

1 **Reconstructing the reproductive mode of an Ediacaran macro-organism**

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11 Enigmatic macrofossils of late Ediacaran age (580–541 million years ago [Ma]) provide the
12 oldest known record of diverse complex organisms on Earth, lying between the microbially-
13 dominated ecosystems of the Proterozoic and the Cambrian emergence of the modern
14 biosphere.¹ Among the oldest and most enigmatic of these macrofossils are the
15 Rangeomorpha, a group characterized by modular, self-similar branching and a sessile
16 benthic habit.^{2,3,4} Localized occurrences of large *in situ* fossilized rangeomorph populations
17 allow fundamental aspects of their biology to be resolved using spatial point techniques.⁵
18 Here, we use such techniques to identify recurrent clustering patterns in the rangeomorph
19 *Fractofusus*, revealing a complex life history of multigenerational, stolon-like asexual
20 reproduction, interspersed with dispersal of waterborne propagules. Ecologically, such a
21 habit would have allowed for both the rapid colonisation of a localized area and transport to
22 new, previously uncolonized areas. The capacity of *Fractofusus* to derive adult morphology
23 via two distinct reproductive modes documents the sophistication of its underlying
24 developmental biology.

25 Late Ediacaran sedimentary strata (~580–541Ma) of Newfoundland and the UK are
26 dominated by rangeomorphs, whose unique self-similar branching construction³ makes
27 resolution of their phylogenetic relationships, or even their basic biology, difficult.¹ The
28 occurrence of rangeomorphs in conspicuously deep-water sediments has led to a general
29 consensus that they were heterotrophic,⁶ while the global distribution of charniids (a
30 rangeomorph sub-group) has been interpreted as evidence for reproduction via waterborne
31 propagules.⁷ In the present study we use spatial statistics and modelling^{5,9} in a novel
32 approach to illuminate the reproductive biology and underlying ecology of one of the most
33 abundantly-preserved rangeomorph fossils, *Fractofusus*.⁸

34
35 We analysed three large bedding-plane assemblages of *Fractofusus* in SE Newfoundland: 1)
36 the ‘D’ surface and 2) the ‘E’ surface at Mistaken Point, Avalon Peninsula;^{8,10} and 3) the H14
37 surface on Bonavista Peninsula (locality 14 of Hofmann et al.)¹¹ (Extended data Fig. 1a-c). A
38 volcanic tuff directly above the ‘E’ surface has been dated to 565 ±3 Ma,¹² which also
39 constrains the age of the underlying ‘D’ surface. Regional lithostratigraphic correlations
40 suggest that the H14 surface is a few million years younger than the Mistaken Point beds.¹¹
41 All three assemblages occur within deep-marine turbidite sequences, with *Fractofusus* fossils
42 preserved as negative epirelief external moulds in siltstone hemipelagites, cast from above by
43 volcanoclastic deposits.⁶

44
45 *Fractofusus* is conspicuously endemic, restricted almost exclusively to southeastern
46 Newfoundland,¹³ where it dominates many macrofossil assemblages.¹⁰ *Fractofusus* has a
47 rounded, elongate spindle-like morphology, with two (arguably three^{2,13}) offset rows of
48 irregularly alternating, self-similar, subdivided frondlets arranged along a central axis.^{2,14}
49 *Fractofusus* specimens range from 1cm to 42cm in length² (Fig. 1a,b); two species have been

50 described, distinguished by their length:width ratios.² The ‘D’ and ‘E’ surfaces are dominated
51 by the elongate form, *Fractofusus misrai* (L/W=3.2, Fig. 1a), whereas the more ovate
52 *Fractofusus andersoni* (L/W=1.6, Fig. 1b) dominates the H14 surface.¹⁰ *Fractofusus* occurs
53 in dense benthic populations and exhibits no evidence of motility or current orientation.²
54 Together with nearest neighbour spatial analyses,¹⁰ these observations point to a sessile,
55 recumbent, benthic mode of life in aggregated communities.

56

57 The spatial positions of *Fractofusus* were mapped to millimetre-scale resolution using
58 differentiated GPS (Extended data Figs. 1d-f) on the two surfaces at Mistaken Point, and by
59 tracing specimen outlines onto acetate sheets at H14; significantly, this latter approach also
60 allowed size data to be recorded (Extended data Fig. 1f). The ‘D’ and ‘E’ surface data were
61 corrected for tectonic deformation prior to analysis (Extended data Fig. 2).⁷ Heterogeneous
62 Poisson models were used to identify possible distortions arising from differential erosion of
63 the bedding planes (Supplementary Table 1). Pair correlation functions (PCF) were
64 calculated to describe the spatial distributions of taxa on each bedding plane.⁵ Monte Carlo
65 simulations¹⁵ and Diggle’s goodness-of-fit test⁵ (the p-value p_d , where $p_d=1$ indicates a perfect
66 model fit and $p_d=0$ indicates no fit), were used to compare the fit of different spatial models
67 to the data (specifically homogeneous and heterogeneous Poisson models¹⁶ and single and
68 double homogeneous and heterogeneous Thomas cluster models).¹⁶ PCFs were also used to
69 describe the spatial distributions of taxa other than *Fractofusus* on the ‘D’ and ‘E’ surfaces.
70 For the H14 surface, spatial relationships between three distinct *Fractofusus* size classes
71 (defined in Methods, Extended data Figs. 3a,b) were analysed by calculating partial PCF⁵ and
72 comparing model fit of bivariate shared parents models (SP) with linked cluster models
73 (LCM).¹⁶ Finally, spatial directionality was investigated by plotting their generalised K-

74 functions¹⁷ from 0° to 360° (isotropy plots), allowing visualisation of the relative directional
75 positions of specimens (Fig. 3).

76

77 Non-random spatial distributions of sessile organisms, i.e. those that do not exhibit complete
78 spatial randomness (CSR), can be explained by either extrinsic factors (e.g. environmental
79 heterogeneities), or intrinsic reproduction.¹⁸ Identifying the processes behind such patterns is
80 not straight-forward; however, extrinsically-induced patterns are generally best modelled by
81 heterogeneous Poisson models,¹⁸ which describe randomly distributed points with a non-
82 uniform density across the sampled area. In contrast, intrinsic processes typically generate
83 Thomas cluster models,¹⁸ where the points within each cluster have a normal density
84 distribution centred on a parent point.

85

86 All three populations of *Fractofusus* were found to be significantly aggregated, conforming
87 closely to homogeneous Thomas cluster models (Fig. 2a). Specimens on the ‘E’ and H14
88 surfaces are aggregated at two spatial scales, forming clusters of clusters (Fig. 2a,b). On the
89 ‘E’ surface, this distribution is best modelled by a nested homogeneous double Thomas
90 cluster model of 23 clusters (radius $r=0.242\text{m}$), each containing 12 smaller clusters
91 ($r=0.074\text{m}$) of 3 specimens ($p_d=0.76$). The H14 surface distribution is best modelled by a
92 nested homogeneous double Thomas cluster model of 24 large clusters ($r=0.237\text{m}$), each
93 containing 6 clusters ($r=0.079\text{m}$) of 8 specimens ($p_d=0.89$). The ‘D’ surface distribution
94 forms discrete clusters (not clusters of clusters), which are best modelled by a single Thomas
95 cluster model ($p_d=0.77$) with 338 *Fractofusus* clusters of 3 specimens ($r = 0.086\text{m}$) (Extended
96 data Tables 1–2). Importantly, the spatial distribution on the ‘E’ surface can also be
97 modelled by the nested double cluster pattern found on the H14 surface (Fig. 2b) (p_d^{Hon}
98 $E=0.51$), strongly implying the same underlying process for both distributions (Fig. 2b,

99 Extended data Table 4). The spatial distribution of *Fractofusus* on the ‘D’ surface is
100 conspicuously similar to that seen in the larger specimens on H14 (Extended data Fig. 4e). By
101 contrast, the spatial distributions of other taxa – *Thectardis*, *Primocandelabrum* and
102 *Charniodiscus* – exhibit fundamentally different magnitudes and spatial scales of
103 aggregation, both to each other and to those of *Fractofusus* (Fig. 2b and Extended data Tables
104 3, 5).

105
106 The close fit of *Fractofusus* spatial distributions to single and nested double Thomas cluster
107 models strongly suggests that they derive from reproductive rather than extrinsic
108 (environmental) factors. Reproductive biology is further corroborated by size analysis of the
109 *Fractofusus* population on the H14 surface (Fig. 2c, Extended data Figs. 4a,c,d), which
110 reveals strikingly different spatial patterns for each of the three size classes (Fig. 2c,
111 Extended data Tables 1–2). Whereas the largest size class (>11.0cm) is randomly distributed
112 ($p_d=0.30$), both the intermediate (5.5–11.0cm) and smallest (<5.5cm) size classes are
113 hierarchically clustered: small individuals cluster around intermediate individuals
114 ($p_d^{LCM}=0.74$ versus $p_d^{SP}=0.03$; Extended data Table 5), which in turn cluster around large
115 individuals ($p_d^{LCM}=0.66$ versus $p_d^{SP}=0.01$). In other words, the smallest specimens form
116 clusters (homogeneous nested double Thomas cluster model ($p_d=0.72$)) around intermediate-
117 sized specimens (homogeneous single Thomas cluster model; $p_d=0.51$), which are themselves
118 clustered around randomly distributed large specimens (homogeneous Poisson model
119 $p_d=0.31$; Figs. 2c, 4, Extended data Fig. 5, Extended data Tables 1–2). Moreover, the
120 isotropy plots for H14 (Fig. 3) show strong directionality for the large size class, but limited
121 directionality for the medium and small size classes. The nested clusters on the ‘E’ and H14
122 surfaces suggest three generations, while the single clusters on the ‘D’ surface suggest two,
123 reflecting an earlier stage in population development. The difference is consistent with the

124 suggestion that the ‘D’ surface records an earlier stage in the ecological succession of
125 Ediacaran macroscopic communities¹⁰ (SI:2:3).

126

127 As with other Ediacaran macrofossils, there is no direct fossil evidence of reproductive habits
128 in *Fractofusus*, but its recurrent distribution on bedding surfaces provides a statistically
129 robust approach for inferring the underlying processes.¹⁹ In modern oceans, large sessile
130 organisms typically reproduce by means of waterborne propagules, fragmentation/budding,
131 and/or stolons (i.e., production of asexual clones that are at least initially connected to the
132 parent by specialized outgrowths).

133

134 Spatial distribution of waterborne propagules – including both sexual and asexual spores, as
135 well as sub-millimetre buds and fragments – are a function of current and rate of sinking.
136 Even with rapid sinking ($\sim 1\text{mm/s}$)²⁰ and slow currents ($\sim 1\text{cm/s}$), propagules released from
137 the dorsal surface of a ‘parental’ *Fractofusus* ($\sim 2\text{--}3\text{cm}$ above the substrate) would have been
138 current aligned²¹ and dispersed by decimetres or more.²² Slow descent times also correspond
139 with right-skewed (mean greater than the median) density distributions.^{20,21} The random
140 spatial distribution of the H14 largest size class likely reflects a large dispersal distance
141 (Extended data Table 1), which coupled with its highly directional isotropy plot (Fig. 3a)
142 indicates that the largest specimens were strongly influenced by currents (c.f. Darroch et
143 al.^{7,10}) As such, they likely derive from waterborne propagules and represent the initial
144 establishment of a *Fractofusus* population on this surface.

145

146 The hierarchically clustered bedding plane distributions of small and medium *Fractofusus* on
147 H14 closely match patterns exhibited by organisms reproducing asexually via stolon-like
148 lateral extensions (Extended data Fig. 5).²³ Cluster distributions of the small and medium

149 size classes are also highly left-skewed (median greater than the mean), with the mean
150 distance from each “parent” to their “offspring” on the order of a few centimetres (Fig. 2a),
151 and offspring exhibiting no significant directionality or current orientation (Fig. 3b–c,
152 Extended data Fig. 3c). The reproducibility of the model distributions across the three
153 bedding-plane assemblages further attests to the indifferent effects of current: the spatial
154 distributions of non-tethered offspring would result in patterns dependent on current velocity,
155 which are unlikely to be consistent across multiple bedding planes in different localities.
156 Moreover, there are no recorded instances of buds or fragmentary specimens of *Fractofusus*
157 in any of its 5000+ documented specimens^{1,10,11,24} (see SI:2.5, SI:3). As such, the
158 *Fractofusus* clusters on the H14 surface are not consistent with waterborne propagules or
159 fragmentation/budding, but are directly comparable to stolon-like reproduction. Other taxa
160 exhibit an intriguing range of non-random habits, and our preliminary analyses indicate that
161 *Primocandelabrum* and *Charniodiscus* may have also reproduced using stolons.

162

163 Reproductive biology lies at the core of ecological and evolutionary dynamics, and its
164 positive identification in Ediacaran microfossils has the potential to illuminate the beginnings
165 of the modern marine biosphere. Previous studies of Ediacaran microfossils have
166 investigated the seasonality of reproduction⁷, identified putative stolons^{28,29}, and inferred
167 sexual or asexual reproduction based on biogeographic distribution or qualitative description
168 of local populations.^{7,10} In the case of phosphatized ‘embryo’ microfossils, internal cell
169 packages have been interpreted as evidence of germ-soma differentiation,³⁰ but it remains to
170 be seen how those fossils relate to the evolution of large and/or complex eukaryotes.

171

172 The identification in *Fractofusus* of a multigenerational asexual clonal phase, interspersed
173 with the release of waterborne propagules, is the first statistically robust account of

174 reproductive life history reported in an Ediacaran macrofossil. Such a strategy would have
175 allowed for the rapid exploitation of localized areas, as well as for transport to new,
176 previously uncolonized areas. The conclusion that *Fractofusus* could switch between
177 reproductive modes further reveals the sophistication of its underlying developmental
178 programme, capable not only of tissue differentiation, but also the generation of new
179 macroscopic individuals from both benthic stolons and waterborne propagules.

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258 **Supplementary Information**

259 Extended Data

260 Supplementary Methods

261 Supplementary Information

262 Supplementary Data

263

264 **Acknowledgements**

265 The Parks and Natural Areas Division, Department of Environment and Conservation,

266 Government of Newfoundland and Labrador provided permits to conduct research within the

267 Mistaken Point Ecological Reserve in 2010, while the Department of Tourism, Culture and

268 Recreation provided permits for paleontological research on the Bonavista Peninsula in 2012.

269 Readers are advised that access to both of the aforementioned fossil localities is by scientific

270 research permit only. Contact the relevant Department listed above for further information.

271 This work has been supported by the Natural Environment Research Council [grant numbers

272 NE/I005927/1 to C.G.K., NE/J5000045/1 to J.J.M., NE/L011409/1 to A.G.L. and
273 NE/G523539/1 to E.G.M.], and a Henslow Junior Research Fellowship from Cambridge
274 Philosophical Society to A.G.L. We thank Marc Laflamme for discussions on this
275 manuscript.

276

277 **Author Contributions**

278 E.G.M conceived the project, collected data on the ‘D’ and ‘E’ surfaces and ran the analyses.
279 C.G.K, A.G.L and J.J. M collected data on the H14 surface. All authors discussed the results
280 and prepared the manuscript.

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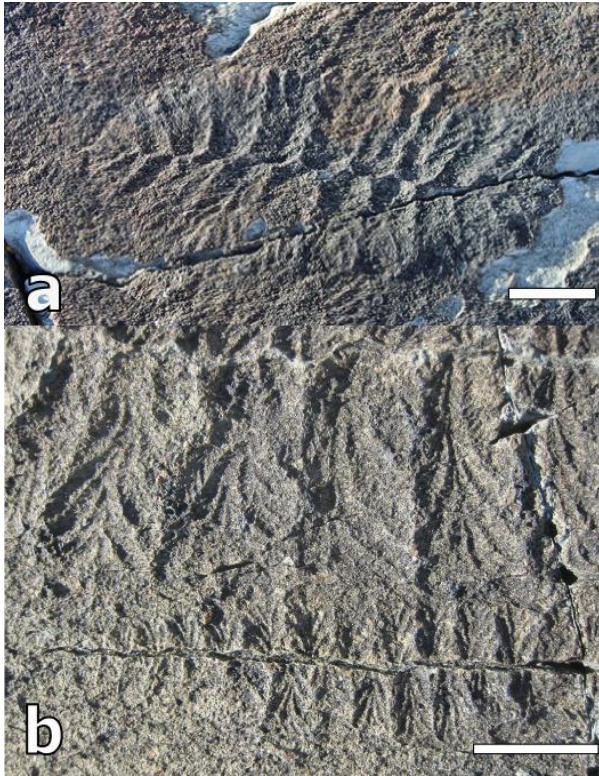
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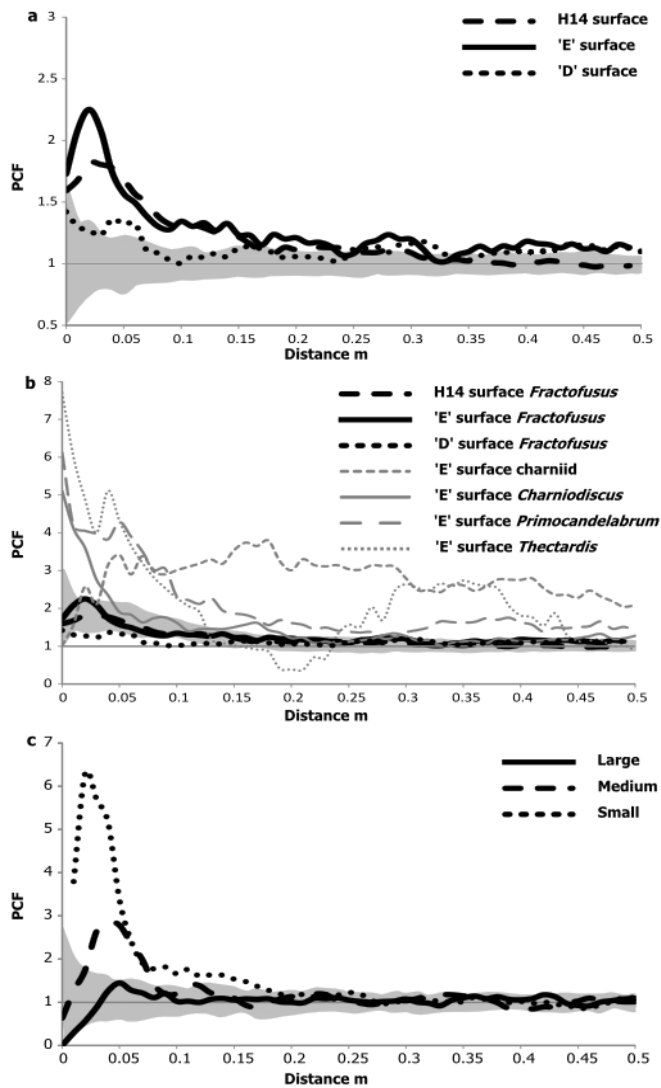
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295 **Figure 1:** **a**, *Fractofusus andersoni* specimen from the H14 surface. **b**, *Fractofusus misrai*
296 from the 'E' surface, showing a large size-class partial specimen (~20cm, above) alongside a
297 small size-class specimen (3.5cm in length, below). Scale bars = 1cm. Photographs are
298 unretrodeformed.

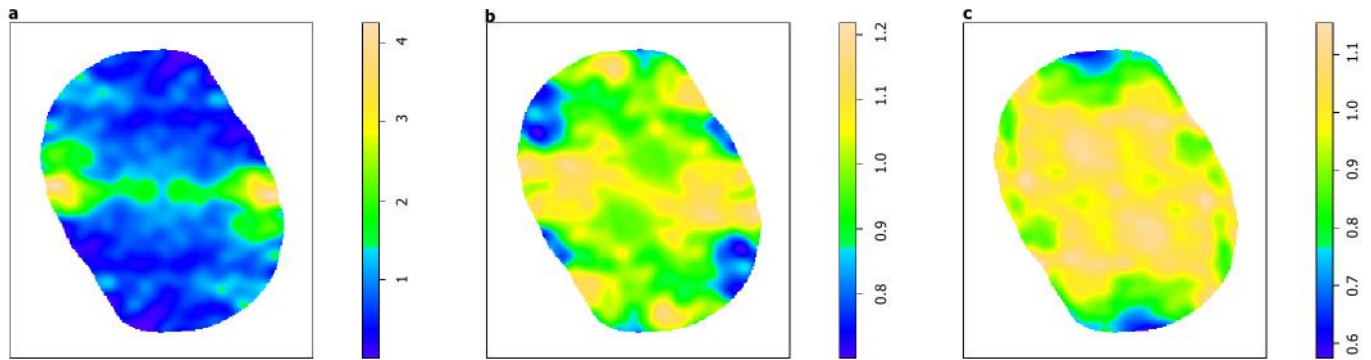


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300 **Figure 2:** PCF for mapped taxa. For all plots the x-axis is the inter-point distance between
 301 organisms in metres. The y-axis PCF=1 indicate CSR, <1 indicates segregation, and >1
 302 indicates aggregation. **a**, PCF for *Fractofusus* on the 'D' surface (1040 specimens), 'E'
 303 surface (1141 specimens) and H14 surface (1214 specimens). Grey shaded area depicts the
 304 bounds of 99 Monte Carlo simulations of CSR. Since the PCF curves are not completely
 305 within these areas, the CSR hypothesis is rejected and one can assume that the *Fractofusus*
 306 distributions on all three surfaces form cluster patterns ($p^D_d < 0.01$, $p^E_d < 0.01$, $p^{H14}_d < 0.01$). **b**,
 307 PCF for non-CSR 'E' surface taxa (charniid 76 specimens, *Charniodiscus* 326 specimens,
 308 *Primocandelabrum* 311 specimens and *Thectardis* 39 specimens). Grey shaded area depicts
 309 99 Monte Carlo simulation of the best-fit H14 surface model of double Thomas cluster

310 process. Note how the 'E' surface *Fractofusus* PCF follows the H14 surface PCF very
311 closely, and can be modelled by the same process ($p_d=0.51$). Other 'E' surface taxa have
312 dramatically different PCF to the *Fractofusus* PCF. **c**, PCF for the three size classes of
313 *Fractofusus* on H14 surface. Grey shaded area depicts the 99 Monte Carlo simulation of CSR
314 . The large size-class (350 specimens) exhibits CSR ($p_d=0.30$), the intermediate size-class
315 (310 specimens) shows aggregation $<0.10\text{m}$ (single Thomas cluster model ($p_d=0.51$)). The
316 small size-class (554 specimens) shows a large aggregation $<0.08\text{m}$ and a lesser aggregation
317 between 0.08m and 0.20m (double Thomas cluster model ($p_d=0.72$)).
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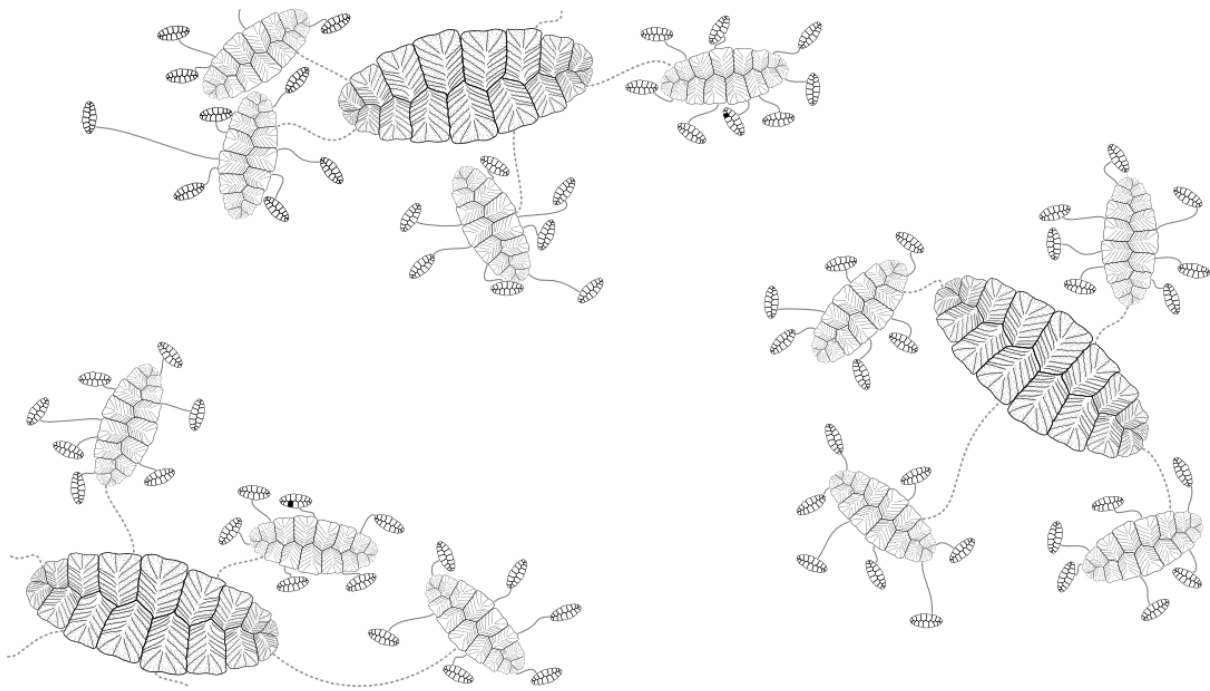
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Figure 3. Isotropy plots from the H14 surface for each size class of *Fractofusus*, providing a visualisation of specimen positions relative to one another. The vertical axis on each subfigure depicts the colour map of specimens/m² normalised to account for different densities between size-classes. A peak (<1) is shown in green or yellow and depicts clustering, while a dip (<1) is shown in blue and depicts segregation. If there are no directional effects then the colour map in every direction from the centre point should be similar. **a**, The large size-class shows strong anisotropy, with aggregation of up to 4 normalised specimens/m². In contrast the **b**, medium and **c**, small size-classes show isotropy, that is a relative evenness of aggregations with a maximum density variation up to 0.5 normalised specimens/m².

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339 **Figure 4:** Schematic diagram showing simplified *Fractofusus* spatial arrangements. The
340 actual number of clusters, and clusters within those clusters, is higher than shown (23 clusters
341 each containing 12 clusters of 3 specimens on the H14 surface), making their direct visual
342 detection challenging. No overlapping specimens are shown because, while the best-fit
343 models allow for overlaps, the observed PCF between the small size-class (Extended data
344 Fig. 4c,d) and the large size-class (Fig. 2b) shows a small segregation (<3cm) away from the
345 model behaviour, and a similar, non-significant segregation for the large size-class.

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349 **Extended Data Figure 1: Map and simplified stratigraphic column showing the position**
350 **of studied bedding planes with bedding plane maps of *Fractofusus*.** **a**, Newfoundland,
351 Eastern Canada. Dashed area indicates region of interest in B. **b**, The Avalon and Bonavista
352 Peninsulas, eastern Newfoundland. Locations of the bedding planes are indicated. **c**,

353 Stratigraphic column (not to scale) compiled of information from the Avalon and Bonavista
354 Peninsulas; lithological units in each region are treated as correlative in this study, but work
355 is ongoing to determine the validity of this assumption. The ‘E’ surface at Mistaken Point has
356 been dated to $565 \pm 3 \text{ Ma}^{12}$. There are currently no available radiometric dates from the
357 Bonavista Peninsula. Maps of *Fractofusus* positions on **d**, the ‘D’ surface, **e**, the ‘E’ surface
358 and **f**, the H14 surface. In Fig. e the largest specimens in light blue, medium specimens in
359 mid blue and smallest specimens in dark blue.

360 **Extended Data Figure 2: Retrodeformation calculations on the Mistaken Point surfaces.**

361 Plots of the lengths versus widths of discs from **a**, the ‘D’ surface, Mistaken Point and **b**, the
362 ‘E’ surface Mistaken Point. The gradient of the line defines the retrodeformation factor,
363 which for ‘D’ surface is 1.35 ± 0.11 ($R^2 = 0.92$), and for ‘E’ surface is 1.71 ± 0.08 ($R^2 = 0.75$).
364 **c**, *Fractofusus* PCF on the ‘E’ surface with (solid black line) and without (dashed black line)
365 retrodeformation. The grey shaded area depicts the boundary of 99 Monte Carlo simulations
366 for the model which provided the best-fit model to the retrodeformed data, which has a good
367 fit on the non-retrodeformed data ($p_d = 0.60$)

368 **Extended Data Figure 3: Size distribution analysis of *Fractofusus* for the H14 surface.**

369 **a**, Size-frequency distributions for *Fractofusus*, and **b**, the results of Bayesian Information
370 Criterion^{52,53} (BIC) (univariate data). Triangles and squares correspond to models assuming
371 equal and unequal variance respectively. High BIC values correspond to a good model fit, so
372 the best-fit model is a three component equal variance model using log-normalized length
373 data. **c-d**, Rose diagrams plotting the directional orientation of the different size classes of
374 *Fractofusus* on H14 surface showing **c**, Large size class (<11.0cm), **d**, Intermediate size class
375 (5.5-11.0cm) and **e**, Small size class (<5.5cm). The angles of the *Fractofusus* central axis
376 relative to North (0°). There is no strong orientation preference for any of the size classes.

377 **Extended Data Figure 4: Distance measures for the size data from H14 surface.** For all
378 plots the x-axis is the inter-point distance between organisms in metres. **a**, Mark correlation
379 function,⁵ where 1 corresponds to a lack of correlation of size, such that *Fractofusus* size is
380 independent and identically distributed. <1 corresponds to a positive dependency (in contrast
381 to PCF) and >1 corresponds to a negative dependency. Fig. a shows that small *Fractofusus*
382 on the H14 surface (<0.3cm) are more likely to be found near each other than expected by
383 random. **b**, The H14 surface PCF (solid line) showing the model that fits the data best, a
384 double Thomas cluster model (dotted line, $p_d=0.89$), and the simulation envelope for 99
385 Monte Carlo simulations (grey shaded area). PCF for the best-fit models for the bivariate
386 size-classes of *Fractofusus* on H14 surface showing: **c**, Linked cluster model for small with
387 medium size classes ($p_d=0.74$) and **d**, Linked cluster model for medium with large size class
388 ($p_d=0.66$). **e**, The PCF of the largest size class of H14 (solid line), showing the CSR Monte
389 Carlo simulation envelope in grey, with the 'D' surface PCF (dotted line, $p_d=0.56$). **f**,
390 Nearest neighbour distances (solid line, $p_d=0.01$) with CSR Monte Carlo simulation envelope
391 in grey.

392

393 **Extended Data Figure 5: Artistic reconstruction of *Fractofusus* on the H14 surface,**
394 **Bonavista Peninsula.** Artwork by C.G.K. The bottom right features a large *Fractofusus*
395 around which there are five to eight medium specimens clustered. Each of the medium
396 specimens also has small specimens clustered around them. The small specimens therefore
397 form an independent double cluster pattern, that is, clusters of clusters.

398

399 **Extended Data Table 1: Best-fit univariate cluster models.** For the heterogeneous
400 backgrounds, the moving window radius is 0.5m using the same taxon density as the taxon
401 being modelled. $p_d=1$ corresponds to a perfect fit of the model on the data, while $p_d=0$

402 corresponds to no fit. The error function of the best-fit model gives the fraction of the total
403 sum of squares for the transformed empirical PCF which are not explained by the model.

404

405 **Extended Data Table 2: Best-fit univariate double cluster models.** Large-scale clusters
406 are determined for the univariate cluster then input into the model, and the small-scale
407 clusters are determined in the double cluster analysis. $p_d = 1$ corresponds to a perfect fit of the
408 model on the data, while $p_d = 0$ corresponds to no fit.

409

410 **Extended Data Table 3: Best-fit univariate cluster models on heterogeneous**
411 **backgrounds for ‘E’ surface taxa.** Univariate clusters, either fitted to the small scale (S)
412 or large scale (L) were modelled on different backgrounds defined by the density map of all
413 taxonomic groups, or Random for charniid. C: Thomas cluster on homogeneous background.
414 CH: Thomas cluster on heterogeneous background. For the heterogeneous backgrounds, the
415 moving window radius is 0.5m since that radius produced the best-fit for Charniids:
416 Heterogeneous Cluster model on a background density constructed from all species: (CH_{all});
417 Ivesheadiamorphs (CH_{Ive}), *Fractofusus* (CH_{Frac}), *Charniodiscus* (CH_{Cha}),
418 *Primocandelabrum* (CH_{Primo}). CSR on heterogeneous background (H). *Bradgatia* (H_{Bra}),
419 Lobate Discs (H_{Lob}), *Thectardis* (H_{The}), Charniid (H_{Char}). $p_d = 1$ corresponds to a perfect fit
420 of the model on the data, while $p_d = 0$ corresponds to no fit. The H14 surface did not possess
421 enough non-*Fractofusus* specimens to perform similar analyses. NA: not applicable.

422

423 **Extended Data Table 4: The best-fit double Thomas cluster models fit onto other taxon**
424 $p_d = 1$ corresponds to a perfect fit of the model on the data, while $p_d = 0$ corresponds to no fit.
425 Note, that while these numbers may seem low (such as the ‘E’ surface fit), they need to be

426 considered in context of the PCF graph (Extended Data Fig. 2b), which clearly shows a good
427 fit to the data, with the small fluctuations of the observed PCF around the model PCF.

428

429 **Extended Data Table 5: Models for bivariate analysis between different size classes of**
430 ***Fractofusus* on the H14 surface.** SP refers to shared parents models, and LCM refers to
431 linked cluster models. $p_d = 1$ corresponds to a perfect fit of the model on the data, while $p_d =$
432 0 corresponds to no fit. The large size class was randomly distributed, but was approximated
433 by a cluster model, which was required for input into Programita.⁹

434