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1 **Title: *Hootia quadriformis* n. gen., n. sp., interpreted as a**
2 **muscular cnidarian impression from the late Ediacaran Period**
3 **(~560 Ma)**

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14 **Key words:** Ediacaran, metazoan, Newfoundland, Cnidaria, muscle

15

16 **Abstract**

17 Muscle tissue is a fundamentally eumetazoan attribute. The oldest evidence for fossilized
18 muscular tissue before the early Cambrian has hitherto remained moot, being reliant upon
19 indirect evidence in the form of late Ediacaran ichnofossils. We here report a candidate
20 muscle-bearing organism, *Hootia quadriformis* n. gen., n. sp., from ~560 Ma strata in
21 Newfoundland, Canada. This taxon exhibits sediment molds of twisted, superimposed fibrous

22 bundles arranged quadrilaterally, extending into four prominent bifurcating corner branches.
23 *Haootia* is distinct from all previously published contemporaneous Ediacaran microfossils in
24 its symmetrically fibrous, rather than frondose, architecture. Its bundled fibers, morphology,
25 and taphonomy compare well with the muscle fibers of fossil and extant Cnidaria,
26 particularly the benthic Staurozoa. *H. quadriformis* thus potentially provides the earliest body
27 fossil evidence for both metazoan musculature, and for Eumetazoa, in the geological record.

28

29 **Main text:** Sediments of late Ediacaran age (~580–541 Ma) record the fossilized remains of
30 a diverse global assemblage of soft-bodied macro-organisms. The biological affinities of
31 these late Ediacaran megafossils remain the subject of considerable debate (*summarized in*
32 *ref. 1*). Following their initial discovery, Ediacaran soft-bodied organisms were commonly
33 assigned to metazoan groups (*see for example ref. 2, or the classification tables in ref. 3, p.*
34 *240–242*). However, the revolution in Ediacaran thinking brought about by the Vendobiont
35 hypothesis of Seilacher [4] led to reconsideration of many of those assignments. Recent years
36 have witnessed a trend towards interpreting individual taxa as candidate stem- and crown-
37 group metazoans. Described with varying degrees of confidence, these currently include
38 potential sponges [5-8], anthozoan, hydrozoan and scyphozoan cnidarians [9-11],
39 ctenophores [12], placozoans [13], early molluscs (*ref. 14; though see ref. 15*), and even
40 ascidian chordates [16]. These fossils are largely found in successions of ~555–541 Ma, in
41 South China, Brazil, the White Sea region of Russia, Namibia, and the Flinders Ranges of
42 South Australia [17, 18]. Further evidence for the presence of metazoans in the late Ediacaran
43 Period, and indirectly for muscular tissue, comes from simple, putatively bilaterian, surface
44 trace fossils from the previously mentioned localities [19-21], horizontal surface traces with
45 crescentic internal divisions made by motile, muscular organisms [22, 23] ~565 Ma [24], and
46 vertical equilibration traces from Newfoundland [23]. Prior to 565 Ma, the potential fossil

47 record of animals is restricted to claims for biomarkers (e.g., demosponge steranes of >635
48 Ma, ref. 25; *though see* ref. 26); various specimens interpreted as possible sponges from the
49 Early and Middle Neoproterozoic (refs 27-29; *though see* ref. 8); and traces of contested age
50 and origin [30-32]. The absence of clear metazoan body fossils until the latest Ediacaran
51 Period renders these earliest reports open to debate. Independent estimates for the first
52 appearance of animals in the Neoproterozoic vary widely, but recent molecular phylogenetic
53 studies predict that most stem-group divergences between extant metazoan phyla occurred
54 within the Cryogenian and Ediacaran Periods [33].

55 Newfoundland, in eastern Canada, contains some of the oldest non-algal Ediacaran
56 macrofossil assemblages, dated to ~579–560 Ma [34]. Although ichnological evidence for the
57 presence of metazoans in assemblages of this age has been reported [22, 23, 35], metazoan
58 body plans have yet to be convincingly demonstrated. We here report *Haootia quadriformis*
59 n. gen., n. sp. (figure 1) from the lower Fermeuse Formation of the Bonavista Peninsula of
60 Newfoundland (~560 Ma; figure S1; Text S1). This organism exhibits structures wholly
61 consistent with collagenous musculature, in the form of twisted and superimposed fibrous
62 bundles arranged in a quadrilaterally symmetrical pattern.

63

64 **Phylum CNIDARIA** Hatschek, 1888 [36]

65 **Genus HAOOTIA gen. nov.**

66 *Derivation of name.* From the Beothuk (language of the indigenous population of
67 Newfoundland) term *Haoot*, meaning *demon*, describing the striking appearance of the
68 holotype.

69 *Type species.* *Haootia quadriformis* n. gen., n. sp.

70 *Diagnosis* (of genus). Soft-bodied, quadrilaterally symmetrical organism possessing a smooth
71 discoidal structure connected by a relatively short stem to a quadrate body comprising
72 numerous regularly-aligned linear fibers. The fibers extend laterally across the body, linking
73 adjacent corners. Converging fibers extend beyond each corner to form an elongate branch,
74 which divides dichotomously to form smaller, distally tapering sub-branches. Smaller
75 branches also emanate from the lateral margins of the quadrate body, and these too branch
76 dichotomously.

77 *Haootia quadriformis* sp. nov.

78 figures 1–2a

79 *Derivation of name.* From the Latin *quadri* (fourfold), and *formis* (form), relating to the
80 quadrilateral symmetry of the organism's body.

81 *Holotype.* The original specimen, discovered by MDB in 2008, remains uncollected in the
82 field according to provincial law in Newfoundland. A plastotype is held within the collections
83 of the Oxford University Museum of Natural History, specimen OUM ÁT.424/p.

84 *Horizon and locality.* From the lower part of the late Ediacaran Fermeuse Formation, St.
85 John's Group [37]. The specimen resides within a turbiditic marine succession (Text S1,
86 figure S2) on the north shore of Back Cove, roughly 1.8 km NNW of the town of Melrose,
87 Bonavista Peninsula, Newfoundland, Canada (figure S1).

88 *Diagnosis.* As per the genus.

89 *Remarks.* *Haootia quadriformis* n. gen., n. sp. is known from the holotype specimen, and one
90 additional incomplete specimen from the Trepassey Formation of Burnt Point, Bonavista
91 Peninsula (figures 1f, S1, S5; designated the paratype). The smaller paratype specimen has

92 been preserved in lateral view, and displays an anchoring support structure, lineated stem,
93 and a furrowed body with apparent branches (figures 1f, S5).

94 *Description.* The non-retrodeformed holotype bears a discoidal structure 56 x 37 mm in
95 diameter, preserved in negative epirelief. The disc interior is smooth, apart from faint
96 concentric ridges at its outer margin (figure 1a), and a small slightly raised central structure
97 of 9 mm diameter with several tight concentric rings (figure 1e). This central structure
98 appears to form the attachment point for a short 7 mm wide, lineated stalk-like structure, 32
99 mm in length, which extends to the center of the quadrate body (figure 1a). The body is
100 preserved as a rectangular sheet 49 x 72 mm in dimension, characterized by well-defined
101 positive epirelief linear ridges (fibers) that are 100–600 μm wide and have peaks spaced 200
102 μm –1 mm apart. Individual fibers are finely lineated, exhibiting a structure composed of
103 bundles of parallel strands (figure 1a–b). In places, these strands split and then re-join (figure
104 1b). At the four corners of the body, the fibers converge to form bundles that progress distally
105 into elongate extensions, here termed branches (figure 1c). Each of the four corner branches
106 bifurcates up to three times, and taper towards their distal end, with those fibers that persist
107 distally decreasing in number after each successive branching point (figures 1a, c). Branches
108 were originally flexible, as demonstrated by 180° changes in direction of some examples to
109 face the predominant flow direction, as inferred from alignment of nearby unipolar
110 rangeomorphs and *Charniodiscus* specimens (figure 1a), and by their apparent ability to
111 become twisted and rotated (figure 1c). Location of the bulk of the organism down-current of
112 the circular disc in both known specimens is consistent with entrainment by a flow on the
113 seafloor prior to burial (figures 1a, 1f, S5).

114 Along the margins of the body sheet, between the four corners, further smaller
115 bundles of linear fibers converge to form small branches that divide dichotomously.

116 Additionally, along the two shorter edges of the compacted body, linear fibers running from
117 the adjacent corners combine to form bundles that bulge in the middle (figure 1a). In contrast,
118 along the two longer edges the fibers are less obviously clustered into discrete structures, and
119 continue broadly parallel to one-another.

120 A prominent linear structure preserved in positive epirelief runs up the center-right of
121 the impression, and the fibers of the surface of the body appear to drape over it (figure 1a).
122 The narrow morphology of this structure and its similar topographic relief to the branches
123 leads us to suggest that it reflects a primary branch from the lower-right corner (as seen in
124 figure 1a), folded beneath the body at the time of burial.

125 *Discussion:* *H. quadriformis* displays several unique morphological traits, the most striking of
126 which is an apparently symmetrical, fibrous body with regularly arranged branches (figure
127 2b). The superficial impression of bilateral symmetry in the holotype (figure 2c) was
128 arguably brought about by oblique collapse and differential contraction of the body.
129 Biostratinomic distortion is further enhanced by tectonic stretching. We thus infer that the
130 original body was quadrilaterally symmetrical in life (figures 2d, 3b), and we suggest that the
131 bedding plane relationships of the holotype specimen indicate composite preservation of a
132 mold of the base of the anchoring adhesive disc, and the upper surface and internal structure
133 of the body. The apparent draping of the quadrate body over the disc edge implies that the
134 body lay above both the disc and stem on the seafloor at the time of burial (figure 1a). On the
135 basis of the position of the disc upstream of the quadrate body, we infer that the disc was a
136 tethering structure similar to those of associated frondose taxa (e.g. figure S3a–c), and that
137 *Haootia* was epibenthic.

138 The complex structure of *H. quadriformis*, with prominent bundles of fibers
139 showing consistent directional changes within a discrete sheet-like structure, is not readily

140 explained by tectonic or sedimentological processes. Unusual environmental taphonomic
141 conditions can also be ruled out, since neighboring specimens of recognizable macrofossil
142 taxa on the bedding planes (e.g. figure 1a) do not differ in preservation or appearance from
143 those found abundantly throughout the region. All other fossil impressions on these surfaces
144 (figure S3) lack fibrous structures of the kind described here.

145

146 *Is this a known Ediacaran macrofossil taxon?*

147 Whereas typical frondose Ediacaran taxa possess either leaf-like morphologies or some
148 evidence for alternating rangeomorph branching elements [38, 39], such features are lacking
149 in *Haootia*. *Primocandelabrum* sp. [37] (figure S6d), a superficially similar contemporaneous
150 rangeomorph bearing multiple branches attached by a stem to a disc, can be distinguished by
151 its lack of quadrilateral symmetry, and its rangeomorph branching. Furthermore, in rare
152 specimens where longitudinal ridges are preserved along the length of a *Primocandelabrum*
153 [40], such ridges are wider, more broadly spaced, and less regular in arrangement than those
154 seen in *Haootia*. The disc in the holotype *Haootia* specimen also differs distinctly from
155 others found on the same surface, being smoother, with lower topographic relief (figure 1a)
156 and fewer concentric rings (figure S3).

157 Examples of putative tissue differentiation in Ediacaran macrofossils have typically
158 proven controversial. Structures interpreted as external sheaths and membranes have been
159 described in *Pteridinium* and *Rangea* from Namibia [41, 42], and in rare rangeomorphs from
160 Newfoundland [43], although the latter examples likely have a sedimentological origin [44].
161 Such claimed sheaths are typically smooth, and lack the fibrous character of *Haootia*. The
162 internal anatomy of other Ediacaran macrofossils is largely inferred from composite
163 impressions explained by biostratinomic collapse of tissues (e.g. ref. 45, fig. 2), or from
164 three-dimensional specimens in-filled by sediment (e.g. refs 46, 47). However, such typically

165 lobate structures do not exhibit the wavy fibrous symmetry of *H. quadriformis*. Whereas the
166 linear fibrous construction of the alga *Flabellophyton* from South China and Australia [48]
167 shows some similarity with fibers of *Haootia*, those fossils lack a large holdfast, a stem-
168 mounted body, or quadrilateral symmetry. It could be argued that the linear fibers in *Haootia*
169 result from the deformation or twisting of a non-muscular integument, but that cannot explain
170 their presence across the whole body, their multi-directionality, or their symmetry. Rough
171 comparison may be made with the ‘crumpled’ margins of *Karakhtia* from the White Sea [49],
172 but the folds in *Karakhtia* are irregular in shape and direction, radiate from the centre of the
173 organism to the outer margin, and become more finely spaced towards the specimen edges.
174 Differences are also apparent when considering linear features associated with ‘mop’
175 structures in Australia. ‘Mop’ plausibly results when a disc, embedded in a microbial mat,
176 has been dragged by unidirectional currents [50] to produce unidirectional or evenly radiating
177 marks. In contrast, *Haootia* fibers form bands that are multidirectional and often run parallel
178 to the margins of the impression, and that appear to converge at both ends (figure 1a).
179 Longitudinal furrows are known within ribbon-like *Harlaniella* [51]. Such linear features
180 demonstrate how individual Ediacaran taxa can exhibit a variety of putative internal
181 morphologies as a result of differential taphonomic processes. Such features will also require
182 explanation, but on the available evidence, we do not consider *Haootia* to represent a
183 taphonomic variant of any currently known Ediacaran taxon. Contemporaneous microbial
184 fabrics can exhibit linear striated morphologies (e.g. Arumberia; ref. 52), but are not typically
185 localized in their occurrence; do not possess a sharp boundary to the impression; and are not
186 known to form symmetrically arranged bifurcating structures.

187

188 *Metazoan affinities?*

189 *Haootia*'s size and complex, regular morphology demand consideration of metazoan
190 affinities. Its symmetry and the lack of evidence for pores or spicules argues against Porifera
191 (*following* ref. 8). The presence of numerous branches, absence of comb rows, and inferred
192 benthic mode of life likewise make comparison with Ctenophora problematic. Possession of
193 quadrilateral structure, a central radial disc, and fibrous soft tissues, clearly invite comparison
194 with living and fossil Cnidaria.

195 Although the extant Phylum Cnidaria includes morphologically and genetically
196 disparate taxa [53, 54], their molecular phylogeny confirms a basal position within the
197 Eumetazoa [55]. Cnidarians are classically united by the possession of cnidocytes,
198 diploblastic construction, and radial symmetry, but suggestions of a wider variety of
199 symmetry states (e.g. refs 56-58) are supported by genetic arguments for the presence of
200 bilateral symmetry in the eumetazoan common ancestor [59], and the presence of a
201 mesoderm-like layer has been recognized in some cnidarian taxa (cf. ref. 60; Text S2).

202 The bundles of fibrous ridges within the body of *Haootia* compare favourably in
203 size, order, and arrangement to the preserved muscular tissue of modern cnidarians.
204 Cnidarians can possess smooth and/or striated muscular tissue [60, 61] (Text S2), both of
205 which can form fibrous bundles arranged in a similar manner to those in *Haootia* [62]
206 (figures 3*a*, S6). Rare fossil examples of cnidarian muscular tissue (e.g. refs 63-65) typically
207 comprise impressions of regularly arranged ridges (e.g. ref. 64, p. 63, fig.55). These are best
208 known in fossil scyphozoan medusae, where coronal and radial muscles of the sub-umbrella
209 are often grouped into bundles (e.g. ref. 66) and are preserved as casts and molds in a
210 taphonomic style similar to that seen in the Ediacaran siliciclastic settings of Newfoundland
211 [67]. The morphology of soft-bodied fossil cnidarians is typically influenced by muscle
212 contraction at the time of burial [64]. Twisting and overlapping of fossil medusa tentacles
213 [68] also compare closely with *Haootia*'s flexible branches. Phalloidin fluorescence reveals

214 that the 1–2.5 μm -width smooth muscle fibers in the extant parasitic hydrozoan *Polypodium*
215 *hydriforme* run longitudinally up the length of the tentacles [62] in an arrangement strikingly
216 similar to individual fibers in *H. quadriformis*. Furthermore, the junction between muscles in
217 the tentacles and those in the body of *P. hydriforme* produces a similar ‘truncated’ surface to
218 the ridges observed in *Haootia* (figure 1d; ref. 62, fig. 4A), and individual fibers can also split
219 and/or join one-another. These morphological and structural similarities lead us to the
220 conclusion that the fibrous structures preserved within *Haootia* may well represent the soft-
221 tissue impressions of cnidarian musculature. If so, this specimen significantly pre-dates
222 previously documented preserved muscular tissues, the oldest of which are early Cambrian in
223 age [69, 70].

224 Striated muscle fibers have been demonstrated to be present in the cubozoan
225 *Tripedalia cystophora* (ref. 71, fig. 5), and although individual fibers are of smaller
226 magnitude than those seen in *Haootia quadriformis*, they are nevertheless very similar in
227 gross morphology. Smooth muscle has also been observed in cnidarians, and can form
228 macroscopic fibrous bundles within the tentacles of several scyphozoans [60] and cubozoans
229 [71, 72]. Distinguishing between bundles of smooth and striated muscle cells in the fossil
230 record is not likely to be possible when only soft tissue impressions are available for study. In
231 the living actinian *Metridium*, the better-developed (smooth) longitudinal muscles are notably
232 found in the ectoderm of the tentacles, with circular muscles located in the endoderm (ref. 73,
233 p. 79; *contra* ref. 74). This differentiation of muscle groups within different tissues may
234 explain why we only see longitudinal ridges along the branches of *Haootia*, with no clear
235 evidence for circular bands.

236 The preservation of muscular tissue in the Phanerozoic is uncommon, and is
237 typically restricted to Konservat Lagerstätten [75]. In many cases, particularly involving

238 arthropod and vertebrate muscle, preservation takes place via authigenic replacement of
239 muscular tissues by calcium phosphate or clay minerals [76], or via sulfurization of organic
240 matter [65]. In the Ediacaran, taphonomic processes were significantly different, and soft-
241 tissue preservation was commonly facilitated by the early diagenetic, microbially-induced
242 casting of fossil exteriors in framboidal pyrite [44, 77], or by rapid burial beneath volcanic
243 ash [78]. Such mouldic preservation is unusual in the Phanerozoic, but has been documented
244 to preserve cnidarians (and significantly impressions of their muscular tissue) at several
245 localities [68].

246 An important consideration is explaining how internal muscle tissues are preserved
247 in this manner, when in other Ediacaran macrofossils we typically only see external
248 morphology. In taphonomic experiments involving modern hydrozoans and scyphozoans,
249 impressions of muscular tissues were not preserved [79, 80]. However, the absence of
250 microbial mats on the experimental surfaces [79], and the desiccation of specimens [80],
251 precludes direct comparison between those studies and Ediacaran taphonomic conditions. We
252 suggest that rapid degradation of an external integument in *Haootia* (such as the epidermis,
253 <50 μ m thick in some modern cnidarians; ref. 81) upon death and burial exposed the
254 relatively more robust muscular tissues, and permitted them to be cast in the same manner as
255 contemporaneous Ediacaran macrofossils.

256 We infer that the muscle-like fibers seen in *Haootia* likely facilitated extension and
257 retraction of branches for gathering food, as with the tentacles of modern cnidarian polyps.
258 We see neither a distinct mouth-like structure nor a gastro-vascular cavity, so their presence
259 must be inferred at the center of the quadrilateral body. Similarly, structures similar to canals
260 or mesenteries are not clearly distinguishable. Interpretation of the disc as a benthic holdfast
261 then implies a polyp-like organism, with a gross body-plan most similar to that of living

262 staurozoans (e.g. figure 3). The fibers within *Haootia* are consistent with the positioning of
263 muscular fibers in the calyx of modern Staurozoa [82] (figure 3a), being longitudinal within
264 the stalk and branches of the specimen but mainly positioned laterally (i.e. parallel to the
265 margins in a manner analogous to coronal musculature in modern forms; ref. 81) in the body.
266 However, the additional marginal branches in *Haootia* are unlike anything seen in
267 staurozoans, which typically possess only eight arms. *Haootia* also lacks fossilized evidence
268 for morphological features such as anchors, gonads, nematocyst clusters, or characteristic
269 tissue structures observed in histological sections through modern Staurozoa (e.g. ref. 81).
270 Since *Haootia* is also considerably larger than most extant Staurozoa, and possesses an
271 unusually large holdfast disc, we are not in a position to assign it to the Class Staurozoa on
272 the basis of available evidence. Cubozoans can also possess bifurcating tentacles and four-
273 fold symmetry, but extant forms are pelagic, not benthic as inferred for *Haootia*.

274 Interestingly, sympleisiomorphies within the Medusozoa have been proposed to
275 include the presence of four intramesogleal muscles [83]. The Medusozoa are usually
276 considered to have a long evolutionary history, with divergence from the Octocorallia
277 conservatively estimated to have taken place at least ~571 Ma [84]. If correct, medusozoan
278 ancestors, and indeed diverse cnidarian ancestors, would be expected within late Ediacaran
279 marine environments. The suggestion that Staurozoa is the sister group to all other
280 medusozoan classes (refs 83, 85, *though see* ref. 55) potentially indicates a similarly ancient
281 evolutionary history for that clade. Further comparisons with the body plans of extant
282 cnidarians are limited by our poor understanding of deep sea forms [86], and the absence of
283 many extinct forms (cf. ref. 56). Until further morphological evidence is obtained, we
284 therefore suggest that the muscular *Haootia quadriformis* n. gen., n. sp. occupied a position
285 within the Cnidaria, and potentially within the stem-group Medusozoa.

286

287 *The significance of a cnidarian at ~560 Ma*

288 Interpretation of *Haootia quadriformis* as a muscular cnidarian leads us to examine the early
289 fossil record of the Phylum Cnidaria. Cnidarians appear to have diversified into several major
290 clades by the middle Cambrian, as evidenced by the presence of probable anthozoan actinians
291 [87-90] and corals [91-94], scyphozoans [95], possible hydrozoans and cubozoans [63, 96],
292 and cnidarians of unknown affinity [97] in lower and middle Cambrian strata, with
293 conulariids [98] and mass strandings of medusae [99, 100] additionally reported in the upper
294 Cambrian [see also ref. 68]. Some of the earliest interpretations of the original Ediacara biota
295 of Australia proposed cnidarian medusoid affinities for discoidal specimens [101-103], but
296 many of these have since been disputed (e.g. refs 68, 104). Similarly, interpretation of *Inaria*
297 as an actinian-grade, muscle-bearing polyp [105] has been questioned following taphonomic
298 and morphodynamic analysis [74]. Other reports of cnidarians in latest Ediacaran rocks
299 include *Pambikalbae* as a ?hydrozoan [106]; interpretation of the tubular fossils *Corumbella*
300 and *Vendoconularia* as scyphozoans similar to the conulariids [9, 11, 107]; discussion of the
301 biomineralized genera *Cloudina* and *Namacalathus* as ‘cnidariomorphs’ [108]; and the
302 possible calcified cnidarian *Namapoikia* [109]. Fossils from the late Ediacaran Doushantuo
303 Formation have been tentatively compared to tabulates [110, 111] and hydrozoans [10].
304 Elsewhere, the recent reinterpretation of certain middle Ediacaran carbonaceous fossils from
305 the Lantian Biota as potential conulariids [112] is of interest. Traces of actinian-like
306 locomotion in deep marine sediments ~565–560 Ma are also germane here [22, 23]. All
307 claims for Neoproterozoic metazoans should be critically assessed on a case-by-case basis,
308 much as with the early sponge fossil record [8]. At the time of writing, however, the studies
309 cited above clearly indicate morphological diversity of fossil cnidarian candidates in the late
310 Ediacaran/early Cambrian. Such fossils have also been used to help calibrate recent
311 molecular estimates of bilaterian-cnidarian divergence during the Ediacaran Period [33].

312 Cnidarian-like body fossils from Newfoundland at ~560 Ma also raise important
313 questions about tissue differentiation, feeding strategy, food sources, and the complexity of
314 late Ediacaran ecosystems. Our interpretation of *Haootia quadriformis* as a muscular
315 metazoan of cnidarian grade arguably represents the earliest known evidence for preservation
316 of muscular tissue in the geological record, and one of the earliest claims for a eumetazoan
317 (*see also* refs 10, 112). *Haootia* therefore delivers a key calibration point for studies of early
318 eumetazoan evolution and body symmetry.
319

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622

623

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635

636 **Figure 1.** *Haootia quadriformis* n. gen., n. sp., lower Fermeuse Formation of Back Cove,
637 Bonavista Peninsula, Newfoundland. **(a)** *H. quadriformis* holotype specimen. Note the
638 negative-relief central disc, interpreted as a holdfast, and the broadly bilaterally symmetrical
639 bundles of linear ridges, extending into discrete bifurcating branches. Inferred current
640 direction indicated by the arrow. **(b)** Fibers running along the right-hand margin of *Haootia*;
641 each fiber is composed of finer, thinner fibers. **(c)** Bottom left corner of *Haootia*, detailing the
642 connection between a primary bifurcating branch and the main body. Note the twisted fibers
643 along the branch. **(d)** Pinching, bundling and superposition of fibers at the base of a
644 subsidiary branch. **(e)** The small circular depression at the centre of the disc, showing
645 mantling parallel fibers forming the base of a short stalk that connects the disc to the body. **(f)**
646 Incomplete paratype specimen of *H. quadriformis*, from the Trepassey Formation of Burnt
647 Point, Bonavista Peninsula. This specimen is preserved on its side, but clearly displays fibers
648 extending up its stem and around the body. A small partially buried holdfast disc is arrowed.
649 Scales bars (a), (c), (f) = 10 mm; (b), (d–e) = 5 mm.

650

651 **Figure 2.** Digitized images of *Haootia quadriformis* n. gen., n. sp., emphasizing the
652 convergence of fibrous linear features at the corners of the body, and the symmetry of the
653 fossil. **(a)** Photograph of the holotype as it appears *in situ*. **(b)** Interpretive sketch of the non-
654 retrodeformed specimen. Labels indicate: a) muscle bundles, b) expanded bundles, c)
655 ‘contracted’ bundles, d) twisting fibers, e) superimposed fibers, f) disc. **(c)** Digitized overlay
656 of the fossil. Symmetrical regions of the organism are color coded. Note the thick bulging of
657 fibers (indicating muscle contraction?) along short axes of the sheet (light green). **(d)** As in
658 (b), but the image has been corrected to account for tectonic deformation on the surface by
659 compressing the disc into a perfectly circular structure (cf. ref. 113, *though see* ref. 114).
660 Scale bar = 10 mm.

661

662 **Figure 3.** (a) The extant staurozoan *Lucernaria quadricornis*, exhibiting a body plan similar
663 to that hypothesized for *Haootia quadriformis* n. gen., n. sp. The Staurozoa are known from a
664 range of marine depositional environments and water depths [83]. (b) Artistic reconstruction
665 of *H. quadriformis*. Scale bars = 10mm.