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1 **The *Beothukis/Culmofrons* problem and its bearing on Ediacaran**
2 **macrofossil taxonomy: evidence from an exceptional new fossil**
3 **locality**

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12

13 **Abstract:** The late Ediacaran siliciclastic successions of eastern Newfoundland, Canada, are
14 renowned for their fossils of soft-bodied macro-organisms, which may include some of the
15 earliest animals. Despite the potential importance of such fossils for evolutionary
16 understanding, the taxonomic framework within which Ediacaran macrofossils are described
17 is not clearly defined. Rangeomorphs from a newly discovered fossil surface on the
18 Bonavista Peninsula, Newfoundland, require us to reconsider contemporary use of
19 morphological characters to distinguish between genera and species within Ediacaran taxa.
20 The new surface exhibits remarkable preservational fidelity, resolving features smaller than
21 0.1mm in dimension in both frondose and non-frondose taxa. Such preservation permits the
22 recognition of rarely-observed fourth- and fifth-order rangeomorph branching, offering

23 unparalleled opportunities to investigate the fine-scale construction of rangeomorph taxa
24 including *Culmofrons plumosa* Laflamme *et al.*, 2012. Our observations enable resolution of
25 taxonomic issues relating to rangeomorphs, specifically overlap between the diagnoses of the
26 frondose genera *Beothukis* Brasier and Antcliffe, 2009 and *Culmofrons*. We propose a
27 taxonomic framework for all Ediacaran macrofossils whereby gross architecture, the
28 presence/absence of discrete morphological characters, and consideration of growth program
29 are used to distinguish genera, whereas morphometric or continuous characters define taxa at
30 the species-level. On the basis of its morphological characters, *Culmofrons plumosa* is herein
31 synonymized to a species (*Beothukis plumosa* comb. nov.) within the genus *Beothukis*. This
32 discussion emphasizes the need to standardize the taxonomic approach used to describe
33 Ediacaran macrofossil taxa at both the genus and species level, and raises important
34 considerations for future formulation of higher-level taxonomic groups.

35

36 **Key words:** Rangeomorph, Ediacaran, Newfoundland, systematics

37

38

39 THE late Ediacaran strata of Newfoundland record some of the oldest fossil evidence for
40 large, soft-bodied organisms. Fossils are typically preserved beneath volcanic tuffs or
41 volcanoclastic sediments, deposited in deep-marine turbiditic environments (Wood *et al.*
42 2003; Ichaso *et al.* 2007; Brasier *et al.* 2013; Mason *et al.* 2013) ~580–560 Ma (Benus 1988;
43 Van Kranendonk *et al.* 2008). The Newfoundland biota includes many taxa whose biological
44 affinities have been widely debated (summarised in Liu *et al.* 2015). In recent years,
45 researchers have tended to interpret Ediacaran macrofossils on a case-by-case basis,
46 proposing that a range of biological groups, including bacteria (Callow and Brasier 2009a;
47 Laflamme *et al.* 2011), and potentially algae (Hofmann *et al.* 2008), fungi (Callow and

48 Brasier 2009b), and metazoans (Liu *et al.* 2014a; Liu *et al.* 2014b), co-existed in the
49 Ediacaran marine ecosystems of Newfoundland.

50 The most abundant and diverse macroscopic group within the Newfoundland
51 successions is the Rangeomorpha (Liu *et al.* 2015), members of which are characterised by
52 the possession of self-similar branching architectures (Narbonne 2004; Brasier *et al.* 2012).
53 The preservation of rangeomorphs in the manner typical of Avalonian (eastern
54 Newfoundland and the southern UK) Ediacaran macrofossils, on siliciclastic bedding planes
55 as external molds and casts (cf. Kenchington and Wilby 2014), contributes to a dearth of
56 diagnostic morphological characters with which to constrain their phylogenetic affinities.

57 There is no clear and consistent taxonomic framework within which to describe
58 Ediacaran macrofossils, many of which are not currently attributable to living clades. Efforts
59 have been made to formulate high-level schemes by grouping genera within higher-order
60 Linnaean ranks (e.g. Sepkoski in Schopf and Klein 1992) or non-Linnaean groupings
61 (Laflamme *et al.* 2013; Grazhdankin 2014). A robust taxonomic framework is important,
62 since the genera and species that form the basis of existing Ediacaran groups have been
63 employed as the foundation both for efforts to determine relationships between taxa, and for
64 discussions of palaeoecological attributes such as diversity, disparity, and population
65 structure (e.g. Clapham *et al.* 2003; Darroch *et al.* 2013). Despite this, there has been little
66 agreement or even discussion of the characters or features that might usefully define
67 Ediacaran genera with respect to species. If we are to make effective progress in Ediacaran
68 palaeobiology, the formulation of generally accepted taxonomic protocols is imperative. This
69 attractive proposition is impeded by the need to consider non-uniformitarian and often
70 abiological interpretations for many preserved structures (e.g. Brasier *et al.* 2013), and by
71 preconceptions of the possible physiology of Ediacaran organisms—necessarily guided
72 primarily by extant taxa— which may introduce artificial biases to taxonomic schemes.

73 However, the greatest limitation to our understanding of the morphological construction and
74 ontogeny of the Ediacaran macrobiota is often the quality of the available fossil record.

75 Much of the progress made in Avalonian Ediacaran palaeobiology stems from data
76 collected at a handful of localities exhibiting high-quality macrofossil preservation (e.g. the
77 ‘D’ and ‘E’ Surfaces of the Mistaken Point Ecological Reserve, or the bedding plane at
78 Spaniard’s Bay; Clapham *et al.* 2003; Narbonne 2004). Recent discoveries have significantly
79 increased the number of known fossil-bearing sites, most notably on the Bonavista Peninsula
80 (O'Brien and King 2004; Hofmann *et al.* 2008), and in Charnwood Forest in the United
81 Kingdom (Wilby *et al.* 2011). A bedding plane on the east coast of Burnt Point, near the town
82 of Port Union, Bonavista Peninsula, formally documented here for the first time (Fig. 1), is
83 remarkable for its high-quality preservation of Ediacaran macrofossils. The horizon exhibits
84 high taxonomic diversity, and a wide size-range of taxa including some of the largest and
85 smallest rangeomorphs yet discovered. The surface is named the MUN Surface to reflect the
86 long history of research on Newfoundland’s Ediacaran successions by researchers from the
87 Memorial University of Newfoundland (MUN). Importantly, preservational fidelity on the
88 MUN Surface permits assessment of the architectural scheme of Brasier *et al.* (2012) in
89 defining rangeomorph taxa. Here we use MUN Surface specimens to; assess the role
90 morphological characters (including those not relating to branching architecture) can play in
91 rangeomorph systematics; resolve a taxonomic conundrum relating to the genera *Beothukis*
92 and *Culmofrons*, and; propose an extension of the classification approach of Brasier *et al.*
93 (2012) for rangeomorphs to other Ediacaran macrofossil groups. We also consider some of
94 the broader issues surrounding incorporation of Ediacaran taxa into higher-level taxonomic
95 groups, which may aid future development of a consistent global higher-rank taxonomic
96 scheme for these perplexing organisms.

97

98 **THE MUN SURFACE FOSSIL ASSEMBLAGE**

99 The MUN Surface lies near the base of the Port Union Member of the Trepassey Formation
100 (cf. O'Brien and King 2005; Fig. 1), within an interval dominated by medium- to thick-
101 bedded buff-grey turbiditic sandstones with soft-sediment deformation, rounded intraclasts,
102 and centimetre- to decimetre-scale carbonate concretions (Supp. Figs 1–2; Supp. Text 1).
103 Fossils are preserved as positive and negative epirelief impressions on a siltstone surface,
104 beneath a ~6 mm-thick fine-grained tuff layer (Supp. Fig. 3), which is itself overlain by 3–20
105 cm-thick beds of grey to grey-green siltstone and coarse sandstones (Supp. Figs 1–2).

106 Fossils on the MUN Surface occur in densities of up to 45 well-preserved
107 individuals/m², with over 250 exceptionally preserved identifiable specimens on a total
108 exposed surface (at low tide) of ~120m² (Figs 2–3, Supp. Fig. 4). Around 500 small,
109 indistinct impressions not included in this biotic density count represent additional poorly
110 preserved juvenile specimens (e.g. Supp. Fig. 4). The most striking fossils are members of the
111 Rangeomorpha (Narbonne 2004; Laflamme *et al.* 2013), and include: at least 40 specimens of
112 a unipolar form (i.e. possessing a single apical generative zone) comparable to *Culmofrons*
113 *plumosa* (Fig. 2A; Supp. Fig. 6; see later discussion); seven large specimens of *Bradgatia* aff.
114 *linfordensis* Boynton and Ford, 1995 (Fig. 2B–C); 43 *Primocandelabrum* sp. Hofmann *et al.*,
115 2008 (Fig. 3A); rare *Fractofusus andersoni* Gehling and Narbonne, 2007 (Fig. 3C); and
116 *Charnia masoni* Ford, 1958 (Fig. 3D). Other taxa include numerous *Charniodiscus* spp.
117 including *C. procerus* Laflamme *et al.*, 2004 (Fig. 3B); isolated holdfast discs; a single partial
118 specimen of the possible cnidarian *Haootia quadriformis* (Liu *et al.* 2014a, fig. 1f);
119 *Thectardis avalonensis* Clapham *et al.*, 2004; four *Hadryniscalia avalonica* Hofmann *et al.*,
120 2008; and several poorly defined ivesheadiomorphs (cf. Liu *et al.* 2011). Specimens range in
121 size from 10 mm to 0.7 m in maximum dimension, and can preserve features ~0.1 mm in
122 dimension (Fig. 2C), a quality of morphological resolution comparable to that of the younger

123 Ediacara Hills (South Australia) and White Sea (Russia) assemblages (e.g. Gehling and
124 Droser 2013). Some rangeomorph specimens exhibit up to five orders of self-similar
125 branching (e.g. Fig. 2C; Supp. Fig. 5), whereas other notable fossil surfaces in Newfoundland
126 typically preserve only two or three. In addition to taxa assignable to known late Ediacaran
127 genera, a dense fabric of 100s of thin filamentous impressions is also present (Fig. 3E).
128 Filamentous structures are arranged in multiple orientations on the bedding plane, and can
129 both drape and underlie macrofossil taxa. Individual filaments are 0.2–0.6 mm in width, but
130 can reach up to 400 mm in length. They exhibit no internal or external ornament, and show
131 no clear branching.

132 A tectonic overprint is evident on the surface, both as two sets of cleavage fractures
133 oriented at 016° and 350° respectively, and as deformation of holdfast discs (assumed from
134 study of multiple specimens to have originally been circular) to oval shapes. The holdfast
135 discs have an aspect ratio (width/length) of 0.73 (mean value taken from 20 specimens to 2
136 d.p., relative standard deviation 6.35%), with long axes oriented along a NNE-SSW axis (i.e.
137 broadly along strike), consistent with regional compressive tectonism associated with the
138 formation of the Catalina Dome.

139

140 **THE TAXONOMY OF EDIACARAN RANGEOMORPHS**

141 Taxonomy forms the framework for many current and previous attempts to understand
142 Ediacaran organisms and their palaeoecology. However, there are no clear definitions of what
143 constitutes a species-level characteristic as opposed to a generic attribute within Ediacaran
144 macrofossil taxonomy, let alone agreement on a framework for the higher-order classification
145 of these taxa. Until we have a better handle on their biological affinities, it is difficult to be
146 sure about how fixed the phenotype of these organisms was, and the extent to which they

147 conform to the morphological and biological species concepts. We consider that as
148 understanding of Ediacaran palaeobiology and palaeoecology improves and attention turns to
149 global questions, a standardized, consistently applied scheme for the diagnosis of Ediacaran
150 macrofossil taxa would be advantageous. Here, we address the characters used to define
151 Ediacaran rangeomorphs in light of the new MUN Surface specimens.

152 The broad concepts of what constitutes a genus, and how genera should be objectively
153 defined, have been long debated (e.g. Calman 1949; Mayr 1963; Melville 1995). Calman
154 (1949, p. 17) notes that the genus “*has no objective existence as a group but is merely a*
155 *convenient device to make easier the cataloguing and handling of numbers of species*”.
156 Calman further proposed that in establishing new genera, distinguishing characters “*should*
157 *be such as we may reasonably suppose [them] to be longer established in phylogeny than*
158 *those distinctive of species*” ... remaining “*unchanged amid variations in other characters*”
159 when assessing a group of related forms (Calman 1949, p. 17).

160 Late Ediacaran fossil assemblages commonly offer only small populations of
161 specimens, of variable preservational quality. Assessment of the variability of characters
162 within populations can therefore be difficult. In recent years, increased awareness and
163 understanding of wider global sections and sedimentological and taphonomic processes has
164 resulted in considerable taxonomic synonymization (see Fedonkin *et al.* 2007). Amongst
165 Avalonian taxa, discoidal forms have largely been synonymized (e.g. Gehling *et al.* 2000),
166 but there has also been much work to formally describe new non-discoidal taxa. Most
167 existing Avalonian Ediacaran genera are monospecific (see Liu *et al.* 2015, table 1). Since
168 rangeomorphs are common in Newfoundland, and are one of the few groups with a widely
169 recognized shared morphological attribute (the possession of self-similar branching within
170 cm-scale specimens; Narbonne 2004; Brasier *et al.* 2012; Hoyal Cuthill and Conway Morris
171 2014), they offer a useful case study for Ediacaran taxonomic questions.

172 Many Ediacaran macro-organisms are preserved only as mould or cast impressions on
173 rock surfaces, so when discussing their taxonomy we are exclusively dealing with
174 morphotypes. Macrofossil taxa in Newfoundland were originally distinguished by the
175 presence or absence of characters such as central rods and stems/stalks, and by variations in
176 gross shape, branch shape, branching angle, number of branches, and polarity (e.g. Hofmann
177 *et al.* 2008; Bamforth and Narbonne 2009; Narbonne *et al.* 2009; Laflamme *et al.* 2012).
178 However, some of these parameters, such as branch angle and number of branches, have
179 since been recognised to vary within populations of certain species, for example through
180 ontogeny (e.g. Liu *et al.* 2012), and have therefore been suggested to be unsuitable for use in
181 taxonomic diagnosis (Wilby *et al.* 2015). There has also been little consistency in whether
182 formal diagnoses have been assigned to the genus (as with *Beothukis*, *Pectinifrons*,
183 *Primocandelabrum*, *Parviscopa*, *Hapsidophyllas*, *Fronidophyllas*, *Vinlandia*), or the species
184 (e.g. *Avalofractus*, *Culmofrons*), in monospecific taxa. Diagnosing the species within a
185 monospecific genus would prevent creation of further species within that genus, so we urge
186 future workers to only diagnose species when multiple species exist within a genus. More
187 enlightening in terms of addressing taxonomic methodologies are taxa with multiple species,
188 such as *Fractofusus* or the arboreomorph *Charniodiscus*, in which gross morphology defines
189 the genus, and variations in frond shape, number of branches, length-width ratios and the
190 presence/absence of subsidiary branches have been considered to be species-level traits (cf.
191 Laflamme *et al.* 2004; Gehling and Narbonne 2007). More recently, the structural
192 architecture of rangeomorph branches has been considered a valid characteristic with which
193 to discriminate between rangeomorph taxa, leading to the formalization of a taxonomic
194 scheme based on branching architecture (Narbonne *et al.* 2009; Brasier *et al.* 2012). This
195 scheme is largely consistent with existing rangeomorph taxonomy, and proposes that the
196 presence or absence of structural features such as holdfast discs, and branching architecture

197 (the way in which branches are arranged within a frond), are genus-level traits, whereas
198 morphometric or continuous characters (such as number of branches and shape of the frond)
199 would either be better suited for the diagnosis of species, or used only with caution as
200 diagnostic criteria, since they may have been subject to ecological or ontogenetic influences
201 (Brasier *et al.* 2012).

202 The MUN Surface specimens conform to the concepts of branch furling, display, and
203 inflation proposed as suitable characters for taxonomic identification within the
204 rangeomorphs (Brasier *et al.* 2012). They may also permit future extension of such concepts
205 to consider variation in branching morphologies within 3rd–5th order sub-units. Exceptionally
206 preserved MUN Surface specimens of unipolar forms similar to *Culmofrons plumosa* warrant
207 further attention, since they lie at the heart of a conundrum that has a bearing on how
208 rangeomorphs are diagnosed.

209

210 *The genera Beothukis and Culmofrons.*

211 *Culmofrons plumosa* was formally described in March 2012 (Laflamme *et al.* 2012), at a
212 similar time to the publication of Brasier *et al.* (September 2012) in which morphological
213 architecture was suggested as a means of characterising rangeomorph taxonomic diagnoses.

214 The genus *Culmofrons* was erected using material from the Mistaken Point region of the
215 Avalon Peninsula (Laflamme *et al.* 2012). *Culmofrons plumosa*, the type species, was
216 diagnosed as follows (note that the generic diagnosis of *Culmofrons* is “as for species”):

217 “Rangeomorph frond with a spatulate to ovate petaloid composed of few (less than five on
218 each side) alternating primary branches forming a zigzagging central axis. Basal primary
219 branches attach directly to a long cylindrical stem and circular unornamented holdfast.

220 Primary branches composed of several (between 8 to 12) sub-rectangular to trapezoidal

221 *secondary modular units oriented perpendicularly to the primary branches. Secondary*
222 *modular units composed of cm-scale rangeomorph frondlets”* (Laflamme *et al.* 2012, p. 195).

223 It is clear from this description, and from images of the type material (Fig. 4C;
224 Laflamme *et al.* 2012), that some of the best-preserved rangeomorph fossils on the MUN
225 Surface are encapsulated by the diagnosis of *C. plumosa* (e.g. Figs 2A, 4B). However, some
226 of these MUN Surface specimens were figured as part of the emended diagnosis of the
227 rangeomorph genus *Beothukis* (Brasier *et al.* 2012, fig. 8B), and provide the basis for the
228 following emended generic diagnosis of *Beothukis*:

229 “*Fronde unipolar, comprising two rows of primary branches arranged in irregularly spaced*
230 *alternations along a furled central axis, forming a linear suture. Inflation of first- and*
231 *second-order branches is moderate to medial. Mature first- and second-order branches*
232 *typically have furled margins, with alignments that are arranged in radiating to subparallel*
233 *series. Rangeomorph elements of the first-order branches are usually undisplayed, whereas*
234 *those of second-order branches are clearly displayed. A basal disc and stem is sometimes*
235 *preserved”* (Brasier *et al.* 2012, p. 1114).

236 As with the diagnosis of *Culmofrons*, it is clear that the MUN Surface material could
237 equally be assigned to the genus *Beothukis* as defined by Brasier *et al.* (2012), though our
238 new material differs in possessing a zigzag rather than a linear central axis. We are thus faced
239 with a taxonomic conundrum that requires resolution.

240 Following the Brasier *et al.* (2012) scheme for classifying rangeomorph genera,
241 focusing solely on branching architecture, requires that the MUN Surface specimens be
242 assigned to *Beothukis*, which has taxonomic priority. However, as stated by Laflamme *et al.*
243 (2012), there are several clear differences between the type material of *Beothukis mistakensis*
244 Brasier and Antcliffe, 2009 (currently the sole species of *Beothukis*), and *Culmofrons*;
245 namely the presence in the latter of a long stem, fewer than five primary branches, and a

246 zigzag central axis (see Table 1; Laflamme *et al.* 2012, p. 197–198; Fig. 4D), and these
247 differences are shared by our specimens (Fig. 4; Supp. Fig. 6). It is therefore imperative to
248 consider whether the morphological details in which these taxa differ reflect species or
249 genus-level characters. Throughout this discussion, we suggest that the taxonomic importance
250 ultimately ascribed to a character is dependent on whether its morphological appearance in an
251 organism is considered to be the result of inherent genetically-based programming, or
252 extrinsic factors in the palaeoenvironment.

253 The course of the midline (straight or zig-zag) is a weak taxonomic character in
254 rangeomorphs since it may be prone to taphonomic variability (Laflamme *et al.* 2007; Brasier
255 *et al.* 2012). In contrast, the presence or absence of a basal disc is considered a key character
256 in the Brasier *et al.* framework, and this line of reasoning could be extended to the presence
257 or absence of a stem. The original diagnosis and description of *Beothukis* (Brasier and
258 Antcliffe 2009) do not mention a stem or a holdfast disc, but the diagnosis was emended by
259 Brasier *et al.* (2012) to state that a “*stem is sometimes preserved*” (2012, p. 1114).
260 Importantly, the emended specific diagnosis of *B. mistakensis* by Narbonne *et al.* (2009)
261 notes that although a stem is typically not present, it can be observed, and is <5% of the
262 length of the frond when present. It therefore appears that although a stem is not frequently
263 seen in *Beothukis mistakensis* (perhaps due to taphonomic reasons), it is present in some
264 specimens. Specimens previously assigned to the genus *Culmofrons* (cf. Laflamme *et al.*
265 2012) possess a stem that comprises 29–42% of the length of the organism (values calculated
266 using data presented in Laflamme *et al.* 2012, table 1), demonstrating that considerable
267 variability in stem length is observed within what has previously been considered to be a
268 single taxon. Given these discussions, it appears that *Culmofrons* and *Beothukis* specimens as
269 previously defined differ not in the presence of a stem, but in its length. The presence/absence
270 of a stem is a key morphological attribute of undoubted value to the organism, but we

271 consider that taxonomic diagnoses should not be based on the inferred ecological function of
272 a morphological characteristic (cf. Laflamme *et al.* 2012) until we can be assured that the
273 character in question represents genetic (as opposed to ontogenetic, taphonomic or
274 ecophenotypic) variability. Since stem length in *Culmofrons* does show variation within
275 populations and is seemingly unlinked to other morphological differences, until further
276 evidence can be presented to the contrary, we consider it appropriate to suggest that stem
277 length in that taxon is likely to be an ecophenotypic trait rather than a genetic one. The length
278 of a stem (relative to total length or frond length) could be regarded as a continuous
279 character. We therefore do not consider stem length as a means to distinguish between
280 closely related taxa at the level of genus.

281 The number of primary branches in rangeomorphs has previously been suggested to
282 be a character that should only be used with caution in their taxonomy (Brasier *et al.* 2012;
283 Wilby *et al.* 2015), since in some taxa it has been demonstrated to vary during ontogeny (e.g.
284 *Charnia* in Antcliffe and Brasier 2007; Liu *et al.* 2012). The number of branches is arguably
285 a continuous character, and therefore we argue that it should only be used as a species- or
286 population-level trait. The suggestion that some taxa have an upper limit on the number of
287 primary branches they possess (e.g. *Culmofrons*), while others seemingly appear to add
288 branches indefinitely (e.g. *Charnia*, Liu *et al.* 2012; Wilby *et al.* 2015), may indicate a
289 substantially different growth program that arguably transcends species-level distinction.
290 Capping the number of primary branches produces a growth plan in *Culmofrons* (Fig. 4C)
291 that—in mature specimens—is entirely dependent on inflation of primary branches and
292 addition only of higher-order (e.g. secondary) branches for growth. In contrast, *B. mistakensis*
293 can have as many as ten primary branches per row (Laflamme *et al.* 2012). Both of these
294 growth plans are compatible with an overall indeterminate mode of growth whereby the
295 organisms continue to grow indefinitely (as seen in other rangeomorphs such as *Charnia*;

296 Wilby *et al.* 2015). Current data suggest that *Culmofrons* had a finite limit on the number of
297 primary branches, whereas *B. mistakensis* did not. This strongly supports distinction of these
298 taxa at a higher taxonomic level than the species. However, we note that few large specimens
299 of *B. mistakensis* have been described, which importantly means we cannot yet be sure that *B.*
300 *mistakensis* did not also cap its branch addition, but at a later stage in its developmental
301 program. As it is currently not possible to refute this possibility, we suggest that it would be
302 unwise to separate these taxa on the basis of assumed differences in growth strategy until
303 further evidence is available.

304 In summary, our assessment of figured material of both *Culmofrons* and *Beothukis*
305 specimens, and material from the MUN Surface, leads us to conclude that differences
306 between these taxa in the linearity of the frond midline and the length of the stem are either
307 continuous variables, or subject to taphonomic influence. Although we also consider the total
308 number of primary branches to be a continuous variable, we recognise that the apparent
309 presence of a discrete cap to the number of primary branches in *Culmofrons* may reflect a
310 significantly different growth program to that seen in *Beothukis*, where branches appear to be
311 added continuously throughout growth. If this is demonstrated to be the case in the future, we
312 would consider such a difference in growth program to be a character of taxonomic
313 significance above the species level. However, given the paucity of large (>25cm) specimens
314 of *B. mistakensis*, we cannot currently refute the possibility that *B. mistakensis* also limits
315 branch addition at a later stage in its growth cycle. We therefore suggest that these organisms
316 can currently be shown to differ only in characters we consider to reflect variation at a
317 species level. We recommend that these taxa are grouped within the same genus, and since
318 *Beothukis* has taxonomic priority, we suggest inclusion of *Culmofrons plumosa* within the
319 genus *Beothukis* to create *Beothukis plumosa* comb. nov. The relevant specimens we describe
320 from the MUN Surface (e.g. Figs 2A, 4B; Supp. Fig. 6; Brasier *et al.* 2012, fig. 8B) are

321 hereby assigned to the newly described *B. plumosa* comb. nov. The emended diagnosis of
322 Brasier *et al.* (2012) for the genus *Beothukis* requires minor changes to the discussion of
323 stems (see below). We also provide emended diagnoses for the species *B. mistakensis* and *B.*
324 *plumosa* comb. nov. to consider their branch architecture, and the importance of the
325 morphological differences between them.

326

327

SYSTEMATIC PALAEOONTOLOGY

328

Genus BEOTHUKIS Brasier and Antcliffe, 2009

329

Type species. *Beothukis mistakensis* Brasier and Antcliffe, 2009, from the late Ediacaran of
330 the Mistaken Point Ecological Reserve, Newfoundland, Canada.

331

332 *Emended diagnosis.* Frond unipolar, comprising two rows of primary branches arranged in
333 irregularly spaced alternations along a furled central axis. Inflation of first- and second-order
334 branches is moderate to medial. Mature first- and second-order branches typically have furled
335 margins, with alignments that are arranged in radiating to sub-parallel series. Rangeomorph
336 elements of the first-order branches are undisplayed, whereas those of second-order branches
337 are clearly displayed. A basal disc and stem can be present.

338

339

Beothukis mistakensis Brasier and Antcliffe, 2009

340

Figure 4A

341

1991 *Rangea* sp.; Gehling, pl. 3.1.

342

1992 “Flat recliner”; Seilacher, p. 608–609, fig. 1 (*partim*, bottom row, third from right), fig.

343

2 (*partim*, upper left).

344

1992 “Folding over”; Seilacher, p. 609, fig. 3 (*partim*, top right).

345

1999 “other form”; Seilacher, p. 98, fig. 3 (*partim*, lower right of fossil block sketches).

346 2001 “Small tree-like form” and “*Charnia* composite morph”; Narbonne, Dalrymple and
347 Gehling, p. 26, pl. 1E and H (*partim*).

348 *non* 2003 “small, unnamed frond-shaped fossil”; Wood, Dalrymple, Narbonne, Gehling and
349 Clapham, p. 1383, fig. 9.

350 2004 Unnamed frond; Laflamme, Narbonne and Anderson, p. 830, fig. 3.1 (*partim*).

351 2004 “short-stemmed rangeomorph frond”; Narbonne, p. 1143, fig. 3B–C.

352 2004 “Bush-like form”; O’Brien and King, p. 207–210, fig. 3f, pl. 5a.

353 2005 “Spatulate rangid” and “short stem rangid”; Narbonne, Dalrymple, Laflamme, Gehling
354 and Boyce, p. 28, pl. 1K and 1N.

355 2007 “Rangeomorph fronds”; Ichaso, Dalrymple and Narbonne, p. 28, fig. 3C–D.

356 2008 “*Charnia antecessens*”; Hofmann, O’Brien and King, p. 17, fig. 13.7 (*pars*), (*non* figs
357 13.8 – 13.10, 15.1–15.5).

358 2008a “Rangeomorph frond”; Laflamme and Narbonne, p. 184, fig. 2.5.

359 2008b “Spatulate rangeomorph”; Laflamme and Narbonne, p. 170, figs 4.4, 4.6, 4.7.

360 2009 *Beothukis mistakensis*; Brasier and Antcliffe, p. 382–383, figs 17a–b, 18a–b.

361 2009 *Beothukis mistakensis*; Narbonne, Laflamme, Greentree and Trusler, p. 508–514, figs
362 3.3 (*partim*), 3.6 (*partim*), 5.1–5.2, 6.1–6.7, 7, 8.1–8.6.

363 2012 *Beothukis mistakensis*; Dornbos, Clapham, Fraiser and Laflamme, p. 58, fig. 5.2c.

364 2012 *Beothukis mistakensis*; Brasier, Antcliffe and Liu, p. 1116, fig. 5C–D.

365 2013 *Beothukis* sp.; Brasier, Liu, Menon, Matthews, McIlroy and Wacey, p. 130, figs 9D,
366 11B–D.

367 2013 *Beothukis*; Darroch, Laflamme and Clapham, p. 596, fig. 2B.

368 2013 *Beothukis mistakensis*; Laflamme, Darroch, Tweedt, Peterson and Erwin, p. 562, fig.
369 2.1–2.4.

- 370 2013 *Beothukis*; Macdonald, Strauss, Sperling, Halverson, Narbonne, Johnston, Kunzmann,
371 Schrag and Higgins, p. 257, fig. 6C.
- 372 2014 *Beothukis mistakensis*; Xiao, p. R121, fig. 1b. [cop. Narbonne *et al.* 2009, fig. 7].
- 373 2014 *Beothukis mistakensis*; Hoyal Cuthill and Conway Morris, p. 13123, fig. 1.
- 374 2014 *Beothukis*; Ghisalberti, Gold, Laflamme, Clapham, Narbonne, Summons, Johnston and
375 Jacobs, p. 2, fig. 1e (*partim*, lower right).
- 376 2014 *Beothukis* cf. *Beothukis mistakensis*; Narbonne, Laflamme, Trusler, Dalrymple and
377 Greentree, p. 215, fig. 6.1–6.7.
- 378 2014 *Beothukis*; Zalasiewicz and Williams, p. 144, fig. 13.
- 379 2015 *Beothukis mistakensis*; Liu, Kenchington and Mitchell, p. 1361, fig. 2B.
- 380 2015 *Beothukis*; Burzynski and Narbonne, p. 37, figs 4a (*partim*, upper left), 5B(b).

381

382 *Emended diagnosis.* Frond unipolar and spatulate to ovate in shape, comprising two rows of
383 five or more primary branches (in specimens of > 2cm in length; juveniles may have fewer)
384 arranged alternately along a furled, broadly linear central axis. First- and second-order
385 branches typically exhibit furled margins, and moderate to medial inflation. Second-order
386 branches are arranged in a radial to sub-parallel arrangement. A circular basal holdfast disc
387 and a short stem are sometimes present, but the length of the stem is typically <5% of the
388 length of the frond when observed.

389

390 *Beothukis plumosa* comb. nov.

391 Figures 2A, 4B–C; Supp. Fig. 6A–J, L(*partim.*), N–P.

392

393 2007 “Frond”; Laflamme, Narbonne, Greentree and Anderson, p. 249, fig. 6d–e.

394 v* 2012 *Culmofrons plumosa*; Laflamme, Flude and Narbonne, p. 196, figs 2.1–2.4, 2.7 (*non*
395 figs 2.5–2.6).

396 v. 2012 “*Beothukis* sp.”; Brasier, Antcliffe and Liu, p. 1120, fig. 8b.

397 2014 *Culmofrons*; Kenchington and Wilby, p. 105, fig. 2a [cop. Brasier *et al.* 2012].

398 2015 *Culmofrons plumosa*; Liu, Kenchington and Mitchell, p. 1361, fig. 2e.

399

400 *Diagnosis.* Frond unipolar and spatulate to ovate in shape, comprising two rows of primary
401 branches (with fewer than five branches in each row) arranged alternately along a furled,
402 often zigzagging central axis. Second-order branches (typically 8–12 per first-order branch,
403 but reducing in number distally) are arranged in a broadly sub-parallel to radiating
404 arrangement. A circular basal holdfast disc and a long cylindrical stem (comprising ~30–40%
405 of the length of the organism) are present. A broad, smooth region is often present at the
406 junction between frond and stem.

407

408 *Discussion.* We note that for the specific case of distinguishing juvenile *B. mistakensis* with
409 relatively few branches from juvenile *B. plumosa* comb. nov., if a clear stem is not evident or
410 the specimen is poorly preserved, it may be advisable to use open nomenclature (*Beothukis*
411 sp.).

412

413 **EXTENSION OF AN ARCHITECTURAL APPROACH TO WIDER EDIACARAN** 414 **TAXONOMY**

415 The discussion above builds upon the use of branching architecture and the presence or
416 absence of key discrete morphological features as generic characters in rangeomorphs, with
417 morphometric or continuous variables used to discriminate between species. Extension of a

418 similar approach to other Ediacaran taxa would be valuable, as would a search for further
419 potential synapomorphies with which to group possible higher-level clades. The most
420 comparable group to consider is the arboreomorph/frondomorph clade (cf. Laflamme *et al.*
421 2013; Grazhdankin 2014), many members of which bear superficial morphological
422 similarities to the rangeomorphs. A lack of rangeomorph elements in arboreomorphs
423 precludes use of the exact terms used by Brasier *et al.* (2012), but detailed study of their
424 architecture may yet reveal comparable variability in branch construction (cf. Laflamme and
425 Narbonne 2008b). The use of branch architecture and presence/absence of stems and
426 holdfasts (i.e. discrete characters) as genus-level characters in the Arboreomorpha, with
427 morphometric differences (i.e. continuous characters) being species-level discriminating
428 characters, should be straight-forward. This approach is broadly consistent with existing
429 *Charniodiscus* taxonomy based on material from Newfoundland (Laflamme *et al.* 2004;
430 Laflamme and Narbonne 2008b).

431 Extension of an architectural approach to non-frondose taxa requires consideration of
432 alternative independent characters that can undergo morphometric or continuous variation.
433 Symmetry has been suggested as a basis for higher order taxonomy (Fedonkin 1985; Erwin *et al.*
434 2011; Laflamme *et al.* 2013), but more subtle characters are required for fine-tuning at the
435 generic and species levels. The concepts of polarity, rows, and inflation (cf. Brasier *et al.*
436 2012) could equally be applied to the ‘pneus’ or ‘segments’ of taxa such as *Dickinsonia* or
437 *Pteridinium*, but other groups such as tubular body fossils (e.g. *Wutubus*; Chen *et al.* 2014),
438 may require inspection of additional features, such as branching style, consistency of width,
439 or segment cross-sectional profile.

440 Difference in growth program between taxa solely growing by inflation, or by both
441 addition and inflation of branches or segments can potentially be of use in distinguishing taxa
442 at the generic or higher levels. However, such distinction should only be accepted if the

443 perceived difference in growth program can be clearly demonstrated, and is not simply a later
444 change in a growth plan common to both taxa (e.g. the limiting of primary branches at eight
445 branches rather than four). Morphological characters used for taxonomic purposes must be
446 clearly independent of ecological, taphonomic and ontogenetic variation.

447 The rationale for grouping Ediacaran macrofossils into higher clades, a topic that has
448 long attracted discussion (e.g. Fedonkin 1985) also requires consideration. Two recent studies
449 have resulted in broadly similar schemes that jointly recognize some groups (e.g. the
450 Rangeomorpha), but differ in suggesting distinct names and characteristic features for some
451 groups (e.g. Arboreomorpha vs. Frondomorpha), or including different taxa within similar
452 overall groups (e.g. the Dickinsoniomorpha; Laflamme *et al.* 2013; Grazhdankin 2014). Both
453 studies take a phenetic approach to classification, with Laflamme *et al.* (2013) explicitly
454 using unique synapomorphies to recognize clades whenever possible. However, both studies
455 also propose groupings diagnosed by non-unique characters or character combinations. For
456 example, the Frondomorpha of Grazhdankin (2014, p. 271–272) are described as taxa
457 “*composed of a large, relatively flattened foliate section, a central stem, and a holdfast or*
458 *rooting anchor*”; a description that could be used to describe several rangeomorphs (e.g.
459 *Trepassia* or *Beothukis*). Similarly, the suggestion that members of the Arboreomorpha
460 possess primary branches that “*end at an outer margin*” (Laflamme *et al.* 2013, following
461 Erwin *et al.* 2011 supplementary information) would lead to the inclusion of rangeomorph
462 specimens such as *Beothukis plumosa* comb. nov. from the MUN Surface (Fig. 4B) within
463 that group. We should perhaps not expect all authors to converge on the same higher-order
464 groupings for Ediacaran taxa, and the debate promoted by the differences their schemes
465 reveal is welcomed. However, the characters by which those groups are distinguished should,
466 where possible, be chosen such that they are unique to the proposed clade, potentially paving
467 the way for future application of phylogenetic approaches to these fossils. Adoption of a

468 ‘bottom up’ approach to Ediacaran macrofossil taxonomy—first reaching agreement on
469 methods to distinguish genera and species before progressing to higher levels—seems an
470 appropriate course of action.

471

472 **CONCLUSIONS**

473 It is hoped that refinement of Ediacaran morphological and taxonomic studies will lead to
474 wider appreciation of the similarities and differences between Ediacaran macrofossil taxa,
475 although we must remember that “*classification can only reflect existing knowledge and must*
476 *be open to modification in the light of further discovery*” (Calman 1949, p. 21). The newly
477 discovered high-definition fossil assemblage of the MUN Surface reveals important
478 morphological and constructional data that guide our interpretation of the biology and
479 palaeoecology of rangeomorphs and associated organisms. Our observations of specimens
480 from the MUN Surface conform to the existing descriptive taxonomic scheme for
481 rangeomorphs (Brasier *et al.* 2012), allowing us to resolve taxonomic problems within the
482 Rangeomorpha, namely the *Beothukis/Culmofrons* dilemma. We suggest that the architectural
483 approach used herein, whereby species are distinguished on the basis of continuous
484 characters whereas genera differ in gross architecture or developmental program, can be
485 extended with modification to aid taxonomic understanding of the
486 Arboreomorpha/Frondomorpha. We also note that certain variables related to size and shape
487 of organisms could be subject to the influences of taphonomy, ontogeny, or ecology, and
488 should therefore only be used in taxonomic diagnoses with caution. Determining the extent of
489 ecophenotypic variation in Ediacaran fossil assemblages may be a worthwhile avenue for
490 future research. Other Ediacaran macrofossil taxa could similarly benefit from this consistent
491 approach to taxonomy, allowing for the fact that higher-level classification of Ediacaran
492 macrofossils is itself in a current state of flux. Consideration of the points outlined herein,

493 and critical appraisal of existing taxonomic schemes, will lead to an increasingly robust
494 framework within which to reconstruct systematic relationships amongst the Ediacaran
495 macrobiota.

496

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507

508 **AUTHOR CONTRIBUTIONS**

509 AGL and JJM jointly discovered the site and conducted the field and laboratory studies. All
510 authors were involved in data analysis and writing the manuscript.

511

512 **DATA ARCHIVING STATEMENT**

513 Data for this study, including information on the sedimentology and stratigraphic setting of
514 the MUN Surface, and six additional figures, are available in the [Dryad Digital Repository]:
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516

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725 **EXPLANATION OF FIGURES AND TABLES**

726

727 **FIG. 1.** Map and stratigraphic column (latter not to scale) showing the location of the MUN
728 Surface. **A)** Newfoundland, Eastern Canada. **B)** The Avalon and Bonavista Peninsulas (see
729 box in **A)**, showing the major Ediacaran fossil localities of Mistaken Point, Spaniard's Bay,
730 Ferryland, and the Catalina Dome. **C)** Geological map of the Catalina Dome (after Hofmann
731 *et al.* 2008), showing major settlements, and the location of the MUN Surface (yellow star).

732 See the column for key to the geological units. Dates in the column are taken from Benus
733 (1988) and Van Kranendonk *et al.* (2008, after Bowring *et al.* 2003), from correlative units
734 on the Avalon Peninsula. Note that these dates have only been published in abstract form.
735 Stratigraphy follows O'Brien and King (2005).

736

737 **FIG. 2.** Ediacaran macrofossils from the MUN Surface, Bonavista Peninsula, Newfoundland.

738 **A)** Unipolar rangeomorph *Beothukis plumosa* comb. nov., preserved in negative epirelief.

739 Note the clearly displayed second-order rangeomorph branches along the length of the frond.

740 **B)** Silicon rubber cast (i.e. positive hyporelief) of a partial *Bradgatia* aff. *linfordensis*

741 specimen. Primary branches are distally inflated, and can reach over 22 cm in length. **C)**

742 Close-up image of *Bradgatia* from the MUN Surface preserved in negative epirelief, showing

743 sub-mm resolution of preserved features. Scale bars = 10 mm.

744

745 **FIG. 3.** Ediacaran macrofossils on the MUN Surface, Bonavista Peninsula, Newfoundland.

746 **A)** Juvenile *Primocandelabrum* sp., exhibiting clear first and second order branching. **B)**

747 *Charniodiscus procerus*. **C)** *Fractofusus* sp. This specimen is too small to confidently

748 identify to species level. **D)** *Charnia masoni*. **E)** Multiple superimposed macroscopic

749 filaments, oriented in a variety of directions. Filaments vary from broadly straight to gently

750 curving. Note the unweathered tuff still covering the surface at top left. A, B, D and E

751 preserved in positive epirelief; **C)**, preserved in negative epirelief. All scale bars = 10 mm

752 except **C)** = 1 mm.

753

754 **FIG. 4.** A comparison of MUN Surface specimens with the type specimens of *Beothukis* and

755 *Culmofrons*. **A)** Holotype specimen of *Beothukis mistakensis*, 'E' Surface, Mistaken Point

756 Ecological Reserve, Newfoundland. **B)** Specimen from the MUN Surface, Burnt Point,

757 Bonavista Peninsula, Newfoundland. **C)** Holotype specimen of *Culmofrons plumosa* from the
758 Lower Mistaken Point surface (cf. Clapham and Narbonne 2002), Mistaken Point Ecological
759 Reserve, Newfoundland. **D)** Schematic diagram of a *Beothukis* frond, annotated to show the
760 morphological features discussed herein. Images have not been retrodeformed, all fossil
761 specimens remain in the field. Rangeomorph branches preserved as negative epirelief
762 impressions. Scale bars = 50 mm, except B = 10 mm.

763

764 **TABLE 1.** Summary of the differences in characters used to diagnose *Beothukis* Brasier *et*
765 *al.*, 2012, and *Culmofrons plumosa* Laflamme *et al.*, 2012. Characters in parentheses are
766 added by us to assist comparison, and have been interpreted from the original diagnoses and
767 descriptions. For those characters that are specified to differ between the two taxa (in italics),
768 we state whether they are discrete or continuous, as discussed in the text. *Note that in the
769 original description of *Beothukis (mistakensis)*, Brasier and Antcliff 2009), neither a stem nor
770 a holdfast disc was mentioned, though a holdfast was later recognized by Narbonne *et al.*
771 (2009).