

# 1 **Filamentous connections between Ediacaran fronds**

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11

12 **Short Title: Ediacaran filamentous connections**

13

14 **Keywords:** Newfoundland; Rangeomorpha; stolon; clonal reproduction; palaeoecology

15

16 **Summary: Fossils of the Ediacaran macrobiota (~571–539 Ma) record phylogenetically**  
17 **diverse marine palaeocommunities, including early animals, which pre-date the**  
18 **‘Cambrian Explosion’ [1–4]. Benthic forms with a frondose gross morphology, assigned**  
19 **to the morphogroups Rangeomorpha [5] and Frondomorpha/Arboreomorpha [6–8], are**  
20 **amongst the most temporally wide-ranging and environmentally tolerant members of**  
21 **the Ediacaran macrobiota [6], and dominated deep-marine ecosystems ~570–560 Ma [9–**  
22 **11]. Investigations into the morphology [12–14], palaeoecology [10,15–16], reproductive**

23 strategies [17–18], feeding methods [9,19] and morphogenesis of frondose taxa together  
24 constrain their phylogenetic position to the metazoan (for Rangeomorpha) or  
25 eumetazoan (e.g. *Arborea*) total groups [14,20], but tighter constraint is currently  
26 lacking. Here we describe fossils of abundant filamentous organic structures preserved  
27 amongst frond-dominated fossil assemblages in Newfoundland (Canada). The filaments  
28 constitute a prominent component of the ecosystems, and exhibit clear physical  
29 associations with at least seven frondose taxa. Individual specimens of one uniterminal  
30 rangeomorph taxon appear to be directly connected by filaments across distances of  
31 centimetres to metres. Such physical linkages are interpreted to reflect evidence for  
32 stolonetic connections: a conclusion with potential implications for the phylogenetic  
33 placement and palaeoecology of frondose organisms. Consideration of extant  
34 stoloniferous organisms suggests that Ediacaran frondose taxa were likely clonal, and  
35 resurrects the possibility that they may have been colonial [e.g. 21–22].

36

37 **Results:** Fossilised macroscopic filamentous structures are here reported from 38 unique  
38 bedding plane horizons (out of 183 studied fossil-bearing horizons) on the Avalon and  
39 Bonavista peninsulas of Newfoundland (Figure S1). Filamentous structures manifest as low  
40 (< 1 mm) positive epirelief impressions, with no visible cell walls, membranes, external  
41 ornamentation, or disarticulation (Figure 1). Filaments are typically 100–1000  $\mu\text{m}$  in width  
42 and 2–40 cm in length, although the longest and thickest examples we have observed (on the  
43 LC6 surface; Figures S1C, S2–S3) measure over four metres in total length. Filament  
44 densities vary between different bedding planes, ranging from occasional individual strands  
45 to hundreds per square metre (extrapolated estimates suggest over 580 filaments/ $\text{m}^2$  from  
46 sections of the MUN Surface, Figure 1C), but densities are largely uniform within individual  
47 bedding plane assemblages. Individual specimens possess broadly constant widths, and

48 traverse bedding planes in multiple directions (Figures 1–3, S2–S4). Where filaments meet,  
49 they are typically superimposed (Figures 1C–D) rather than cross-cutting, strongly suggesting  
50 that they are not trace fossils [23]. Rarely, observed filamentous structures dichotomously  
51 bifurcate (Figure 3F), while some examples are seemingly arranged into bundles from which  
52 individual filaments can radiate (Figure 1C). Small bulges along the length of some filaments  
53 are also observed, often at triple junction branching points (Figure 3F).

54 Filaments follow relatively straight paths, but slight to significant curvature in most  
55 specimens (even doubling back on themselves in places; e.g. Figures 1B–C, 2B), and bending  
56 around the holdfast structures of frondose macrofossils (Figure 1E), indicates that they were  
57 originally flexible structures. Across studied filament populations, filaments show no  
58 consistent preferential alignment with fracture/cleavage planes or frond orientations (e.g.  
59 Figures 1C, 2A). Thin sections reveal no three-dimensional sub-surface expression or  
60 preserved organic material, and confirm that filaments are not associated with sub-surface  
61 fracture planes (Figure S1E). Together, these observations imply that the filamentous  
62 structures were benthic, and we interpret observed specimens to have lain above/on seafloor-  
63 covering microbial mats at the point of burial. However, the gradual fading of many  
64 specimens into bedding surfaces suggests that filaments may also have lain partially beneath  
65 the sediment, or within microbial mats, outside the plane of preservation. We cannot refute  
66 the possibility that smaller filaments may reflect torn, fragmented, or partially degraded  
67 specimens.

68 Ediacaran frondose taxa are typically constructed of one or multiple fronds, and often possess  
69 a basal holdfast structure interpreted to have anchored them to the seafloor, as well as a stem  
70 to elevate the frond into the water column [12]. Filaments occur alongside all frondose  
71 Ediacaran macrofossil taxa described from Newfoundland to date, and could both overlie,  
72 and lie beneath, the fronds and stems of such organisms. Of the 38 surfaces on which we

73 have documented filamentous impressions, they occur alongside frondose taxa on 27  
74 surfaces, alongside only discoidal specimens on nine surfaces, and as the only fossil  
75 impressions on two surfaces. Several specimens of an undescribed uniterminal rangeomorph  
76 taxon on the LC6 surface exhibit filaments terminating at/converging upon the outer margin  
77 of their holdfast discs (e.g. Figures 2–3). In one specimen, a large, unbroken filament  
78 traverses the bedding plane for 4.1 m and terminates at the holdfast of a frond. It then doubles  
79 back for 46 cm and terminates at the holdfast of another similarly-sized specimen of the same  
80 taxon, before continuing on a curving trajectory for 90 cm to terminate at a small circular  
81 bulge, from which two additional filamentous impressions radiate (Figures 2A, 3, S2). These  
82 specific filaments can exhibit branching along their length, and in places comprise multiple  
83 discrete strands (Figure 3). A second pair of fronds of the same taxon (Figure 2D–E) lie along  
84 another single filament of >2.23 m in length (Figure S3), while at least three other specimens  
85 of the same taxon on that surface possess holdfasts that exhibit direct contact with  
86 filamentous structures, many of which clearly change their course to converge on the  
87 holdfasts (e.g. Figure 2B).

88 Seven specimens of small frondose organisms termed ‘ostrich feathers’ [10] on the LC6  
89 surface are observed to possess filamentous structures of variable length that radiate from  
90 their holdfast margins (Figure 4E). This variation in length in individual specimens is distinct  
91 from the radial ‘rays’ possessed by contemporary *Hiemalora* discs, which are typically of  
92 equal length in individual specimens [e.g. 24, figure 9].

93 Several other frondose taxa exhibit one or multiple filaments terminating at or bisecting their  
94 holdfast margin (e.g. the frondomorph/arboreomorph *Charniodiscus*, and the rangeomorphs  
95 *Charnia* and *Primocandelabrum*; Figure 4B–D). We also observe rare examples of single  
96 filaments terminating at one end of small *Fractofusus andersoni* specimens on the Brasier

97 and H14 surfaces (e.g. Figure 4A), aligning with the trajectory of the organism's midline, and  
98 not emerging on the other side of the specimen.

99 Comparable filamentous structures to those seen in Newfoundland are recognised from the  
100 Memorial Craggs [25, figure 5D], and 'Bed B' (Figure S4A–D) [26] surfaces of Charnwood  
101 Forest (U.K.), occurring in relatively low densities directly adjacent to frondose macrofossils  
102 (Figure S4A). Negative hyporelief linear structures in the frond-bearing Ediacara Member of  
103 South Australia (Figure S4G), and the Lyamtsa and Verkhovka formations of the White Sea  
104 region, Russia (Figure S4E–F), share morphological (e.g. their size and shape) and  
105 taphonomic (negative hyporelief/positive epirelief surface impressions of low topography)  
106 similarities with the Newfoundland structures, but require further investigation to confirm a  
107 common origin.

108

109 **Discussion:** The 1000s of filamentous fossils in Newfoundland do not exhibit cellular  
110 preservation, annulations, striations or ornamentation, and maintain constant width along  
111 their length. Specimens could reach large size (Figures S2–S3), appear to have been flexible  
112 (Figures 1B,E, 2B, 4D), could cluster into bundles (Figure 1C), could dichotomously branch  
113 (Figure 3F), are inferred to have been benthic, and could terminate at (or radiate from)  
114 holdfast structures or assumed growth axes of frondose taxa (Figures 2–4). There is no link  
115 between the filaments and cleavage or fracture planes either at the surface (Figures 2A, S3) or  
116 in thin section (Figure S1E), ruling out a tectonic origin. The non-uniform orientations of  
117 filaments on bedding planes (Figures 1–3) indicate that they have not undergone significant  
118 current alignment and were therefore unlikely to have been tethered to the substrate at just  
119 one point.

120 Previously described Ediacaran filamentous microfossil impressions are not directly  
121 comparable to those described herein. Filamentous structures from Spain and Namibia  
122 interpreted as vendotaenids [27–28], as well as structures from the Drook Formation of  
123 Newfoundland [29–30], can be of comparable width, but are typically just a few centimetres  
124 in length, are preserved in far lower densities, and possess more sinuous morphologies than  
125 these Newfoundland specimens. Possible algal fossils described from shallow marine  
126 assemblages of the White Sea [31–32] only reach a few millimetres in length, and are found  
127 in small, dispersed clusters on the bedding surfaces. A single figured specimen from the  
128 Khatyspyt Formation of Siberia documents physical filamentous connections between  
129 macroscopic circular carbonaceous compression fossils, within successions that contain  
130 frondose taxa [33], but includes no further description.

131 Other modern and extinct organisms with a macroscopic filamentous appearance include  
132 several Neoproterozoic forms of a few centimetres in length [28,34–36], which have been  
133 compared with macroalgae [28,34], metazoans [37], or the sheathes of sulfur bacteria [38]  
134 and cyanobacteria [39]. The filaments we describe are too large to be attributed to most  
135 extant bacterial groups, including giant bacteria [40] and those capable of undergoing  
136 filamentation [41]. Algal fossils can show some similarities to this material [27,35], but the  
137 deep-marine depositional setting inferred for the Conception Group in Newfoundland [42]  
138 would preclude benthic photosynthetic lifestyles. Algae could have been washed into these  
139 depositional settings, but the abundance and extensive lateral distributions of filaments on  
140 bedding planes, and their apparent connections to holdfasts of frondose taxa, are difficult to  
141 explain in that scenario. The taphonomic style and branching of the filaments bears passing  
142 resemblance to certain late Ediacaran biotic sedimentary surface textures (e.g. ‘Arumberia’;  
143 [43]), but such impressions usually show a preferential alignment and regular spacing on a

144 given surface, and overwhelmingly occur in shallower sedimentary facies that do not contain  
145 Ediacara-type macrofossils.

146 The filaments described herein exhibit widths at least an order of magnitude larger than those  
147 of the largest modern fungal hyphae. Meanwhile, clear superposition rather than truncation  
148 (e.g. Figure 1C–D) renders an ichnological explanation unlikely [23]. Filamentous  
149 components of contemporary Ediacaran macrofossils such as the long filamentous ‘string’ of  
150 *Hadrynichorde* or the radial ‘rays’ of *Hiemalora* are distinctive structures, with consistent  
151 spatial associations relative to their respective body impressions [24]. *Hiemalora* typically  
152 possesses ~10–80 individual rays [44], which radiate in all directions from an attachment  
153 point at the margin of the disc, and which usually all terminate at similar distances of a few  
154 centimetres. This is in contrast to the small number of filaments (<8) associated with  
155 individual holdfasts seen amongst our material, which can extend over distances of many  
156 centimetres (e.g. Figure 2). To the best of our knowledge, there are no described extant or  
157 fossilized discrete, filamentous organisms that exhibit all aforementioned characters.

158 Strong circumstantial evidence for termination of filaments at frond holdfasts suggests a  
159 physical association with Ediacaran frondose taxa. Such an association could be direct (i.e.  
160 the filaments are part of the macro-organisms), or indirect (with the filaments being  
161 independent organisms engaging with the fronds passively, symbiotically or parasitically, as  
162 seen for example in the interactions between extant plants and mycorrhizal fungal networks  
163 [45]). An indirect relationship for the filaments with the frondose taxa cannot be ruled out,  
164 but is considered less likely since all observed filament-mediated connections between  
165 frondose specimens on individual surfaces are intraspecific (Figures 2–3). On the >200 m<sup>2</sup>  
166 bedding plane LC6, which exhibits thousands of thin filamentous impressions, the majority of  
167 the few thick ( $\geq 1$  mm width) filamentous structures converge on holdfasts of a single, un-  
168 named, rangeomorph taxon (Figure 2), seemingly passing adjacent holdfasts of other taxa

169 without exhibiting any obvious relationship with them (Figures S2–S3), despite high frond  
170 densities.

171 There is no indication that the filamentous structures were rigid (given their propensity to  
172 bend/change direction in many examples), implying that they were not biomineralized.

173 Amongst extant marine taxa, non-mineralized filamentous outgrowths of comparable gross  
174 morphology occur in algae (where they link individual fronds), certain metazoans (where  
175 they link polyps/individuals), and fungal mycelia. The outgrowths typically fulfil  
176 stabilization, defence, nutrient transport, or (asexual) reproductive roles involving budding or  
177 stoloniferous growth, for example in extant algae (e.g. the green alga *Caulerpa*), terrestrial  
178 plants, and metazoans including sponges [46], colonial cnidarians [47], entoprocts [48] and  
179 bryozoans [49]. These different functions of filamentous outgrowths are not mutually  
180 exclusive, and all remain potential candidates for the function of the Ediacaran filaments we  
181 describe, given available evidence and sedimentary context.

182 Independent assessment of the spatial distribution of the rangeomorph taxon *Fractofusus* on  
183 Ediacaran bedding planes predicted a stolon-like asexual reproductive strategy in the life  
184 cycle of that organism [17]. We are yet to observe *Fractofusus* specimens actually connected  
185 to each other by filaments, but filaments are observed in abundance on several surfaces  
186 containing *Fractofusus* (e.g. bed H14), where they rarely terminate at the ends of small  
187 *Fractofusus* specimens (Figure 4A). *Fractofusus* specimens possessing such filaments are  
188 never the very smallest, but typically measure 1.5–3 cm in length. Further support for a stolon  
189 interpretation is provided by the presence of bulbous thickenings at filament branch points  
190 (e.g. Figure 3F), which are morphologically comparable to the branch nodes seen in some  
191 stoloniferous metazoans [50]. If the filamentous structures do reflect stolon-like projections  
192 with a solely reproductive role, large specimens might be expected to connect to smaller  
193 ones. However, in examples of connected uniterminal rangeomorph specimens on bed LC6



194 (Figures 2–3), both specimens in any given pair are of a similar large size, and are thus  
195 interpreted as ‘mature’ individuals of a similar developmental stage. This may indicate that,  
196 even if reproduction was the primary reason for stolon formation, the connections between  
197 specimens may have remained active for a considerable period following establishment of the  
198 individuals on the substrate, perhaps to facilitate nutrient transfer between individuals to  
199 counter the inferred nutrient-poor deep-water settings of the Conception Group [51; though  
200 see 18]. A stoloniferous habit is also consistent with observations that in cases where fronds  
201 are seemingly connected, the filament often continues beyond the frond after meeting it (e.g.  
202 Figure 2D–E), and that multiple filaments may converge upon a single holdfast (Figures 2B–  
203 C, F).

204 The filamentous structures may ultimately provide novel morphological characters with  
205 which to assess Ediacaran fronds, but the prevalence of stolon-like structures amongst extant  
206 eukaryotes means that, in isolation, stolon-like growth cannot constrain the phylogenetic  
207 position of Ediacaran frondose taxa. However, multiple modern stoloniferous eukaryotes –  
208 independent of phylogeny – are modular, clonal, and in some cases, colonial organisms [52].  
209 Ediacaran frondose taxa have previously been proposed to be clonal or colonial, albeit by  
210 viewing individual specimens as colonies on the basis of their highly-compartmentalized  
211 morphology [see 22 and references therein]. In recent years, such interpretations have lost  
212 support as comparisons between frondose taxa and extant colonial cnidarians have been  
213 questioned [53]. A clonal facet to frond biology would raise the prospect that individual  
214 fronds were ‘unitary’ entities (ramets) within a larger benthic, interconnected clonal colony.  
215 This intriguing possibility could explain several aspects of frond palaeoecology (e.g. the  
216 dominance of particular taxa on individual surfaces), and has implications for our views of  
217 senescence, reproduction [17] and damage response [54] within these early metazoan  
218 communities. Clonal reproduction in Ediacaran fronds could also have allowed for rapid

219 colonisation of the seafloor, or re-establishment of communities following sediment influx  
220 events [e.g. 55, see also 17]. The observed filaments may therefore have favoured rapid  
221 community succession by frondose taxa over non-frondose competitors in environments  
222 prone to episodic sedimentation [17], potentially in addition to engineering increased  
223 ecosystem habitability for those taxa by binding/stabilising soft substrates.

224 Recognition of direct associations between organic filamentous structures and benthic  
225 frondose organisms offers new insight into late Ediacaran palaeocommunities. The profusion  
226 of filaments on Newfoundland bedding planes indicates that they were an important, and  
227 perhaps even integral, ecological component of frondose Ediacaran taxa and ecosystems. A  
228 stoloniferous interpretation of apparent filamentous connections between frondose taxa  
229 implies clonal reproduction in these organisms, and may offer support to the view that these  
230 early macroscopic metazoans were non-unitary.

231

232 **Acknowledgments:** This research has been supported by the Natural Environment Research  
233 Council [Independent Research Fellowship, grant number NE/L011409/2 to A.G.L., and  
234 GW4 DTP Studentship NE/L002434/1 to F.S.D.]. A.G.L. received additional support from a  
235 Henslow Junior Research Fellowship from the Cambridge Philosophical Society; the  
236 National Geographic Global Exploration Fund (GEFNE22-11); and the Joseph Burr Tyrrell  
237 Fund of the Geological Society (London). F.S.D. received additional funding from a Merton  
238 College (Oxford) Junior Research Fellowship, and a Research Fellowship from the Royal  
239 Commission for the Exhibition of 1851. The field assistance of J. Stewart, J. Matthews, D.  
240 Grazhdankin and E. Liu, the museum assistance of M. Binnie (South Australia Museum), the  
241 laboratory support of A. Dennis, and the data analysis of K. Dunn are gratefully  
242 acknowledged. This work has benefited from enjoyable discussions with D. McIlroy, M.

243 Brasier, L. Herringshaw, E. Mitchell and C. Kenchington, and from comprehensive reviews  
244 by R. Wood, L. Tarhan and G. Budd.

245

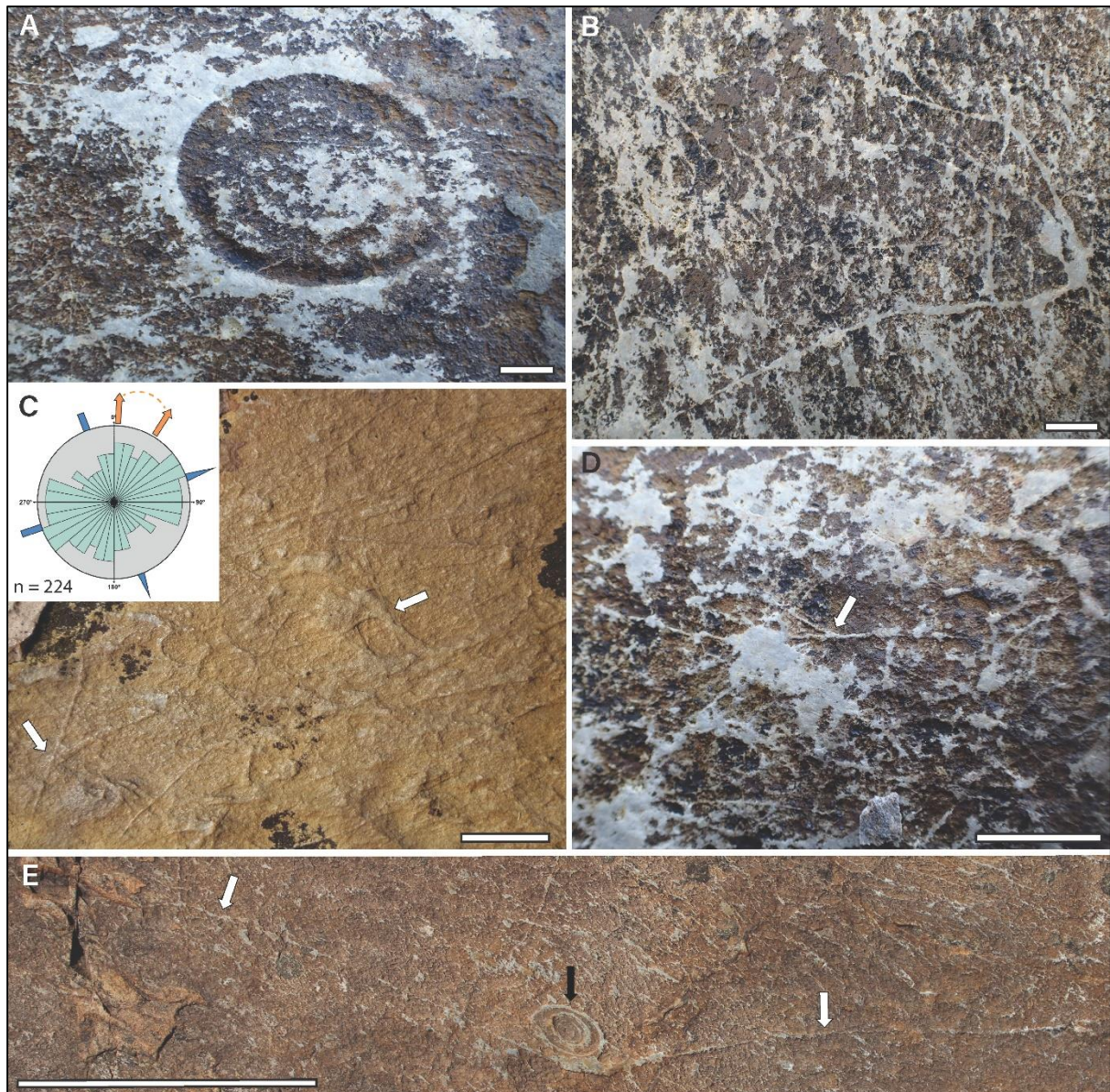
246 **Author Contributions:** A.G.L. conceptualized, developed and conducted formal analysis for  
247 this research. A.G.L. and F.S.D. investigated the findings, collected field data, and wrote the  
248 paper.

249

250 **Declaration of interests:** The authors declare no competing interests.

251

252 **Figure Legends:**



253

254 **Figure 1. Filamentous macrofossils from the Bonavista Peninsula, Newfoundland.**

255 Filaments are preserved as positive epirelief impressions beneath fine-grained tuffs. **(A)**

256 Negative epirelief holdfast, with positive epirelief filaments running across (inferred to be

257 beneath) and around it. PU13 Surface. **(B)** Dense superimposed filament assemblages,

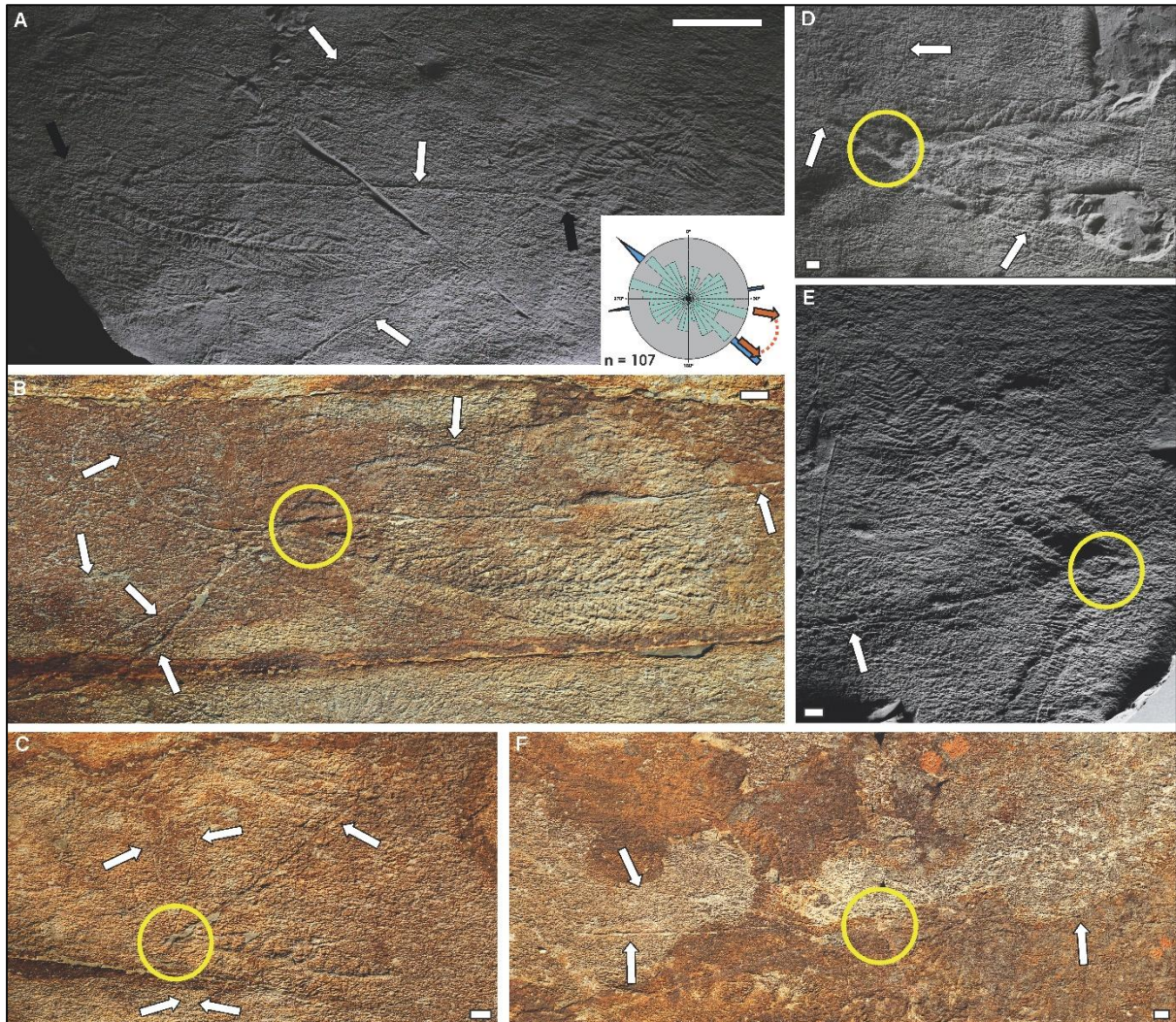
258 showing superposition and directional changes, PU13 Surface. **(C)** Abundant filaments from

259 the MUN Surface. Note filament superposition (arrowed at left) and bundling (arrowed at

260 right). Inset: orientations of all filaments present on cast CAMSM X 50340.1 CST1, from the

261 MUN Surface. Orange arrows denote the range of orientations of frondose taxa (indicating

262 perceived current direction). Blue bars indicate primary fracture directions. **(D)** Further  
 263 filaments, including one specimen that overlies another (arrowed, PU13 Surface). **(E)**  
 264 Filamentous structure (white arrows) seemingly wrapped around a concentric holdfast disc  
 265 (black arrow). All scale bars = 10 mm, except E = 10 cm. See also Figure S1.

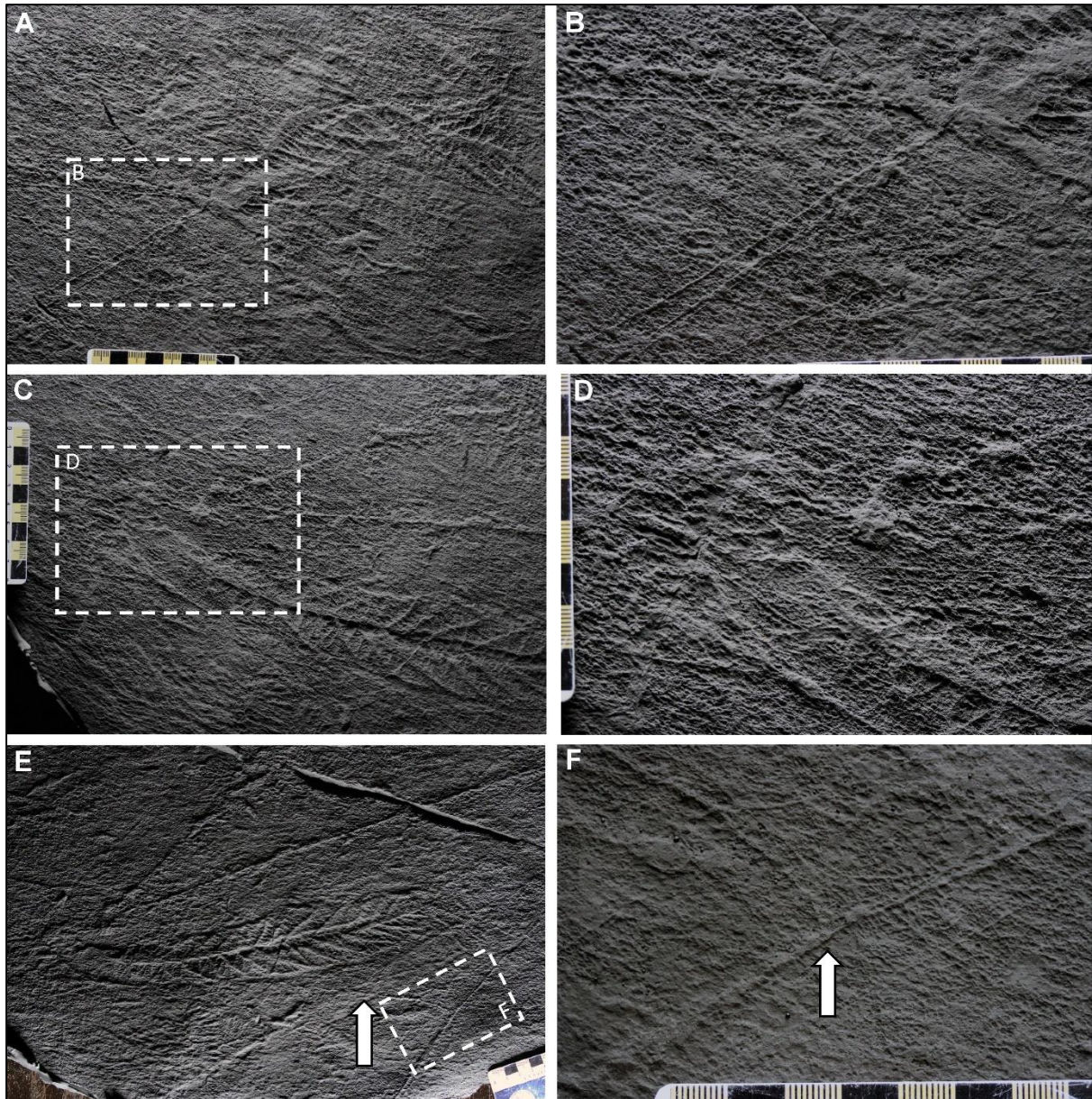


266  
 267 **Figure 2. Rangeomorph fronds and associated filaments on the LC6 Surface, Little**  
 268 **Catalina, Newfoundland.** **(A)** Two large rangeomorph fronds, seemingly connected by a  
 269 filamentous structure (white arrows) that transits between their holdfasts (black arrows) and  
 270 then continues across the surface, tracing an inverted ‘z’ shape on the surface (photograph  
 271 from cast CAMSM X 50341.4 CST1). See Figures 3 and S2 for additional images. Inset:  
 272 orientations of all filaments present on this cast. Orange arrows denote the range of

273 orientations of frondose taxa (indicating perceived current direction). Blue bars indicate  
274 primary (thick) and secondary (thin) cleavage directions. **(B–F)** Further examples of multiple  
275 filaments (arrowed) converging on the holdfasts (circled) of rangeomorph specimens. The  
276 specimens in (D: CAMSM X 50341.2 CST1) and (E: CAMSM X 50341.3 CST1) lie along  
277 the same filament (see Figure S3), which continues beyond both of them. All examples are of  
278 the same, as yet un-named, rangeomorph taxon. Scale bars A = 10 cm, B–F = 10 mm.

279

280



281

282 **Figure 3. Close up images of seemingly connected rangeomorphs on the LC6 Surface**

283 **(cast CAMSM X 50341.4 CST1). (A–B)** The rangeomorph frond on the right of Figure 2A

284 with multiple filamentous structures converging on its holdfast disc. **(C–D)** The large

285 rangeomorph at left in Figure 2A, showing the spatial relationship between its holdfast and

286 prominent filaments, which terminate at the holdfast margin. **(E)** Zoomed out view of the

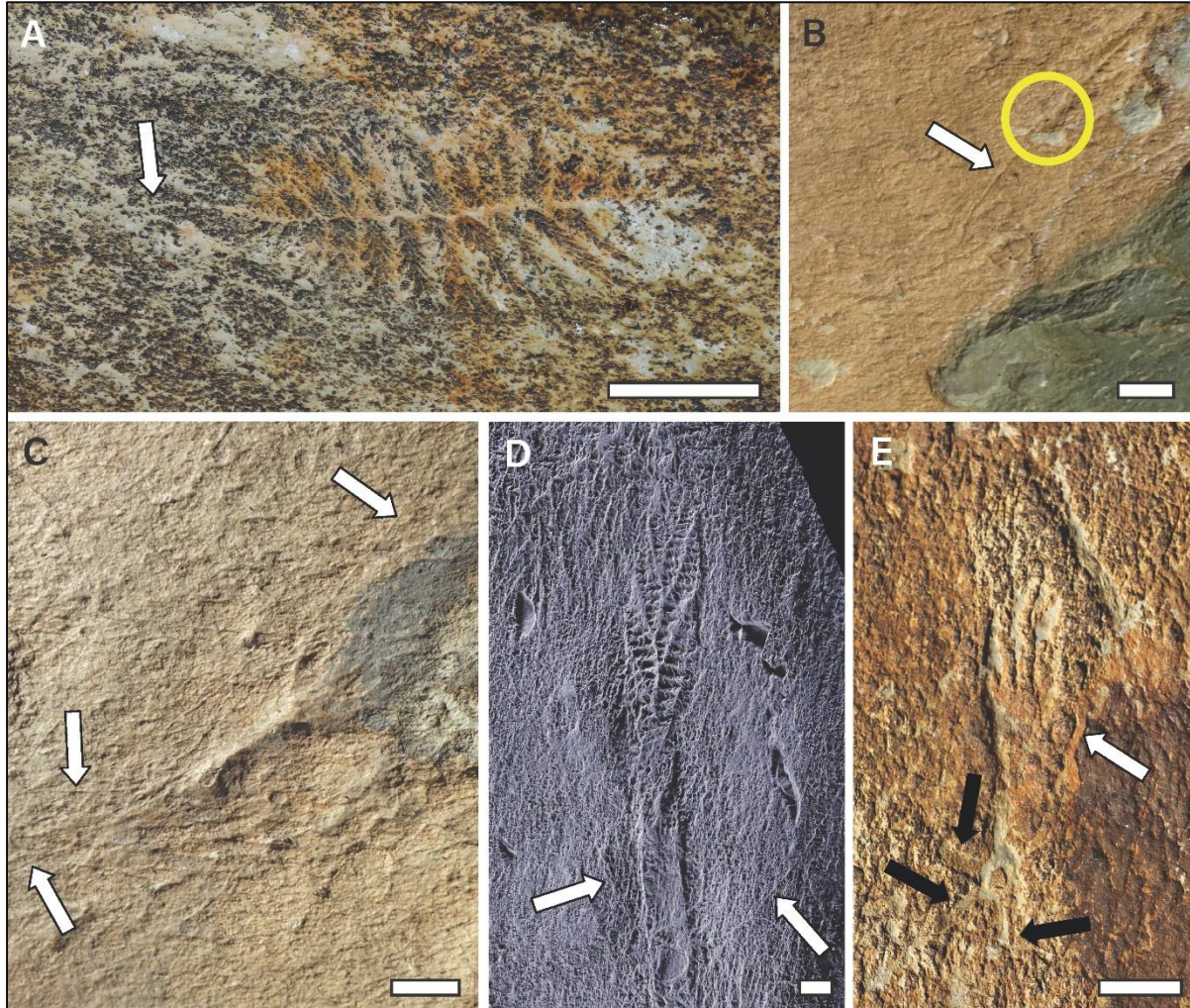
287 frond in (C) showing how the filament leading to the second frond (bottom of Figure 2A)

288 branches ~20 cm before reaching that specimen, with the branching filament (arrowed)

289 possessing a trajectory that directly intersects the holdfast of the frond in (C). **(F)** Close up of

290 the bulbous branching junction (arrowed) between the filaments in (E). N.B. additional  
291 thinner filaments traverse the surface in multiple directions nearby. Scale bar gradations in  
292 centimetres and millimetres.

293



294

295 **Figure 4. Filamentous macrofossils (arrowed) terminating at Ediacaran frondose taxa.**

296 (A) *Fractofusus andersoni* from bed BR5, MPER, with a filament seemingly extending from

297 one end of the specimen midline. (B) Filaments on the MUN Surface, including one

298 specimen that terminates at the holdfast disc (circled) of a small *Charniodiscus* specimen. (C)

299 *Primocandelabrum* sp. (MUN Surface), with associated filaments (arrowed) that appear to

300 terminate at its holdfast. (D) *Charnia masoni* (cast CAMSM X 50341.5 CST1) from the LC6

301 surface, associated with two prominent curving filaments (arrowed) that converge on its

302 holdfast. (E) 'Ostrich feather' specimen from the LC6 surface. Note the ray-like projections



303 of variable length emanating from the holdfast disc (black arrows), with one filament (white  
304 arrow) extending from the holdfast over a greater distance of several centimetres. Scale bars  
305 = 10 mm.

306

## 307 **STAR Methods:**

### 308 **LEAD CONTACT AND MATERIALS AVAILABILITY**

#### 309 *Materials Availability Statement*

310 New casts/fossil replicas generated for this study are housed in the collections of the  
311 Sedgwick Museum, Department of Earth Sciences, University of Cambridge. Specific  
312 accession numbers are provided in the main text/figure captions, and denoted with a CAMSM  
313 prefix in the text. CAMES refers to specimens in the Department of Earth Sciences,  
314 University of Cambridge. Material can be viewed upon arrangement with the Sedgwick  
315 Museum curatorial staff.

316 All original material from Newfoundland remains in the field. Access to field  
317 localities for scientific research is by permit only. Applications to obtain a permit to work  
318 within the Mistaken Point Ecological Reserve should be directed to the Department of  
319 Fisheries and Land Resources, Government of Newfoundland and Labrador  
320 ([www.flr.gov.nl.ca/natural\\_areas/wer/r\\_mpe/permits.html](http://www.flr.gov.nl.ca/natural_areas/wer/r_mpe/permits.html)). For more information please  
321 contact the Reserve Manager. Permits for palaeontological research elsewhere in  
322 Newfoundland, including all sites on the Bonavista Peninsula, are required under the  
323 Palaeontological Resource Regulations of the Historic Resources Act (Regulation 67/11), and  
324 issued by the Department of Tourism, Business and Innovation. Enquiries should be directed  
325 to the Provincial Archaeologist.

326

327 *Lead Contact Information*

328 Requests for information should be directed to and will be fulfilled by the Lead Contact, Alex  
329 Liu (agscl2@cam.ac.uk).

330

### 331 **EXPERIMENTAL MODEL AND SUBJECT DETAILS**

332 All original fossil material used in this study remains in the field, and individual specimens  
333 have not been allocated accession numbers. Exceptions to this are:

- 334 • One thin section through a filamentous impression from the MUN Surface, Bonavista  
335 Peninsula, Newfoundland, Canada (Cambridge Department of Earth Sciences  
336 Collections number CAMES N12-PU9-1A).
- 337 • One rock sample of a microbial mat surface with filamentous impressions from the  
338 Ediacaran Lyamtsa Formation, White Sea Coast, Russia (Cambridge Department of  
339 Earth Sciences Collections number CAMES WS17-LY2-1).

340 Casts of Ediacaran partial bedding planes containing impressions of studied rangeomorph  
341 fossils (representing multiple taxa) and filaments were also studied and imaged. Figured  
342 specimens can be found on the following casts:

- 343 • Sedgwick Museum Collections numbers CAMSM X 50340.1 CST1, and CAMSM X  
344 50341.1 CST1 to 50341.5 CST1, from Newfoundland, Canada.
- 345 • British Geological Survey Collections number BGS GSM 105875, mould 6, which is  
346 a cast of the Ediacaran North Quarry Bed B fossil surface, Charnwood Forest,  
347 Leicestershire, U.K.

348

### 349 **METHOD DETAILS**

350 Filamentous fossils are observed in association with frondose taxa of the Ediacaran  
351 macrobiota on 38 distinct fossil-bearing bedding plane horizons on the Avalon and Bonavista

352 peninsulas of eastern Newfoundland, Canada. They are most abundant in the Briscal,  
353 Mistaken Point, Trepassey and Fermeuse Formations of the Conception and St. John's  
354 Groups. The material figured herein is derived primarily from four fossil-bearing horizons,  
355 namely: the MUN and PU13 surfaces within the Port Union Member of the Trepassey  
356 Formation [56], and the LC6 surface within the Catalina Member of the Trepassey Formation  
357 (see bed LC6 in [57]), all of which lie within the Catalina Dome antiform of the Bonavista  
358 Peninsula (Figure S1); and the Brasier Surface (BR5, see [58]) within the Briscal Formation  
359 at Mistaken Point Ecological Reserve (MPER). Precise locality information for these sites  
360 cannot be published since they are protected by Provincial legislation, but GPS co-ordinates  
361 are available from the authors upon request.

362         Filamentous fossils are preserved as positive epirelief casts on bedding plane surfaces,  
363 within terrigenous and volcanogenic sedimentary rock successions deposited in sub-photic  
364 marine slope and basin depositional environments [42, 57, 59]. Preservation quality of the  
365 fossils is often patchy on individual surfaces, but can be locally exceptional, with the  
366 distribution of high-quality preservation dictated by both original and modern taphonomic  
367 processes [57, 60]. Filamentous fossils are not seen on all fossil-bearing surfaces, even when  
368 preservation of other taxa is relatively good (e.g. on the Mistaken Point 'D' Surface). This  
369 suggests that in addition to a modern taphonomic control on the presence and abundance of  
370 filamentous fossils (their very low topographic relief results in increased susceptibility to loss  
371 due to physical weathering), their distributions may also reflect primary ecological, or  
372 taphonomic (e.g. growth within microbial mats/substrate), controls.

373         Provincial law prohibits collection of fossil specimens in Newfoundland, so  
374 filamentous material was either photographed in the field, or moulded using silicon rubber  
375 under the conditions of scientific research permits (see details above), with replica casts

376 produced later in the laboratory. The specimen subjected to thin sectioning originates from a  
377 sedimentary sample collected prior to 2011.

378         Specimens of filamentous fossils from Charnwood Forest, U.K. (see Figure S4), were  
379 identified either directly on bedding planes (at Memorial Crag), or from casts of the North  
380 Quarry Bed B fossil surface displayed at the New Walk Museum, Leicester [see 26]. These  
381 casts were originally taken from moulds housed at the British Geological Survey (BGS),  
382 Keyworth, U.K. Original specimens and latex peels from the Ediacara Member of the  
383 Rawnsley Quartzite, South Australia were studied and photographed in the South Australia  
384 Museum, Adelaide, or observed in the field at Ediacara Conservation Park and Nilpena  
385 National Heritage Site in South Australia. Russian material from the Lyamtsa and Verkhovka  
386 Formations was observed in the field at sites along the Solza River and the White Sea  
387 summer coast.

388

### 389 **QUANTIFICATION AND STATISTICAL ANALYSIS**

390 Filament densities were calculated either by counting in the field, or by counting individual  
391 specimens on casts of key surfaces under controlled lighting conditions in the laboratory. For  
392 beds LC6 and MUN, orientations of filaments on the surfaces were obtained from casts  
393 CAMSM X 50341.4 CST1 and CAMSM X 50340.1 CST1 respectively. The casts were fixed  
394 in place on a flat, non-metallic surface, and a compass was used to measure filament  
395 orientation over the area represented by the cast, with each measured filament then marked to  
396 ensure no duplication of measurements. Primary cleavage directions, and frond orientations,  
397 were measured from the casts at the same time. Since filament orientations are bidirectional  
398 (there is no single polarity to a filament), a second value for orientation of each specimen was  
399 obtained by adding 180° to the measured orientation (explaining why the presented rose  
400 diagrams are bi-radially symmetrical). V=Orientation values were plotted as rose diagrams

401 using Rozeta 2.0. For the LC6 surface,  $n = 107$  (number of individual measured filaments),  
402 and data are presented in Figure 2A. The MUN surface data are presented in Figure 1C,  
403 where  $n = 224$ .

404

#### 405 *Normalized data for frond-filament interactions*

406 It would be desirable to include normalized data regarding the nature of the relationship  
407 between fronds and filaments on the studied bedding surfaces, to determine whether their  
408 inferred associations are statistically significant. Specifically, the possibility that observed  
409 physical contact between filaments and the holdfasts of frondose specimens could be a  
410 chance occurrence is something that could be investigated. We considered this problem at  
411 length, and ultimately did not provide such data because we do not deem the surfaces to  
412 faithfully reflect original abundances and morphologies of the features of interest. We  
413 question whether observed filaments faithfully reflect the original morphologies (particularly  
414 lengths) of the specimens; whether all filaments and fronds in the palaeocommunity are  
415 recorded on the surface; and whether the filaments were entirely surficial features (i.e. it is  
416 possible that they were intertwined with the substrate). These concerns mean that any  
417 normalized data we could present would not necessarily be reliable or meaningful. The  
418 following points explain our reasoning for not including normalized data in the manuscript.

419

#### 420 *The influence of taphonomy*

421 In order to obtain meaningful spatial data regarding the relationships between fronds and  
422 filaments, a sufficient/representative areal extent of preserved bedding plane is required.  
423 Since the filaments are small, and oriented in all directions, such a surface must exhibit 100%  
424 exposure at a level of preservational quality sufficient to permit recognition of both fronds  
425 and filaments if they are present. Sadly, such surfaces are rarely encountered. The fossil sites

426 in Newfoundland possess the most abundant record of filamentous structures we have  
427 observed, and thus offer the best prospects for spatial studies. Filaments are not found on all  
428 surfaces, and it is difficult to determine whether they were ever originally present on a  
429 surface, since their low topographic relief is readily effaced and worn away by modern  
430 weathering and erosional processes [60]. Many large surfaces with excellent preservation of  
431 fronds do not preserve filamentous impressions (e.g. the Mistaken Point 'D' and 'E'  
432 surfaces).

433           Where filaments can be observed, portions of their host bedding planes are often not  
434 amenable to study, either because the surface is cleaved or locally/patchily weathered (e.g.  
435 bed BR5), or because ash coverage remains on top of parts of the surface. On other surfaces,  
436 filaments are either very rare, or the surface itself is smaller than that required for meaningful  
437 statistical assessment. Further surfaces that possess sufficient exposure and areal extent suffer  
438 in having undergone preferential loss of fidelity of either filaments or fronds owing to their  
439 specific weathering/erosional regime (spalling or effacement [60]), and quantitative data from  
440 such surfaces would therefore be questionable. These factors combine to leave us with only  
441 two suitable surfaces where meaningful coverage of well-preserved fronds and filaments is  
442 available.

443           The low topographic relief of filaments also means that it is often difficult to see  
444 them in the field, so for quantitative data, replica casts studied under controlled lighting  
445 conditions are required. Our figured cast of bed LC6, one of the best available surfaces for  
446 preservation of fronds and filaments, covers an area of  $\sim 0.5\text{m}^2$ , but it was clear when taking  
447 orientation measurements that filament distribution, even on a 'densely populated' surface, is  
448 uneven and reveals patches on a scale of tens of centimetres. These patches may be  
449 taphonomic or original, but any cast smaller than this size is unlikely to permit recognition of  
450 such variation.

451

452 *The nature of filamentous connections and holdfast preservation*

453 Our interpretation of the filamentous structures suggests that although observed examples lay  
454 on the surface of the ancient seafloor at the time of burial, it is entirely possible that they  
455 could also lie beneath or within the microbial mat communities, where they would not  
456 necessarily be included on the plane of preservation. It is also possible that individual  
457 filaments wove into and out of the plane of preservation, perhaps providing an explanation  
458 for the difficulty encountered in identifying a clear termination point for many of them. We  
459 can only assume that all filaments that were present at the time of burial are observable today  
460 if we can be confident that they were originally only present *on* the bed surface. However, if  
461 they did extend into the mat, there may have been many filamentous structures present within  
462 the assemblage that were not preserved at the horizon of preservation. We cannot currently  
463 discriminate between these possibilities beyond the discussion already included in the main  
464 text. There are also examples of fronds and stems preserved without a visible discoidal  
465 holdfast, most likely because the disc was buried beneath the mat. In such cases, the areal  
466 extent of the disc can only be estimated, rather than directly measured, and it may therefore  
467 not be possible to determine whether there are direct terminations of filaments at such  
468 structures. Obtaining accurate numbers, orientations and positions of filaments and discs,  
469 which constitute the necessary data required to calculate the likelihood of chance encounters  
470 between filaments and frondose taxa, is therefore fraught with uncertainty regarding whether  
471 what we are seeing is a faithful reflection of the original palaeocommunity. Since we are  
472 unable to quantify the magnitude of the likely influence of these factors on the observed  
473 surfaces, we do not deem it possible to present meaningful data concerning this question at  
474 the current time.

475

476 *Additional influences*

477 We must also consider original ecological variation. We interpret the observation of a  
478 filament in association with a disc in a fossil assemblage to suggest that filaments may have  
479 been associated with fronds. However, the absence of a filament terminating at a  
480 frond/holdfast does not imply that there wasn't one originally. The filament could have  
481 detached before burial; it could lie outside of the plane of preservation; or it could have  
482 simply never been there at all. Distinguishing between these possibilities is currently not  
483 possible, and further complicates efforts to statistically determine the relative number of  
484 chance encounters. It is also possible that more than one biological entity is represented  
485 amongst the broad 'filament' grouping we observe.

486           In sum, we could obtain spatial data to provide estimates of chance encounters, but  
487 in most cases it would not be possible to demonstrate that the data would be representative of  
488 the original palaeocommunity. Even if it were, the way in which we interpret the assemblage  
489 could bias our wider interpretations.

490

#### 491 **DATA AND CODE AVAILABILITY**

492 This study did not generate/analyse datasets/code other than the filament orientation dataset  
493 for the rose plots presented in the published article.

494

#### 495 **KEY RESOURCES TABLE**

496 Please see the accompanying file.

497

498 **Supplementary Information** in the form of a Supplementary File with four supplemental  
499 figures can be found at [xxxxxxx](#).



500

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