

# Filamentous connections between Ediacaran fronds

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**Short Title: Ediacaran filamentous connections**

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

There is no indication that the filamentous structures were rigid (given their propensity to bend/change direction in many examples), implying that they were not biomineralized. Amongst extant marine taxa, non-mineralized filamentous outgrowths of comparable gross morphology occur in algae (where they link individual fronds), certain metazoans (where they link polyps/individuals), and fungal mycelia. The outgrowths typically fulfil stabilization, defence, nutrient transport, or (asexual) reproductive roles involving budding or stoloniferous growth, for example in extant algae (e.g. the green alga *Caulerpa*), terrestrial plants, and metazoans including sponges [46], colonial cnidarians [47], entoprocts [48] and bryozoans [49]. These different functions of filamentous outgrowths are not mutually exclusive, and all remain potential candidates for the function of the Ediacaran filaments we describe, given available evidence and sedimentary context.

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



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

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

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## **Figure Legends:**

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

Filaments are preserved as positive epirelief impressions beneath fine-grained tuffs. **(A)**  
Negative epirelief holdfast, with positive epirelief filaments running across (inferred to be  
beneath) and around it. PU13 Surface. **(B)** Dense superimposed filament assemblages,  
showing superposition and directional changes, PU13 Surface. **(C)** Abundant filaments from  
the MUN Surface. Note filament superposition (arrowed at left) and bundling (arrowed at  
right). Inset: orientations of all filaments present on cast CAMSM X 50340.1 CST1, from the  
MUN Surface. Orange arrows denote the range of orientations of frondose taxa (indicating  
perceived current direction). Blue bars indicate primary fracture directions. **(D)** Further  
filaments, including one specimen that overlies another (arrowed, PU13 Surface). **(E)**  
Filamentous structure (white arrows) seemingly wrapped around a concentric holdfast disc  
(black arrow). All scale bars = 10 mm, except E = 10 cm. See also Figure S1.

**Figure 2. Rangeomorph fronds and associated filaments on the LC6 Surface, Little Catalina, Newfoundland.** (A) Two large rangeomorph fronds, seemingly connected by a filamentous structure (white arrows) that transits between their holdfasts (black arrows) and then continues across the surface, tracing an inverted ‘z’ shape on the surface (photograph from cast CAMSM X 50341.4 CST1). See Figures 3 and S2 for additional images. Inset: orientations of all filaments present on this cast. Orange arrows denote the range of orientations of frondose taxa (indicating perceived current direction). Blue bars indicate primary (thick) and secondary (thin) cleavage directions. (B–F) Further examples of multiple filaments (arrowed) converging on the holdfasts (circled) of rangeomorph specimens. The specimens in (D: CAMSM X 50341.2 CST1) and (E: CAMSM X 50341.3 CST1) lie along the same filament (see Figure S3), which continues beyond both of them. All examples are of the same, as yet un-named, rangeomorph taxon. Scale bars A = 10 cm, B–F = 10 mm.

**Figure 3. Close up images of seemingly connected rangeomorphs on the LC6 Surface (cast CAMSM X 50341.4 CST1).** (A–B) The rangeomorph frond on the right of Figure 2A with multiple filamentous structures converging on its holdfast disc. (C–D) The large rangeomorph at left in Figure 2A, showing the spatial relationship between its holdfast and prominent filaments, which terminate at the holdfast margin. (E) Zoomed out view of the frond in (C) showing how the filament leading to the second frond (bottom of Figure 2A) branches ~20 cm before reaching that specimen, with the branching filament (arrowed) possessing a trajectory that directly intersects the holdfast of the frond in (C). (F) Close up of the bulbous branching junction (arrowed) between the filaments in (E). N.B. additional thinner filaments traverse the surface in multiple directions nearby. Scale bar gradations in centimetres and millimetres.

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

(A) *Fractofusus andersoni* from bed BR5, MPER, with a filament seemingly extending from one end of the specimen midline. (B) Filaments on the MUN Surface, including one specimen that terminates at the holdfast disc (circled) of a small *Charniodiscus* specimen. (C) *Primocandelabrum* sp. (MUN Surface), with associated filaments (arrowed) that appear to terminate at its holdfast. (D) *Charnia masoni* (cast CAMSM X 50341.5 CST1) from the LC6 surface, associated with two prominent curving filaments (arrowed) that converge on its holdfast. (E) ‘Ostrich feather’ specimen from the LC6 surface. Note the ray-like projections of variable length emanating from the holdfast disc (black arrows), with one filament (white arrow) extending from the holdfast over a greater distance of several centimetres. Scale bars = 10 mm.

**STAR Methods:**

**LEAD CONTACT AND MATERIALS AVAILABILITY**

*Materials Availability Statement*

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

All original material from Newfoundland remains in the field. Access to field localities for scientific research is by permit only. Applications to obtain a permit to work

within the Mistaken Point Ecological Reserve should be directed to the Department of Fisheries and Land Resources, Government of Newfoundland and Labrador ([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 contact the Reserve Manager. Permits for palaeontological research elsewhere in Newfoundland, including all sites on the Bonavista Peninsula, are required under the Palaeontological Resource Regulations of the Historic Resources Act (Regulation 67/11), and issued by the Department of Tourism, Business and Innovation. Enquiries should be directed to the Provincial Archaeologist.

#### *Lead Contact Information*

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

## **EXPERIMENTAL MODEL AND SUBJECT DETAILS**

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

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

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

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

## **METHOD DETAILS**

Filamentous fossils are observed in association with frondose taxa of the Ediacaran macrobiota on 38 distinct fossil-bearing bedding plane horizons on the Avalon and Bonavista peninsulas of eastern Newfoundland, Canada. They are most abundant in the Briscal, Mistaken Point, Trepassey and Fermeuse Formations of the Conception and St. John's Groups. The material figured herein is derived primarily from four fossil-bearing horizons, namely: the MUN and PU13 surfaces within the Port Union Member of the Trepassey Formation [56], and the LC6 surface within the Catalina Member of the Trepassey Formation (see bed LC6 in [57]), all of which lie within the Catalina Dome antiform of the Bonavista Peninsula (Figure S1); and the Brasier Surface (BR5, see [58]) within the Briscal Formation at Mistaken Point Ecological Reserve (MPER). Precise locality information for these sites cannot be published since they are protected by Provincial legislation, but GPS co-ordinates are available from the authors upon request.

Filamentous fossils are preserved as positive epirelief casts on bedding plane surfaces, within terrigenous and volcanogenic sedimentary rock successions deposited in sub-photic marine slope and basin depositional environments [42, 57, 59]. Preservation quality of the fossils is often patchy on individual surfaces, but can be locally exceptional, with the distribution of high-quality preservation dictated by both original and modern taphonomic processes [57, 60]. Filamentous fossils are not seen on all fossil-bearing surfaces, even when

preservation of other taxa is relatively good (e.g. on the Mistaken Point ‘D’ Surface). This suggests that in addition to a modern taphonomic control on the presence and abundance of filamentous fossils (their very low topographic relief results in increased susceptibility to loss due to physical weathering), their distributions may also reflect primary ecological, or taphonomic (e.g. growth within microbial mats/substrate), controls.

Provincial law prohibits collection of fossil specimens in Newfoundland, so filamentous material was either photographed in the field, or moulded using silicon rubber under the conditions of scientific research permits (see details above), with replica casts produced later in the laboratory. The specimen subjected to thin sectioning originates from a sedimentary sample collected prior to 2011.

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

## QUANTIFICATION AND STATISTICAL ANALYSIS

Filament densities were calculated either by counting in the field, or by counting individual specimens on casts of key surfaces under controlled lighting conditions in the laboratory. For beds LC6 and MUN, orientations of filaments on the surfaces were obtained from casts



CAMSM X 50341.4 CST1 and CAMSM X 50340.1 CST1 respectively. The casts were fixed in place on a flat, non-metallic surface, and a compass was used to measure filament orientation over the area represented by the cast, with each measured filament then marked to ensure no duplication of measurements. Primary cleavage directions, and frond orientations, were measured from the casts at the same time. Since filament orientations are bidirectional (there is no single polarity to a filament), a second value for orientation of each specimen was obtained by adding 180° to the measured orientation (explaining why the presented rose diagrams are bi-radially symmetrical). V=Orientation values were plotted as rose diagrams using Rozeta 2.0. For the LC6 surface, n = 107 (number of individual measured filaments), and data are presented in Figure 2A. The MUN surface data are presented in Figure 1C, where n = 224.

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

It would be desirable to include normalized data regarding the nature of the relationship between fronds and filaments on the studied bedding surfaces, to determine whether their inferred associations are statistically significant. Specifically, the possibility that observed physical contact between filaments and the holdfasts of frondose specimens could be a chance occurrence is something that could be investigated. We considered this problem at length, and ultimately did not provide such data because we do not deem the surfaces to faithfully reflect original abundances and morphologies of the features of interest. We question whether observed filaments faithfully reflect the original morphologies (particularly lengths) of the specimens; whether all filaments and fronds in the palaeocommunity are recorded on the surface; and whether the filaments were entirely surficial features (i.e. it is possible that they were intertwined with the substrate). These concerns mean that any

normalized data we could present would not necessarily be reliable or meaningful. The following points explain our reasoning for not including normalized data in the manuscript.

#### *The influence of taphonomy*

In order to obtain meaningful spatial data regarding the relationships between fronds and filaments, a sufficient/representative areal extent of preserved bedding plane is required. Since the filaments are small, and oriented in all directions, such a surface must exhibit 100% exposure at a level of preservational quality sufficient to permit recognition of both fronds and filaments if they are present. Sadly, such surfaces are rarely encountered. The fossil sites in Newfoundland possess the most abundant record of filamentous structures we have observed, and thus offer the best prospects for spatial studies. Filaments are not found on all surfaces, and it is difficult to determine whether they were ever originally present on a surface, since their low topographic relief is readily effaced and worn away by modern weathering and erosional processes [60]. Many large surfaces with excellent preservation of fronds do not preserve filamentous impressions (e.g. the Mistaken Point ‘D’ and ‘E’ surfaces).

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

two suitable surfaces where meaningful coverage of well-preserved fronds and filaments is available.

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

#### *The nature of filamentous connections and holdfast preservation*

Our interpretation of the filamentous structures suggests that although observed examples lay on the surface of the ancient seafloor at the time of burial, it is entirely possible that they could also lie beneath or within the microbial mat communities, where they would not necessarily be included on the plane of preservation. It is also possible that individual filaments wove into and out of the plane of preservation, perhaps providing an explanation for the difficulty encountered in identifying a clear termination point for many of them. We can only assume that all filaments that were present at the time of burial are observable today if we can be confident that they were originally only present *on* the bed surface. However, if they did extend into the mat, there may have been many filamentous structures present within the assemblage that were not preserved at the horizon of preservation. We cannot currently discriminate between these possibilities beyond the discussion already included in the main text. There are also examples of fronds and stems preserved without a visible discoidal holdfast, most likely because the disc was buried beneath the mat. In such cases, the areal

extent of the disc can only be estimated, rather than directly measured, and it may therefore not be possible to determine whether there are direct terminations of filaments at such structures. Obtaining accurate numbers, orientations and positions of filaments and discs, which constitute the necessary data required to calculate the likelihood of chance encounters between filaments and frondose taxa, is therefore fraught with uncertainty regarding whether what we are seeing is a faithful reflection of the original palaeocommunity. Since we are unable to quantify the magnitude of the likely influence of these factors on the observed surfaces, we do not deem it possible to present meaningful data concerning this question at the current time.

#### *Additional influences*

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

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

## DATA AND CODE AVAILABILITY

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

## KEY RESOURCES TABLE

Please see the accompanying file.

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

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