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25

## INTRODUCTION: THE IMPORTANCE OF TAPHONOMY

26

27 Taphonomic analyses can provide valuable insights into a spectrum of  
28 paleobiological questions, including biology, tissue composition, and paleoecology, as  
29 well aspects of the paleoenvironment such as sediment pore-water composition and ocean  
30 water geochemistry. In celebrated examples, unique taphonomic windows and  
31 exceptional preservation have allowed fundamental questions about a group to be  
32 resolved. Ediacaran macrofossils are amongst the least-well understood of any  
33 macrobiotic assemblage in terms of their biology, paleoecology, and phylogenetic  
34 affinity. A thorough understanding of the processes involved in their preservation is  
35 required to distinguish between taphonomic artifact and genuine morphological features.  
36 Accordingly, there is a long history of actualistic taphonomic analyses undertaken on this  
37 biota, combining field-based observations with petrographic and experimental data.  
38 Furthermore, recent research has demonstrated that the coincidence of multiple  
39 taphonomic windows operating on the same organisms allow us to resolve fundamental  
40 questions regarding the taphonomic processes themselves; each window provides a test-  
41 bed against which the others can be compared. Of all Ediacaran macrofossil assemblages,  
42 those traditionally referred to as the 'Ediacara biota' (e.g. Gehling, 1999; Narbonne,  
43 2005) have been the most intensively scrutinised, and thus form the focus of this  
44 discussion.

45

46 The most notable difference between the Ediacaran and the Phanerozoic is the  
abundance of moldic preservation of soft parts in sand-grade sediments, but the

47 differences in geochemistry and taphonomic processes between the two are not yet fully  
48 understood. There remain fundamental questions regarding life and its preservation in the  
49 Ediacaran, including the composition of the soft parts of the organisms, the taphonomic  
50 biases imparted by the various paleoenvironments in which the organisms lived, and the  
51 relationship between organism, microbial mat, and sediment. Only by understanding the  
52 taphonomy of these organisms can we begin to confidently elucidate other aspects of  
53 their biology. Herein, we review Ediacaran diversity and paleobiology, discussing the  
54 dominant preservational styles, the importance of microbial mats, and a few intriguing  
55 oddities. We explore the limitations to our current knowledge, and suggest future  
56 directions for research in this fascinating Period.

57

### 58 **Ediacaran macrofossils – it's life, but not as we know it!**

59 The Ediacaran Period (635-541 Ma; Knoll et al., 2004) hosts the earliest  
60 macrofossils currently known from the rock record. These include the ~600 Ma Lantian  
61 biota (Yuan et al., 2011), and the much more widely-studied assemblages commonly and  
62 collectively referred to as the Ediacara biota (e.g. Gehling, 1999; Narbonne, 2005; see  
63 MacGabhann, 2014 for a discussion). Assemblages included in the latter biota span some  
64 40 Ma of Earth history, from immediately after the Gaskiers glaciation to the base of the  
65 Cambrian (Fedonkin et al., 2007; Narbonne et al., 2012), and shape our ideas of early  
66 metazoan evolution and the development of Phanerozoic ecosystem structure. They also  
67 provide a means of calibrating molecular clocks and the origination of metazoan clades  
68 (Erwin et al., 2011). They are thought by many to include some of the earliest metazoans  
69 (e.g. Narbonne, 2005), but interpretations regarding their phylogenetic affinity are as

70 varied as the organisms themselves. They have been interpreted as, or allied to, stem- or  
71 crown-group metazoans (e.g. Glaessner, 1979; Clapham et al., 2003; Sperling and  
72 Vinther, 2010; Sperling et al., 2011), algae (Ford, 1958), xenophyophores (large benthic  
73 foraminifera; Seilacher et al., 2003), fungal-grade organisms (Peterson et al., 2003), an  
74 extinct Kingdom (the Vendobionta; Seilacher, 1984, 1992) and even lichens (Retallack,  
75 1994). Part of this confusion is, at least in part, attributable to the historic treatment of the  
76 biota as one phylogenetic group, when it almost certainly includes representatives from  
77 many disparate clades (Xiao and Laflamme, 2009; Erwin et al., 2011). Treatment of the  
78 organisms on a 'case by case basis' will, no doubt, lead to a clearer understanding of the  
79 diversity and biology of the organisms present.

80         Most workers now recognize several distinct groups (Fedonkin et al., 2007;  
81 Laflamme et al., 2013), including: 1) rangeomorphs, characterised by repeated branching  
82 which creates a pseudo-fractal, "modular" architecture (Narbonne, 2004; Brasier et al.,  
83 2012); 2) arboreomorphs, which are similar in gross appearance to rangeomorphs but  
84 have a different (non-fractal) branching pattern; 3) kimberellomorphs, which are  
85 bilaterally symmetrical, display clearly defined anterior-posterior differentiation and have  
86 at least three concentric zones; 4) erniettomorphs, which are modular and consist of  
87 tubular units, and 5) dickinsoniomorphs, which are also modular but show anterior-  
88 posterior differentiation. Four additional groups are defined based purely on their  
89 symmetry: bilateralomorphs (which are likely polyphyletic; Laflamme et al., 2013),  
90 triradialomorphs, tetradialomorphs, and pentaradialomorphs (Laflamme et al., 2013).  
91 Although considered phylogenetically distinct, individuals of all described groups  
92 comprise serially-repeated units.

93 Three assemblages have been proposed: the Avalon, White Sea and Nama  
94 assemblages (Waggoner, 2003). Whilst these correlate broadly with current  
95 understanding of paleogeography and age, debate as to the extent of the influence of  
96 depositional environment on biotic composition of any given site persists (Grazhdankin,  
97 2004; Droser et al., 2006; Gehling and Droser, 2013). Understanding the  
98 paleoenvironment of a site, and thus the biases imposed on taphonomic processes, is of  
99 critical importance in assessing the fidelity of the fossil assemblage to the life assemblage  
100 (e.g. Grazhdankin et al., 2008).

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

110

### 111 **Peeking through the taphonomic windows at a soft-bodied world**

112 The Ediacaran is conspicuous for its sheer abundance of soft-tissue preservation.  
113 Dozens of sites are known from across five continents, and include representatives from  
114 multiple paleoenvironmental settings hosting abundant and diverse communities. They  
115 allow a glimpse onto a world populated almost entirely by soft-bodied organisms.

116 Without such abundant preservation of these soft parts, we would have little knowledge  
117 of macro-benthic life during most of this critical interval of Earth history; mineralization  
118 in macro-organisms only evolves in the terminal Ediacaran (e.g. Grant, 1990; Grotzinger  
119 et al., 2000; Penny et al., 2014), and the makers of known trace fossils largely remain  
120 elusive.

121         Many aspects of the Ediacaran paleoenvironment differed to the Phanerozoic, and  
122 different taphonomic biases held sway: sediment surfaces were sealed by microbial mats,  
123 scavenging and deep bioturbation were absent, and the organisms were largely sessile and  
124 immotile. Consequently, there was a lack of disturbance and an attendant lack of  
125 significant time-averaging. Microbes are often cited as key to preservation (e.g. Briggs,  
126 2003; Raff and Raff, this volume), and they formed ubiquitous mats in the Ediacaran (see  
127 *Binding it all together*, below). It also had a potentially very different sedimentary and  
128 oceanic chemistry, with lower seawater sulfate concentrations (Canfield et al., 2008),  
129 abundant labile dissolved organic carbon in the deep oceans (Sperling et al., 2011), and a  
130 condensed sediment-water geochemical profile, favoring early diagenetic mineralization  
131 (Callow and Brasier, 2009b).

132         The multiple views provided onto the community by the different taphonomic  
133 windows, coupled with the lack of significant time-averaging, give us greater confidence  
134 in the relative completeness of ecosystems. This has allowed inferences about community  
135 successions (Clapham et al., 2003), evolutionary progressions (Xiao and Laflamme,  
136 2009) and ecological interactions to be made (Clapham and Narbonne, 2002; Clapham et  
137 al., 2003; Droser et al., 2006; Darroch et al., 2013). Nevertheless, details of the anatomy  
138 of many Ediacaran organisms are largely unknown. Only external and, rarely, internal

139 surfaces are preserved (Meyer et al., 2014a, 2014b); in marked contrast to the  
140 Phanerozoic, convincing evidence of preserved internal structures is virtually absent  
141 (though see Dzik, 2002, 2003; Narbonne, 2004).

142

## 143 **VARIETY IS THE SPICE OF LIFE**

144

145 The taphonomic windows through which we can view the biota are many and  
146 varied, each giving us a different perspective on their biology. Crucially, some organisms  
147 are preserved in more than one taphonomic mode, allowing the biases induced by each  
148 mode to be ascertained (e.g. Grazhdankin et al., 2008). Ediacaran preservation is  
149 dominated by three major taphonomic modes: 1) moldic; 2) replication by early  
150 diagenetic minerals; and 3) carbonaceous compression, each of which are detailed below.  
151 Two or more modes sometimes combine in an individual specimen (Fig. 1; Cai et al.,  
152 2012). The mode in which a fossil is preserved depends on a variety of factors, many of  
153 which are still incompletely understood, but which include the nature of the burial  
154 sediment and depositional environment (Narbonne, 2005), the nature of the microbial  
155 community (Gehling, 1999; Gehling et al., 2005), and the chemistry of the pore waters  
156 (Mapstone and McIlroy, 2006; Callow and Brasier, 2009b).

157

### 158 **Upsides and downsides: moldic preservation**

159 Moldic preservation is the most abundant and typical preservational style of the  
160 Ediacaran (Fig. 2–4; e.g. Gehling, 1999; Steiner and Reitner, 2001; Narbonne, 2005;  
161 Grazhdankin et al., 2008; Cai et al., 2012) but, barring a handful of exceptional examples

162 (e.g. MacGabhann et al., 2007), is largely unknown outside of this Period. Terms used to  
163 describe the nature of the molds, and their relationship to the beds preserving the fossils,  
164 were introduced by Glaessner and Wade (1966). Features observed on the top surface of a  
165 bed are termed epirelief (Fig. 2), and those seen on the base of a bed are hyporelief (Fig.  
166 3). Features which form hollows or depressions have negative relief (Fig. 2a,c,d,f; Fig.  
167 3a,b,c) and those which protrude above the substrate surface have positive relief (Fig.  
168 2b,e; 3e). The sense of relief is thought to involve an interplay between the relative  
169 resistance of the soft parts to collapse, and the timing of substrate lithification (Gehling,  
170 1999; Narbonne, 2005): more robust or recalcitrant parts collapse or decay more slowly,  
171 and so are cast by still-soft material from the underlying bed being injected upwards  
172 (creating negative hyporelief; Fig. 3a,b,c/positive epirelief impressions; Fig. 2b,e), whilst  
173 more fragile, fluid-filled or labile parts collapse or decay quickly, creating impressions  
174 which are filled and presumably cast by material from the overlying bed subsiding into  
175 the void (resulting in positive hyporelief; Fig. 3e/negative epirelief impressions; Fig.  
176 2a,c,d,e; Fig. 4). The latter process likely requires stabilization of the lower surface of the  
177 organism prior to complete decay in order to retain the observed level of morphological  
178 detail (Darroch et al., 2012). Both senses of relief may be seen even within a single  
179 specimen, and in different specimens of the same taxon from different localities (Fig. 2b–  
180 e). In the Avalon Assemblage sites of Newfoundland and Charnwood Forest, the fossils  
181 are only seen preserved as epirelief impressions (Fig. 2; Fig. 4); the counterparts are as  
182 yet unknown.

183         The influence of the nature of the surrounding sediment and the depositional  
184 environment on the taphonomy of an organism is apparent from the four styles of moldic

185 preservation proposed by Narbonne (2005), but is not yet completely understood. He  
186 considers “Conception-style” preservation to be attributable to early diagenesis of  
187 reactive minerals in a smothering volcanic ash. In contrast, the classic White Sea  
188 Assemblage sites of Australia preserve their fossils on the bases of event beds  
189 (hyporelief), for which Narbonne (2005) coined the term “Flinders-style” (Fig. 3c,e). This  
190 style is also observed in the sandstone-and-shale facies of the White Sea (Grazhdankin,  
191 2004), and has been suggested to be characteristic of shallow-marine environments  
192 between fair- and storm-wave base. In both regions, fossils may in whole or in part be  
193 preserved as positive or negative relief features. In his “Fermeuse-style preservation”,  
194 only the bases of holdfasts, and trace fossils, are preserved (Narbonne, 2005). In “Nama-  
195 style preservation” (Narbonne, 2005), named after its occurrence in the Nama Group of  
196 Namibia, three-dimensional internal and external molds of fossils (Fig. 3d,f,g) are  
197 preserved within storm event beds and channel-fill deposits deposited above fair-weather  
198 wave base. Whilst it has also been reported from the Spaniard’s Bay locality of  
199 Newfoundland (Fig. 4; Narbonne, 2004), other authors have interpreted the taphonomic  
200 mode there to be more akin to death mask preservation, with the higher relief of the  
201 fossils attributable to their preservation within scours in the underlying bed (Brasier et al.,  
202 2013). Regardless, the exquisite preservation on this bed is remarkable, and is dependent  
203 on a so-far unique combination of taphonomic artifice. This likely includes the burial of  
204 the frond within sediment (Brasier et al., 2013), which exposed the entirety of the frond  
205 to mineralizing pore waters, and unusually rapid and thorough mineralization, which was  
206 potentially a function of pore water chemistry with favorable iron and sulfur ion  
207 concentrations (see discussion of death mask preservation below).

208           Several taphonomic experiments have sought to replicate moldic preservation of  
209 soft parts, but these have typically used specimens from only one species (Darroch et al.,  
210 2012) or one phylum (Seilacher, 1984; Norris, 1989; Bruton, 1991). This limits their  
211 usefulness in interpreting the soft-part composition or phylogenetic affinity of the fossils,  
212 as limited comparison between tissue types or phyla can be made (under the same set of  
213 experimental parameters). Indeed, the different responses and preservation potential of  
214 the cnidarian taxa studied by Norris (1989) hints at the importance of the structure and  
215 composition of an organism on its taphonomy. Under favorable conditions, medusoids  
216 and chondrophorans produce simple concentric or radial impressions; pennatulids appear  
217 more susceptible to contraction even under burial and compression, with the stalk and  
218 polyps producing clear impressions, but most branches retracting into an indistinct mass.  
219 Interestingly, no impression of musculature was produced in these experiments (Norris,  
220 1989); its preservation in the Phanerozoic typically involves phosphatization (Briggs,  
221 2003 and refs. therein), which seems to play only a minor role in the Ediacaran outside of  
222 Doushantuo-type preservation (Schiffbauer et al., this volume). Is the absence of  
223 musculature in the Ediacaran original, or due to failure of preservation? Additionally,  
224 only the influence of the content of organic matter in the sediment was investigated  
225 (Norris, 1989; Darroch et al., 2012); other parameters (e.g. grain size, composition) exert  
226 an as yet unquantified influence. These experiments have also been conducted under an  
227 array of environmental conditions, from water-covered (Bruton, 1991; Darroch et al.,  
228 2012) to water-saturated with compression (Norris, 1989) to dry (beach strandline;  
229 Bruton, 1991). Interestingly, experiments conducted under water but without mats or  
230 compression result in poor or absent impressions, as the buoyancy of the decaying

231 organism lifts it off the sediment surface (Norris, 1989; Bruton, 1991). Whilst these  
232 experimental approaches represent great leaps forward in our taphonomic understanding,  
233 greater finesse is required to determine the relative influences of the many variables (see  
234 Sansom, this volume).

235 *Breaking the mold: Gehling's death mask hypothesis.—*

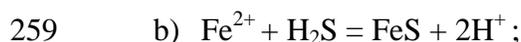
236 Once formed, the impressions must be rapidly stabilized in order to be preserved.  
237 Groundbreaking work into understanding this mode of preservation, and particularly how  
238 biological structures could be preserved in their original positive relief, was made by  
239 Gehling (1999), based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

- 241 1) Organisms living on a microbial mat were smothered by sediment;
- 242 2) Labile or fluid-filled organisms/tissues decayed rapidly, leaving impressions  
243 which were infilled by sediment from the overlying bed, while more robust  
244 organisms/tissues persisted;
- 245 3) Sulfur-reducing bacteria exploited the organic material of both carcasses and  
246 mat, releasing reduced sulfur compounds which combined with iron in the sediment,  
247 resulting in the formation of pyrite. This pyrite coated the lower surface of the now-  
248 collapsed labile organisms/tissues, and the upper surface of the recalcitrant  
249 organisms/tissues, stabilizing the impressions and forming the so-called “death mask”;
- 250 4) Death masks which formed over more recalcitrant tissues were infilled from  
251 below by still-unlithified sediment.

252

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

257



261

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

274 This model has since been expanded upon (Gehling et al., 2005; Mapstone and  
275 McIlroy, 2006; Laflamme et al., 2011), as its ubiquity and variability has become

276 appreciated. Comparable pyrite sole veneers have been described from the Amadeus  
277 Basin of Australia (Mapstone and McIlroy, 2006), and inferred from hematite partings  
278 (Gehling et al., 2005) and Fe and S within preserved microbial mats (Laflamme et al.,  
279 2011) from Newfoundland. Fossils from the Nama Group were originally thought to have  
280 been preserved via a different process (Narbonne, 2005), but this has since been  
281 questioned (Meyer et al., 2014a, 2014b). These fossils have a thin coating of pyrite that  
282 lines the voids left by the external walls of the organism. The thinness of the pyrite  
283 coating has been attributed to the dearth of organic matter in the system; in the absence of  
284 a microbial mat, the sole source of organic matter was the carcass and sediment (Meyer et  
285 al., 2014a, 2014b). Pyritization has also been implicated in the preservation of specimens  
286 from the White Sea (Dzik, 2003) and the Gaojiashan biota (Cai et al., 2012), and replaces  
287 the organic wall of frond stems from Siberia (Steiner and Reitner, 2001).

288         Formation of a pyritiferous sole veneer or parting is also key in the recovery of  
289 the fossils: it provides a surficial horizon which is more susceptible to weathering than  
290 the bulk rock (Mapstone and McIlroy, 2006; Meyer et al., 2014a, 2014b), allowing the  
291 rocks to split along those horizons where fossils have been preserved. The red iron-oxide  
292 and iron-oxyhydroxide staining resulting from this weathering also aids field  
293 identification of likely fossil-bearing surfaces (Fig. 3e,f; Gehling et al., 2005).

294         If pyrite is the only mineral involved in making the death mask, then the level of  
295 morphological detail retained in fossils is difficult to reconcile with their collapse and/or  
296 decay prior to pyritization (which does not occur until step 3 of Gehling's 1999 model).  
297 Recent evidence suggests that either authigenic aluminosilicate templating (see below) or

298 the microbial mat (see *Binding it all together*, below) may have stabilized the impression  
299 during the earliest stages of its formation (Darroch et al., 2012).

300

301 **Coatings of clay – the timing of aluminosilicate mineralization.**

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

319 Clay minerals and pyrite appear involved in the preservation of fossils from the  
320 Doushantuo and Dengying formations (Anderson et al., 2011) and from the Gaojiashan

321 Lagerstätte (Cai et al., 2012; Meyer et al., 2012). In the Gaojiashan Lagerstätte, three-  
322 dimensional fossils which have the finest level of three-dimensional morphological detail  
323 are pervasively pyritized (Fig. 1a,b,f); two-dimensional carbonaceous compression fossils  
324 are stabilized by Fe-rich clay minerals (Fig. 1c,d,e,g). Based on their composition,  
325 spheroidal aggregate habit, and the fact that the fossils they template retain poorer  
326 morphological detail, these clays are thought to reflect relatively late diagenetic  
327 replacement of an earlier mineral which stabilized the fossil but which formed later in the  
328 diagenetic sequence than pyrite (which is associated with the best fossils).

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

343 to record authigenic aluminosilicate and pyrite growth in a decaying biofilm which had  
344 completely surrounded the holdfast during life (Laflamme et al., 2011).

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

348

#### 349 **Caught on film: carbonaceous compressions**

350 Carbon compression fossils are best known from Chinese localities, with  
351 examples from the Gaojiashan Lagerstätte (Fig. 1c,d; Cai et al., 2012), Doushantuo  
352 Formation (Fig. 5a; Anderson et al., 2011), Miaohe (Xiao et al., 2002; Zhu et al., 2008),  
353 Lantian (Fig. 5c–f; Yuan et al., 2011) and Jinxian (Zhang et al., 2006) biotas, and also  
354 from the Denying Formation (Sun, 1986). Preservation of fossils in this mode has enabled  
355 inferences about the nature of the original composition of the organism (i.e.,  
356 recalcitrance) and, by extension, phylogenetic affinity (Zhu et al., 2008) to be made.  
357 Assemblages of the ~550 – 590 Ma Miaohe biota are found in black shales in the  
358 Yangtze Gorges, and host a diverse range of macrofossils, many of which are interpreted  
359 as algae based on the sub-millimetric resolution of preservation and the observation of  
360 delicate thalli-like structures (Xiao et al., 2002). Specimens preserved in a comparable  
361 manner to the Miaohe fossils are documented from the White Sea and from Siberia,  
362 where they occur in finely-laminated, silicified calcareous mudstones of the Khatyspyt  
363 Formation (Steiner and Reitner, 2001; Grazhdankin et al., 2008). Kerogenization of  
364 carbonaceous compressions has been documented from the Gaojiashan, and has been  
365 inferred to have contributed to stabilization of the fossils (Cai et al., 2012).

366           Although the paleoenvironments are very different, carbonaceous compression  
367 fossils do not seem to differ from typical Phanerozoic fossils such as Carboniferous  
368 plants (see Locatelli, this volume) preserved in this way: at first glance, they appear to be  
369 a simple film of organic carbon compressed onto the sediment surface. However, the  
370 extent of microbial influence in their preservation is uncertain, particularly for those  
371 fossils which also have a moldic component. Although comparisons have been made  
372 between Ediacaran carbonaceous compressions which are associated with clay minerals  
373 and/or pyrite, and preservation in the Burgess Shale (e.g. Anderson et al., 2011; Cai et al.,  
374 2012; Meyer et al., 2012), the presence or influence of any differences in sedimentology,  
375 pore water chemistry or even nature of microbial community on preservation between the  
376 sites is unknown. Given the uncertainty regarding the phylogenetic affinity and biological  
377 composition of Ediacaran organisms, it is also unclear to what degree the composition of  
378 tissues would affect the quality or type of preservation within this taphonomic spectrum.

379

### 380 **Bridging the taphonomic void**

381           The large number of biotas now known enables the preservation of single taxa to  
382 be compared across different paleoenvironments and taphonomic windows, and thus the  
383 biases imparted by each to be elucidated (Fig. 5; Grazhdankin et al., 2008; Zhu et al.,  
384 2008). This promises to allow original ecological variability in assemblages to be  
385 distinguished from secondary, taphonomic effects. The exclusion of certain organisms  
386 from deposits in which fossils are preserved as carbonaceous compressions has been  
387 shown to be a purely taphonomic artifact, and may record differences in original tissue  
388 composition (Grazhdankin et al., 2008). In the Khatyspyt Formation of Siberia, fossils are

389 preserved in two, facies-dependent, modes: as carbonaceous compressions and by  
390 authigenic carbonate cementation. *Charnia* is commonly found in the latter, but is only  
391 observed in the former as “phantoms” where it fortuitously distorts co-occurring  
392 carbonaceous films (Grazhdankin et al., 2008). In some cases, individual fossils are  
393 preserved in multiple modes, suggesting a complex taphonomic pathway (Cai et al.,  
394 2012). The fine balance between these modes may provide insights into the nature of the  
395 original organic material, and/or the chemistry of the host sediment. In order to preserve a  
396 carbonaceous compression, decay by sulfate-reducing bacteria, and hence pyrite  
397 formation, must be halted early. This may be accomplished by overwhelming the system  
398 with disseminated organic carbon, or by limiting diffusion of sulfate from seawater into  
399 the sediment.

400

#### 401 **BINDING IT ALL TOGETHER: THE IMPORTANCE OF MICROBIAL MATS**

402

403 In contrast to much of the Phanerozoic, microbial mats played a conspicuous role  
404 in the preservation of soft parts in the Ediacaran, and may be at least partly responsible  
405 for the comparative abundance of soft-tissue preservation at this time (Seilacher, 1984;  
406 Gehling et al., 2005). Their ubiquity on the sea-floor is widely supported by a myriad of  
407 field and petrographic fabrics (e.g. Gehling, 1999; Steiner and Reitner, 2001; Noffke et  
408 al., 2002; Gehling et al., 2005; Grazhdankin and Gerdes, 2007; Callow and Brasier,  
409 2009b; Wilby et al., 2011; Lan and Chen, 2012). These fabrics include microbially-  
410 induced sedimentary structures (“MISS”, *sensu* Noffke et al., 2001) such as wrinkle  
411 marks, reticulate network fabrics, old elephant skin textures and pustular fabrics (see

412 Gehling, 1999, and refs. therein), as well as “bubble trains” (Laflamme et al., 2012;  
413 though see Brasier et al., 2013 for an alternative explanation of these structures). Despite  
414 this abundant evidence, there are only scant reports of microbial body fossils outside of  
415 the Doushantuo Formation of China (Hofmann et al., 1979; Callow and Brasier, 2009a).

416         The timing of pyritization relative to collapse of the organism as per the death  
417 mask model (see discussion above), and the attendant difference in sense of relief of the  
418 resultant fossil, testifies to the importance of microbes in Ediacaran preservation (Gehling  
419 et al., 2005; Narbonne, 2005). Sites in the Flinders Ranges with thicker microbial mats  
420 (evidenced by prominent surface textures) show negative hyporelief preservation of  
421 fossils: pyrite formed before collapse of the organisms. By comparison, sites with thinner  
422 microbial mats (relatively subdued microbial textures) exhibit composite and shallow,  
423 positive hyporelief preservation: pyrite formed after collapse of the organisms. Therefore,  
424 a thicker mat induced earlier formation of a death mask. Similarly, Narbonne (2005)  
425 attributes “Flinders-style” preservation to rapid mineralization related to the presence of  
426 the thick mats which could develop in the environments where this style is common  
427 (Seilacher, 1984; Gehling, 1999). In contrast, he suggests that organisms preserved either  
428 by poor examples of “Flinders-style” preservation or by “Nama-style” preservation are  
429 attributable to their occurrence in environments above fair-weather wave base, which  
430 would have lacked a well-developed mat. In contrast, “Fermeuse-style” preservation has  
431 been suggested to have arisen from failure of the overlying bed to lithify before complete  
432 decay of the organism, due to either an absence of a mat, or the presence of a mat  
433 composed entirely of heterotrophic and/or sulfur-oxidizing bacteria (Narbonne, 2005).

434           Additionally, the extracellular polymeric substance (EPS) produced by the  
435 microbial mat likely played an important role in the initial formation and stabilization of the  
436 fossil impression by binding the sediment grains prior to precipitation of authigenic  
437 minerals (Darroch et al., 2012). In a series of experiments, the impressions which retained  
438 the finest morphological detail and lasted the longest were those that contained microbial  
439 mats (Darroch et al., 2012). These samples preserved exceptional detail (as scored on  
440 their taphonomic index) for two weeks after death of the subject, compared to one week  
441 in samples with no mat. In mat-hosted samples, precipitation of pyrite precursors initiated  
442 after just one day and reached maximum extent after two weeks. In samples without  
443 mats, pyrite precursors initiated after two weeks in unsterilized sand, and failed to initiate  
444 in sterilized sand. The importance of microbial mats in preservation is highlighted when  
445 this recent experimental approach is compared with those conducted in the 1980s and  
446 1990s, particularly given the relatively low return rate of recognizable impressions in  
447 experimental runs with otherwise similar conditions (Norris, 1989).

448

#### 449           ***ASPIDELLA* EVERYWHERE! THE ABUNDANCE OF HOLDFASTS**

450

451           Without doubt, the most abundant macrofossils found throughout the Ediacaran  
452 are discoidal. The majority of these belong to the taxon *Aspidella*, which brings under its  
453 umbrella many different, and previously taxonomically distinguished, forms (Gehling et  
454 al., 2000). They are thought to principally represent holdfasts (Gehling et al., 2000;  
455 Laflamme et al., 2011; MacGabhann, 2007), and may be so profuse that they entirely  
456 cover bedding surfaces, as seen in the Fermeuse Formation of Newfoundland (Fig. 6e).

457 Only rarely are holdfasts preserved on the same horizon as their fronds (e.g. in  
458 Charnwood Forest, Fig. 2b,d; Wilby et al., 2011); in most localities, either one or the  
459 other is preserved. Most holdfasts were likely buried within the sediment, in whole or in  
460 part, and their frequent concentric rings are generally interpreted as collapse structures.  
461 On certain surfaces, only fronds of certain taxa are associated with holdfasts (e.g.  
462 *Charniodiscus* in Mistaken Point, Newfoundland). In these cases, the holdfasts are  
463 typically positive epirelief, and have been inferred to record upper surfaces of holdfasts  
464 which protruded above the mat surface in life and were preserved before their collapse by  
465 rapid mineralization of the ash (Conception-style preservation; Narbonne, 2005). Fronds  
466 on these surfaces which appear without associated holdfasts (e.g. *Charnia*) may have had  
467 ones which remained entirely buried within the sediment during their life and death  
468 (Laflamme et al., 2007), and so are out of the plane of preservation. Some localities  
469 preserve only holdfasts and trace fossils (“Fermeuse-style” preservation; Narbonne,  
470 2005).

471         There may be several taphonomic reasons for the relative abundance of holdfasts  
472 to fronds. First, their *in vivo* position within the sediment means that, even if the holdfasts  
473 collapse after death or are tugged out, they may still leave an expression, such as collapse  
474 structures formed as sediment falls back into the void left after decay (Narbonne, 2005),  
475 and shear structures (Tarhan et al., 2010), respectively. Secondly, their anchorage within  
476 (Laflamme et al., 2011) or beneath (Mapstone and McIlroy, 2006) the mat means that  
477 they are less likely than the frond to be tugged out and removed by the current. Thirdly,  
478 their presence within or close to the zone of active diagenesis (the “mixed layer”; Callow  
479 and Brasier, 2009b) gives them a higher preservation potential. Finally, there is some

480 evidence that holdfasts were made of more resistant material; they may be preserved as  
481 carbonaceous compressions while stems are replicated by pyrite (Steiner and Reitner,  
482 2001), or as positive epirelief structures while fronds are preserved in negative epirelief  
483 (Fig. 2e; 4a,b,d,f; Narbonne, 2005). Their comparative persistence may lead to their  
484 preservation even in conditions conducive to only slow mineralization (cf. Darroch et al.,  
485 2012).

486

## 487 **UNRAVELLING THE RAVAGES OF TIME: BIOSTRATINOMY AND THE** 488 **GRADATION OF FORMS**

489

490 Biostratinomy encompasses the effects of post-mortem compaction, contraction  
491 (whether by dehydration or bacterial decay), folding, and transport (Gehling et al., 2005),  
492 which necessarily influence the final morphology of the fossil. Compared to the  
493 Phanerozoic, fewer biostratinomic processes operated in Ediacaran times. Scavengers  
494 consume or disarticulate carcasses, but are unknown from the Period, and bioturbation  
495 was limited. Those processes which would have endured throughout the Proterozoic into  
496 the Phanerozoic are microbial decay and abiotic (physical) disturbance. Syn- or post-  
497 mortem distortion of the morphology of the organism by physical processes has been  
498 recorded from localities around the globe, and includes wrinkling (Gehling, 1991),  
499 folding (Seilacher, 1992) and ripping (Runnegar and Fedonkin, 1992). If different parts of  
500 an organism had dissimilar rheologies, they will be affected differently by shared  
501 biostratinomic processes. For example, the crenellated part of *Kimberella* shows  
502 comparatively greater deformation or wrinkling than the rest of the organism, and is

503 accordingly inferred to have been a broad, flattened “foot” which was less robust than a  
504 surrounding, unmineralized shell (Fig. 3a; Fedonkin and Waggoner, 1997).

505         In fossils from Newfoundland, the quality of preservation is seen to decrease  
506 along their length; there is greater opportunity for sediment to settle beneath the more  
507 distal and lateral parts of the frond during felling (Laflamme et al., 2007). Fronds of  
508 increasing size may show variations in susceptibility to current-induced stacking of  
509 branches and compression of overall form. The observed change from I to V to U and to  
510 O plan-view morphology in *Bradgatia* with overall increase in size may thus reflect  
511 increased resistance to this process (Brasier et al., 2013), rather than a purely ontogenetic  
512 signal (Flude and Narbonne, 2008). On a finer scale, the branching pattern of  
513 rangeomorphs may also be affected during the burial event, for example the current-  
514 induced imbrication of primary branches recorded in specimens from Spaniard’s Bay,  
515 Newfoundland (Fig. 4; Brasier et al., 2013). If this interpretation is correct, it is  
516 unnecessary for these branches to have been either constrained in a sheath or attached to  
517 each other, as has been proposed for some taxa (Narbonne et al., 2009).

518

### 519 **Sweeping up: interpreting “mops”**

520         The potential extent of modification of form by physical disruption is further  
521 evidenced by so-called “mop” structures (Tarhan et al., 2010). They have a highly  
522 variable appearance and relief, but are consistently aligned parallel to ripped-up stems on  
523 the same bed, have well-defined distal margins, and subparallel internal lineations that  
524 are orthogonal to the margin. There is a gradation from typical *Aspidella* holdfasts to full  
525 “mop”, consistent with these structures representing an effect imposed upon an organism

526 rather than a discrete taxon. “Mops” are thus interpreted to be the result of current shear  
527 on frond holdfasts; the fronds themselves are not preserved, and are suggested to have  
528 been either torn off by the current or held above the preservational surface (Tarhan et al.,  
529 2010). They may alternatively have been held out of the plane of preservation. Upstream  
530 parts of “mops” have a range of distal margin shapes, and are interpreted as buckled and  
531 compressed parts of the holdfast, whereas downstream, linear structures are interpreted as  
532 torsion-induced stretch marks. The smallest “mops” are expressed solely as distortion of  
533 the surrounding sediment, suggesting that the smallest fronds were removed entirely. This  
534 may provide an explanation for the lack in many communities of specimens below a few  
535 centimeters. Alternatively, it may be that the entire mop spectrum represents disturbance  
536 and distortion of the microbial mat arising from plucking out of the holdfast, and are  
537 therefore a form of MISS (Laflamme, pers. comm.. 2014).

538

### 539 **Is it all rot? Iveshediomorphs**

540 Forms currently referred to as “iveshediomorphs” (Fig. 6a–d) are contentious, and  
541 include a wide spectrum of morphologies. These were originally described from  
542 Charnwood Forest as discrete taxa, and include *Ivesheadia*, *Blackbrookia*, *Pseudovendia*  
543 and *Shepshedia* (Boynton and Ford, 1979, 1995); similar forms in Newfoundland are  
544 referred to as “pizza discs”, “lobate discs” and “bubble discs” (Narbonne et al., 2001;  
545 Laflamme et al., 2012). A full spectrum between such forms and fronds exhibiting fine  
546 detail has been documented from several bedding planes in Newfoundland, leading to the  
547 interpretation of “ivesheadiomorphs” as the remnants of dead organisms which were in  
548 the process of microbial decay at the time of burial (Liu et al., 2011). The irregular,

549 unusually high relief and often network-like internal features of these forms were  
550 suggested to represent a conflation of sediment trapped by EPS and gas derived from the  
551 decay process (Liu et al., 2011). However, other authors have suggested alternative  
552 explanations: Laflamme et al. (2012) interpret these structures as purely microbial in  
553 origin, and Wilby et al. (2011) propose that at least some of the forms may be created by  
554 differential loading on the fossil-bearing surface following collapse of organisms within  
555 the overlying bed.

556

### 557 **All full up: the timing of sand infills**

558 Resolution of both the mechanism and timing (*in vivo* or post-mortem) of  
559 sediment infill is of great significance for current interpretations of the biology of the  
560 organisms in which they are found. Rangeomorphs and erniettomorphs have been  
561 interpreted as osmotrophs, absorbing dissolved organic carbon from the water column  
562 (Laflamme et al., 2009). The proposed model requires the organisms to have had a very  
563 small (< 2 %) volume of metabolically-active material, which could potentially have been  
564 achieved by *in vivo* incorporation of sediment (Laflamme et al., 2009). If this can be  
565 demonstrated, then an osmotrophic mode of life is plausible; if not, then the inert material  
566 must be a fluid, which might be expected to exert its own influence on the rheology of the  
567 organism and on its taphonomic behaviour.

568 Sand fills observed in stalks of fronds from the Amadeus Basin exhibit ripple  
569 cross-lamination contiguous to that of the surrounding sediment, and are convincingly  
570 demonstrated to record post-mortem slumping of sediment into the stalk (Mapstone and  
571 McIlroy, 2006). In contrast, it has been suggested that sand in the holdfasts (“bulbs”) and

572 central stalks of fossils of *Rangea* from Namibia was incorporated into the body of the  
573 organism during life, based on the similarity of the sediment within the “bulb” and stalk  
574 to that infilling the gutter casts below the fossil (Vickers-Rich et al., 2013). A similar *in*  
575 *vivo* fill has been interpreted in holdfasts from the Fermeuse Formation of Newfoundland  
576 (see *Aspidella* section above; Laflamme et al., 2011).

577         If this *in vivo* interpretation holds, then such a fill could have served to stabilise or  
578 anchor the organisms. However, a post-mortem infilling might explain the recorded  
579 presence of a gap in the sediment fill part way up the stalk (Vickers-Rich et al., 2013),  
580 their Fig. 7.3,7.4), which is hard to reconcile with the *in vivo* interpretation. In contrast, a  
581 taphonomic sand infill is more difficult to argue for specimens of taxa such as *Ernietta*  
582 which are preserved as three-dimensional sediment casts. There are no obvious tears or  
583 punctures through which sediment could enter, and it might be expected that a post-  
584 mortem fill would be less pervasive than an *in vivo* one, either restricted to a few  
585 (damaged) individuals or to partial infills. If these fossils represent templates of the  
586 external surface which have been infilled by uncemented sediment (Meyer et al., 2014a,  
587 2014b), how did this sediment penetrate a more-or-less continuous veneer after its  
588 formation? Perhaps these organisms did have an *in vivo* fill; in that case, how was this  
589 achieved?

590         Fully understanding the biostratinomy of the organisms can be hugely useful in  
591 determining various aspects of their biology. The observation of torsion-induced stretch  
592 marks in holdfasts indicates both that these were firmly anchored in the sediment, and  
593 that they were sufficiently elastic to deform rather than snap or tear. This, in turn, casts  
594 doubt on interpretations of structures such as “mops” and isolated *Aspidella* specimens

595 which invoke ripping off the frond. We can infer that tissues which do show evidence of  
596 tearing under the same conditions were likely more rigid. That organisms can fold over  
597 indicates a certain degree of flexibility, and the style of fold can provide additional  
598 information on body rheology: assuming no decay had occurred, those that kink over at a  
599 sharp line (e.g. dickinsoniids) were likely more rigid/solid than those which show more  
600 sinuous or irregular folds (e.g. the rangeomorph, *Fractofusus*).

601

602 **KNOW YOUR LIMITS: PRESERVATIONAL BIASES AND UNKNOWABLE**  
603 **UNKNOWNNS**

604

605 Although soft-tissue preservation is reasonably common in the Ediacaran, with  
606 bed after bed preserving fossils, it is by no means perfect, and has its own inherent  
607 problems and biases. Two-dimensional records of three-dimensional organisms are by  
608 their very nature either composite (with structures at multiple levels in the organism  
609 compressed together into one plane) and/or partial; usually, only one side of an organism  
610 is cast. This is most problematic for organisms with a highly three-dimensional  
611 morphology, such as multifoliate rangeomorphs (*sensu* Laflamme and Narbonne, 2008)  
612 and erniettomorphs, as opposed to flatter organisms such as unifoliate rangeomorphs  
613 (*sensu* Laflamme and Narbonne, 2008) and dickinsoniids. Imagine how the two-  
614 dimensional impression of a bushy plant would compare to its three-dimensional  
615 morphology, and how much more complex and confused, and less representative of the  
616 living morphology, this would be in contrast to the compression of a plant like a fern.

617 This is exemplified in the changing morphology and decreased clarity of branching of  
618 *Bradgatia* with increasing size (see *Biostratinomy* section above).

619 As in any Lagerstätte, we must still consider what has not been preserved, in  
620 terms of both parts of the organisms and of whole organisms. For those specimens which  
621 have been transported and deposited in death assemblages (Namibian channel-fill  
622 deposits), we have lost information regarding their *in situ* ecology, such as their relative  
623 abundances and spatial distributions, as well as their position relative to the sediment-  
624 water interface. The limits of the resolution of preservation also render invisible any  
625 meiofauna which may have been present, and so we have no knowledge of these  
626 components of the ecosystem (Sperling et al., 2013). Any organism capable of motility  
627 (Liu et al., 2010) has a greatly reduced chance of being captured in the ecosystem than its  
628 sessile compatriots. Despite early (now-refuted) suggestions of discoidal fossils as  
629 medusoids (e.g. Sprigg, 1947, 1949; Glaessner and Wade, 1966), there is to date no  
630 convincing evidence of pelagic forms. As such, we have no knowledge whatsoever of the  
631 macroscopic life which may have been present in the water column during the Ediacaran.  
632 By extension, if these organisms did have a planktonic dispersal stage (discussed in  
633 Darroch et al., 2013), it is unlikely that this would be captured. Apparent support for such  
634 a life stage is the lack of preserved individuals smaller than a centimeter, despite sub-  
635 millimetric preservation, and that even the very smallest fossils currently known are  
636 identical in morphology to adult forms (Liu et al., 2012, 2013).

637 For the organisms that we do see, the overwhelming dominance of two-  
638 dimensional, external moldic preservation means that we have little, if any, evidence of  
639 internal anatomy. Reported examples of internal “struts” in rangeomorphs from

640 Spaniard's Bay (Narbonne, 2004) have subsequently been explained as branches filled by  
641 sediment casting the underside of the upper surface and creating positive epirelief  
642 impressions (Fig. 4b,c), rather than casting the lower surface and creating negative  
643 epirelief impressions (Fig. 4a,d,e,f), as is typical at this locality (Brasier et al., 2013). The  
644 ridges originally interpreted as struts are accordingly inferred to be the divisions between  
645 higher-order branches (Brasier et al., 2013). The differential collapse of branches within  
646 the frond (Fig. 4b) could be taken to suggest the *in vivo* presence of a hydrostatic skeleton  
647 which became punctured and subsequently deflated, but could alternatively simply record  
648 relaxation in response to decay (Brasier et al., 2013). Discrimination between the  
649 competing hypotheses will remain challenging until further evidence comes to light.

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

657 Explanations for the absence of internal structures in Ediacaran fossils include: 1)  
658 decay outpaced their fossilization; 2) the microenvironment created by their decay inside  
659 the body cavity was not conducive to fossilization; 3) the extrinsic environment was  
660 incompatible with their fossilization, perhaps because of sediment sealing; 4)  
661 comparatively low oceanic sulfate concentrations (e.g. Canfield et al., 2008) favored  
662 pyritization of the organisms' external surface; or 5) the organisms lacked substantive

663 internal structures. Until sufficient and suitable fossils are available to permit the  
664 undertaking of destructive analyses (e.g. Laflamme et al., 2011), resolution of this  
665 question may remain elusive.

666

## 667 **CONCLUSIONS AND QUANDARIES**

668

669 Exciting progress is being made in several fields of Ediacaran endeavour,  
670 including paleoecology (Clapham and Narbonne, 2002; Clapham et al., 2003; Darroch et  
671 al., 2013), anatomy (e.g. Fedonkin and Waggoner, 1997; Narbonne et al., 2009; Brasier et  
672 al., 2012; Vickers-Rich et al., 2013), ontogeny (e.g. Laflamme et al., 2004; Antcliffe and  
673 Brasier, 2007) and phylogentic relationships (e.g. Erwin et al., 2011; Laflamme et al.,  
674 2013). Taphonomic processes and biases impact all aspects of paleobiology; an  
675 understanding of these is therefore paramount if we are to further elucidate the nature of  
676 the original organisms and their communities. Great strides are being made, with elegant  
677 experimental work (McIlroy et al., 2009; Darroch et al., 2012) enhancing detailed  
678 petrographic and field-based studies (e.g. Gehling, 1999; Xiao et al., 2005; Grazhdankin  
679 et al., 2008; Laflamme et al., 2011). Taphonomic modes as disparate as moldic  
680 preservation, pyritization, carbonaceous compression, clay mineral precipitation, and  
681 carbonate mineralization are all observed in Ediacaran sites across the globe, sometimes  
682 with multiple modes within a single fossil (Cai et al., 2012). There does appear to be a  
683 broad correlation between taphonomic style and depositional environment (e.g.  
684 Narbonne, 2005; Grazhdankin et al., 2008), with moldic and death mask preservation  
685 most common in siliciclastic and volcanoclastic settings, and carbonaceous compression

686 fossils occurring predominantly in shales and carbonates. Clay mineralization appears to  
687 occur in all environments. However, the extent of the influence exerted by  
688 paleoenvironment, and of the disparate factors this includes, remains uncertain. Fifteen  
689 years on from the proposal of the death mask model (Gehling, 1999), perhaps it is time to  
690 consider how the plethora of biotas featuring pyritization relate to this model, and to one  
691 another.

692         The location of an organism with respect to the sediment-water interface imparts a  
693 significant taphonomic bias, as those structures which were located within the sediment  
694 during life were more readily preserved in death. This bias is a likely cause of the greater  
695 abundance of holdfasts with respect to fronds (see *Aspidella* section above). Other  
696 taphonomic biases are much more poorly understood, with a few rare exceptions (e.g. the  
697 scarcity of rangeomorphs in Miaohe-type preservation; Grazhdankin et al., 2008).  
698 Elucidation of these biases is of absolute import for paleoecological studies: as they  
699 become known, we can begin to appreciate which site-to-site differences in assemblage  
700 composition are original (ecological), and which are secondary (taphonomic overprint).

701         Perhaps the most appropriate way to investigate these biases is through expansive  
702 experimental work. Such studies may also help to answer why moldic preservation is so  
703 prevalent in the Ediacaran as opposed to the Phanerozoic. The effects of a range of  
704 physical and chemical parameters have been tested in various taphonomic experiments  
705 (see e.g. Briggs, 2003, and refs. therein; Sansom, this volume). However, such studies  
706 have yet to be systematically extended to investigate systems which would be more  
707 applicable to the Ediacaran, e.g. those with microbial mats (with the exception of Darroch  
708 et al., 2012). Trace metals such as molybdenum, which are limiting nutrients for life (e.g.

709 (Glass et al., 2012), are becoming widely used as tracers of productivity and ocean redox  
710 conditions in the Proterozoic (e.g. Scott et al., 2008), but nothing is known about their  
711 specific effects on decay-related microbial activity, and therefore on taphonomy.

712 A major caveat to such taphonomic experimentation is the enduring uncertainty  
713 surrounding the original biological composition of Ediacaran organisms, which will  
714 likely only be resolved upon discovery of an assemblage preserving cellular-level detail.  
715 Currently, inferences regarding relative degrees of robustness and rigidity may be made  
716 based on biostratigraphic grounds, but these can only tell us so much. Taphonomic  
717 experiments sampling a wide variety of tissue and cell types from as many branches of  
718 the tree of life as possible may provide our best hope: by comparing the behaviours of  
719 different biological compositions to features seen in fossils, it may be possible to relate  
720 the two, and consequently to infer the original composition of the organism or its parts.  
721 Of course, this must be repeated for the many potential variables already discussed in  
722 order for any such inferences to be made with any degree of confidence, rendering the  
723 number of experiments required unfeasible.

724 One quandary peculiar to Avalon Assemblage localities is the true nature(s) of  
725 “ivesheadiomorphs”. Do all “ivesheadiomorphs” as currently defined (Liu et al., 2011)  
726 have the same genesis? Are they all taphomorphs of known taxa? Are they all microbial  
727 colonies (Laflamme et al., 2012)? Do any represent discrete macro-organisms (Boynton  
728 and Ford, 1979, 1995)? Do some have a different origin? The answers to these questions  
729 have great potential impacts for several aspects of paleoecological studies, including  
730 living biomass, species diversity and disparity, and spatial distributions: if these  
731 structures are dead and decaying organisms, they must inherently have a different effect

732 on the rest of the community than if they were living organisms. Whatever they are, why  
733 is their occurrence seemingly restricted to Avalonian, deep-water systems? Is this an  
734 environmental signal, or a function of the microbial community present? If they really do  
735 include taphomorphs, could different organisms have created distinguishably different  
736 forms, and could these be related back to their progenitors (cf. Liu et al., 2011)?

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

740

741

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748

## References

- 750 Anderson, E.P., Schiffbauer, J.D., and Xiao, S., 2011, Taphonomic study of Ediacaran  
751 organic-walled fossils confirms the importance of clay minerals and pyrite in  
752 Burgess Shale-type preservation: *Geology*, v. 39, p. 643–646, doi:  
753 10.1130/G31969.1.
- 754 Antcliffe, J.B., and Brasier, M.D., 2007, *Charnia* and sea pens are poles apart: *Journal of*  
755 *the Geological Society*, v. 164, p. 49–51, doi: 10.1144/0016-76492006-080.
- 756 Billings, E., 1872, Fossils in Huronian Rocks: *Canadian Naturalist and Quarterly Journal*  
757 *of Science*, v. 6, p. 478.

- 758 Boynton, H.E., and Ford, T.D., 1995, Ediacaran fossils from the Precambrian (Charnian  
759 Supergroup) of Charnwood Forest, Leicestershire, England: *Mercian Geologist*, v.  
760 13, p. 165–182.
- 761 Boynton, H.E., and Ford, T.D., 1979, *Pseudovendia charnwoodensis* – a new  
762 Precambrian arthropod from Charnwood Forest, Leicestershire: *Mercian*  
763 *Geologist*, v. 7, p. 175–177.
- 764 Brasier, M.D., Antcliffe, J.B., and Liu, A.G., 2012, The architecture of Ediacaran Fronds:  
765 *Palaeontology*, v. 55, p. 1105–1124, doi: 10.1111/j.1475-4983.2012.01164.x.
- 766 Brasier, M.D., Liu, A.G., Menon, L., Matthews, J.J., McIlroy, D., and Wacey, D., 2013,  
767 Explaining the exceptional preservation of Ediacaran rangeomorphs from  
768 Spaniard’s Bay, Newfoundland: A hydraulic model: *Precambrian Research*, v.  
769 231, p. 122–135, doi: 10.1016/j.precamres.2013.03.013.
- 770 Briggs, D.E.G., 2003, The role of decay and mineralization in the preservation of soft-  
771 bodied fossils: *Annual Review of Earth and Planetary Sciences*, v. 31, p. 275–301,  
772 doi: 10.1146/annurev.earth.31.100901.144746.
- 773 Bruton, D.L., 1991, Beach and laboratory experiments with the jellyfish *Aurelia* and  
774 remarks on some fossil “medusoid” traces, *in* Simonetta, A.M. and Conway  
775 Morris, S. eds., *The Early Evolution of Metazoa and the Significance of*  
776 *Problematic Taxa*, Cambridge, UK, Cambridge University Press, p. 125–129.
- 777 Butterfield, N.J., Balthasar, U., and Wilson, L.A., 2007, Fossil Diagenesis in the Burgess  
778 Shale: *Palaeontology*, v. 50, p. 537–543, doi: 10.1111/j.1475-4983.2007.00656.x.
- 779 Cai, Y., Schiffbauer, J.D., Hua, H., and Xiao, S., 2012, Preservational modes in the  
780 Ediacaran Gaojiashan Lagerstätte: Pyritization, aluminosilicification, and  
781 carbonaceous compression: *Palaeogeography, Palaeoclimatology, Palaeoecology*,  
782 v. 326–328, p. 109–117, doi: 10.1016/j.palaeo.2012.02.009.
- 783 Callow, R.H.T., and Brasier, M.D., 2009a, A solution to Darwin’s dilemma of 1859:  
784 exceptional preservation in Salter’s material from the late Ediacaran  
785 Longmyndian Supergroup, England: *Journal of the Geological Society*, v. 166, p.  
786 1–4, doi: 10.1144/0016-76492008-095.
- 787 Callow, R.H.T., and Brasier, M.D., 2009b, Remarkable preservation of microbial mats in  
788 Neoproterozoic siliciclastic settings: Implications for Ediacaran taphonomic  
789 models: *Earth-Science Reviews*, v. 96, p. 207–219, doi:  
790 10.1016/j.earscirev.2009.07.002.
- 791 Canfield, D.E., Simon W. Poulton, Knoll, A.H., Narbonne, G.M., Ross, G., Goldberg, T.,  
792 and Strauss, H., 2008, Ferruginous Conditions Dominated Later Neoproterozoic  
793 Deep-Water Chemistry: *Science*, v. 321, p. 949–952, doi: 10.2307/20144603.

- 794 Chen, Z., Zhou, C., Meyer, M., Xiang, K., Schiffbauer, J. D., Yuan, X., and Xiao, S.,  
795 2013, Trace fossil evidence for Ediacaran bilaterian animals with complex  
796 behaviors: *Precambrian Research*, v. 224, p. 690–701.
- 797 Clapham, M.E., and Narbonne, G.M., 2002, Ediacaran epifaunal tiering: *Geology*, v. 30,  
798 p. 627–630, doi: 10.1130/0091-7613(2002)030<0627:EET>2.0.CO;2.
- 799 Clapham, M.E., Narbonne, G.M., and Gehling, J.G., 2003, Paleoecology of the Oldest  
800 Known Animal Communities: Ediacaran Assemblages at Mistaken Point,  
801 Newfoundland: *Paleobiology*, v. 29, p. 527–544.
- 802 Darroch, S.A.F., Laflamme, M., and Clapham, M.E., 2013, Population structure of the  
803 oldest known macroscopic communities from Mistaken Point, Newfoundland:  
804 *Paleobiology*, v. 39, p. 591–608, doi: 10.1666/12051.
- 805 Darroch, S.A.F., Laflamme, M., Schiffbauer, J.D., and Briggs, D.E.G., 2012,  
806 Experimental formation of a microbial death mask: *PALAIOS*, v. 27, p. 293–303,  
807 doi: 10.2110/palo.2011.p11-059r.
- 808 Droser, M.L., Gehling, J.G., and Jensen, S.R., 2006, Assemblage palaeoecology of the  
809 Ediacara biota: The unabridged edition?: *Palaeogeography, Palaeoclimatology,*  
810 *Palaeoecology*, v. 232, p. 131–147, doi: 10.1016/j.palaeo.2005.12.015.
- 811 Dzik, J., 2003, Anatomical Information Content in the Ediacaran Fossils and Their  
812 Possible Zoological Affinities: *Integrative and Comparative Biology*, v. 43, p.  
813 114–126, doi: 10.2307/3884846.
- 814 Dzik, J., 2002, Possible ctenophoran affinities of the precambrian “sea-pen” *Rangaea*:  
815 *Journal of Morphology*, v. 252, p. 315–334, doi: 10.1002/jmor.1108.
- 816 Erwin, D.H., Laflamme, M., Tweedt, S.M., Sperling, E.A., Pisani, D., and Peterson, K.J.,  
817 2011, The Cambrian Conundrum: Early Divergence and Later Ecological Success  
818 in the Early History of Animals: *Science*, v. 334, p. 1091–1097, doi:  
819 10.1126/science.1206375.
- 820 Farrell, Ú., 2014, Pyritization of soft-tissues in the fossil record: an overview:  
821 *Paleontological Society Special Publication*,.
- 822 Fedonkin, M.A. (Mikhail A.), Gehling, J.G., Grey, K., Narbonne, G.M., and Vickers-Rich,  
823 P., 2007, The rise of animals: evolution and diversification of the kingdom  
824 animalia: Baltimore, Md., John Hopkins University Press, xv, 326 p. p.
- 825 Fedonkin, M.A., and Waggoner, B.M., 1997, The Late Precambrian fossil *Kimberella* is a  
826 mollusc-like bilaterian organism: *Nature*, v. 388, p. 868–871.
- 827 Flude, L.I., and Narbonne, G.M., 2008, Taphonomy and ontogeny of a multibranching  
828 Ediacaran fossil: *Bradgatia* from the Avalon Peninsula of Newfoundland:  
829 *Canadian Journal of Earth Sciences*, v. 45, p. 1095–1109, doi: 10.1139/E08-057.

- 830 Ford, T.D., 1958, Pre-Cambrian Fossils from Charnwood Forest: Proceedings of the  
831 Yorkshire Geological and Polytechnic Society, v. 31, p. 211–217, doi:  
832 10.1144/pygs.31.3.211.
- 833 Gaines, R.R., Kennedy, M.J., and Droser, M.L., 2005, A new hypothesis for organic  
834 preservation of Burgess Shale taxa in the middle Cambrian Wheeler Formation,  
835 House Range, Utah: Interpretation of Biological and Environmental Changes  
836 across the Neoproterozoic-Cambrian Boundary Interpretation of Biological and  
837 Environmental Changes, v. 220, p. 193–205, doi: 10.1016/j.palaeo.2004.07.034.
- 838 Gehling, J.G., 1999, Microbial Mats in Terminal Proterozoic Siliciclastics: Ediacaran  
839 Death Masks: PALAIOS, v. 14, p. 40, doi: 10.2307/3515360.
- 840 Gehling, J.G., 1991, The case for Ediacaran fossil roots to the metazoan tree: Geological  
841 Society of India Memoir, v. 20, p. 181–224.
- 842 Gehling, J.G., and Droser, M.L., 2013, How well do fossil assemblages of the Ediacara  
843 Biota tell time?: *Geology*, v. 41, p. 447–450, doi: 10.1130/G33881.1.
- 844 Gehling, J.G., Droser, M.L., Jensen, S.R., and Runnegar, B.N., 2005, Ediacaran  
845 organisms: relating form and function., *in* Briggs, D.E.G. ed., *Evolving Form and*  
846 *Function: Fossils and Development: Proceedings of a symposium honoring Adolf*  
847 *Seilacher for his contributions to paleontology, in celebration of his 80th birthday,*  
848 *New Haven, Peabody Museum of Natural History, Yale University, p. 43–67.*
- 849 Gehling, J.G., Narbonne, G.M., and Anderson, M.M., 2000, The first named Ediacaran  
850 body fossil, *Aspidella terranovica*: *Palaeontology*, v. 43, p. 427–456, doi:  
851 10.1111/j.0031-0239.2000.00134.x.
- 852 Glaessner, M.F., 1979, Precambrian, *in* Robinson, R.A. and Teichert, C. eds., *Treatise on*  
853 *Invertebrate Paleontology, Part A, Boulder, CO/Lawrence, KS, Geological*  
854 *Society of America, Kansas Press, p. A79–118.*
- 855 Glaessner, M.F., and Wade, M., 1966, The late Precambrian fossils from Ediacara, South  
856 Australia: *Palaeontology*, v. 9, p. 599–628.
- 857 Glass, J.B., Axler, R.P., Chandra, S., and Goldman, C.R., 2012, Molybdenum limitation  
858 of microbial nitrogen assimilation in aquatic ecosystems and pure cultures:  
859 *Frontiers in Microbiology*, v. 3, doi: 10.3389/fmicb.2012.00331.
- 860 Grant, S.W., 1990, Shell structure and distribution of Cloudina, a potential index fossil  
861 for the terminal Proterozoic: *American Journal of Science*, v. 290-A, p. 261–294.
- 862 Grazhdankin, D., 2004, Patterns of distribution in the Ediacaran biotas: facies versus  
863 biogeography and evolution: *Paleobiology*, v. 30, p. 203–221.

- 864 Grazhdankin, D.V., Balthasar, U., Nagovitsin, K.E., and Kochnev, B.B., 2008,  
865 Carbonate-hosted Avalon-type fossils in arctic Siberia: *Geology*, v. 36, p. 803–  
866 806, doi: 10.1130/G24946A.1.
- 867 Grazhdankin, D., and Gerdes, G., 2007, Ediacaran microbial colonies: *Lethaia*, v. 40, p.  
868 201–210, doi: 10.1111/j.1502-3931.2007.00025.x.
- 869 Grotzinger, J.P., Watters, W.A., and Knoll, A.H., 2000, Calcified Metazoans in  
870 Thrombolite-Stromatolite Reefs of the Terminal Proterozoic Nama Group,  
871 Namibia: *Paleobiology*, v. 26, p. 334–359, doi: 10.2307/2666114.
- 872 Hua, H., Pratt, B. R., and Zhang, L., 2003, Borings in *Cloudina* shells: complex predator-  
873 prey dynamics in the terminal Neoproterozoic: *Palaios*, v. 18, p. 454–459.
- 874 Hofmann, H.J., Hill, J., and King, A.F., 1979, Late Precambrian microfossils,  
875 southeastern Newfoundland.: Current Research, Part B, Geological Survey of  
876 Canada, v. 79-1B, p. 83–98.
- 877 Knoll, A.H., Walter, M.R., Narbonne, G.M., and Christie-Blick, N., 2004, A New Period  
878 for the Geologic Time Scale: *Science*, v. 305, p. 621–622, doi:  
879 10.1126/science.1098803.
- 880 Laflamme, M., Darroch, S.A.F., Tweedt, S.M., Peterson, K.J., and Erwin, D.H., 2013,  
881 The end of the Ediacara biota: Extinction, biotic replacement, or Cheshire Cat?:  
882 *Gondwana Research*, v. 23, p. 558–573, doi: 10.1016/j.gr.2012.11.004.
- 883 Laflamme, M., and Narbonne, G.M., 2008, Ediacaran fronds: *Palaeogeography*,  
884 *Palaeoclimatology*, *Palaeoecology*, v. 258, p. 162–179, doi:  
885 10.1016/j.palaeo.2007.05.020.
- 886 Laflamme, M., Narbonne, G.M., and Anderson, M.M., 2004, Morphometric Analysis of  
887 the Ediacaran Frond *Charniodiscus* from the Mistaken Point Formation,  
888 Newfoundland: *Journal of Paleontology*, v. 78, p. 827–837.
- 889 Laflamme, M., Narbonne, G.M., Greentree, C., and Anderson, M.M., 2007, Morphology  
890 and taphonomy of an Ediacaran frond: *Charnia* from the Avalon Peninsula of  
891 Newfoundland: Geological Society, London, Special Publications, v. 286, p. 237–  
892 257, doi: 10.1144/SP286.17.
- 893 Laflamme, M., Schiffbauer, J.D., and Narbonne, G.M., 2012, Deep-water microbially  
894 induced sedimentary structures (MISS) in deep time; the Ediacaran fossil  
895 Ivesheadia: Special Publication - Society for Sedimentary Geology, v. 101, p.  
896 111–123.
- 897 Laflamme, M., Schiffbauer, J.D., Narbonne, G.M., and Briggs, D.E.G., 2011, Microbial  
898 biofilms and the preservation of the Ediacara biota: *Lethaia*, v. 44, p. 203–213,  
899 doi: 10.1111/j.1502-3931.2010.00235.x.

- 900 Laflamme, M., Xiao, S., and Kowalewski, M., 2009, Osmotrophy in modular Ediacara  
901 organisms: Proceedings of the National Academy of Sciences of the United States  
902 of America, v. 106, p. 14438–14443, doi: 10.1073/pnas.0904836106.
- 903 Lan, Z.-W., and Chen, Z.-Q., 2012, Exceptionally preserved microbially induced  
904 sedimentary structures from the Ediacaran post-glacial successions in the  
905 Kimberley region, northwestern Australia: Precambrian Research, v. 200–203, p.  
906 1–25, doi: 10.1016/j.precamres.2012.01.006.
- 907 Liu, A.G., McIlroy, D., Antcliff, J.B., and Brasier, M.D., 2011, Effaced preservation in  
908 the Ediacara biota and its implications for the early macrofossil record:  
909 EDIACARAN TAPHOMORPHS: Palaeontology, v. 54, p. 607–630, doi:  
910 10.1111/j.1475-4983.2010.01024.x.
- 911 Liu, A.G., McIlroy, D., Matthews, J.J., and Brasier, M.D., 2012, A new assemblage of  
912 juvenile Ediacaran fronds from the Drook Formation, Newfoundland: Journal of  
913 the Geological Society, v. 169, p. 395–403, doi: 10.1144/0016-76492011-094.
- 914 Liu, A.G., McIlroy, D., Matthews, J.J., and Brasier, M.D., 2013, Exploring an Ediacaran  
915 “nursery”: growth, ecology and evolution in a rangeomorph palaeocommunity:  
916 Geology Today, v. 29, p. 23–26, doi: 10.1111/j.1365-2451.2013.00860.x.
- 917 Liu, A.G., McIlroy, D., and Brasier, M.D., 2010, First evidence for locomotion in the  
918 Ediacara biota from the 565 Ma Mistaken Point Formation, Newfoundland:  
919 Geology, v. 38, p. 123–126, doi: 10.1130/G30368.1.
- 920 Locatelli, E. R., 2014, The exceptional preservation of plant fossils: a review of  
921 taphonomic pathways and biases in the fossil record: Paleontological Society  
922 Special Publication,.
- 923 MacGabhann, B.A., 2007, Discoidal fossils of the Ediacaran biota: a review of current  
924 understanding: Geological Society, London, Special Publications, v. 286, p. 297–  
925 313, doi: 10.1144/SP286.21.
- 926 MacGabhann, B.A., 2014, There is no such thing as the “Ediacara Biota:” Geoscience  
927 Frontiers, v. 5, p. 53–62, doi: 10.1016/j.gsf.2013.08.001.
- 928 MacGabhann, B.A., and Murray, J., 2010, Non-mineralised discoidal fossils from the  
929 Ordovician Bardahessiagh Formation, Co. Tyrone, Ireland: Irish Journal of Earth  
930 Sciences, v. 28, p. 1–12, doi: 10.3318/IJES.2010.28.1.
- 931 MacGabhann, B.A., Murray, J., and Nicholas, C., 2007, *Ediacaria booleyi*: weeded from  
932 the Garden of Ediacara?: Geological Society, London, Special Publications, v.  
933 286, p. 277–295, doi: 10.1144/SP286.20.
- 934 Mapstone, N.B., and McIlroy, D., 2006, Ediacaran fossil preservation: Taphonomy and  
935 diagenesis of a discoid biota from the Amadeus Basin, central Australia:  
936 Precambrian Research, v. 149, p. 126–148, doi: 10.1016/j.precamres.2006.05.007.

- 937 McIlroy, D., Brasier, M.D., and Lang, A.S., 2009, Smothering of microbial mats by  
938 macrobiota: implications for the Ediacara biota: *Journal of the Geological Society*,  
939 v. 166, p. 1117–1121, doi: 10.1144/0016-76492009-073.
- 940 Meyer, M., Elliott, D., Schiffbauer, J. D., Hall, M., Hoffman, K. H., Schneider, G.,  
941 Vickers-Rich, P., and Xiao, S., 2014a, Taphonomy of the Ediacaran fossil  
942 *Pteridinium simplex* preserved three-dimensionally in mass flow deposits, Nama  
943 Group, Namibia: *Journal of Paleontology*, v. 88, p. 240–252.
- 944 Meyer, M., Elliott, D., Wood, A.D., Polys, N.F., Colbert, M., Maisano, J.A., Vickers-  
945 Rich, P., Hall, M., Hoffman, K.H., Schneider, G., and Xiao, S., 2014b, Three-  
946 dimensional microCT analysis of the Ediacara fossil *Pteridinium simplex* sheds  
947 new light on its ecology and phylogenetic affinity: *Precambrian Research*, v. 249,  
948 p. 79–87, doi: 10.1016/j.precamres.2014.04.013.
- 949 Meyer, M., Xiao, S., Gill, B. C., Schiffbauer, J. D., Chen, Z., Zhou, C., and Yuan, C.,  
950 2014c, Interactions between Ediacaran animals and microbial mats: insights from  
951 *Lamonte trevallis*, an new trace fossil from the Dengying Formation of South  
952 China: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 396, p. 62–74.
- 953 Meyer, M., Schiffbauer, J. D., Xiao, S., Cai, Y., and Hua, H., 2012., Taphonomy of the  
954 late Ediacaran enigmatic ribbon-like fossil *Shaanxilithes*: *Palaios*, v. 27, p. 354–  
955 372.
- 956 Narbonne, G.M., 2004, Modular Construction of Early Ediacaran Complex Life Forms:  
957 *Science*, v. 305, p. 1141–1144.
- 958 Narbonne, G.M., 2005, THE EDIACARA BIOTA: Neoproterozoic Origin of Animals  
959 and Their Ecosystems: *Annual Review of Earth and Planetary Sciences*, v. 33, p.  
960 421–442, doi: 10.1146/annurev.earth.33.092203.122519.
- 961 Narbonne, G.M., Dalrymple, R.W., and Gehling, J.G., 2001, Neoproterozoic fossils and  
962 environments of the Avalon Peninsula, Newfoundland, *Guidebook, Trip B5*..
- 963 Narbonne, G.M., Laflamme, M., Greentree, C., and Trusler, P., 2009, Reconstructing a  
964 Lost World: Ediacaran Rangeomorphs from Spaniard’s Bay, Newfoundland:  
965 *Journal of Paleontology*, v. 83, p. 503–523, doi: 10.2307/29739123.
- 966 Narbonne, G.M., Xiao, S., Shields, G.A., and Gehling, J.G., 2012, Chapter 18 - The  
967 Ediacaran Period, *in* Gradstein, F.M., Ogg, J.G., Schmitz, M.D., and Ogg, G.M.  
968 eds., *The Geologic Time Scale*, Boston, Elsevier, p. 413–435.
- 969 Noffke, N., Gerdes, G., Klenke, T., and Krumbein, W.E., 2001, Microbially Induced  
970 Sedimentary Structures: A New Category within the Classification of Primary  
971 Sedimentary Structures: *Journal of Sedimentary Research*, v. 71, p. 649–656, doi:  
972 10.1306/2DC4095D-0E47-11D7-8643000102C1865D.

- 973 Noffke, N., Knoll, A.H., and Grotzinger, J.P., 2002, Sedimentary Controls on the  
974 Formation and Preservation of Microbial Mats in Siliciclastic Deposits: A Case  
975 Study from the Upper Neoproterozoic Nama Group, Namibia: *PALAIOS*, v. 17,  
976 p. 533–544, doi: 10.2307/3515692.
- 977 Norris, R.D., 1989, Cnidarian taphonomy and affinities of the Ediacara biota: *Lethaia*, v.  
978 22, p. 381–393, doi: 10.1111/j.1502-3931.1989.tb01439.x.
- 979 Orr, P.J., Briggs, D.E.G., and Kearns, S.L., 1998, Cambrian Burgess Shale Animals  
980 Replicated in Clay Minerals: *Science*, v. 281, p. 1173–1175, doi:  
981 10.2307/2895499.
- 982 Page, A., Gabbott, S.E., Wilby, P.R., and Zalasiewicz, J.A., 2008, Ubiquitous Burgess  
983 Shale–style “clay templates” in low-grade metamorphic mudrocks: *Geology*, v.  
984 36, p. 855–858, doi: 10.1130/G24991A.1.
- 985 Penny, A.M., Wood, R., Curtis, A., Bowyer, F., Tostevin, R., and Hoffman, K.-H., 2014,  
986 Ediacaran metazoan reefs from the Nama Group, Namibia: *Science*, v. 344, p.  
987 1504–1506, doi: 10.1126/science.1253393.
- 988 Peterson, K.J., Waggoner, B., and Hagadorn, J.W., 2003, A fungal analog for  
989 Newfoundland Ediacaran fossils?: *Integrative and Comparative Biology*, v. 43, p.  
990 127–136.
- 991 Raff, R.A., and Raff, E.C., 2014, The role of biology in the fossilization of embryos and  
992 other soft-bodied organisms: microbial biofilms and lagerstätten: *Paleontological*  
993 *Society Special Publication*,.
- 994 Retallack, G.J., 1994, Were the Ediacaran Fossils Lichens?: *Paleobiology*, v. 20, p. 523–  
995 544, doi: 10.2307/2401233.
- 996 Runnegar, B.N., and Fedonkin, M.A., 1992, Proterozoic metazoan body fossils, *in*  
997 Schopf, J.W. and Klein, C. eds., *The Proterozoic Biosphere, A Multidisciplinary*  
998 *Study*, New York, Cambridge University Press, p. 369–387.
- 999 Sansom, R. S., 2014, Experimental decay of soft tissues: *Paleontological Society Special*  
1000 *Publication*,.
- 1001 Schiffbauer, J. D., Wallace, A. F., Broce, J., and S. Xiao., 2014, Exceptional fossil  
1002 conservation through phosphatization: *Paleontological Society Special*  
1003 *Publication*,.
- 1004 Scott, C., Lyons, T.W., Bekker, A., Shen, Y., Poulton, S.W., Chu, X., and Anbar, A.D.,  
1005 2008, Tracing the stepwise oxygenation of the Proterozoic ocean: *Nature*, v. 452,  
1006 p. 456–459, doi: 10.1038/nature06811.
- 1007 Seilacher, A., 1999, Biomat-Related Lifestyles in the Precambrian: *PALAIOS*, v. 14, p.  
1008 86–93, doi: 10.2307/3515363.

- 1009 Seilacher, A., 1984, Late Precambrian and Early Cambrian Metazoa: Preservational or  
1010 Real Extinctions?, in Holland, H.D. and Trendall, A.F. eds., Patterns of Change in  
1011 Earth Evolution, Dahlem Workshop Reports Physical, Chemical, and Earth  
1012 Sciences Research Reports 5, Springer Berlin Heidelberg, p. 159–168.
- 1013 Seilacher, A., 1992, Vendobionta and Psammocorallia: lost constructions of Precambrian  
1014 evolution: Journal of the Geological Society, v. 149, p. 607–613, doi:  
1015 10.1144/gsjgs.149.4.0607.
- 1016 Seilacher, A., Grazhdankin, D., and Legouta, A., 2003, Ediacaran biota: The dawn of  
1017 animal life in the shadow of giant protists: Paleontological Research, v. 7, p. 43–  
1018 54, doi: 10.2517/prpsj.7.43.
- 1019 Sperling, E.A., Frieder, C.A., Raman, A.V., Girguis, P.R., Levin, L.A., and Knoll, A.H.,  
1020 2013, Oxygen, ecology, and the Cambrian radiation of animals: Proceedings of  
1021 the National Academy of Sciences,, p. 201312778, doi:  
1022 10.1073/pnas.1312778110.
- 1023 Sperling, E.A., Peterson, K.J., and Laflamme, M., 2011, Rangeomorphs, Thectardis  
1024 (Porifera?) and dissolved organic carbon in the Ediacaran oceans: Geobiology, v.  
1025 9, p. 24–33, doi: 10.1111/j.1472-4669.2010.00259.x.
- 1026 Sperling, E.A., and Vinther, J., 2010, A placozoan affinity for *Dickinsonia* and the  
1027 evolution of late Proterozoic metazoan feeding modes: Placozoan affinity for  
1028 Dickinsonia: Evolution & Development, v. 12, p. 201–209, doi: 10.1111/j.1525-  
1029 142X.2010.00404.x.
- 1030 Sprigg, R.C., 1947, Early Cambrian (?) Jellyfishes from the Flinders Ranges, South  
1031 Australia: Transactions of The Royal Society of South Australia, v. 71, p. 212–  
1032 224.
- 1033 Sprigg, R.C., 1949, Early Cambrian “Jellyfishes” of Ediacara, South Australia and Mount  
1034 John, Kimberley District, Western Australia: Transactions of The Royal Society  
1035 of South Australia, v. 73, p. 72–99.
- 1036 Steiner, M., and Reitner, J., 2001, Evidence of organic structures in Ediacara-type fossils  
1037 and associated microbial mats: Geology, v. 29, p. 1119–1122, doi: 10.1130/0091-  
1038 7613(2001)029<1119:EOOSIE>2.0.CO;2.
- 1039 Sun, W., 1986, Late precambrian pennatulids (sea pens) from the eastern Yangtze Gorge,  
1040 China: Paracharnia gen. nov.: Precambrian Research, v. 31, p. 361–375, doi:  
1041 10.1016/0301-9268(86)90040-9.
- 1042 Tarhan, L.G., Droser, M.L., and Gehling, J.G., 2010, Taphonomic Controls on Ediacaran  
1043 Diversity: Uncovering the Holdfast Origin of Morphologically Variable  
1044 Enigmatic Structures: PALAIOS, v. 25, p. 823–830, doi: 10.2110/palo.2010.p10-  
1045 074r.

- 1046 Vickers-Rich, P., Ivantsov, A.Y., Trusler, P.W., Narbonne, G.M., Hall, M., Wilson, S.A.,  
1047 Greentree, C., Fedonkin, M.A., Elliott, D.A., Hoffmann, K.H., and Schneider,  
1048 G.I.C., 2013, Reconstructing Rangepa: New Discoveries from the Ediacaran of  
1049 Southern Namibia: *Journal of Paleontology*, v. 87, p. 1–15, doi: 10.1666/12-  
1050 074R.1.
- 1051 Wade, M., 1969, Medusae from uppermost Precambrian or Cambrian sandstones, central  
1052 Australia: *Palaeontology*, v. 12, Part 3, p. 351–365.
- 1053 Waggoner, B., 2003, The Ediacaran biotas in space and time: Integrative and  
1054 *Comparative Biology*, v. 43, p. 104–113.
- 1055 Wilby, P.R., Carney, J.N., and Howe, M.P.A., 2011, A rich Ediacaran assemblage from  
1056 eastern Avalonia: Evidence of early widespread diversity in the deep ocean:  
1057 *Geology*, v. 39, p. 655–658, doi: 10.1130/G31890.1.
- 1058 Xiao, S., Droser, M., Gehling, J.G., Hughes, I.V., Wan, B., Chen, Z., and Yuan, X., 2013,  
1059 Affirming life aquatic for the Ediacara biota in China and Australia: *Geology*, v.  
1060 41, p. 1095–1098, doi: 10.1130/G34691.1.
- 1061 Xiao, S., and Laflamme, M., 2009, On the eve of animal radiation: phylogeny, ecology  
1062 and evolution of the Ediacara biota: *Trends in Ecology & Evolution*, v. 24, p. 31–  
1063 40, doi: 10.1016/j.tree.2008.07.015.
- 1064 Xiao, S., Shen, B., Zhou, C., Xie, G., and Yuan, X., 2005, A uniquely preserved  
1065 Ediacaran fossil with direct evidence for a quilted bodyplan: *Proceedings of the*  
1066 *National Academy of Sciences of the United States of America*, v. 102, p. 10227–  
1067 10232, doi: 10.1073/pnas.0502176102.
- 1068 Xiao, S., Yuan, X., Steiner, M., and Knoll, A.H., 2002, Macroscopic Carbonaceous  
1069 Compressions in a Terminal Proterozoic Shale: A Systematic Reassessment of the  
1070 Miaohu Biota, South China: *Journal of Paleontology*, v. 76, p. 347–376, doi:  
1071 10.2307/1307146.
- 1072 Yuan, X., Chen, Z., Xiao, S., Zhou, C., and Hua, H., 2011, An early Ediacaran  
1073 assemblage of macroscopic and morphologically differentiated eukaryotes:  
1074 *Nature*, v. 470, p. 390–393, doi: 10.1038/nature09810.
- 1075 Zhang, X., Hua, H., and Reitner, J., 2006, A new type of Precambrian megascopic fossils:  
1076 the Jinxian biota from northeastern China: *Facies*, v. 52, p. 169–181, doi:  
1077 10.1007/s10347-005-0027-z.
- 1078 Zhu, M., Gehling, J.G., Xiao, S., Zhao, Y., and Droser, M.L., 2008, Eight-armed Ediacara  
1079 fossil preserved in contrasting taphonomic windows from China and Australia:  
1080 *Geology*, v. 36, p. 867–870, doi: 10.1130/G25203A.1.
- 1081

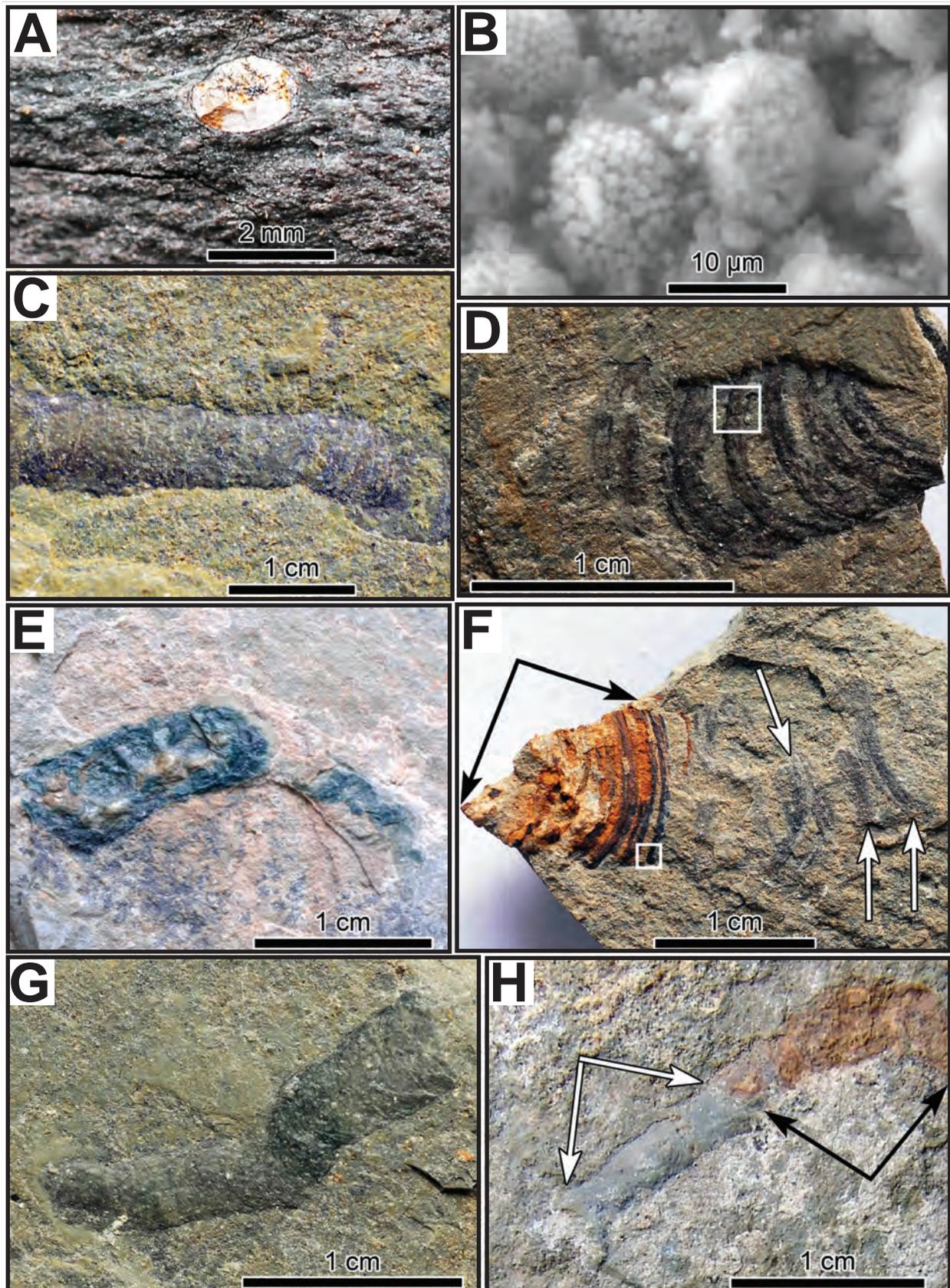


FIGURE 1.—Preservation of single fossils from the Gaojiashan biota in multiple taphonomic styles, reproduced from Cai et al., 2012 with the permission of Elsevier. All reflected light photographs except b (SEM photomicrograph). a) Cross-section through a pyritized *Conotubus hemiannulatus* specimen; b) pyrite framboids on the exterior of the specimen in a); c, d) carbonaceous compression fossils; e) replication by green-coloured aluminosilicate minerals; f) specimen exhibiting both pyritization (rust-coloured 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 via ESEM EDS.

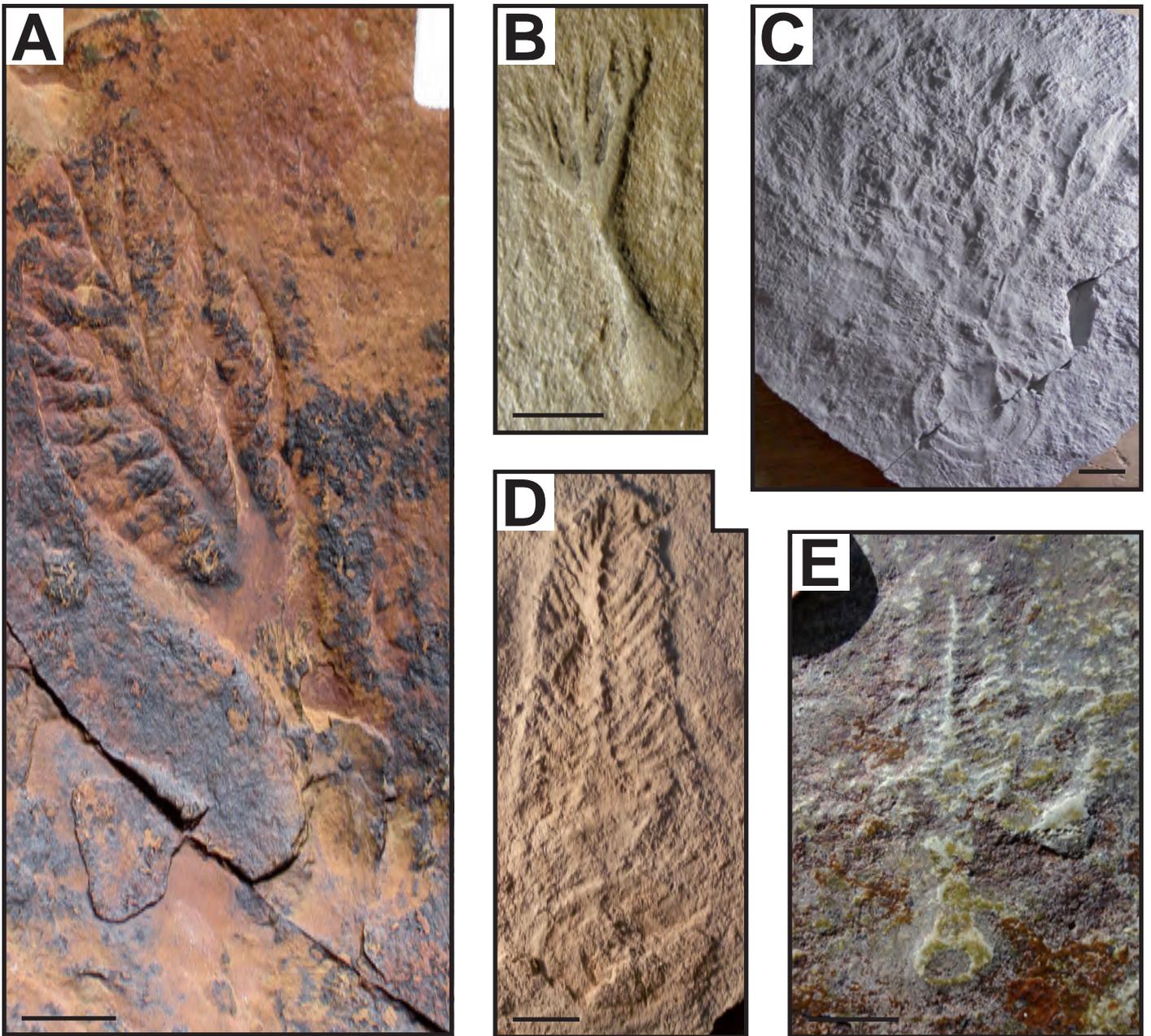


FIGURE 2.—a) Exceptional preservation in the Avalon Assemblage - a *Culmofrons* specimen from the Bonavista Peninsula, Newfoundland. Note that the frondose portion of the fossil is preserved in negative epirelief, and the stalk is preserved in positive relief. Photo courtesy of Alex Liu. b) Small *Primocandelabrum* specimen from the Bonavista Peninsula, with holdfast, stalk and branch axes preserved in positive epirelief. The frondose portions are not evident in this fossil. c) A *Primocandelabrum* specimen from Charnwood Forest, UK. Note that in contrast to b, the stalk and holdfast are preserved in negative epirelief, indicating a difference in the relative timings of collapse and lithification of the beds in the two sites. Plaster cast of GSM 105969; d) *Charniodiscus* specimen from Charnwood Forest, with central and branch axes preserved in low positive epirelief, and the holdfast in negative epirelief. Plaster cast of GSM 106069; e) *Charniodiscus* specimen from the Bonavista Peninsula, Newfoundland, with central and branch axes and the holdfast all preserved in positive epirelief. Scale bars are 2 cm (a, c, d) and 1 cm (b, e).

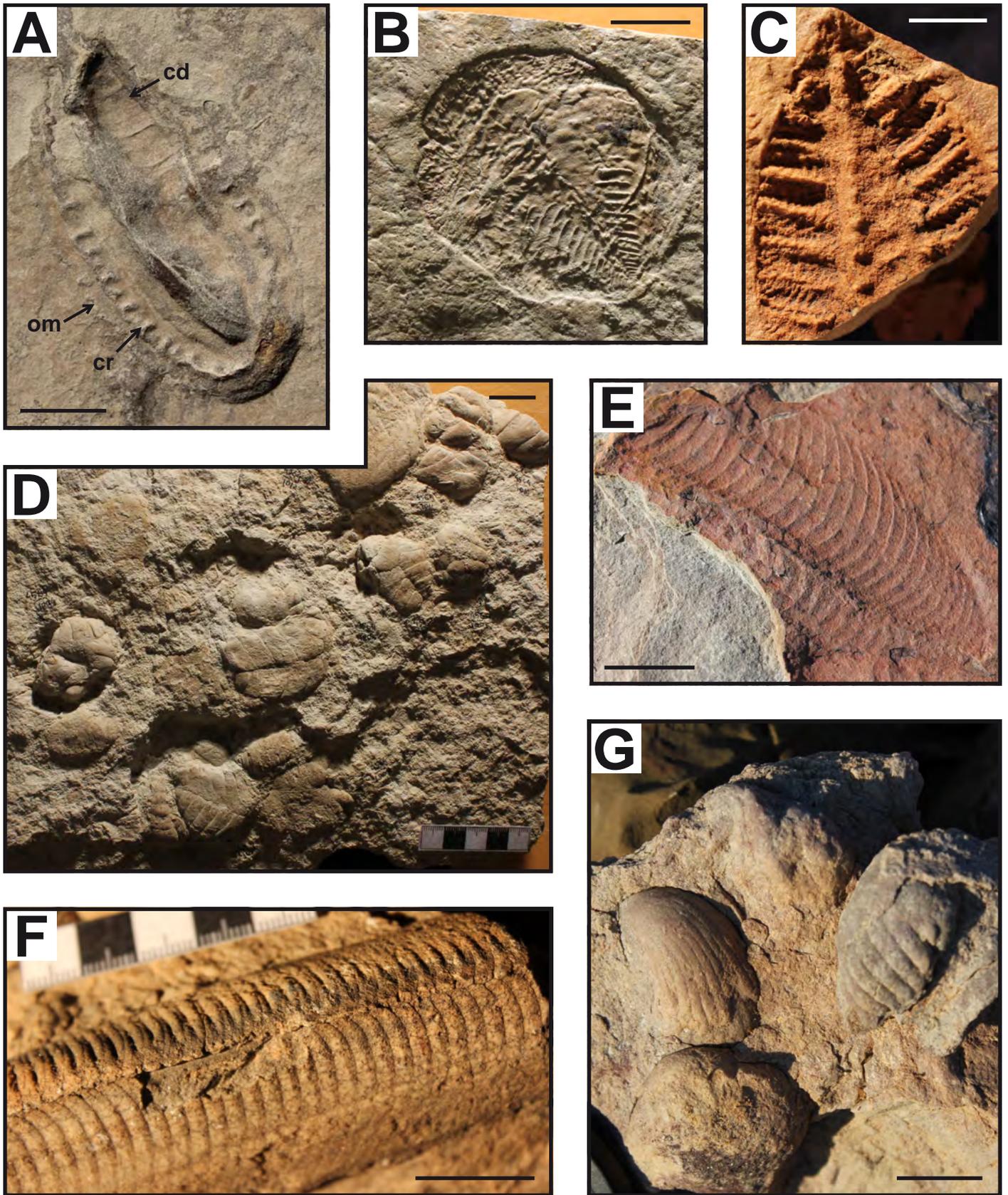


FIGURE 3.—Examples of mouldic preservation from the White Sea (a, b, d) and Namibia (c, e, f, g). a) *Kimberella* displaying three distinct zones (om = outer margin; cr = crenellated part; cd = central depression); b) *Yorgia* with a disturbed proximal region (upper left); c) *Rangea* with clear rangeomorph 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.

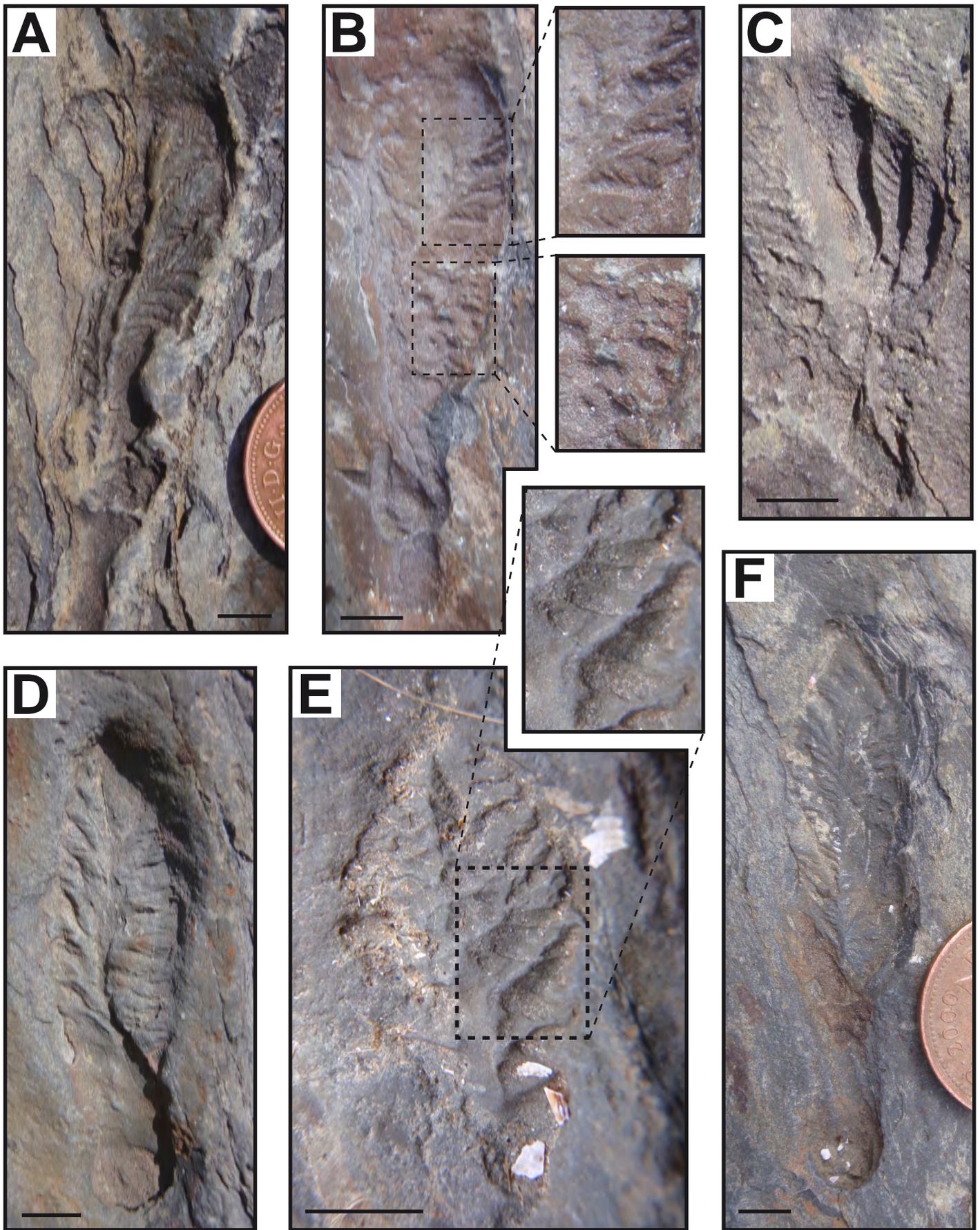


FIGURE 4.—Specimens from Spaniard's Bay, Newfoundland. a) *Bradgatia* with exquisite preservation down one side only; b) *Beothukis* with good, negative epirelief, distal (upper insert) and poorer, positive epirelief, proximal preservation (lower insert); c) unidentified frond with relatively high relief 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. All scale bars: 5 mm.

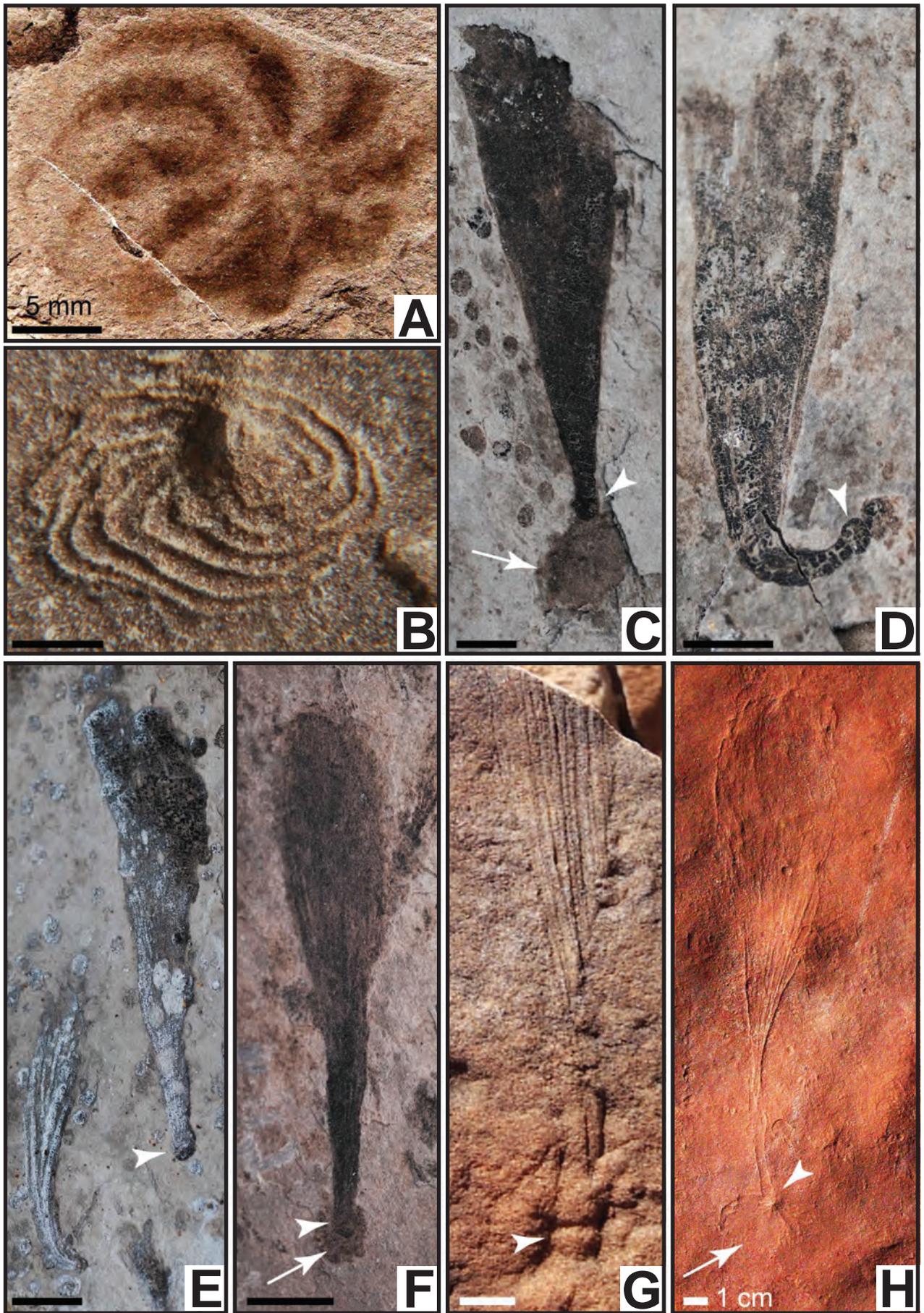


FIGURE 5.— One species preserved in multiple taphonomic modes. Reproduced from Xiao et al., 2013 with permission from GSA. a) *Eoandromeda octobrachiata* preserved in black shale, from the uppermost Doushantuo Formation at Wenghui (China); b) *E. octobrachiata* preserved as a siliclastic mold from the Ediacara Member sandstone (South Australia); c–f): *Flabelophyton lantianensis* preserved in black shales of the lower Lantian Formation (South China); g, h) similar forms from the 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.

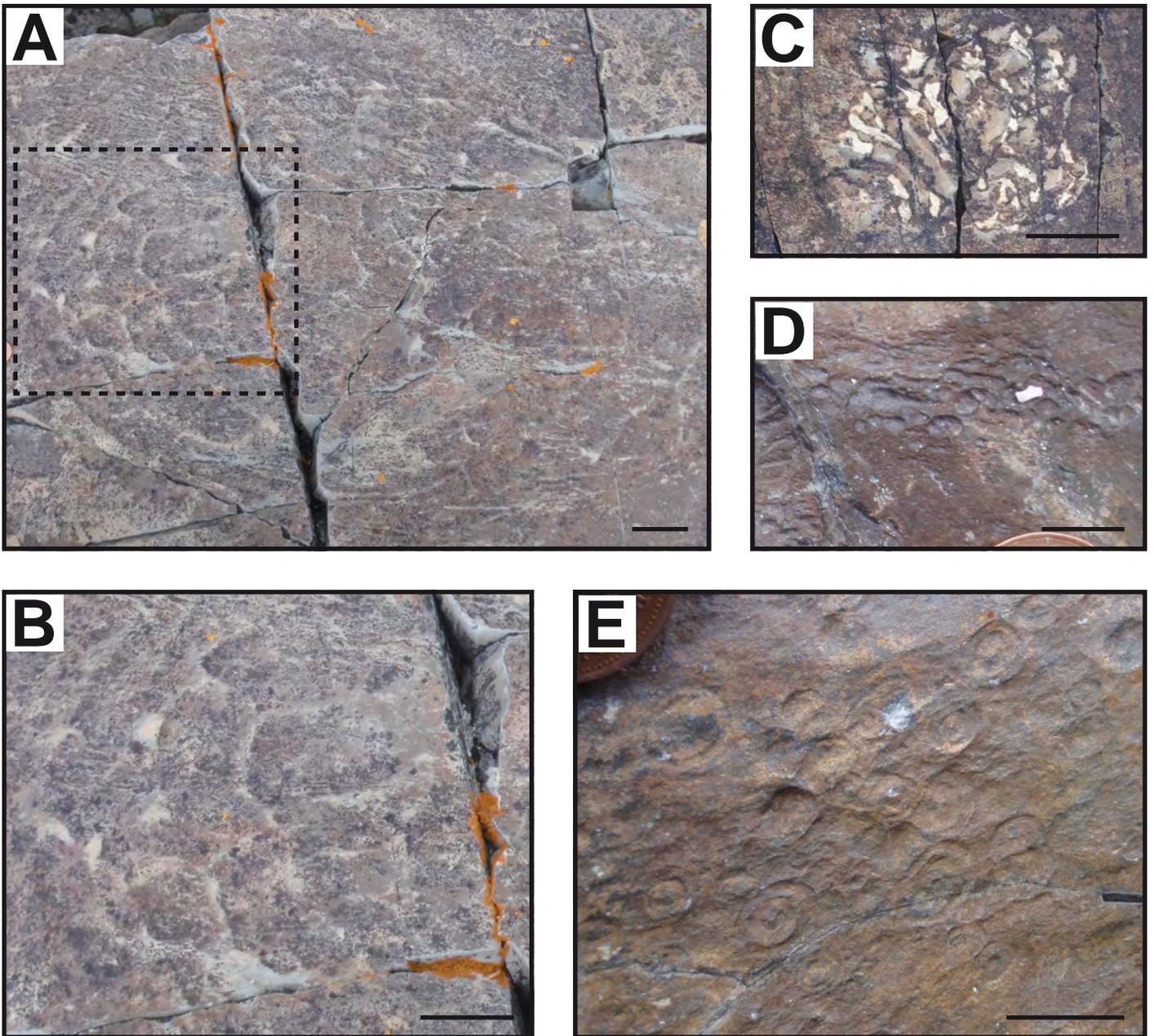


FIGURE 6.—a) Large ikaite holdfast from Bonavista Peninsula, Newfoundland; b) inset of a) showing reticulate network texture; c) “pizza disc” *sensu* Narbonne 2001 from the Mistaken Point Ecological Reserve, Newfoundland; d) “bubble strip” *sensu* Laflamme et al. 2012 from Spaniard’s Bay, Newfoundland; e) numerous small *Aspidella* holdfasts from Ferryland, Newfoundland. Scale bars are 5 cm (a, b, c) and 1 cm (d, e).