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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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13

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  $\mu\text{m}$  wide and have peaks spaced 200  
102  $\mu\text{m}$ –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  $\mu\text{m}$ -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 $\mu$ 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, sympleiomorphies 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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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.