1 **The macroalga *Bosworthia* from the Cambrian Burgess Shale and**
2 **Kaili biotas of North America and China**

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11

12 **Abstract.**—A comprehensive restudy of all material assigned in previous reports to
13 the noncalcified macroalgal genus *Bosworthia* Walcott from the Burgess Shale
14 Formation (Cambrian Stage 5) of western Canada and the slightly older Kaili
15 Formation of South China, together with investigation of previously unpublished
16 material, indicates important morphological differences between the two species
17 heretofore included within the genus. On the basis of these differences, *B. gyges* is
18 removed from the genus and assigned to *Walcottophycus* gen. nov. Most specimens
19 previously assigned to *Bosworthia* from the Cambrian of China, including those
20 assigned to *B. simulans* Walcott, are transferred to *W. gyges*, and it is concluded that
21 *Bosworthia* remains unknown in China. Morphological details for this material when
22 evaluated in the context of molecular clock studies and other fossil macroalgae
23 indicate that *B. simulans* may belong to the extant red algal subclass
24 Rhodymeniophycidae (Florideophyceae) and indicate that *W. gyges* may be an early
25 form of bryopsidalean alga within the Chlorophyta.

26

27 *Keywords:* Cambrian, *Bosworthia*, Kaili biota, Burgess Shale, macroalgae

28

29 **1. Introduction**

30 Walcott (1919) erected the macroalgal genus *Bosworthia* to accommodate
31 three specimens from the Greater Phyllopod Bed of the Burgess Shale Formation
32 (Cambrian Stage 5) at the Fossil Ridge (now Walcott Quarry) site, two of which were
33 assigned to the type species, *B. simulans* Walcott, and the third to *B. gyges* Walcott.
34 No additional Burgess Shale specimens have been formally assigned to *Bosworthia*
35 since that initial study, and Walcott's sparse descriptions constitute the only formal
36 taxonomic treatment of this material to date. Specimens attributed to *Bosworthia*,
37 however, have been reported from the Kaili Formation of China (Cambrian stages 4–
38 5) (Mao et al., 1994; Yang et al., 1999; Yang, 2006; Zhao et al., 2011). To develop a
39 better understanding of this material, a detailed study was undertaken that included all
40 specimens previously assigned to *Bosworthia* from the Burgess Shale and Kaili
41 biotas, as well as a large number of unpublished specimens from the latter. Results
42 indicate that the Burgess Shale material is best placed among two genera, and that
43 *Bosworthia* (sensu stricto) remains unknown from the Cambrian of China.

44

45 **2. Material and methods**

46 The *Bosworthia* type material was examined using a binocular microscope at
47 the Smithsonian Institution National Museum of Natural History. Kaili Formation
48 study material, totaling over 30 specimens, was studied in similar fashion at Guizhou
49 University. For all study specimens, high-resolution morphometric data was collected
50 from digital images using the open source program ImageJ. Scanning electron

51 microscope (SEM) study of GTBM-9-2-636 from the Kaili Formation was conducted
52 using an FEI Quanta 250 FEG at the Subsurface Energy Materials Characterization
53 and Analysis Laboratory (SEMCAL), School of Earth Sciences, Ohio State
54 University. The specimen was imaged uncoated under low vacuum, and backscattered
55 electron (BSE) images were obtained using an accelerating voltage of 15 keV.
56 Repository abbreviations as follows: GTB, GTBM, GTBJ, Guizhou University,
57 Guiyang, China; USNM, Smithsonian Institution National Museum of Natural
58 History, Washington D.C., USA.

59

60 **3. Results**

61 *3.1 Burgess Shale Formation material*

62 Walcott's two syntypes of *Bosworthia simulans*, USNM 35426 and USNM
63 35427, show a similar style of preservation, each specimen consisting of a thin
64 slightly glossy film with a faint silvery cast. In direct light, they are only just
65 discernible from the surrounding shale (Plate I, 3). In polarized light, however, the
66 contrast between specimen and matrix is enhanced, and the specimens, therefore, are
67 more apparent (Plate I, 1, 4). The thallus of USNM 35426, as preserved on the slab
68 surface, has a maximum width of 70 mm and comprises a number of branches arrayed
69 in radial fashion around a dark, roughly ovoid central area with a maximum
70 dimension of 6 mm (Plate I, 1; Fig. 1). Additional details for the central area are not
71 apparent. The number of branches extending from the central area is difficult to
72 determine because of overlaps, but appears to be between 4 and 6. Branches have a
73 sinuous character and show repeated dichotomous branching. In some places, equal
74 (isotomous) branching is evident, especially at lower levels of branching, but it cannot
75 be determined if this pattern applies throughout, in part because of overlaps. The best

76 preserved branch (top center of Plate I, 1) has a total length of at least 77 mm, as
77 measured along the curvature, and shows at least five levels of branching, the distance
78 from the base to the first branch point being roughly 20 mm. Spacing between
79 successive branch points is approximately 11, 6, 26, and 4 mm. Branch width in most
80 but not all cases decreases from one level to the next, the succession for the first five
81 levels being 2.3, 2.0, 1.5, 1.6, and 1.0 mm, as measured at the mid-point of each level.
82 Between branch points, branch width is roughly constant. Other branches for this
83 specimen, although less well preserved, appear to show a similar morphology. The
84 angle of divergence at branch points is typically between 40 and 50 degrees, and inner
85 margins of bifurcations often have a u-shaped form. Branch margins throughout are
86 smooth and entire, without serrations or teeth (Plate I, 2). No definitive natural branch
87 terminations are present despite the fact that several branches appear to show blunt
88 endings. Close inspection reveals most of these to be interruptions caused by
89 discontinuities of shale laminae resulting from uneven splitting, and the other
90 instances are not convincing because no clear margins are present. Original three-
91 dimensional branch form appears to have been that of a thin ribbon rather than
92 cylindrical, as longitudinal creases are only weakly developed in a few small
93 localized areas, and some of the branches are folded back on themselves (e.g., near
94 arrow in Plate I, 1). The entire specimen by virtue of the overall arrangement of
95 branches on the slab surface presents the appearance of a thallus buried in life
96 position and compressed flat by a rapid influx of sediment essentially directly from
97 above. USNM 35427, as proposed by Walcott (1919), can be readily understood as a
98 thallus with a morphology similar to that of USNM 35426, but buried on its side and
99 thereby presented on the slab surface in lateral view. Maximum width for this
100 specimen is similar to that for USNM 35426 (79 vs. 70 mm). Images of this specimen

101 taken in polarized light (Plate I, 4) show enhanced morphological detail in
102 comparison to the photograph published by Walcott (1919, pl. 58, fig. 1). In
103 particular, a portion of the specimen shows six branches arranged in a radial pattern
104 and converging on a single point, each branch having a width of 2.3 mm in the area of
105 convergence (left arrow in Plate I, 4). Such an arrangement points to this area as
106 being the basal part of the thallus. Evidence of a holdfast in this area is lacking, but
107 branch widths in this part of the specimen match those in the lower part of USNM
108 35426. Walcott (1919) regarded the left side of the specimen, as oriented in Plate I, 4,
109 as the base. In the new interpretation, most of the branches are swept to one side of
110 the base, overall branch length is somewhat shorter than in USNM 35426 (ca. 55 vs
111 77 mm), and branch portions on the far left correspond to distal elements, these
112 having a width comparable to distal elements in USNM 35426 (ca. 1 mm in both
113 specimens). Branching details for individual branches are difficult to discern because
114 of overlaps, but in some areas clear dichotomous branching is evident with
115 divergence angles of about 40 degrees (right arrow in Plate I, 4). The form of the
116 branch tips is also difficult to discern because of overlaps. Walcott's photograph
117 shows a multitude of rounded tips, but these were added by hand-retouching, a
118 practice acknowledged in that report (Walcott, 1919, p. 225), and rounded
119 terminations are not definitively present at these locations or elsewhere on the
120 specimen. For both USNM 35426 and USNM 35427, branch interiors presented a
121 featureless appearance when examined under a binocular microscope.

122 Walcott's only specimen of *B. gyges*, USNM 35428, shows a preservational
123 style similar to USNM 35426 and 35427. The thallus comprises a tightly packed
124 cluster of branches arising from a central base and preserved in lateral view, the
125 whole having a gentle curvature and a length of 40 mm as measured along the arc

126 (Plate II, 1; Fig. 2). Thallus width is 2.5 mm at the base, gradually expanding to 15
127 mm at the top. It is not clear whether the branches had this compact arrangement in
128 life, or were instead swept into this position by currents just prior to burial. Width for
129 each branch is approximately 1 mm; branches maintain a more or less constant width
130 along their length, but tapering is evident in the last few millimeters. Most branches
131 appear to extend the full length of the thallus. No branches show definitive evidence
132 of bifurcation. It is possible, however, that infrequent bifurcations are present but
133 concealed by the tightly packed arrangement of the branches, especially near the base
134 as margins of individual branches are not well defined in this area, even in polarized
135 light images. Creases or folds are not evident, but branch surfaces have a subtle
136 fibrous texture (Plate II, 13).

137 Examination of Walcott Quarry material in the collections of the Royal
138 Ontario Museum brought to the attention of the authors by J.-B. Caron revealed no
139 specimens that could be assigned with confidence to either *B. simulans* or *B. gyges*. A
140 few ribbon-like specimens, all less than 15 mm in length, might be fragments of *B.*
141 *simulans* based on width dimensions (1–2 mm), but none of this material shows the
142 specific pattern of dichotomous branching characteristic of the taxon. In an
143 unpublished PhD dissertation, Satterthwait (1976, p. 37–38) attributed material from
144 collections of Walcott Quarry material made by the Geological Survey of Canada to
145 *B. simulans*. Satterthwait (1976) illustrated two specimens, but neither has been
146 accessioned on an individual basis in the GSC collections (M. Coyne, pers. comm.).
147 The specimen illustrated in pl. III, fig. 4 of Satterthwait (1976) might be an early
148 growth stage. It consists of six branches arranged in a rosette pattern, the longest
149 having a length of 13 mm and a width of 3 mm, but none of the branches show
150 dichotomous branching. There is little doubt, however, that the specimen illustrated

151 in pl. III, fig. 6 of Satterthwait (1976) is a further specimen of *B. simulans*. This
152 specimen appears to consist of a jumble of branch fragments, the longest of which has
153 a length of 50 mm, a maximum width of 2.5 mm, and displays clear dichotomous
154 branching. Although these GSC specimens do not shed additional light on the gross
155 morphology of *B. simulans*, peels produced from this material indicate a lack of
156 cellular-level details and reproductive structures (Satterthwait, 1976), a finding
157 consistent with our observations of the USNM material using light microscopy.

158

159 3.2 Kaili Formation material

160 Both *Bosworthia simulans* and *B. gyges* have been reported from the Kaili
161 Formation of South China. The total number of published specimens is small, and
162 most of the Chinese *Bosworthia* material has been attributed to *B. simulans*. Mao et
163 al. (1994, pl. II, figs. 2–5) illustrated four specimens as *B. simulans*, GTB-22-1-165,
164 GTB-5-2-98, GTB-8-3-64, and GTB-15-19-1. Yang et al. (1999) assigned two
165 additional specimens to *B. simulans*, GTB-9-1-304 and GTB-5-2-98 (the latter is not
166 the same specimen as GTB-5-2-98 from Mao et al., 1994), but rejected a *Bosworthia*
167 affinity for all of the Mao et al. (1994) material except GTB-22-1-165 (erroneously
168 listed as GTB-22-1-105), placing GTB-5-2-98 (listed as GTB-12-2-208) and GTB-8-
169 3-64 in the new taxa *Kailiphyton simulans* Yang et Zhao and *Palaeospinella typica*
170 Yang et Zhao, respectively. We concur that the specimens removed from *Bosworthia*
171 by Yang et al. (1999) differ significantly from GTB-22-1-165 and the Burgess Shale
172 type material, and they will not be considered further herein. An additional specimen,
173 GTBM-9-2-636, was illustrated as *B. simulans* in a comprehensive overview of the
174 Kaili Biota by Zhao et al. (2011, fig. 248).

175 Among the foregoing, GTB-22-1-165 and GTBM-9-2-636 appear to represent
176 thalli that are complete or nearly so. From published photographs, GTB-22-1-165
177 comprises upwards of 20 elongate branches that arise and diverge from a common
178 basal area (Plate II, 2). Each branch is approximately 26 mm long and 1 mm wide.
179 Branch width remains more or less constant along length, but tapering is evident near
180 the ends. Branches do not show evidence of bifurcation, but overlaps are present and
181 it is possible that minor branching occurs near the base. GTBM-9-2-636 is similar to
182 GTB-22-1-165 in all key respects, differing only in having branches that are slightly
183 longer (30 vs. 26 mm) and fewer in number (Plate II, 10, 15). Both specimens show a
184 fibrous texture on the branch surfaces. In BSE images of GTBM-9-2-636, internal
185 filaments are evident, these having a diameter of 13 to 25 μm and running roughly
186 parallel to the long axis of the branch (Fig. 3). Preservation is poor, but branching of
187 the filaments seems to be present in some places. Internal details for these structures
188 are lacking, so here “filament” is applied in a general sense rather than to denote a
189 chain of cells attached end to end. SEM analyses indicate that the specimen is
190 carbonaceous, the composition being essentially identical to that of *Fuxianospira*
191 specimens from the same unit (see LoDuca et al., in press). Specimens listed as GTB-
192 9-1-304 and GTB-5-2-98 in Yang et al. (1999) have a width and shape consistent with
193 these being detached branches from thalli similar to GTB-22-1-165. For all of this
194 previously described material, folds are lacking, indicating that the branches may
195 have been cylindrical in life as opposed to flat blades.

196 In the Yang et al. (1999) report, a single specimen, GTB-22-1-186, was
197 assigned to *Bosworthia gyges* (Plate II, 3). A further specimen, GTM-22-4-20 (note:
198 the prefix should be GTB and will be listed as such hereafter), was assigned to *B.*
199 *gyges* in a comprehensive overview of the algal component of the Kaili Biota by

200 Yang (2006). From the published photograph it is evident that the thallus of GTB-22-
201 1-186 comprises numerous elongate parallel-sided branches arising from a common
202 base. Branches are 20 to 25 mm in length and up to 1 mm in width with no clear
203 evidence of bifurcation. Branches are in close contact along most of their length, so
204 that the thallus has a narrow, belt-like form. GTB-22-4-20 is similar to GTB-22-1-186
205 in most regards but shows a distinct difference in that the branches are lanceolate,
206 rather than parallel-sided, and some of the branches are significantly wider at the
207 midpoint (up to 2 mm vs. 1mm).

208 During the present study, more than thirty previously unpublished specimens
209 comparable to GTB-22-1-165 and GTB-22-1-186 were examined. Morphometric data
210 for most of these specimens is provided in Table 1. Specimen GTBM-9-5-2300 (Plate
211 II, 4) is typical of this material and affords a good view of the individual branches.
212 The thallus of this specimen is preserved as a black to dark brown film on the surface
213 of the slab and comprises approximately 10 elongate branches. These arise and
214 diverge from a common base evident at the center of the specimen (Plate II, 15), but
215 evidence of a holdfast is lacking. Branches preserving the complete length reach a
216 length of 23 mm in each case and show similar widths, the maximum width ranging
217 between 0.7 and 1.0 mm. For individual branches, width remains roughly constant
218 along the length but tapers in the few millimeters near the base and tip. Branch sides
219 are smooth, straight, and entire, without teeth, undulations, or protuberances, and
220 branch surfaces have a subtle fibrous texture (Plate II, 14). Most of the branches have
221 a flexuous form, but none show folding. Definitive evidence of bifurcation is lacking,
222 but it is possible that branching occurs very near the base. No reproductive structures
223 are evident. The other study specimens (Plate II, 5–12; Plate III, 1–6) show a
224 morphology similar to GTBM-9-5-2300, including a fibrous texture on branch

225 surfaces, but variation is evident between specimens in terms of branch length,
226 ranging from a minimum of 10 mm to a maximum of 42 mm (Table 1), and
227 maximum branch width, ranging from 0.6 to 1.2 mm (Table 1). Between-specimen
228 variation is also evident in the arrangement of the individual branches, these in some
229 cases forming a tight, narrow bundle (e.g., Plate II, 9) and in others having a more
230 open distribution, similar to that shown by GTBM-9-5-2300 (e.g., Plate II, 5; Plate
231 III, 3), and in the total number of branches per thallus, this ranging from as few as two
232 to as many as 20 or more (Table 1), the precise number being difficult to determine
233 for many specimens because of overlaps. Small thalli, such as GTBM-9-5-969 (Plate
234 III, 3), are likely early growth stages because they resemble larger thalli in all respects
235 except branch length. Some specimens appear to represent individual, detached
236 branches (e.g., Plate III, 6). None of the specimens show definitive evidence of a
237 holdfast.

238

239 **4. Discussion**

240 Detailed examination of Walcott's *Bosworthia* material indicates that the two
241 syntypes of *B. simulans* are similar in terms of overall thallus size and form, and
242 details for the branches, including branch width and branching pattern. On this basis,
243 we concur with Walcott's assessment that the two specimens are conspecific. Walcott
244 (1919) did not designate a holotype for *B. simulans*. Herein, we designate USNM
245 35426 as the lectotype because details of the branching pattern are more apparent on
246 this specimen than on USNM 35427.

247 Our restudy indicates that the *B. gyges* holotype, USNM 35428, differs
248 significantly in several respects from the *B. simulans* type material as well as from
249 material illustrated as *B. simulans* by Satterthwait (1976). In describing the difference

250 between *B. gyges* and *B. simulans*, Walcott (1919, p. 242) noted only “This species
251 differs from *B. simulans* in its compact thallus and less flexuous branches.”
252 Additional key differences identified during the present investigation include
253 narrower width for the branches (1 mm vs. 2.3 mm near the base), rarity or complete
254 lack of dichotomous branching, and a different surface texture (fibrous as opposed to
255 smooth). On the basis of these differences, particularly with respect to branching
256 details, USNM 35428 is regarded herein as belonging to a genus apart from
257 *Bosworthia*, and a new genus, *Walcottophycus*, is erected to accommodate this
258 specimen (see Section 5).

259 Our findings for the Chinese material indicate that GTB-22-1-165, GTB-22-1-
260 186, GTBM-9-2-636 and all of the previously unpublished study specimens have a
261 branch width, shape, surface texture, and branching pattern comparable to USNM
262 35428. Accordingly, all of this material is herein regarded to be conspecific (see
263 Section 5). Such an outcome significantly bolsters interpretation of USNM 35428 as a
264 complete and intact algal thallus representing a distinct genus in the Burgess Shale
265 Formation, despite the fact that it remains the only specimen of its kind known from
266 this unit. Notably, GTB-22-1-165 does not exhibit the tightly packed (“compact”)
267 arrangement of the branches shown by USNM 35428, and it is on this basis that this
268 specimen in previous reports was assigned to *B. simulans* as opposed to *B. gyges*
269 (Mao et al., 1994; Yang et al., 1999; Yang, 2006). From the new Chinese material,
270 however, it is clear that branch arrangement varies widely between specimens and,
271 therefore, lacks taxonomic value.

272 Thorough search of the extensive Kaili Formation collections housed at
273 Guizhou University failed to reveal any material with a branch width and branching
274 pattern similar to *B. simulans*. It is concluded, therefore, that *Bosworthia* does not

275 occur in the Kaili biota, nor is it presently known from anywhere outside of the
276 Burgess Shale Formation in British Columbia.

277

278 **5. Systematic palaeontology**

279 ?Division Chlorophyta

280 ***WALCOTTOPHYCUS*** Wu et LoDuca, *gen. nov.*

281 *Type: Walcottophycus gyges* (Walcott, 1919), by monotypy.

282 *Diagnosis:* Thallus typically comprising 5 to 20 branches; all branches united
283 at base. Branch width 0.7–1.1 mm, width uniform along length, tapering in the last
284 few millimeters; branch length typically 20 to 45 mm, all branches for a given thallus
285 of similar length. Bifurcation of branches rare or absent; branch margins entire;
286 internal construction consisting of multiple thin filaments 13 to 25 μm in width and
287 arranged parallel to the long axis of the branch, these imparting a subtle fibrous
288 texture to the branch surface.

289 *Etymology:* In honor of Charles Doolittle Walcott, discoverer of the Burgess
290 Shale biota.

291 *Discussion:* Fossil macroalgal genera similar to *Walcottophycus* include
292 *Fractibeltia* Yang et Zhao (in Yang et al., 1999), *Leafiophyton* Yang, 2006, and
293 *Buthotrephis* Hall, 1847. *Fractibeltia*, a genus currently known only from the Kaili
294 Formation, differs in that the individual branches are laminate and lanceolate in form,
295 the midpoint being several times wider than the top or bottom (Yang et al., 1999).
296 Accordingly, we regard GTM-22-4-20 from Yang (2006) as belonging to *Fractibeltia*
297 rather than *Walcottophycus*. An additional difference between these genera is that
298 filaments within the branches of *Fractibeltia* are typically more conspicuous than
299 those of *Walcottophycus*. *Fractibeltia* was characterized by Yang (2006) as a thallus

300 with a terminal split or rupture, although this feature could be an artifact due to
301 taphonomic tearing. Like *Fractibeltia*, *Leafiophyton* is known only from the Kaili
302 Formation and differs from *Walcottophycus* in being characterized by branches with a
303 lanceolate form. As defined in Yang (2006), *Leafiophyton* shows an additional
304 difference in that it has a differentiated holdfast and a poorly defined stipe.
305 *Buthotrephis*, a taxon well known from the Ordovician and Silurian of North
306 America, is similar to *Walcottophycus* in that it comprises narrow branches, and some
307 specimens assigned to this taxon show an internal network of fine filaments (White,
308 1902). Unlike *Walcottophycus*, dichotomous branching is conspicuous. Given the
309 similarity in construction, however, it is possible that *Buthotrephis* diverged from
310 *Walcottophycus* or a similar ancestor. *Algites* Seward, 1894, is an extremely poorly
311 circumscribed genus erected to encompass all fossil macroalgal forms lacking
312 sufficient detail in terms of reproductive structures and/or internal structure to allow
313 confident assignment to living genera. The two species assigned to *Algites* by Seward
314 (1894), both from the Cretaceous of England, *A. valdensis* and *A. catenelloides*, differ
315 from *Walcottophycus* in that they display conspicuous dichotomous branching, but *A.*
316 *enteromorphoides* Basson et Wood, 1970, from the Devonian of Missouri, is similar
317 in that the branches have a similar size and shape and lack bifurcation. No specimens
318 of *A. enteromorphoides* have been found with branches united at the base, however,
319 these instead occurring only as isolated blades (Basson and Wood, 1970). The
320 macroscopic phototroph *Marpolia* Walcott, 1919, regarded as a cyanobacterium
321 (Conway Morris and Robison, 1988), is abundant in both the Burgess Shale and Kaili
322 biotas. It differs conspicuously from *Walcottophycus* in that each branch is an
323 individual filament, 0.1 mm in diameter. In addition, the filaments tend to be shorter
324 than the branches of *Walcottophycus* and often have a branched morphology.

325 *Fuxianospira* Chen et Zhou, 1997, also occurs in both the Burgess Shale and Kaili
 326 biotas (LoDuca et al., in press) and has tubes roughly the same width as the branches
 327 of *Walcottophycus*. Specimens of the former differ from the branches of
 328 *Walcottophycus* in that they have undulating sides, always occur singly, and never
 329 contain internal filaments. *Yuknessia* Walcott, 1919, erected as a genus of macroalga
 330 by Walcott (1919) on the basis of specimens from the Burges Shale Formation, also
 331 comprises tubes similar in some respects to the branches of *Walcottophycus*.
 332 However, recent SEM study of the holotype and similar forms from the Burgess Shale
 333 Formation and Cambrian of Utah indicated the presence of fuselli, and the genus was
 334 redescribed as a colonial hemichordate (LoDuca et al., 2015).

335

336 ***Walcottophycus gyges* (Walcott, 1919) Wu et LoDuca *comb. nov.*** (Plates II,
 337 III; Figures 2, 3)

338

339 *Basionym:* *Bosworthia gyges* Walcott, 1919, Cambrian Geology and
 340 Paleontology IV, no. 5 Middle Cambrian algae. Smithsonian Miscellaneous
 341 Collections, 67: p. 242, plate 58, fig. 2 = holotype, USNM 35428.

342

343 *Synonymy and selected references*

344 1919 *Bosworthia gyges* Walcott, p. 242, pl. 58, fig. 2

345 1966 *Bosworthia gyges* Walcott; Johnson, p. 68, pl. 57, fig. 3

346 1994 *Bosworthia simulans* Walcott; Mao et al., p. 346-347, pl. II, fig. 2

347 1999 *Bosworthia simulans* Walcott; Yang et al., p. 285, pl. I, figs. 1, 2, 4

348 1999 *Bosworthia gyges* Walcott; Yang et al., p. 285, pl. II, fig. 2

349 2006 *Bosworthia simulans* Walcott; Yang, p. 136-137, pl. VII, figs. 1, 2, 4

350 2006 *Bosworthia gyges* Walcott; Yang, p. 137, pl. VIII, fig. 2
 351 2011 *Bosworthia simulans* Walcott; Zhao et al., p. 192-193, fig. 248
 352
 353 *Referred material:* USNM 35428, GTBM-9-1-9465, GTBM-9-2-636, GTBM-
 354 9-5-4195, GTBM-9-5-2300, GTBM-9-2-1112, GTB-22-1-186, GTB-22-1-165,
 355 GTBJ-13-2, GTB-13-3-29, GTBM-9-4-2004, GTBM-9-7-997, GTBM-9-2-4943,
 356 GTBM-9-5-5912, GTBM-9-3-461, GTBM-9-4-1407, GTBM-9-5-969a,b, GTBM-9-1-
 357 627a,b, GTBM-9-4-544, GTBM-9-4-2066, GTBM-9-2-1514, GTBM-9-2-3247, GTB-
 358 20-386, GTB-21-119a,b, GTBM-9-1-567, GTBJ-14-1-193a,b, GTBM-9-2-1997,
 359 GTBM-9-5-362, GTBM-9-2-453, GTBM-9-5-3818, GTBM-9-2-994.
 360 *Occurrence:* Greater Phyllopod Bed, Burgess Shale Formation, Fossil Ridge
 361 (Walcott Quarry), British Columbia (Cambrian Series 3, Stage 5); Kaili Formation,
 362 Wuliu-Zengjiaya (GTB), Miabanpo (GTBM), and Jinyinshan (GTBJ) sections,
 363 Guizhou Province, China (Cambrian Series 3, stages 4-5).
 364 *Discussion:* Within the Kaili biota, *Walcottophycus* is the second most
 365 abundant macrophyte genus, comprising 15% of the flora. *Fractibeltia* also comprises
 366 15% of the flora while *Marpolia* is the most abundant macrophyte, comprising 40%
 367 of the flora (Wu, 2011).
 368 In addition to material formally assigned to *W. gyges* herein, it is likely that
 369 specimens illustrated as *Enteromorphites* in Yang (2006, plate X, 3–6) and as
 370 *Eoulothrix* in Yang (2006, plate X, 8; plate XV, 3; plate XVI, 1, 3, 6) also belong to
 371 *W. gyges*. These specimens could not be located during the present study, and the
 372 published photographs in this case do not provide enough resolution to allow for
 373 definitive identification.

374 Babcock et al. (2011), in describing material referred therein to *Yuknessia*
375 from the Huaqiao Formation of Hunan Province, tentatively assigned all Kaili
376 Formation material illustrated as *Bosworthia simulans* in Mao et al. (1994) to
377 *Yuknessia simplex*, pending further study. The specimen illustrated in plate II, figure 2
378 of Mao et al. (1994), GTB-22-1-165 (Plate 2, 2), is assigned herein to *Walcottophycus*
379 *gyges*.

380 Makhaev (1939), in a report on the Cambrian stratigraphy of the Maya River
381 Basin in eastern Russia, introduced the species name *Bosworthia siberica* for material
382 from the Lower Gerbian beds. The material was not formally described or illustrated,
383 no catalog numbers were provided, and the current whereabouts of the specimens are
384 unknown. Given this state of affairs, the taxonomic status of this material must be
385 regarded as uncertain.

386

387 **6. Phylogenetic affinity of *Bosworthia* and *Walcottophycus***

388 Walcott (1919) assigned *Bosworthia simulans*, and thereby *Bosworthia*, to the
389 Rhodophyta, basing this assignment on an overall thallus form that compared well
390 with the extant rhodophyte *Dumontia filiformis* (now *D. contorta*). The dichotomous
391 branching pattern characteristic of *B. simulans*, however, is also known among extant
392 chlorophytes and phaeophytes, including, for the latter, *Dictyota*, as noted by Walcott
393 (1919). A phaeophyte affinity for *Bosworthia* appears unlikely on the basis of
394 molecular clock studies, which point to a post-Paleozoic origin for the Phaeophyta
395 (Silberfeld et al., 2010; Brown and Sorhannus, 2010). In addition, the higher-level
396 affinities of the few Ediacaran and Paleozoic taxa previously described as
397 phaeophytes, such as *Miaohephyton* Steiner, 1994 (see Xiao et al., 1998) and
398 *Thalassocystis* Taggart et Parker, 1976, remain to be confirmed because

399 morphological features interpreted to be characteristic of phaeophyceans could have
400 evolved convergently in other algal groups (Brown and Sorhannus, 2010; Butterfield,
401 2015). Among extant chlorophytes, thalli comparable to *Bosworthia* in size and gross
402 morphology are found among the bryopsidalean genus *Codium*. The thalli of *Codium*
403 are composed of dense bundles of siphons, but there is no evidence of such a structure
404 in *B. simulans*. Moreover, molecular clock analyses indicate that *Codium* diverged
405 from a structurally simple bryopsidalean ancestor late in the Paleozoic, during the
406 Carboniferous or Permian (Verbruggen et al., 2009). By contrast, all available
407 evidence from thallus morphology and molecular clock analyses agrees with a red
408 algal interpretation. In particular, extant genera within the floridiophycean subclass
409 Rhodymeniophycidae, such as *Chondrus* and *Mastocarpus*, have dichotomously
410 branched thalli that compare well with *B. simulans*, including in terms of branch
411 width and internode lengths. Notably, these genera have a tough, cartilaginous
412 character that might favor their preservation as fossils. *Thallophyca* Zhang, 1989, and
413 *Paramecia* Zhang et Yuan, 1992, from the Doushantuo Formation of China, indicate
414 that floridiophycean algae had originated by the Ediacaran (Xiao et al., 2004, 2014).
415 The pseudoparenchymatous thalli of these likely coralline algae appear to contain
416 carposporophytes, suggesting the presence of a triphasic lifecycle that is typical for
417 extant Floridiophyceae. Because the coralline algae are not an early-diverging lineage
418 in the Floridiophyceae (Le Gall et al., 2007), the initial diversification of
419 Floridiophyceae must have occurred well prior to 600 million years ago. This is
420 supported by molecular clock analyses, which indicate divergence between
421 Floridiophyceae and Bangiales during the early Neoproterozoic, and origination of
422 the Rhodymeniophycidae by the latest Neoproterozoic or earliest Paleozoic (Parfrey
423 et al., 2011; De Clerck et al., 2012; Yang et al., 2016). Features that would

424 unequivocally confirm a rhodymeniophycidaen affinity for *B. simulans*, however, are
425 lacking. In particular, the specimens show no evidence of reproductive features, such
426 as tetrasporangial sori or cystocarps. Nonetheless, it is possible, given the limited
427 sample size, that the specimens do not represent fertile thalli, and it is also
428 conceivable that such features, if present, might escape preservation.

429 Given the available evidence, *Bosworthia* is best regarded as a
430 rhodymeniophycidaen red alga. However, because so many critical features remain
431 unknown, such as reproductive structures, cellular-level details, and chlorophyll
432 composition, the possibility remains that it belongs to an algal clade with no living
433 descendents.

434 Yang et al. (1999) and Yang (2006) interpreted material assigned herein to
435 *Walcottophycus gyges* as red algae. Their interpretation was based on beaded
436 structures that were said to be present in the material. However, these structures are
437 not clearly illustrated or described, and even if they are present they are not diagnostic
438 of red algae. Such structures were not observed among the other material assigned to
439 *W. gyges* during the present study. Instead, an internal construction consisting of thin
440 filaments is indicated (Fig. 3). This internal construction when combined with overall
441 thallus form yields an assemblage of characteristics not known for extant members of
442 either the red or brown algae. Conversely, the thalli of extant multiaxial bryopsidalean
443 green algae, the interiors of which comprise dense networks of thin interwoven
444 siphons, are broadly similar. For many taxa within this group, the siphons have
445 conspicuously inflated terminations (e.g., *Halimeda*, *Codium*), but others have
446 siphons with a simpler form and such is the case for *Avrainvillea* (see Littler and
447 Littler, 1992), the siphons of which are roughly comparable to the filaments of *W.*
448 *gyges* in terms of both general form and width (20–60 vs. 13–25 μm). The oldest

449 likely multiaxial bryopsidaleans are specimens of *Dimorphosiphon* from the mid-
450 Ordovician (reviewed in Boyd, 2007). These calcified macroalgae are roughly 35 Ma
451 younger than *Walcottophycus*, but such forms may have evolved from noncalcified
452 ancestors with similar multiaxial thalli. Two key factors, however, cast doubt on
453 crown-group placement of *Walcottophycus* within the Bryopsidales. First, no living
454 multiaxial bryopsidalean algae are known with an overall thallus form closely
455 comparable to *Walcottophycus*. Second, and more importantly, molecular clock
456 analyses indicate that extant bryopsidaleans with complex multiaxial thalli originated
457 no earlier than the Carboniferous (Verbruggen et al., 2009). The possibility remains,
458 however, that *Walcottophycus* belongs to a clade of bryopsidalean algae with no
459 living descendents. Such an interpretation is supported by molecular evidence
460 indicating multiple independent origins of complex multiaxial thalli within the
461 Bryopsidales (Verbruggen et al., 2009). Thus, on the basis of the available evidence,
462 *W. gyges* is tentatively regarded herein as belonging to an extinct clade within the
463 Bryopsidales. It must be noted, however, that it cannot be determined from the
464 evidence at hand whether thallus organization was truly siphonous. For this reason, as
465 well as a lack of information about chlorophyll composition, such an interpretation
466 must be treated with particular caution. Detailed studies of fossil taxa with a similar
467 internal construction, such as the Silurian taxon *Buthotrephis newlini* White, 1902,
468 may yet shed further light on this issue.

469

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487

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 584

585

FIGURE CAPTIONS

586 **Plate I.** Type material of *Bosworthia simulans* Walcott, Burgess Shale Formation,
587 Greater Phyllopod Bed (35k locality), Fossil Ridge (Walcott Quarry), British
588 Columbia. Scale bar: 10 mm (1, 4) and 5 mm (2, 3).

589 1 Lectotype, USNM 35426, polarized light.

590 2 Enlargement of area indicated by arrow in (1) showing details of branch
591 surfaces, margins, and dichotomous branching pattern, polarized light.

592 3 Same area as shown in (2), but in direct light.

593 4 Syntype, USNM 35427, left arrow indicates inferred base of thallus, right
594 arrow indicates branching similar to USNM 35426, polarized light.

595

596 **Plate II.** *Walcottophycus gyges* (Walcott) from the Burgess Shale and Kaili
597 formations. All specimens photographed dry in direct light. Scale bar: 10 mm (1–10,
598 12), 4 mm (11), 2.5 mm (13, 15), and 2 mm (14).

599 1 Holotype, USNM 35428, Burgess Shale Formation, Greater Phyllopod Bed
600 (35k locality), Fossil Ridge (Walcott Quarry), British Columbia.

601 2 GTB-22-1-165, specimen attributed to *B. simulans* in Mao et al. (1994) and
602 Yang et al. (1999), Kaili Formation, Guizhou Province, China. Photograph
603 from Mao et al. (1994).

604 3 GTB-22-1-186, specimen described as *B. gyges* in Yang et al. (1999), Kaili
605 Formation, Guizhou Province, China. Photograph from Yang et al. (1999).

606 4 GTBM-9-5-2300, Kaili Formation, Guizhou Province, China.

607 5 GTBM-9-5-4195, Kaili Formation, Guizhou Province, China.

608 6 GTBM-21-119b, Kaili Formation, Guizhou Province, China.

609 7 GTBM-9-2-994, Kaili Formation, Guizhou Province, China.

- 610 8 GTB-13-3-29, Kaili Formation, Guizhou Province, China.
- 611 9 GTBM-9-3-461, Kaili Formation, Guizhou Province, China.
- 612 10 GTBM-9-2-636, specimen illustrated as *Bosworthia simulans* in Zhao et al.
- 613 (2011), Kaili Formation, Guizhou Province, China.
- 614 11 Enlargement of upper part of specimen shown in (10).
- 615 12 GTBM-9-5-362, Kaili Formation, Guizhou Province, China.
- 616 13 Enlargement of upper part of specimen shown in (1).
- 617 14 Enlargement of area indicated by arrow in (4).
- 618 15 Enlargement of basal part of specimen shown in (4).

619

620 **Plate III.** *Walcottophycus gyges* (Walcott) from the Kaili Formation, Guizhou
 621 Province, China. All specimens photographed dry in direct light. Scale bar: 10 mm.

- 622 1 GTBM-9-5-5912.
- 623 2 GTBM-9-1-627a.
- 624 3 GTBM-9-5-969a.
- 625 4 GTBM-9-4-1407.
- 626 5 GTBM-9-2-1514.
- 627 6 GTBM-9-2-3247.

628

629 **Fig. 1.** Interpretive drawing of USNM 35426 (see Plate 1, 1).

630

631 **Fig. 2.** Interpretive drawing of USNM 35428 (see Plate 2, 1).

632

633 **Fig. 3.** BSE image of upper part of GTBM-9-2-636 (arrow in Plate II, 10) showing
 634 thin filaments within branches. Scale bar: 1 mm.

Specimen Number	Maximum Branch Length	Maximum Branch Width	Number of Branches
USNM 35428	45.0	1.0	10+
GTB-22-1-165	26.0	1.0	20+
GTB-22-1-186	23.0	1.0	8+
GTBM-9-2-636	30.0	1.0	5+
GTBM-9-1-9465	21.0	1.0	5?
GTBM-9-5-4195	24.0	1.0	10+
GTBM-9-5-2300	23.0	0.7	9+
GTBM-9-2-1112	40.0	0.7	20+
GTBJ-13-2	25.0	1.0	1 or 2
GTB-13-3-29	12.0	0.7	2
GTBM-9-4-2004	28.0	1.0	11+
GTBM-9-7-997	27.0	1.2	3
GTBM-9-2-4943	25.0	1.0	1
GTBM-9-5-5912	33.0	1.0	6+
GTBM-9-3-461	20.0	0.7	4+
GTBM-9-4-1407	35.0	1.0	3 or 4
GTBM-9-5-969a	10.0	0.6	7
GTBM-9-1-627a	20.0	1.0	4
GTBM-9-4-544	20.0	0.6	2+
GTBM-9-4-2066	22.0	1.1	7+
GTBM-9-2-1514	37.0	1.0	5
GTBM-9-2-3247	28.0	1.1	10+
GTB-20-386	21.0	0.7	5+
GTB-21-119b	24.0	1.0	6+
GTBM-9-1-567	24.0	0.6	7+
GTBJ-14-1-193a	38.0	1.5	2
GTBM-9-2-1997	16.0	0.6	4+
GTBM-9-5-362	25.0	1.0	12
GTBM-9-2-453	13.0	0.7	8+
GTBM-9-5-3818	28.0	0.8	12
GTBM-9-2-994	42.0	1.2	6+

Table 1

Morphometric data for specimens assigned herein to *Walcottophycus gyges*.
Measurements in mm.

Figure 1

Figure &

Figure ' .