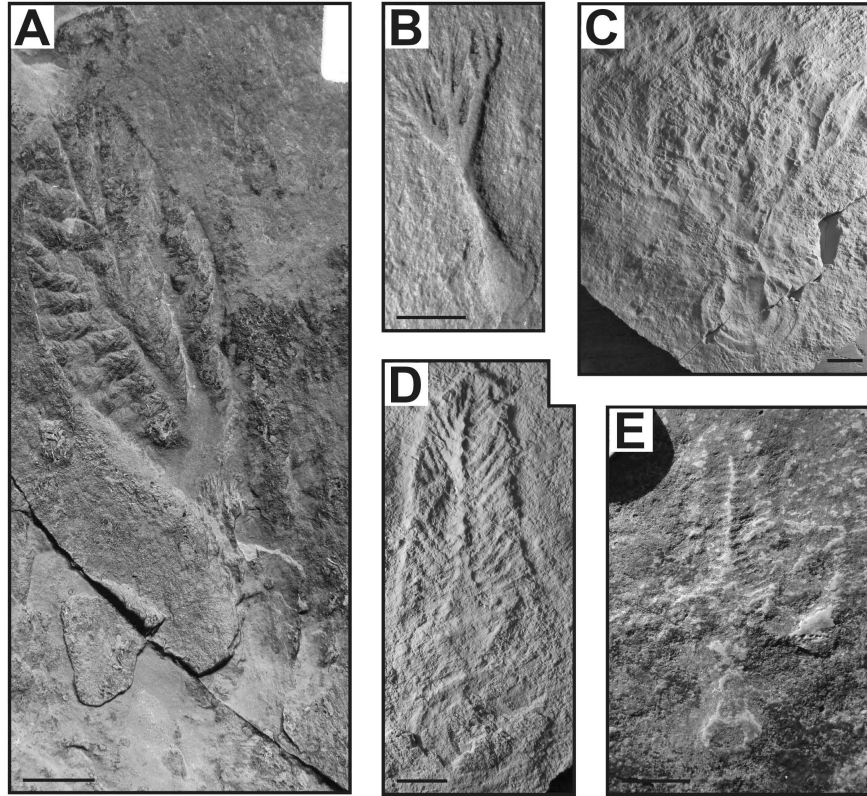
FIGURE 2.—Exceptional preservation in the Avalon Assemblage. A) *Culmofrons* (Bonavista Peninsula, Newfoundland). Note frondose portion preserved in negative epirelief, and stalk preserved in positive relief; photo courtesy of Alex Liu. B) Small *Primocandelabrum* (Bonavista Peninsula) with holdfast, stalk, and branch axes preserved in positive epirelief. C) Plaster cast of *Primocandelabrum (*Charnwood Forest, UK; GSM 105969). In contrast to (B), the stalk and holdfast are preserved in negative epirelief, indicating a difference in relative timings of collapse and lithification of beds at the two sites. D) Plaster cast of *Charniodiscus* (Charnwood Forest, UK; GSM 106069) with central and branch axes preserved in low positive epirelief and holdfast in negative epirelief. E) *Charniodiscus* (Bonavista Peninsula, Newfoundland) with central and branch axes and the holdfast preserved in positive epirelief. Scale bars = 2 cm (A, C–D); and 1 cm (B, E). Color figure available online at <http://paleosoc.org/shortcourse2014.html>

preservation (Fig. 3C, E). This style is also observed in the sandstone-and-shale facies of the White Sea (Grazhdankin, 2004), and has been suggested to be characteristic of shallow-marine environments between fair-weather and storm wave base. In both regions, fossils may be preserved, in whole or in part, as positive or negative relief features. In 'Fermeuse-style' preservation, only trace fossils and the bases of holdfasts are preserved (Narbonne, 2005). In 'Nama-style' preservation (Narbonne, 2005), named after its occurrence in the Nama Group of Namibia, three-dimensional internal and external molds of fossils (Fig. 3D, F–G) are preserved within storm event beds and channel-fill deposits deposited above fair-weather wave base. While this type of preservation has been reported from the Spaniard's Bay locality of Newfoundland

(Fig. 4; Narbonne, 2004), other authors have interpreted the taphonomic mode at that locality to be more akin to death-mask preservation, with the higher relief of the fossils attributable to their preservation within scours in the underlying bed (Brasier et al., 2013). Regardless, preservation on this bed is remarkable, and dependent on a unique (to date) combination of taphonomic circumstances; there may be as-yet undiscovered examples of this style of preservation. There is an element of serendipity to preservation here, which required several processes to operate in concert. This likely included burial of organisms within the sediment (Brasier et al., 2013), exposing the entirety of the frond portion to mineralizing pore waters, coupled with unusually rapid and thorough mineralization, which was potentially a function of pore-water chemistry with favorable
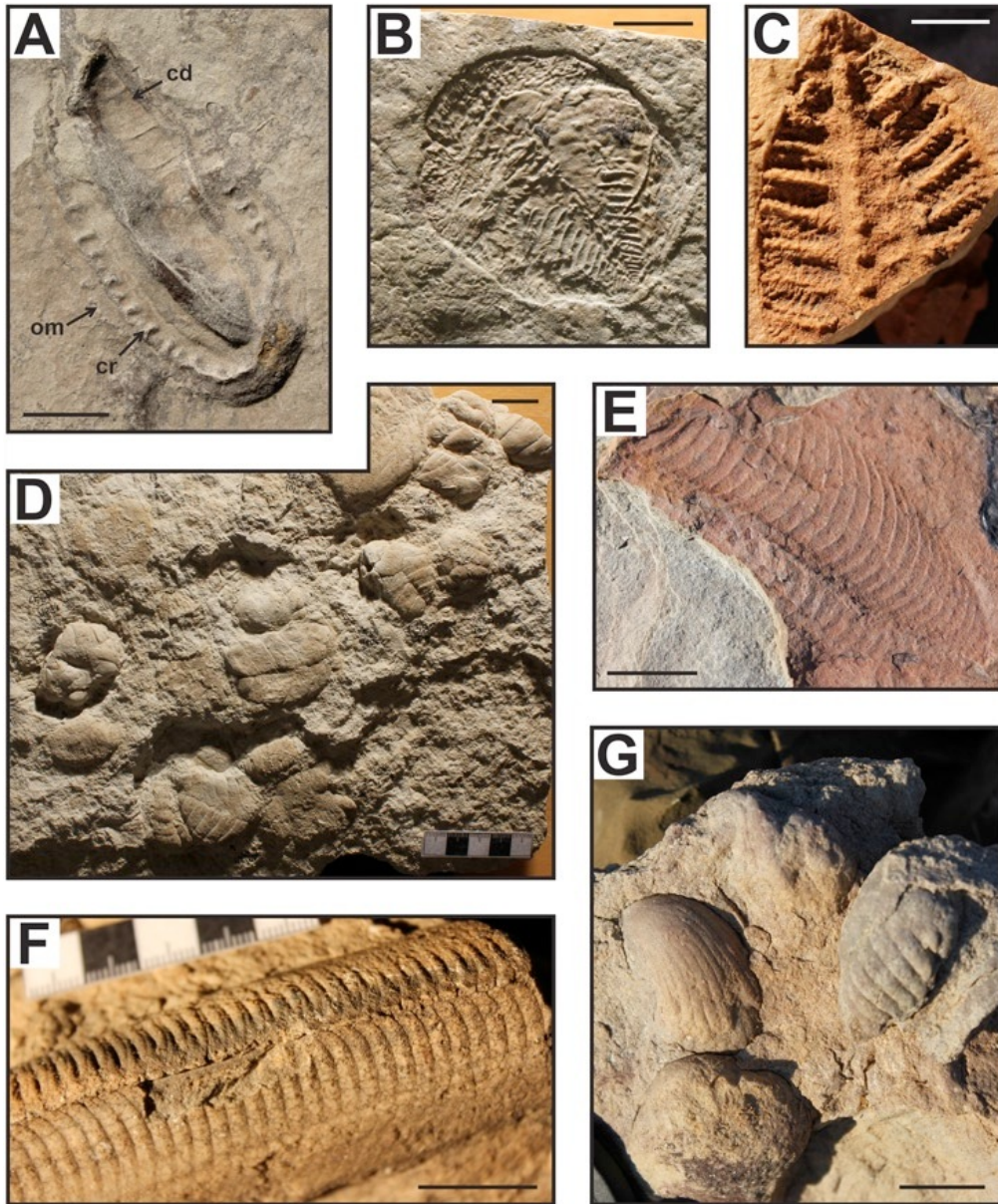
FIGURE *3*.—Examples of moldic preservation from the White Sea (A–B, D) and Namibia (C, E–G). A) *Kimberella* displaying three distinct zones (om = outer margin; cr = crenellated part; cd = central depression). B) *Yorgia* with a disturbed proximal region (upper left). C) *Rangea* with clear rangeomorph branching. D) Death assemblage of *Ventogyrus*. E) *Pteridinium* specimen with prominent red staining on the bed surface. F) *Pteridinium*. g) *Ernietta*. Scale bars are 1 cm (A–B) and 2 cm (C–G). All images courtesy of Marc Laflamme.

iron and sulfur ion concentrations (see discussion of death-mask preservation below).

Several taphonomic experiments have sought to replicate moldic preservation of soft parts; these typically have used specimens from one species (Darroch et al., 2012) or one phylum (Seilacher, 1984; Norris, 1989; Bruton, 1991). This limits their usefulness in interpreting the soft-part composition or phylogenetic affinity of the fossils because of the limited number of tissue types and phyla that have been included in such experiments (and also because each study used disparate experimental parameters, rendering them unsuitable for direct comparison to each other). Indeed, the different responses and preservation potential of the cnidarian taxa studied by Norris (1989) hints at the importance of the structure and composition of an organism
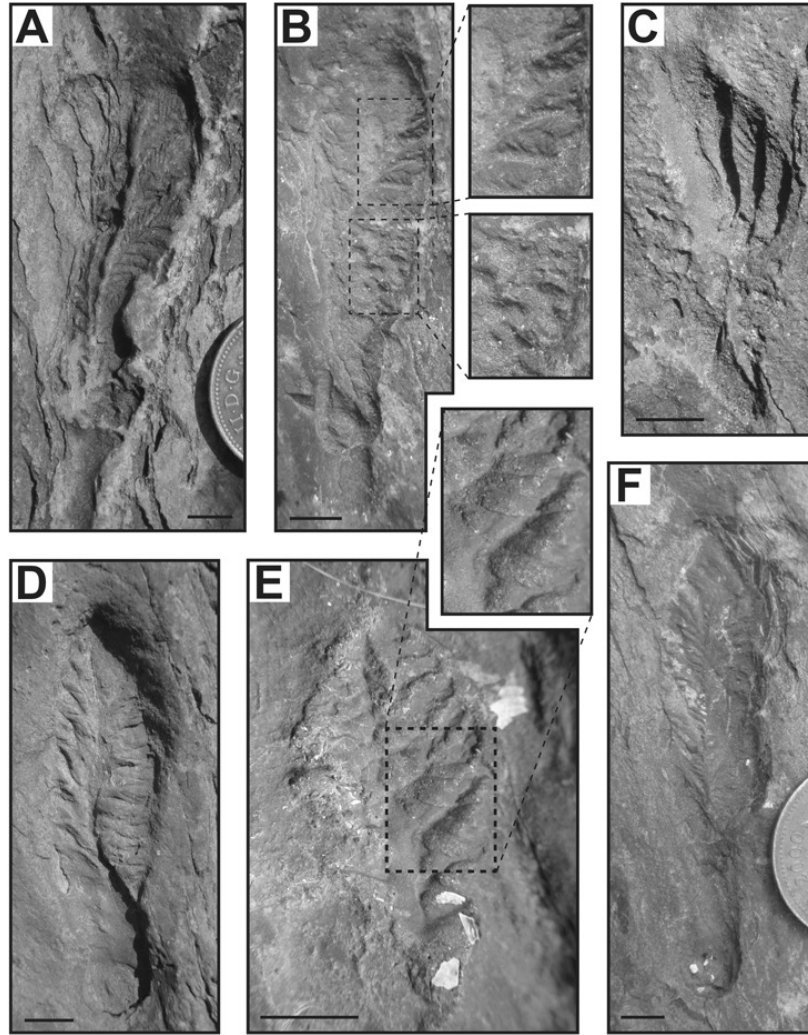
FIGURE *4*.—Specimens from Spaniard's Bay, Newfoundland. A) *Bradgatia* with exquisite preservation down one side only. B) *Beothukis* with good, negative epirelief, distal (upper insert) and poorer, positive epirelief, proximal preservation (lower insert). C) Unidentified frond with relatively high relief on the right, and lower relief on the left. D) *Beothukis* with a prominent disc structure at the base and either a basal sheath or current scour (smooth area). E) *Charnia* with negative epirelief preservation. F) *Trepassia* with exquisite preservation and a basal sheath/current scour. Scale bars=5 mm. Color figure available online at <http://paleosoc.org/shortcourse2014.html>

on its taphonomy. Under favorable conditions, medusoids and chondrophorans produce simple concentric or radial impressions; pennatulids appear more susceptible to contraction even under burial and compression, with the stalk and polyps producing clear impressions, but most branches retracting into an indistinct mass. Interestingly, no impression of musculature was produced in these experiments (Norris, 1989): its preservation in the Phanerozoic typically involves phosphatization (see Briggs, 2003 and references therein), which seems to play only a minor role in the Ediacaran outside of Doushantuo-type preservation (Schiffbauer et al., 2014). A question is therefore raised: is the absence of musculature in the Ediacaran original, or due to failure of preservation?

Additionally, only the influence of the content of organic matter in the sediment was investigated (Norris, 1989; Darroch et al., 2012); other parameters (e.g., grain size, composition) exert an as yet unquantified influence. These experiments have also been conducted under an array of environmental conditions, from water-covered (Bruton, 1991; Darroch et al., 2012) to water-saturated with compression (Norris, 1989), to dry-beach strandline (Bruton, 1991). Interestingly, experiments conducted under water but without

mats or compression result in poor or absent impressions because the buoyancy of the decaying organism lifts it off the sediment surface (Norris, 1989; Bruton, 1991). While these experimental approaches represent great leaps forward in taphonomic understanding, greater finesse is required to determine the relative influences of the many variables (see Sansom, 2014).

Breaking the mold: Gehling's death mask hypothesis.—Once formed, impressions must be rapidly stabilized in order to be preserved. Groundbreaking work into understanding this mode of preservation, and particularly how biological structures could be preserved in their original positive relief, was made by Gehling (1999), based on observations of fossils from the Flinders Ranges. The elegant 'death mask' hypothesis he proposed consists of four main stages:

1) Organisms living on a microbial mat were smothered by sediment;

2) Labile or fluid-filled organisms/tissues decayed rapidly, leaving impressions that were infilled by sediment from the overlying bed, while more robust organisms/tissues persisted;

3) Sulfur-reducing bacteria exploited the organic material of both carcasses and mat, releasing reduced sulfur compounds that combined with iron in the sediment, resulting in the formation of pyrite. This pyrite coated the lower surface of the now-collapsed labile organisms/tissues, and the upper surface of the resistant organisms/tissues, stabilizing the impressions and forming the 'death mask';

4) Death masks that formed over more resistant tissues were infilled from below by still-unlithified sediment.

The pyrite thus formed is observed on the base of the event bed as part of a sole veneer of sediment grains infilled by interstitial pyrite; this layer is typically no more than a few sand grains thick (Gehling et al., 2005; Mapstone and McIlroy, 2006). The reactions involved are summarized here (Gehling et al., 2005):

$$SO_4 + CH_4 = H_2S + 2OH^- + CO_2;$$

$$Fe^{2+} + H_2S = FeS + 2H^+;$$

$$FeS + H_2S + 2R = FeS_2 + 2HR$$
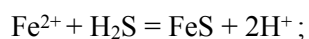
(R = organic compounds).

Several factors influence pyrite precipitation, which in turn influences the anatomical fidelity of the resulting impression (Darroch et al., 2012; Meyer et al., 2014b). In pyritization, a balance exists between the quantity, quality, and distribution of organic matter, and the availability of sulfate and iron ions in the system (see Farrell, 2014). The comparative prevalence of this taphonomic mode in Ediacaran systems can be attributed to two main factors. First, the buried microbial mat provided both a diverse population of decay bacteria and a ready supply of organic matter at the horizon which hosts the fossils (Gehling, 1999). Second, sealing of the sediment by reestablishment of a microbial mat on top of the event bed may have been particularly important in isolating the now anoxic/dysoxic pore waters from the oxic water column above, controlling the availability of sulfate ions and maintaining anoxic pore waters in even porous sediments (Gehling et al., 2005; Callow and Brasier, 2009b).

This model has since been expanded upon (Gehling et al., 2005; Mapstone and McIlroy, 2006; Laflamme et al., 2011) as its ubiquity and variability has become appreciated. Comparable pyrite sole veneers have been described from the Amadeus Basin of Australia (Mapstone and McIlroy, 2006), and inferred from hematite partings (Gehling et al., 2005) and Fe and S within preserved microbial mats (Laflamme et al., 2011) from Newfoundland. Fossils from the Nama Group were originally thought to have been preserved by a different process (Narbonne, 2005), but this has since been questioned (Meyer et al., 2014a, b). These fossils have a thin coating of pyrite that lines the voids left by the external walls of the organism. The thinness of the pyrite coating has been attributed to the dearth of organic matter in the system: in the absence of a microbial mat, the only sources of organic matter were the carcass and the sediment (Meyer et al., 2014a, b). Pyritization has also been implicated in preservation of specimens from the White Sea (Dzik, 2003) and the Gaojiashan biota (Cai et al., 2012), and it replaces the organic wall of frond stems from Siberia (Steiner and Reitner, 2001).

Formation of a pyritiferous sole veneer or parting is also key in the recovery of the fossils: it provides a surficial horizon that is more susceptible to weathering than the bulk rock (Mapstone and McIlroy, 2006; Meyer et al., 2014a, 2014b), causing the rocks to split along those horizons where fossils have been preserved.

The red iron-oxide and iron-oxyhydroxide staining resulting from this weathering also aids in field identification of likely fossil-bearing surfaces (Fig. 3E–F; Gehling et al., 2005).

If pyrite is the only mineral involved in making a death mask, then the level of morphological detail retained in fossils is difficult to reconcile with their collapse and/or decay prior to pyritization, which does not occur until step 3 of Gehling's (1999) model. As described below, recent evidence suggests that either authigenic aluminosilicate templating or microbial mats may have stabilized impressions during the earliest stages of their formation (Darroch et al., 2012).

Coatings of clay: the timing of aluminosilicate mineralization.

The role and importance of clay minerals in soft tissue preservation is controversial, but they have been generated experimentally during early stages of decay (Darroch et al., 2012). Clays are most famously invoked in the preservation of Burgess Shale fossils, although the precise timing of clay formation is debated (Orr et al., 1998; Gaines et al., 2005; Butterfield et al., 2007; Page et al., 2008; Anderson et al., 2011). Authigenic clays were first suggested to have played a role in the preservation of Ediacaran fossils by Wade (1969), and they have recently been noted in association with fossils in several Ediacaran localities. In the Amadeus Basin, aluminosilicates occur as part of a complex suite of very early diagenetic minerals, which consist of authigenic quartz, illite, K-feldspar, chlorite, smectite, glauconite, and hematite after pyrite (Mapstone and McIlroy, 2006). These cements fill interstitial space between the sand grains of the enclosing sediment, and stabilized the fossil impressions throughout burial. In addition to the interstitial minerals, Mapstone and McIlroy (2006) noted a matted fabric of clay minerals, hematite, and silt grains, which form a superficial coating on the fossils. Rather than representing a death mask, which would have also included pyrite framboids, they interpreted this coating to record fine particles falling out of suspension onto the associated mat prior to burial (Mapstone and McIlroy, 2006).

Clay minerals and pyrite appear to be involved in the preservation of fossils from the Doushantuo and Dengying formations (Anderson et al., 2011) and from the Gaojiashan Lagerstätte (Cai et al., 2012; Meyer et al., 2012). In the Gaojiashan Lagerstätte, three-dimensional fossils

that have the finest level of three-dimensional morphological detail are pervasively pyritized (Fig. 1A–B, F); two-dimensional carbonaceous compression fossils are stabilized by Fe-rich clay minerals (Fig. 1C–E, G). Based on mineralogical composition and spheroidal aggregate habit, these Fe-rich clays are though to reflect relatively late diagenetic replacement of an earlier mineral. Although the original mineral served to stabilize the fossil, it likely formed later in the diagenetic sequence than pyrite; fossils templated by clays retain poorer morphological detail than those associated with pyrite.

An association of pyrite and Fe- and Mg-rich aluminosilicates has also been documented from the Fermeuse Formation in Newfoundland (Laflamme et al., 2011), which is notable for its abundance of discoidal fossils assigned to *Aspidella terranovica* (Billings, 1872; Gehling et al., 2000). This study found that *Aspidella* specimens interpreted as holdfasts were preserved in three dimensions, and were coated in a thin layer of fine-grained material. The interior of the holdfast and the surrounding sediment are composed of sand-sized grains, principally composed of Si and Na (analyzed using EDS). The interior sediment is slightly richer in Al, Ca, K, Fe, Na, Mg, P, and Mn, but poorer in C. This is thought to record a vital effect, with sediment inferred to have been incorporated into the holdfast during life (Laflamme et al., 2011). Alternatively, it could record post-mortem precipitation of clay minerals within the holdfast as a function of its specific decay microenvironment. The finer-grained material coating the fossils has higher concentrations of Al, Mg, Fe, Ti, K, Mg, and S than both the holdfast interior and the exterior sediment. This finer-grained layer, which is of variable thickness, has been interpreted to record authigenic aluminosilicate and pyrite growth in a decaying biofilm that had completely surrounded the holdfast during life (Laflamme et al., 2011).

Authigenic chlorite preserves compressed discs in the Jinxian biota, which are found in stratigraphic association with carbonaceous compressions of *Chuaria*, *Shousienia*, and *Tawuia* (Zhang et al., 2006).

Caught on film: carbonaceous compressions

Carbon compression fossils are best known from Chinese localities, with examples from the Gaojiashan Lagerstätte (Fig. 1C–D; Cai et al., 2012), Doushantuo Formation (Fig. 5A; Anderson
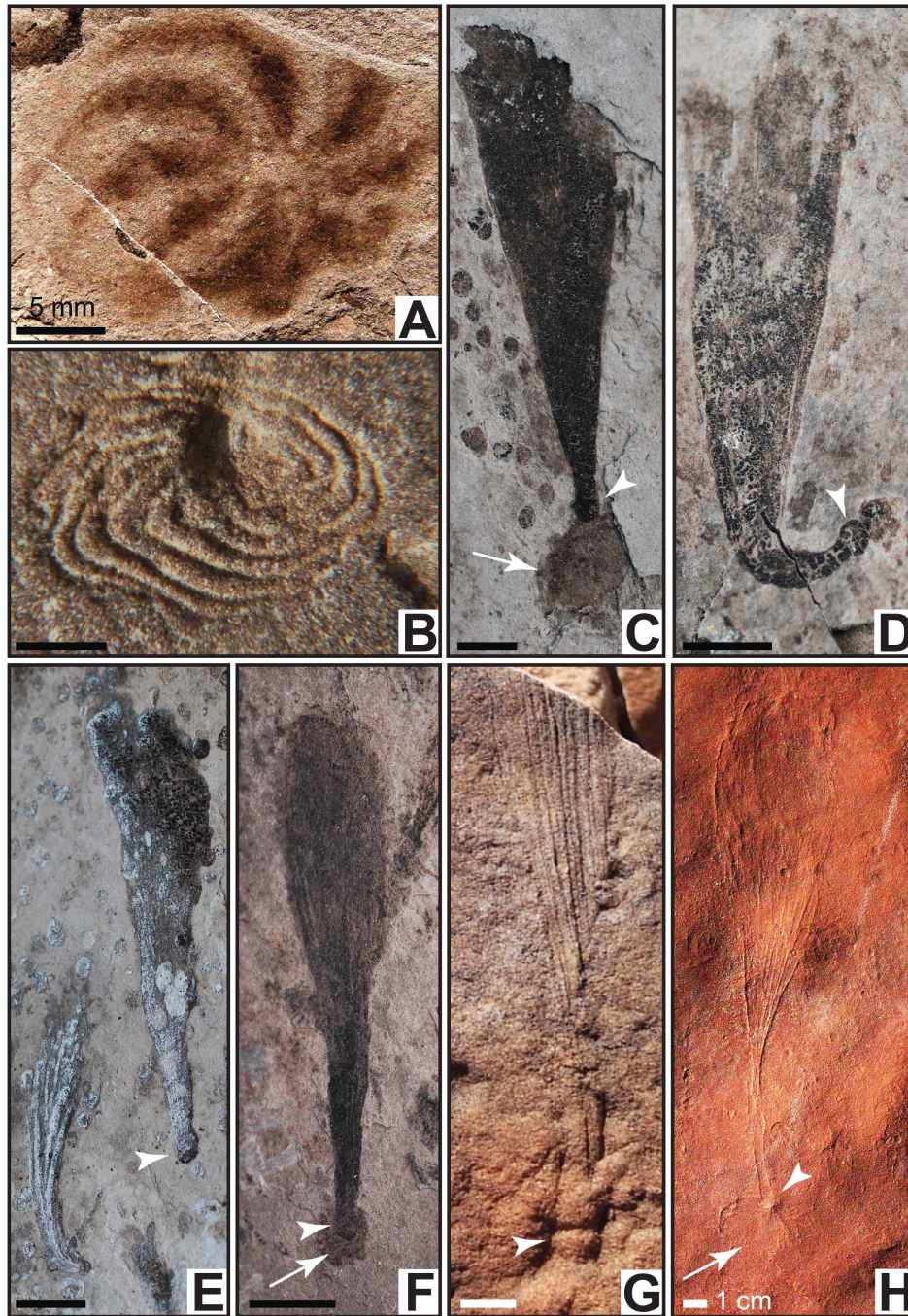
FIGURE 5.—One species preserved in multiple taphonomic modes. A) *Eoandromeda octobrachiata* preserved in black shale, uppermost Doushantuo Formation, Wenghui, China. B) *E. octobrachiata* preserved as a siliclastic mold, Ediacara Member sandstone, South Australia. C–F): *Flabelophyton lantianensis* preserved in black shales of the lower Lantian Formation, South China. G, H) Similar forms, Ediacara Member sandstone, Australia. Arrowheads point to globose holdfasts, and arrows point to organic mass at base. Black scale bars = 5 mm, white scale bars = 1 cm. Reproduced from Xiao et al. (2013) with permission from The Geological Society of America.

et al., 2011), Miaohe (Xiao et al., 2002; Zhu et al., 2008), Lantian (Fig. 5C–F; Yuan et al., 2011) and Jinxian (Zhang et al., 2006) biotas, and the Denying Formation (Sun, 1986). Preservation of fossils in this mode has enabled inferences to be made about the nature of the original composition of the organism and, by extension, its phylogenetic affinity (Zhu et al., 2008).

Assemblages of the ~550–590 Ma Miaohe biota are found in black shales in the Yangtze Gorges, and host a diverse range of macrofossils, many of which are interpreted as algae based on the sub-millimeter resolution of preservation and the observation of delicate thalli-like structures (Xiao et al., 2002). Specimens preserved in a comparable manner to the Miaohe fossils are documented from the White Sea and from Siberia, where they occur in finely laminated, silicified calcareous mudstones of the Khatyspyt Formation (Steiner and Reitner, 2001; Grazhdankin et al., 2008). Kerogenization of carbonaceous compressions has been documented from the Gaojiashan Lagerstätte, and has been inferred to have contributed to stabilization of the fossils (Cai et al., 2012).

Although the paleoenvironments are very different, carbonaceous compression fossils do not seem to differ from typical Phanerozoic fossils, such as Carboniferous plants (see Locatelli, 2014), preserved in this way: at first glance, they appear to be a simple film of organic carbon compressed onto the sediment surface. However, the extent of microbial influence in their preservation is uncertain, particularly for those fossils that also have a moldic component. Although comparisons have been made between Ediacaran carbonaceous compressions that are associated with clay minerals and/or pyrite, and preservation in the Burgess Shale (e.g., Anderson et al., 2011; Cai et al., 2012; Meyer et al., 2012), the presence or influence of any differences in sedimentology, pore-water chemistry or even the nature of the microbial community on preservation between the sites is unknown. Given the uncertainty regarding the phylogenetic affinity and biological composition of Ediacaran organisms, it is also unclear to what degree the composition of tissues would affect the quality or type of preservation within this taphonomic spectrum.

Bridging the taphonomic void

The large number of biotas now known enables the preservation of single taxa to be compared across different paleoenvironments and taphonomic windows, and thus the biases imparted by each to be elucidated (Fig. 5; Grazhdankin et al., 2008; Zhu et al., 2008). This promises to allow original ecological variability in assemblages to be distinguished from taphonomic effects. The exclusion of certain organisms from deposits in which fossils are preserved as carbonaceous compressions has been shown to be a purely taphonomic artifact, and may record differences in original tissue composition (Grazhdankin et al., 2008). In the Khatyspyt Formation of Siberia, fossils are preserved in two facies-dependent modes: as carbonaceous compressions and by authigenic carbonate cementation. *Charnia* is commonly found in the latter, but is only observed in the former as 'phantoms,' where it distorts co-occurring carbonaceous films (Grazhdankin et al., 2008). In some cases, individual fossils are preserved in multiple modes, suggesting a complex taphonomic pathway (Cai et al., 2012). The fine balance between these modes may provide insights into the nature of the original organic material, and/or the chemistry of the host sediment. In order to preserve a carbonaceous compression, decay by sulfate-reducing bacteria, and hence pyrite formation, must be halted early. This may be accomplished by overwhelming the system with disseminated organic carbon, or by limiting diffusion of sulfate from seawater into the sediment.

BINDING IT ALL TOGETHER: THE IMPORTANCE OF MICROBIAL MATS

In contrast to much of the Phanerozoic, microbial mats played a conspicuous role in the preservation of soft parts in the Ediacaran, and may be at least partly responsible for the comparative abundance of soft-tissue preservation at this time (Seilacher, 1984; Gehling et al., 2005). Their ubiquity on the seafloor is widely supported by a myriad of field and petrographic fabrics (e.g., Gehling, 1999; Steiner and Reitner, 2001; Noffke et al., 2002; Gehling et al., 2005; Grazhdankin and Gerdes, 2007; Callow and Brasier, 2009b; Wilby et al., 2011; Lan and Chen, 2012). These fabrics include microbially induced sedimentary structures (MISS, *sensu* Noffke et al., 2001) such as wrinkle marks, reticulate network fabrics, old elephant skin textures, and pustular fabrics (see Gehling, 1999, and references therein), as well as 'bubble trains' (Laflamme et al., 2012; but see Brasier et al., 2013 for an alternative explanation of these structures). Despite this abundant evidence, there are few reports of microbial body fossils outside of the Doushantuo Formation of China (Hofmann et al., 1979; Callow and Brasier, 2009a).

The timing of pyritization relative to collapse of the organism as per the death-mask model (see discussion above), and the consequent difference

in sense of relief of the resultant fossil, testifies to the importance of microbes in Ediacaran preservation (Gehling et al., 2005; Narbonne, 2005). Sites in the Flinders Ranges with thicker microbial mats, as evidenced by prominent surface textures, show negative hyporelief preservation of fossils, with pyrite having formed before collapse of the organisms. By comparison, sites with thinner microbial mats mats, as evidenced by relatively subdued microbial textures, exhibit composite and shallow, positive hyporelief preservation, with pyrite having formed after collapse of the organisms. Therefore, it may be concluded that a thicker mat induced earlier formation of a death mask. Similarly, Narbonne (2005) attributed Flinders-style preservation to rapid mineralization related to the presence of the thick mats which could develop in the environments where this style is common (Seilacher, 1984; Gehling, 1999). Narbonne (2005) also suggested that organisms preserved either by poor examples of Flinders-style preservation or by Nama-style preservation are attributable to their occurrence in environments above fair-weather wave base, which would have lacked a well-developed mat. In contrast, Fermeuse-style preservation has been suggested to have arisen from failure of the overlying bed to lithify before complete decay of the organism, due to either an absence of a mat, or the presence of a mat composed entirely of heterotrophic and/or sulfur-oxidizing bacteria (Narbonne, 2005).

Additionally, the extracellular polymeric substance (EPS) produced by the microbial mat likely played an import role in the initial formation and stabilization of the fossil impression by binding sediment grains prior to precipitation of authigenic minerals (Darroch et al., 2012). In a series of experiments, the impressions that retained the finest morphological detail and lasted the longest were those that contained microbial mats (Darroch et al., 2012). These samples preserved exceptional detail (as scored on their taphonomic index) for two weeks after death of the subject, compared to one week in samples with no mat. In mat-hosted samples, precipitation of pyrite precursors initiated after just one day, and reached maximum extent after two weeks. In samples without mats, pyrite precursors initiated after two weeks in unsterilized sand, and failed to initiate in sterilized sand. The importance of microbial mats in preservation is highlighted when the experimental approach of Darroch et al. (2012) is compared with experiments conducted in the 1980s and 1990s, particularly given the relatively low return rate of recognizable impressions in experimental runs with otherwise similar conditions (Norris, 1989).

ASPIDELLA EVERYWHERE! THE ABUNDANCE OF HOLDFASTS

Without a doubt, the most abundant macrofossils found throughout the Ediacaran are discoidal. The majority of these belong to the taxon *Aspidella*, which brings together many different, and previously taxonomically distinguished, forms (Gehling et al., 2000). They are thought to principally represent holdfasts (Gehling et al., 2000; MacGabhann, 2007; Laflamme et al., 2011), and may be so abundant that they entirely cover bedding surfaces, as seen in the Fermeuse Formation of Newfoundland (Fig. 6E). Holdfasts are rarely preserved on the same horizon as their fronds (e.g., in Charnwood Forest, Fig. 2 B, D; Wilby et al., 2011); in most localities, either one or the other is preserved. Most holdfasts were likely buried within the sediment, in whole or in part, and their frequent concentric rings are generally interpreted as collapse structures. On certain surfaces, only fronds of certain taxa are associated with holdfasts (e.g., *Charniodiscus* in Mistaken Point, Newfoundland). In these cases, the holdfasts are typically preserved in positive epirelief, and have been inferred to record upper surfaces of holdfasts that protruded above the mat surface in life, and were cast before collapse by rapid mineralization of the ash (Conception-style preservation). Fronds on these surfaces that lack associated discs (e.g., *Charnia*) may have had holdfasts that remained entirely buried within the sediment during their life and death (Laflamme et al., 2007), and so are out of the plane of preservation. Some localities preserve only holdfasts and trace fossils (Fermeuse-style preservation).

There may be several taphonomic reasons for the relative abundance of holdfasts to fronds. First, the *in vivo* position of holdfasts within the sediment means that even if they collapsed after death or were tugged out, they may still have left a trace in the rock. Such traces include collapse structures formed as sediment fell back into the void left after decay (Narbonne, 2005), and shear structures (Tarhan et al., 2010), respectively. Second, anchorage within (Laflamme et al., 2011) or beneath (Mapstone and McIlroy, 2006) the mat
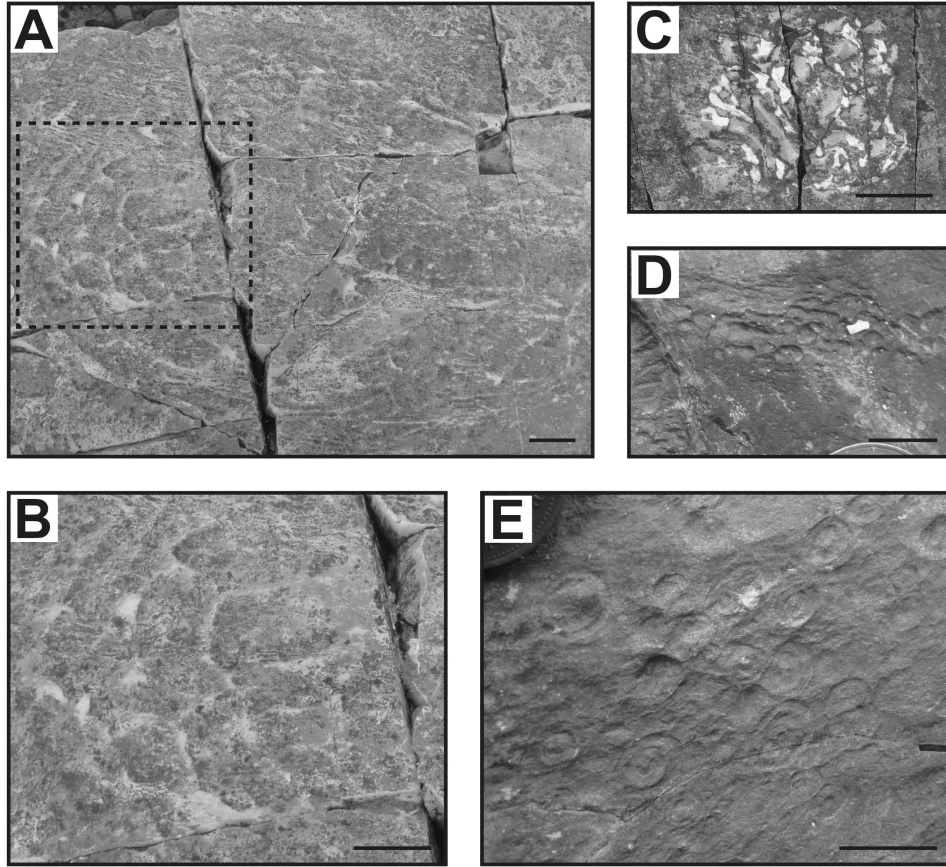
FIGURE *6*.—Fossils from Newfoundland, Canada. A) Large iveshediomorph from Bonavista Peninsula; B) detail of square outlined in (A) showing reticulate network texture. C) 'Pizza disc' (*sensu* Narbonne, 2001) from the Mistaken Point Ecological Reserve. D) 'Bubble strip' (*sensu* Laflamme et al., 2012) from Spaniard's Bay. E) numerous small *Aspidella* holdfasts from Ferryland. Scale bars = 5 cm (A–C) and 1 cm (D–E). Color figure available online at <http://paleosoc.org/shortcourse2014.html>

means that holdfasts were less likely than the frond to be tugged out and removed by the current. Third, their presence within or close to the zone of active diagenesis (the 'mixed layer'; Callow and Brasier, 2009b) gave them a higher preservation potential. Finally, there is some evidence that holdfasts were made of more resistant material; they may be preserved as carbonaceous compressions where stems were replicated by pyrite (Steiner and Reitner, 2001), or as positive epirelief structures where fronds were preserved in negative epirelief (Figs. 2E; 4A–B, D, F; Narbonne, 2005). Their comparative persistence may have lead to their preservation even under conditions conducive to only slow mineralization (c.f., Darroch et al., 2012).

UNRAVELING THE RAVAGES OF TIME: BIOSTRATINOMY AND THE GRADATION OF FORMS

Biostratinomy encompasses the effects of post-mortem compaction, contraction (whether by dehydration or bacterial decay), folding, and transport (Gehling et al., 2005), which necessarily influence the final morphology of the fossil. Compared to the Phanerozoic, fewer biostratinomic processes operated in Ediacaran times. Scavengers that consume or disarticulate carcasses are unknown from the Period, and bioturbation was limited. Those processes that would have endured throughout the Proterozoic into the Phanerozoic are microbial decay and abiotic (physical) disturbance. Syn- or post-mortem distortion of the morphology of organisms by physical processes has been

recorded from localities around the globe, and includes wrinkling (Gehling, 1991), folding (Seilacher, 1992), and ripping (Runnegar and Fedonkin, 1992). If parts of an organism have dissimilar rheologies, they will be affected differently by shared biostratinomic processes. For example, the crenellated part of *Kimberella* shows comparatively greater deformation or wrinkling than the rest of the organism, and is accordingly inferred to have been a broad, flattened 'foot,' which was less robust than a surrounding unmineralized 'shell' (Fig. 3A; Fedonkin and Waggoner, 1997). Additionally, in fossils from Newfoundland, the quality of preservation decreases along their length; there was greater opportunity for sediment to settle beneath the more distal and lateral parts of the frond during felling (Laflamme et al., 2007).

Fronds of increasing size may show variations in susceptibility to current-induced stacking of branches and compression of overall form. The observed change in plan-view morphology in *Bradgatia* with overall increase in size from 'I' to 'V' to 'U' and to 'O' may thus reflect increased resistance to this process (Brasier et al., 2013), rather than a purely ontogenetic signal (Flude and Narbonne, 2008). On a finer scale, the branching pattern of rangeomorphs may also be affected during the burial event, as seen in the current-induced imbrication of primary branches recorded in specimens from Spaniard's Bay, Newfoundland (Fig. 4; Brasier et al., 2013). If this interpretation is correct, it is unnecessary for these branches to have been either constrained in a sheath or attached to each other, as has been proposed for some taxa (Narbonne et al., 2009).

Sweeping up: interpreting 'mops'

The potential extent of modification of form by physical disruption is further evidenced by so-called 'mop structures' (Tarhan et al., 2010). These forms have a highly variable appearance and relief, but are consistently aligned parallel to ripped-up stems on the same bed, have well-defined distal margins, and subparallel internal lineations that are orthogonal to the margin. There is a gradation from typical *Aspidella* holdfasts to full mop structures, consistent with these structures representing an effect imposed upon an organism, rather than a discrete taxon. Mops are thus interpreted to be the result of current shear on frond holdfasts; the fronds themselves are not preserved, and are suggested to have been torn off by the current or held above the preservational

surface (Tarhan et al., 2010). Alternatively, they may have been held out of the plane of preservation. Upstream parts of mops have a range of distal margin shapes, and are interpreted as buckled and compressed parts of holdfasts, whereas downstream, linear structures are interpreted as torsion-induced stretch marks. The smallest mops are expressed solely as a distortion of the surrounding sediment, suggesting that the smallest fronds were removed entirely. This may explain the lack of specimens below a few centimeters in many communities. Alternatively, it may be that the entire mop spectrum represents disturbance and distortion of the microbial mat arising from plucking out of the holdfast, and therefore are a form of MISS (Laflamme, pers. comm. 2014).

Is it all rot? Iveshediomorphs

Forms currently referred to as 'iveshediomorphs' (Fig. 6A–D; Liu et al., 2011) are contentious, and include a wide spectrum of morphologies. These were originally described from Charnwood Forest as discrete taxa, and include *Ivesheadia*, *Blackbrookia*, *Pseudovendia,* and *Shepshedia* (Boynton and Ford, 1979, 1995); similar forms in Newfoundland are referred to as 'pizza discs,' 'lobate discs, and 'bubble discs' (Narbonne et al., 2001; Laflamme et al., 2012). A full spectrum between such forms and fronds exhibiting fine detail has been documented from several bedding planes in Newfoundland, leading to the interpretation of ivesheadiomorphs as the remnants of dead organisms that were in the process of microbial decay at the time of burial (Liu et al., 2011). The irregular, unusually high relief and often network-like internal features of these forms were suggested to represent a conflation of sediment trapped by EPS and gas derived from the decay process (Liu et al., 2011). However, other authors have suggested alternative explanations. Laflamme et al. (2012) interpreted these structures as purely microbial in origin, and Wilby et al. (2011) proposed that at least some of the forms may have been created by differential loading on the fossil-bearing surface following collapse of organisms within the overlying bed.

All full up: the timing of sand infills

Resolution of the mechanism and timing (*in vivo* or post-mortem) of sediment infill is of great significance for current interpretations of the biology of the organisms in which such fills are

found. Rangeomorphs and erniettomorphs have been interpreted as osmotrophs, absorbing dissolved organic carbon from the water column (Laflamme et al., 2009). The proposed model requires the organisms to have had a very small (< 2%) volume of metabolically active material, which potentially could have been achieved by *in vivo* incorporation of sediment (Laflamme et al., 2009). If this could be demonstrated, then an osmotrophic mode of life is plausible; if not, then the inert material must have been a fluid, which might be expected to exert its own influence on the rheology of the organism and, consequently, on its taphonomic behavior. If this *in vivo* fill interpretation holds, then such a fill could have additionally served to stabilize or anchor the organisms.

Sand fills observed in stalks of fronds from the Amadeus Basin exhibit ripple cross-lamination contiguous to that of the surrounding sediment, and are convincingly demonstrated to record post-mortem slumping of sediment into the stalk (Mapstone and McIlroy, 2006). In contrast, it has been suggested that sand in the holdfasts ("bulbs") and central stalks of *Rangea* fossils from Namibia was incorporated into the body of the organism during life, based on the similarity of the sediment within the bulb and stalk to that infilling the gutter casts below the fossil (Vickers-Rich et al., 2013). A similar *in vivo* fill has been interpreted in holdfasts from the Fermeuse Formation of Newfoundland (described above; Laflamme et al., 2011).

However, a post-mortem infilling might explain the recorded presence of a gap in the sediment fill partway up the stalk (Vickers-Rich et al., 2013; fig. 7.3, 7.4), which is hard to reconcile with the *in vivo* interpretation. In contrast, a taphonomic sand infill is more difficult to argue for specimens of taxa such as *Ernietta,* which are preserved as three-dimensional sediment casts. There are no obvious tears or punctures through which sediment could enter, and it might be expected that a post-mortem fill would be less pervasive than an *in vivo* one, either restricted to a few (damaged) individuals or to partial infills. If these fossils represent templates of the external surface that were infilled by uncemented sediment (Meyer et al., 2014a, b), how did this sediment penetrate a more-or-less continuous veneer after its formation? Perhaps these organisms did have an *in vivo* fill; in that case, how was this achieved?

Fully understanding the biostratinomy of the organisms can be very useful in determining various aspects of their biology. The observation of torsion-induced stretch marks in holdfasts indicates that these were firmly anchored in the sediment, and that they were sufficiently elastic to deform rather than snap or tear. This, in turn, casts doubt on interpretations of structures such as 'mops' and isolated *Aspidella* specimens that invoke ripping off the frond. A reasonable inference is that tissues showing evidence of tearing under the same conditions were likely more rigid. That organisms can fold over indicates a certain degree of flexibility, and the style of fold can provide additional information on body rheology. Assuming no decay had occurred, those that kink over at a sharp line (e.g., dickinsoniids) were likely more rigid/solid than those which show more sinuous or irregular folds (e.g., the rangeomorph *Fractofusus*).

KNOW YOUR LIMITS: PRESERVATIONAL BIASES AND UNKNOWABLE UNKNOWNS

Although soft-tissue preservation is reasonably common in the Ediacaran, with bed after bed preserving fossils, it is by no means perfect, and has its own inherent problems and biases. Two-dimensional records of three-dimensional organisms are, by their very nature, either composite (with structures at multiple levels in the organism compressed together into one plane) or partial (usually only one side of an organism is cast). This is most problematic for organisms with a highly three-dimensional morphology, such as multifoliate rangeomorphs (*sensu* Laflamme and Narbonne, 2008) and erniettomorphs, as opposed to flatter organisms such as unifoliate rangeomorphs (*sensu* Laflamme and Narbonne, 2008) and dickinsoniids. Imagine how a two-dimensional impression of a bushy plant compares to its three-dimensional morphology, and how much more complex and less representative of the living morphology this would be in contrast to the compression of a plant like a fern. This is exemplified in the changing morphology and decreased clarity of branching of *Bradgatia* with increasing size (see Biostratinomy, above).

As in any Lagerstätte, what has not been preserved must also be considered, both in terms of parts of organisms and entire taxa. For specimens that have been transported and deposited in death assemblages (e.g., Namibian channel-fill deposits), information has been lost

regarding their in-situ ecology, such as their relative abundances and spatial distributions, as well as their *in vivo* position relative to the sediment-water interface. The limits of the resolution of preservation also render invisible any meiofauna which may have been present, so there is no knowledge of these components of the ecosystem (Sperling et al., 2013). Any organism capable of motility (Liu et al., 2010) has a greatly reduced chance of being preserved in an ecosystem than its sessile compatriots. Despite early (now-refuted) suggestions of discoidal fossils as medusoids (e.g., Sprigg, 1947, 1949; Glaessner and Wade, 1966), there is no convincing evidence of pelagic forms. As such, nothing is known of the macroscopic life that may have been present in the water column during the Ediacaran. By extension, if any of these known organisms did have a planktonic dispersal stage (discussed in Darroch et al., 2013), it is unlikely that this would be preserved. Apparent support for such a life stage is the lack of preserved individuals smaller than a centimeter, despite sub-millimetric preservation, and that the smallest fossils currently known are identical in morphology to adult forms (Liu et al., 2012, 2013).

For the organisms that are observed, the overwhelming dominance of two-dimensional, external moldic preservation means that there is little, if any, evidence of internal anatomy. Reported examples of internal 'struts' in rangeomorphs from Spaniard's Bay (Narbonne, 2004) have subsequently been explained as branches filled by sediment casting the underside of the upper surface and creating positive epirelief impressions (Fig. 4B–C), rather than casting the lower surface and creating negative epirelief impressions (Fig. 4A, D–F), as is typical at this locality (Brasier et al., 2013). The ridges originally interpreted as struts were consequently inferred to be the divisions between higher-order branches (Brasier et al., 2013). The differential collapse of branches within the frond (Fig. 4B) could be taken to suggest the *in vivo* presence of a hydrostatic skeleton that became punctured and subsequently deflated, but could alternatively simply record relaxation in response to decay (Brasier et al., 2013). Discrimination between the competing hypotheses will remain challenging until further evidence comes to light.

True three-dimensional preservation of fossils is rare, restricted to occurrences of Nama-style preservation (Narbonne, 2005) and within certain carbonate deposits (Xiao et al., 2005; Grazhdankin et al., 2008). Most fossils have relief, but are essentially two-dimensional in the sense that only one side, or a composite of both sides, of the organism is captured. This means that for the majority of specimens, there is no evidence for what the other side looked like. There is also little indication of the original volume of the organism due to both biostratinomic and burial compaction.

Explanations for the absence of internal structures in Ediacaran fossils include: 1) decay outpaced fossilization; 2) the microenvironment created by decay inside the body cavity was not conducive to fossilization; 3) the extrinsic environment was incompatible with fossilization, perhaps because of sediment sealing; 4) comparatively low oceanic sulfate concentrations (e.g., Canfield et al., 2008) favored pyritization of the organisms' external surface; or 5) the organisms lacked substantive internal structures. Until sufficient and suitable fossils are available to permit the undertaking of destructive analyses (e.g., Laflamme et al., 2011), resolution of this question may remain elusive.

CONCLUSIONS AND QUANDARIES

Exciting progress is being made in several fields of Ediacaran research, including paleoecology (Clapham and Narbonne, 2002; Clapham et al., 2003; Darroch et al., 2013), anatomy (e.g., Fedonkin and Waggoner, 1997; Narbonne et al., 2009; Brasier et al., 2012; Vickers-Rich et al., 2013), ontogeny (e.g., Laflamme et al., 2004; Antcliffe and Brasier, 2007) and phylogentic relationships (e.g., Erwin et al., 2011; Laflamme et al., 2013). Taphonomic processes and biases affect all aspects of paleobiology; an understanding of these is paramount if the nature of the original organisms and their communities is to be elucidated. Great strides are being made with experimental work (McIlroy et al., 2009; Darroch et al., 2012), which enhances results from detailed petrographic and field-based studies (e.g., Gehling, 1999; Xiao et al., 2005; Grazhdankin et al., 2008; Laflamme et al., 2011). Taphonomic modes as disparate as moldic preservation, pyritization, carbonaceous compression, clay mineral precipitation, and carbonate mineralization are all observed in Ediacaran sites across the globe, sometimes with multiple modes within a single fossil (Cai et al., 2012). There appears to be a broad correlation

between taphonomic style and depositional environment (e.g., Narbonne, 2005; Grazhdankin et al., 2008), with moldic and death-mask preservation most common in siliciclastic and volcaniclastic settings, and carbonaceous compression fossils occurring predominantly in shales and carbonates. Clay mineralization appears to occur in all environments. However, the extent of the influence exerted by paleoenvironment, and of the disparate factors this includes, remains uncertain. Fifteen years after the proposal of the death mask model (Gehling, 1999), perhaps it is time to consider how the plethora of biotas featuring pyritization relate to this model and to one another.

The location of an organism with respect to the sediment-water interface imparts a significant taphonomic bias because structures that were located within the sediment during life were more readily preserved in death. This bias is a likely cause of the greater abundance of holdfasts as compared to fronds (see discussion above). Other taphonomic biases are more poorly understood, with a few exceptions (e.g., the scarcity of rangeomorphs in Miaohe-type preservation; Grazhdankin et al., 2008). Elucidation of these biases is critical for paleoecological studies because, as they become known, primary versus secondary site-to-site differences in assemblage composition can be determined.

Perhaps the most appropriate way to investigate these biases is through experimental work. Such studies may also help to answer why moldic preservation is so prevalent in the Ediacaran as opposed to the Phanerozoic. The effects of a range of physical and chemical parameters have been tested in various taphonomic experiments (e.g., Briggs, 2003, and references therein; Sansom, 2014). However, such studies have yet to be systematically extended to investigate systems which would be more applicable to the Ediacaran, e.g., those with microbial mats (with the exception of Darroch et al., 2012). Trace metals such as molybdenum, which are limiting nutrients for life (e.g., Glass et al., 2012), are becoming widely used as tracers of productivity and ocean redox conditions in the Proterozoic (e.g., Scott et al., 2008), but nothing is known about their specific effects on decay-related microbial activity, and, therefore, on taphonomy.

A major caveat to such taphonomic experimentation is the uncertainty surrounding the original biological composition of Ediacaran organisms, which will likely only be resolved upon discovery of an assemblage preserving cellular-level detail. Currently, inferences regarding relative degrees of robustness and rigidity may be made based on biostratinomic grounds, but this only reveals a certain amount. Taphonomic experiments sampling a wide variety of tissue and cell types from as many branches of the tree of life as possible may provide the best results: by comparing the behaviors of different biological compositions to features seen in fossils, it may be possible to relate the two, and, consequently, to infer the original composition of the organism or its parts. Of course, this should be repeated for the potential variables already discussed in order for any such inferences to be made with any degree of confidence, rendering the number of experiments required to be unworkable.

A quandary peculiar to Avalon Assemblage localities is the true nature(s) of ivesheadiomorphs. Do all ivesheadiomorphs (as currently defined by Liu et al., 2011) have the same genesis? Are they all taphomorphs of known taxa? Are they all microbial colonies (Laflamme et al., 2012)? Do any represent discrete macro-organisms (Boynton and Ford, 1979, 1995)? Do some have a different origin? The answers to these questions have great potential impacts for several aspects of paleoecological studies, including living biomass, species diversity and disparity, and spatial distributions. If these structures represent dead and decaying organisms, they must have had a different effect on the rest of the community than if they were living organisms. Whatever they are, why is their occurrence seemingly restricted to Avalonian, deep-water systems? Does this represent an environmental signal, or is it a function of the microbial community of the time? If these fossils do include taphomorphs, could different organisms have created distinguishably different forms, and could these be related back to their progenitors (cf., Liu et al., 2011)?

Paradigm shifts in understanding will probably depend not on the development of analytical techniques, but rather on the discovery of new, higher-resolution preservational windows.

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