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8 **Title: Extending beyond Gondwana: Cretaceous Cunoniaceae from western North**
9 **America**

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32 Summary

- 33 • Cunoniaceae are important elements of rainforests across the Southern Hemisphere.
34 Many of these flowering plants are considered Paleo-Antarctic Rainforest Lineages that
35 had a Gondwanan distribution since the Paleocene. Fossils of several modern genera
36 within the family, such as *Ceratopetalum*, have indicated biogeographic connections
37 between South America and Australia in the Cenozoic.
- 38 • Here, we report a dramatic geographic range extension for *Ceratopetalum*, and
39 Cunoniaceae as a whole, based on two exceptionally preserved fossil winged fruits from
40 Campanian (~82-80 Ma) deposits on Sucia Island, Washington state, USA. The fossils
41 were studied using physical sectioning, light microscopy, microCT scanning, and
42 multiple phylogenetic analyses.
- 43 • The fossil fruits share diagnostic characters with *Ceratopetalum* such as the presence of
44 four to five persistent calyx lobes, a prominent nectary disk, persistent stamens, a semi-
45 inferior ovary, and two persistent styles. Based on morphological comparisons with fruits
46 of extant species and support from phylogenetic analyses, the fossils are assigned to a
47 new species *Ceratopetalum suciensis*.
- 48 • These fossils are the first unequivocal evidence of crown Cunoniaceae from the
49 Cretaceous of North America, indicating a more complicated biogeographic history for
50 this important Gondwanan family.

51 **Keywords:** biotic exchange, *Ceratopetalum*, Cretaceous, Cunoniaceae, fossil fruits, Gondwana,
52 phylogenetics

54 Introduction

56 Southern Hemisphere rainforests share remarkably similar plant taxonomic associations
57 across far flung landmasses such as Australia, New Zealand, Fiji, New Guinea, and South
58 America (Kooyman *et al.*, 2014). Although these ecosystems currently are separated by great
59 distances, the fossil record has shown that prior to the final break up of Gondwana during the
60 Eocene, important components of these southern rainforests were assembling in present day
61 South America, Australia, and Antarctica. Thus, the plants that constitute Gondwanan floras are
62 known as Paleo-Antarctic Rainforest Lineages (PARLs), some of which include Podocarpaceae,

63 Nothofagaceae, Myrtaceae, Proteaceae, and Cunoniaceae (Kooyman *et al.*, 2014). Many PARLs
64 are important components of present-day temperate to tropical rainforests in the Southern
65 Hemisphere and their fossil records remain critical for investigating the assembly and
66 biogeographic history of these ecosystems (Barreda *et al.*, 2021). Therefore, many of these
67 clades are often used as study systems for understanding the evolution of southern rainforests
68 including Cunoniaceae.

69 Cunoniaceae today comprise 300 species and 27 genera that have a typical PARL
70 distribution and dominate some southern rainforests (Bradford *et al.*, 2004; Kooyman *et al.*,
71 2014). It has long been thought that this family has been restricted to the Southern Hemisphere
72 since the latest Cretaceous (Santonian-Maastrichtian) as indicated by wood and pollen from
73 South America and Antarctica (Cranwell, 1959; Askin, 1992; Baldoni & Askin, 1993; Poole *et*
74 *al.*, 2000a, 2003). However, it is uncertain if these previously reported Cretaceous fossils
75 represent crown members of Cunoniaceae, which makes it difficult to infer when the family
76 originated.

77 Extant genera of the family began to appear during the Paleogene with one of the more
78 conspicuous fossil representatives being *Ceratopetalum* Sm. (Holmes & Holmes, 1992; Barnes
79 & Hill, 1999; Gandolfo & Hermsen, 2017). Today, this genus consists of eight species that are
80 restricted to eastern Australia and Papua New Guinea (Rozefelds & Barnes, 2002) and can
81 dominate rainforests in these regions (Burges & Johnston, 1953; Baur, 1957; Webb, 1978).

82 Here we report two three-dimensionally preserved fruits of *Ceratopetalum* from the
83 Northern Hemisphere, namely, the Late Cretaceous of western North America. The fossil fruits
84 have the diagnostic character combination of the genus and comparative analysis indicates that
85 the fossils represent a new species. Our findings indicate: 1) the diversification of Cunoniaceae
86 was well underway during the Cretaceous; 2) *Ceratopetalum* and crown Cunoniaceae have a
87 biogeographic history in the Northern Hemisphere; and 3) the historical distributions of other
88 important PARLs may have extended beyond Gondwana in the past.

90 **Materials and Methods**

91
92 Two three-dimensionally preserved fruits are preserved within calcium carbonate
93 concretions that were exposed along Henry Point on Sucia Island, Washington state, USA.

94 Cretaceous exposures on Sucia Island (and Little Sucia Island) belong to the Cedar District
95 Formation of the Nanaimo Group and are Campanian in age based on biostratigraphy and
96 magnetostratigraphy (~82-80 Ma; Ward *et al.*, 2012). The reported Cretaceous biota from these
97 deposits include cornalean fruits, ammonites, terrestrial gastropods, inoceramid bivalves, and a
98 theropod femur (Ward, 1978; Roth, 2000; Ward *et al.*, 2012; Peacock & Sidor, 2015; Atkinson,
99 2016).

100 Specimens were imaged using a Nikon SMZ25 stereomicroscope with a Nikon DS-Fi3
101 camera attachment (Nikon Corporation, Tokyo, Japan). One specimen (KUPB 19169) was
102 imaged for internal morphology revealed by the initial fracture. The specimen was then glued
103 back together for X-ray micro-computed tomography (μ CT) and physical sectioning using the
104 cellulose acetate peeling (Joy *et al.*, 1956). Several peels were mounted on microscope slides
105 using the mounting medium Eukitt (O. Kindler GmbH, Freiberg, Germany). All specimens
106 housed in the Division of Paleobotany Collections, Biodiversity Institute, University of Kansas
107 (KUBP).

108 One fossil specimen (KUPB 19169) and seven fruits of five extant species of
109 *Ceratopetalum* (Table S1) were μ CT scanned at the University of Michigan CTEES facility
110 using a Nikon XT H 225ST industrial μ CT system with a Perkin Elmer 1620 X-ray detector
111 panel and a tungsten reflection target. Scan conditions for the fossil were set at 128 KV, 145 μ A,
112 and used a 1 mm copper filter and obtained 20.84 μ m pixel size resolution. Scan conditions for
113 the extant fruits are presented in Table S2. The program Inspect-X (Nikon Corporation, Tokyo,
114 Japan) acquired scans that were segmented (from serial longitudinal digital sections) using the
115 software Mimics 22.0 (Materialise, Leuven, Belgium) to reconstruct three-dimensional images of
116 the fruits. Avizo 9 Lite 3D (Thermo Fisher Scientific, Massachusetts, USA) was used for fruit
117 measurements. Data are archived on Morphosource (Boyer *et al.*, 2016) under project title “3D
118 morphology of *Ceratopetalum* fruits (Cunoniaceae).”

119 In order to test our systematic assignment of the Cretaceous fruits to Cunoniaceae, we
120 analyzed them via the phyloscan method (Schönenberger *et al.*, 2020), which uses a
121 comprehensive angiosperm floral character matrix with a molecular backbone to assess the most
122 parsimonious position(s) of fossil flowers across the angiosperm phylogeny. This method allows
123 us to quickly assess phylogenetic affinities of the fossils and to easily exclude angiosperm clades
124 that may have similar (helicopter-like) fruits but a different floral plan. Since the studied fossil

125 fruits have a number of persistent floral structures preserved, they were easily analyzed using
126 this method. The original floral matrix and backbone did not include *Ceratopetalum*. The genus
127 is morphologically distinct in Cunoniaceae, so the extant species, *C. gummiferum* Sm. was added
128 to the matrix and grafted to the backbone phylogeny with its phylogenetic position based on
129 Bradford and Barnes (2001). The backbone phylogeny and matrix are presented in Supporting
130 Information Notes S1 and S2. Phyloscanning was used to assess two equivocal cunoniaceous
131 fossils, *Tropidogyne pentaptera* Poinar & Chambers (Poinar & Chambers, 2017) and *Platydiscus*
132 *peltatus* Schönenberger & Friis (Schönenberger *et al.*, 2001). Phyloscan outputs can be found in
133 Supporting Information Figs. S1-S6. Scoring justifications are detailed in the Supporting
134 Information Methods S1.

135 After confirming the familial assignment of the studied fossil fruits, we conducted
136 additional phylogenetic analyses to test the systematic affinities of the Sucia Island fruits to
137 *Ceratopetalum*. More specifically, Bayesian phylogenetic analyses that focus on relationships
138 within Cunoniaceae were conducted using combined morphological and molecular datasets. The
139 combined datasets have a more thorough sampling of species within the family which provides
140 for a more precise systematic assessment of the fossils compared to the familial/ordinal level
141 assessment of the phyloscan. Two Bayesian analyses were conducted. In the first analysis the
142 Cretaceous fruits of this study were the only fossils included. In the second analysis, ten
143 additional extinct species with preserved reproductive structures were included to further test the
144 phylogenetic position of these fruits because fossils can affect the position of other fossils in
145 such analyses (Manos *et al.*, 2007; Ronquist *et al.*, 2012a). These analyses used a morphological
146 dataset from Jud and Gandolfo (2020), which was modified to include the additional fossil taxa
147 resulting in a dataset of 54 taxa (43 extant, 11 fossils) and 58 morphological characters. The
148 modified matrix is available online via Morphobank (project P3906, matrix 27164; O'Leary &
149 Kaufman, 2011). The matrix was then combined with *rbcL* and *trnL-trnF* data from the sampled
150 extant taxa. Sequences were obtained from GenBank (Table S3). Molecular data were aligned in
151 Aliview (Larsson, 2014) using Mafft (Katoh & Standley, 2013). PartitionFinder2 (Lanfear *et al.*,
152 2016) was used with AICc model selection to search for the optimal partitioning scheme and
153 models of molecular evolution. The most optimal scheme was GTR+G+I model for the *rbcL* data
154 and a GTR+G model for the *trnL-trnF* data. Mkv model (Lewis, 2001) was used for the
155 morphological data. The Bayesian phylogenetic analyses were conducted using MrBayes 3.2.7a

156 (Ronquist *et al.*, 2012b) on the CIPRES Science Gateway (Miller *et al.*, 2011). The analysis used
157 Markov chain Monte Carlo for two independent runs with four chains running for 100 million
158 generations, sampling every 10000 generations, with a 25% burn-in. The standard deviation of
159 split frequencies was below 0.02; and, Tracer 1.7 (Rambaut *et al.*, 2018) was used to confirm
160 convergence with all ESS values well above 200. All tree files are available in Notes S3.

161

162 **Results**

163

164 ***Systematics***

165 Order – Oxalidales Bercht & J. Presl

166 Family – Cunoniaceae R. Br. 1814

167 Tribe – Schizomerieae J.C. Bradford & R.W. Barnes 2001

168 Genus – *Ceratopetalum* Sm. 1793

169 Species – *Ceratopetalum suciensis* Tang & Atkinson, sp. nov. (Figs. 1a-c, 2, 3)

170 Specific diagnosis. Fruit body up to 4.0 mm wide and 5.75 mm long. Calyx lobes up to 3.0-4.0
171 mm wide and 11.0 mm long, oblong with slightly acute apex and up to five vascular bundles.

172 Secondary bundles in calyx lobes diverging throughout the entire length of wing at 45-90°.

173 Nectary, annular ring up to 0.38-0.60 mm tall, with conspicuous lobes bordering each stamen.

174 Styles up to 2.47 mm long in fruit. Ovary diameter 3.62-4.0 mm.

175 Etymology. The specific epithet refers to Sucia Island where the fossils were recovered.

176 Holotype. KUPB 19169 (Figs. 1b, 1c, 2d-g, 3).

177 Paratype. KUPB 19168 (Figs. 1a, 2a-c).

178 Type locality. Henry Point, Sucia Island, Washington State, USA (48.749330°N,
179 122.900798°W).

180 Stratigraphy. Cedar District Formation.

181 Age. Early to Middle Campanian (ca. 82-80 Ma).

182

183 ***Description***

184 The two three-dimensionally preserved fruits are radially symmetrical with an epigynous
185 perianth and androecium (Figs. 1a, b). The calyx, nectary, androecium, and styles are persistent;
186 petals and internal tissues are not preserved. The width of the fruit body, excluding the wings, is

187 3.62-4.00 mm and the length of the fruit body is 5.75 mm from the base to the tip of the styles.
188 There are four to five calyx lobes per fruit that extend outward forming wings, giving the fruit a
189 helicopter-like morphology (Figs. 1a, c). Most wings are abraded; however, one specimen has an
190 entire wing preserved (Fig. 1a) with smooth margins and it is 11.0 mm long. Wings from both
191 specimens range from 3.0-4.0 mm wide. This wing is elliptic in shape with a slightly acute apex
192 and attenuate base that gradually narrows towards the base.

193 Although internal preservation is limited, calyx venation can be easily observed as dark
194 “coalified” tissue. Five primary veins can be seen entering the base of the wing with secondary
195 veins diverging from primary veins throughout the entire wing length. The divergence of
196 secondary veins range from 45-90°. The marginal veins in the wing connect to other marginal
197 veins of adjacent wings via an inter-wing vein located at the outer edge of the nectary between
198 each calyx lobe (Fig. 2b). The nectary is an annular ring (Fig. 2c) with prominent lobes that
199 border each stamen as revealed by the μ CT-scanned specimen and cellulose acetate peels (Figs.
200 2d-g, 3a). The nectary is 0.38-0.60 mm tall.

201 Three-dimensional renderings from segmentation of μ CT data reveal a diplostemonous
202 androecium with abraded filaments that are 1.21-1.89 mm long. Anthers were not preserved. The
203 outer whorl of stamens is opposite the wings (calyx lobes) while the inner whorl of stamens
204 alternates with the wings (Figs. 1c, 2d, 3e).

205 The ovary is 3.62-4.00 mm in diameter and is semi-inferior in which the apex of the
206 ovary slightly extends above the insertion of the calyx and androecium. The μ CT scan and
207 sections of one specimen (KUPB 19169) reveals two free styles that are pressed against one
208 another for most of their length (Fig. 3). In particular, Fig. 3b clearly shows the two separate and
209 appressed styles. Both styles are 2.47 mm long. Stigmas are inconspicuous or not preserved.

210

211 **Remarks**

212 *Ceratopetalum suciensis* possesses a combination of wing shape and venation characters
213 that indicate it is a new species (Tables S4 and S5). Moreover, these characters are often used to
214 taxonomically compare fruits of extinct species to those of living ones (e.g., Barnes & Hill,
215 1999; Gandolfo & Hermsen, 2017). It is worth noting that *C. suciensis* is based on the most
216 completely preserved fossil fruits of *Ceratopetalum*, to date, while other described fossils tend to

217 lack preservation of other informative structures such as stamens and styles (see Table S4),
218 which makes taxonomic comparisons straightforward.

219 Wing shape of both extant and extinct species of *Ceratopetalum* can be oblong, obovate,
220 or elliptic. Wing bases can range from constricted to not constricted at all and wing apices range
221 from acute to obtuse in shape. The fruit wings of *C. suciensis* fall within the range of variation
222 seen in extant and fossil species, but the wing base is unique in being attenuate with a gradual
223 basipetal constriction. Fruit wings of the Australian *C. virchowii* F. Muell. is the only living
224 species in this genus with conspicuously constricted fruit wing bases (Rozeffelds & Barnes, 2002;
225 Table S5). However, this extant species differs from *C. suciensis* by having a fruit wing shape
226 that is typically obovate and with an abrupt constriction of the wing base rather than an elliptic
227 wing shape with a gradually narrowing base. Therefore, based on fruit wing shape, *C. suciensis*
228 differs from all extant species of *Ceratopetalum*.

229 Among reported fossil *Ceratopetalum* species, *C. edgardoromeroi* Gandolfo & Hermsen
230 from the Eocene of Patagonia (Gandolfo & Hermsen, 2017), is the only one to have a gradually
231 narrowing wing base that is similar to *C. suciensis*. This fossil species differs from *C. suciensis*
232 by having a rounded wing apex (Table S4). In addition, *C. edgardoromeroi* has fruits with ovate
233 wings (Gandolfo & Hermsen, 2017) while *C. suciensis* has fruit wings that are elliptic. Overall,
234 *C. suciensis* has a unique wing shape among all reported extinct species of *Ceratopetalum*.

235 Additionally, fruit wing venation patterns vary and are taxonomically informative within
236 *Ceratopetalum*. Most living species have three primary veins that enter each fruit wing (Table
237 S5; Dickison, 1975; Barnes & Hill, 1999; Matthews *et al.*, 2001; Gandolfo & Hermsen, 2017).
238 *Ceratopetalum succirubrum* C. T. White and *C. virchowii*, from Australia are the only two living
239 species with more than three primary veins, which is similar to *C. suciensis*. However, these two
240 species differ from *C. suciensis* by consistently having fruit wings with more than five primary
241 veins. In addition, the fruits of *C. succirubrum* and *C. virchowii* have wings with secondary veins
242 that are restricted to the distal half (Barnes & Hill, 1999) while those of *C. suciensis* have wings
243 with secondary veins that diverge throughout their entire length. The combination of wing
244 venation characters in *C. suciensis* is unique when compared to living species of *Ceratopetalum*.

245 Like their living counterparts, most extinct *Ceratopetalum* species have three primary
246 veins in each wing (Table S4; Barnes & Hill 1999; Gandolfo & Hermsen 2017). Similar to *C.*
247 *suciensis*, *C. priscum* Holmes and Holmes (Holmes & Holmes, 1992) and *C. wilkinsonii* (Ett.)

248 Holmes and Holmes (Holmes & Holmes, 1992) from the Miocene and Eocene-Oligocene of
249 Australia, are the only extinct species in this genus that have fruit wings with more than three
250 primary veins. These two fossil species differ from *C. suciensis*, however, by having fruits with
251 up to four primary veins in each wing rather than five. In addition, fruits of *C. priscum* and *C.*
252 *wilkinsonii* lack persistent stamens, which differs from *C. suciensis* (Table S4).

253 It is clear that both specimens of *C. suciensis* differ from living *Ceratopetalum* species by
254 consistently having a unique wing shape and five primary veins in each fruit wing. Known fruits
255 of extinct *Ceratopetalum* all have wings with less than five primary veins and those with four
256 veins lack persistent stamens. Due to these differences, the *Ceratopetalum* fossils described in
257 this study clearly have a unique combination of characters and are, therefore, assigned to a new
258 species, *Ceratopetalum suciensis* sp. nov. Tang & Atkinson.

259

260 ***X-ray micro-computed tomography (μCT) of Ceratopetalum fruits***

261 The μCT scans of the fossil fruit, KUPB 19169, revealed four calyx lobes, eight
262 persistent stamens, a semi-inferior ovary, nectary lobes, and two appressed styles (Figs. 1c, 2d-e,
263 3a-b, 3e-f; Videos S1-S3, S5). The calyx lobes have abraded apices and expand out to form
264 radiating wings (Fig. 1c). The persistent stamens form two whorls that alternate with and are
265 opposite of the wings (Fig. 3e). Nectary lobes border each stamen (Figs. 2d).

266 Scans of five extant *Ceratopetalum* species display the presence of 4-6 calyx lobes,
267 persistent stamens, semi-inferior ovaries, a nectary disk, and 2-3 appressed styles on the fruits
268 (Figs. 1d, 4, 5; Videos S4-S5). The calyx lobes expand in size to form radiating wings that
269 resemble a helicopter-like fruit morphology (Fig. 1d, 4a-c). Stamens form two alternating whorls
270 on each fruit (Figs. 1d, 4b, 5). There are four wings, eight stamens, and two styles present on
271 each *C. succirubrum* fruit (Fig. 1d). *Ceratopetalum apetalum* D. Don, *C. corymbosum* C.T.
272 White, and *C. virchowii* all have five wings present with ten stamens and two appressed styles
273 (Figs. 4b, 4c); the scans of fruits from these species reveal a morphology similar to that of *C.*
274 *suciensis*. *Ceratopetalum gummiferum* is the only specimen to have highly dissected petals
275 persistent on the fruit (Figs. 4a, 5a). There are six petals present, 12 stamens, and three styles on
276 the fruit of *C. gummiferum* (Figs. 5a, 5c).

277

278 ***Phylogenetic analyses***

279 In the initial phyloscan analysis, the most parsimonious positions of *Ceratopetalum*
280 *suciensis* were recovered on four branches leading to *Saxifraga cernua* L. (Saxifragaceae), the
281 order Saxifragales, stem Fagales, and *Ceratopetalum gummiferum* (Figs. S1, S2). Flowers of
282 *Tropidogyne pentaptera* Poinar & Chambers (Poinar & Chambers, 2017) have most
283 parsimonious positions in several distantly related taxa such as *Vahlia capensis* (L.f.) Thunb.
284 (Vahliaceae), *Donatia fascicularis* J.R. Forst. & G. Forst. (Stylidiaceae), and the order
285 Saxifragales (Figs. S3, S4). The most parsimonious positions of *Platydiscus peltatus*
286 Schönenberger & Friis (Schönenberger *et al.*, 2001) were recovered within the order
287 Saxifragales, specifically on the branch leading to *Aphanopetalum resinosum* Endl.
288 (Aphanopetalaceae) and on the branch leading to the families Tetracarpaceae, Penthoraceae, and
289 Haloragaceae (Figs. S5, S6).

290 Both Bayesian phylogenetic analyses with increased sampling of Cunoniaceae recovered
291 *C. suciensis* within *Ceratopetalum*. The first analysis recovered *C. suciensis* with extant
292 *Ceratopetalum* in a trichotomy (posterior probability = 1.0; Fig. 6). The second analysis (with
293 ten additional fossil taxa) recovered *C. suciensis* within a clade (polytomy) comprising all other
294 fossil and extant *Ceratopetalum* species (posterior probability = 0.72; Fig. 7).

295

296 **Discussion**

297

298 ***Cretaceous Ceratopetalum***

299 Based on multiple lines of evidence, the Sucia Island fruits are assigned to *Ceratopetalum*
300 as a new species, *C. suciensis*. Phylogenetic analyses in this study support the systematic
301 assignment of the Sucia Island fruits to the genus *Ceratopetalum*. Using the recent phyloscan
302 method (Schönenberger *et al.*, 2020), four most parsimonious positions of *C. suciensis* were
303 recovered along branches leading to Saxifragales, *Saxifraga cernua* (Saxifragaceae), the stem
304 lineage of Fagales, and *Ceratopetalum gummiferum* (crown group Cunoniaceae). Helicopter-like
305 fruits with expanded calyx lobes are not present in the order Saxifragales (Carlswald *et al.*, 2011)
306 and fruits of Fagales are typically nuts or samaras (Kubitzki *et al.*, 1993; Larson-Johnson, 2016).
307 Some fagalean taxa have helicopter-like fruits such as the juglandaceous *Cruciptera* Manchester
308 and *Polyptera* Manchester et Dilcher and the betulaceous *Asterocarpinus* Manchester and Crane,
309 but the fruit wings in these genera are derived from bracts (Manchester & Dilcher, 1982;

310 Manchester & Crane, 1987; Manchester, 1991; Manchester & Dilcher 1997), rather than perianth
311 as seen in *C. suciensis*. In addition, no reported stem Fagales have a fruit morphology similar to
312 *C. suciensis* (see Larson-Johnson, 2016). Therefore, Saxifragales and stem Fagales are excluded
313 from taxonomic consideration. The extinct genus *Calycites* Massalongo, of unknown familial
314 affinity, also has an epigynous perianth and produces helicopter-like fruits (Crane, 1988).
315 Distinct midribs on the fruit wings and longitudinal ribbing present on the ovary of *Calycites*
316 differentiates this genus from *C. suciensis*. Furthermore, persistent floral characters other than
317 calyx lobes are not known for *Calycites*. Additionally, branches leading to other angiosperm
318 families that produce helicopter fruits such as Caprifoliaceae (see Crane 1988), Malphigiaceae,
319 and Dipterocarpaceae were not recovered as most parsimonious positions for *C. suciensis* so these
320 families were excluded from taxonomic consideration. This is due to differences in overall floral
321 morphology. For instance, Caprifoliaceae flowers are typically zygomorphic with a fused
322 perianth (Hofmann & Bittrich, 2016), flowers in Malphigiaceae have superior ovaries (Anderson,
323 1979), and most Dipterocarpaceae flowers have a superior ovary and a single style with a
324 stylopodium (Ashton, 2003). Our Bayesian phylogenetic analyses that focused on Cunoniaceae
325 also support the placement of *C. suciensis* fruits within the genus *Ceratopetalum*.

326 The fruit morphology of *C. suciensis* is clearly diagnostic of the genus *Ceratopetalum*.
327 As shown in our microCT scans and in previous studies, extant *Ceratopetalum* fruits are
328 characterized by the presence of four to six persistent calyx lobes, a prominent nectary disk,
329 inter-wing veins, persistent stamens, a semi-inferior ovary that slightly extends above the
330 attachment of the perianth, and two (rarely three) persistent styles (Hoogland, 1960; Dickison,
331 1984; Barnes & Hill, 1999; Fortune Hopkins & Hoogland, 2002; Rozefelds & Barnes, 2002).
332 Persistent petals on the fruits are absent in the genus with the exception of *C. gummiferum*. The
333 calyx lobes are extensively expanded giving the fruit a helicopter-like morphology and have
334 three to many primary veins (Dickison, 1975; Barnes & Hill, 1999; Table S5). In addition,
335 located in the sinus area between adjacent calyx lobes, there are inter-wing veins that connect
336 lateral veins of adjacent wings (Barnes & Hill, 1999; Gandolfo & Hermsen, 2017). The
337 androecium is diplostemonous with two alternating whorls of eight to ten stamens. The two
338 styles are closely appressed to one another. These characters are used to identify *Ceratopetalum*
339 in the fossil record (Holmes & Holmes, 1992; Barnes & Hill, 1999; Gandolfo & Hermsen, 2017)
340 and, as documented in the description, *C. suciensis* clearly has all of these characters.

341

342 ***Origin and evolution of Cunoniaceae***

343 There is much uncertainty surrounding the age and early evolution of Cunoniaceae.
344 Divergence time estimates of stem ages for the family range from 90.9 to 66.55 Ma (Magallón *et*
345 *al.*, 2015; Ramírez-Barahona *et al.*, 2020). Moreover, reported crown ages of Cunoniaceae range
346 from 83.32 to 63.49 Ma (Heibl & Renner, 2012; Ramírez-Barahona *et al.*, 2020). Much of this
347 uncertainty in the age of this family comes from the difficulty of distinguishing stem and crown
348 members from Cretaceous deposits.

349 Prior to this study, the only accepted Cretaceous fossils for the family were pollen and
350 wood from the Santonian-Maastrichtian of Antarctica and Patagonia (Cranwell, 1959; Askin,
351 1992; Baldoni & Askin, 1993; Poole *et al.*, 2000a, 2003; Carpenter & Rozefelds, 2020);
352 however, due to the limited taxonomic resolution of these particular structures, it is unclear
353 whether those fossils are stem or crown members. Moreover, there are a few equivocal reports of
354 cunoniaceous flowers from Late Cretaceous deposits including *Tropidogyne* Chambers, Poinar &
355 R.T. Buckley from the Cenomanian of Myanmar (Chambers *et al.*, 2010; Poinar & Chambers,
356 2017, 2019; Poinar Jr. *et al.*, 2021) and *Platydiscus* Schönenberger & Friis from the Santonian-
357 Campanian of Europe (Schönenberger *et al.*, 2001). These fossils have been challenged as being
358 cunoniaceous (see Gandolfo & Hermsen, 2017; Jud *et al.*, 2018; Carpenter & Rozefelds, 2020)
359 because their floral morphology is not entirely consistent with the crown group of the family.
360 Our phyloscan analysis recovered multiple most parsimonious positions for *Tropidogyne*
361 *pentaptera* among several eudicot families, none of which are Cunoniaceae. In addition, crown
362 Cunoniaceae were not recovered as a most parsimonious position for *Platydiscus peltatus*.
363 Overall, the phyloscan analyses suggest that *Tropidogyne* and *Platydiscus* are not assignable to
364 crown (or stem) Cunoniaceae or even Oxalidales.

365 Recent studies have described extinct genera assignable to crown Cunoniaceae based on
366 fossil flowers from the lowermost Paleocene (Danian) of Patagonia (Jud *et al.*, 2018; Jud &
367 Gandolfo, 2020). These reports clearly indicate that the diversification of the family was well
368 underway by the Cretaceous-Paleogene boundary. Until now, extant genera have yet to be
369 identified prior to the Eocene, suggesting that the early evolution of crown Cunoniaceae
370 primarily comprised a diversification of extinct genera near the Cretaceous-Paleogene boundary
371 of Gondwana. However, our report of *Ceratopetalum suciensis* provides the first unequivocal

372 evidence for crown Cunoniaceae in the Cretaceous, which indicates that the initial diversification
373 of the family was well underway by the Campanian and comprised at least one extant genus as
374 well. Based on this report, a conservative minimal clade age for the family can be considered as
375 80 Ma.

376

377 ***Paleobiogeographic implications***

378 Although the breakup of Gondwana began during the Jurassic, many of the landmasses
379 that made up the southern super continent were still united or in close enough proximity to one
380 another to allow dispersal and migration across one another throughout the Mesozoic and into
381 the Paleogene. As detailed by the fossil record, biogeographic connections between Australia,
382 South America, and Antarctica were the last to persist until the Eocene (discussed in Wilf et al.
383 2013). These connections facilitated a nearly continuous rainforest biome across these three
384 continents and the constituent plants that comprised them are known as Paleo-Antarctic
385 Rainforest Lineages (PARLs; discussed in Kooyman *et al.*, 2014; Wilf *et al.*, 2019). While some
386 PARLs, such as Araucariaceae and Winteraceae, were nearly cosmopolitan during the Mesozoic
387 (Kunzmann, 2007; Kooyman *et al.*, 2014; Brea *et al.*, 2021), most are traditionally thought to
388 have been restricted to the Southern Hemisphere throughout their evolutionary history; this
389 includes *Ceratopetalum* and other Cunoniaceae.

390 Prior to this study, the entire reported biogeographic history of Cunoniaceae was
391 restricted to the Southern Hemisphere (discussed in Carpenter & Rozefelds, 2020).
392 Cunoniaceae fossil pollen and wood have been recovered from the Late Cretaceous (Santonian-
393 Maastrichtian) of Patagonia and Antarctica (Cranwell, 1959; Askin, 1992; Baldoni & Askin,
394 1993; Poole *et al.*, 2000a, 2003) and at the onset of the Cenozoic Cunoniaceae were diverse in
395 South America and Australia (Holmes & Holmes, 1992; Barnes & Hill, 1999; Barnes *et al.*,
396 2001; Gandolfo & Hermsen, 2017; Jud *et al.*, 2018; Jud & Gandolfo, 2020). These, along with
397 slightly younger records, reflect that the family was part of the expansive Gondwanan rainforest
398 biome during the Late Cretaceous and Paleogene (Kooyman *et al.*, 2014; Barreda *et al.*, 2021),
399 prior to the final breakup of the super continent. This biogeographic pattern is well exemplified
400 by *Ceratopetalum*. Previously, fossil *Ceratopetalum* was only known from the Cenozoic of
401 Patagonia and Australia (Holmes & Holmes, 1992; Barnes & Hill, 1999; Gandolfo & Hermsen,
402 2017) and today the genus is restricted to eastern Australia and Papua New Guinea. However,

403 our report of *Ceratopetalum* fruits from the Campanian of western North America dramatically
404 expands the family's paleogeographic range and provides a Northern Hemisphere legacy for
405 what was formerly considered a strictly Southern Hemisphere lineage.

406 This dramatic geographic range expansion is somewhat consistent with the hypothesis of
407 a North American-South American-Antarctic (NA-SA-A) biotic exchange that occurred during
408 the Late Cretaceous and the Paleogene (Case *et al.*, 2000, 2005; Goin *et al.*, 2006). This
409 hypothesis is largely based on reports of primarily Northern Hemisphere vertebrates, such as
410 hadrosaurs and nodosaurids, recovered from Coniacian-Maastrichtian deposits in Antarctica.
411 Based on stratigraphic and biogeographic occurrences it has been suggested that these
412 vertebrates expanded their ranges into South America from North America and later into
413 Antarctica (Case *et al.*, 2000; Lamanna *et al.*, 2019). Some fossil marsupials show a similar
414 pattern as well (Case *et al.*, 2005; Goin *et al.*, 2006). Concerning this biotic exchange hypothesis,
415 fossil plants have been discussed to a limited degree (Wilf *et al.*, 2013) with some lineages
416 showing a North America to South America-Antarctica migration during the Cretaceous and
417 Paleogene, including *Regnellidium* (Batten *et al.*, 2011; Cúneo *et al.*, 2013) and some
418 nymphaleans (Gandolfo & Cuneo, 2005; Friis *et al.*, 2017). Poole *et al.* (2000b) reported
419 *Sassafrasoxylon* Brezinová et Süss from Late Cretaceous deposits in Antarctica and cautiously
420 discussed that *Sassafras* J. Presl, which today is restricted to the Northern Hemisphere, may have
421 had a Gondwanan origin. Recent work by Viñola-López *et al.* (2021) revealed terrestrial plant
422 and animal assemblages from Campanian-Maastrichtian deposits in Cuba indicating that islands
423 in the Caribbean Seaway may have facilitated NA-SA-A biotic exchanges during the Late
424 Cretaceous.

425 Considering that Cunoniaceae wood and pollen from Antarctica are nearly
426 contemporaneous with *C. suciensis*, the Cretaceous distribution of Cunoniaceae fits well within
427 the NA-SA-A scenario. This distribution could be explained by long distance dispersal and/or
428 migration, similar to the vertebrates discussed above. However, it is also reasonable to suggest
429 that *Ceratopetalum* and Cunoniaceae as a whole were cosmopolitan in the past, as seen in
430 Araucariaceae and Winteraceae (Kunzmann, 2007; Brea *et al.*, 2021). Regional extinctions
431 within northern regions since the Cretaceous likely restricted the family's geographic range to
432 the Southern Hemisphere, but it is striking that there are no other reliable fossil records of
433 Cunoniaceae elsewhere in the Northern Hemisphere. We also note that it is probably pre-mature

434 to infer whether *Ceratopetalum* and Cunoniaceae originated in the Northern Hemisphere or the
435 Southern Hemisphere. As more fossils are recovered from undersampled regions across the
436 world, more light will be shed on these biogeographic patterns. Nonetheless, given the
437 previously recorded current and Cenozoic distribution of *Ceratopetalum*, the recovery of *C.*
438 *suciensis* from the Cretaceous of the western coast of North America suggests a more
439 complicated biogeographic history for this important Paleo-Antarctic Rainforest Lineage and
440 potentially others.

441

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443

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457

458 **Author contributions:**

459 K.K.T. and B.A.A. conceptualized the project. B.A.A. designed the methodology. S.Y.S.
460 collected micro-CT data and K.K.T. prepared 3-dimensional reconstructions and datasets to carry
461 out analyses. K.K.T. wrote the original draft of the manuscript. All authors contributed to the
462 review and edits of subsequent drafts of the manuscript.

463

464 **Data and materials availability:** *Ceratopetalum suciensis* fossils are curated at the University
465 of Kansas Paleobotanical Collections (Biodiversity Institute) on behalf of the Washington State
466 Parks Commission. Extant fruits were provided by L.H. Bailey Hortorium Herbarium and
467 Harvard University Gray Herbarium (Table S1). All micro-CT scans can be accessed on
468 Morphosource under the project title “3D Morphology of Ceratopetalum fruits (Cunoniaceae)”.
469 GenBank accession numbers can be found in the Supporting Information (Table S3). Data
470 associated with phylogenetic analyses can be found on Morphobank (project P3906, matrix
471 27164) or in the Supporting Information.

472

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673

674

675 Supporting Information

676 The following Supporting Information is available for this article:

677 **Fig. S1** “Fan” shaped phyloscan output for *Ceratopetalum suciensis*.

678 **Fig. S2** “Long” shaped phyloscan output for *Ceratopetalum suciensis*.

679 **Fig. S3** “Fan” shaped phyloscan output for *Tropidogyne pentaptera*.

680 **Fig. S4** “Long” shaped phyloscan output for *Tropidogyne pentaptera*.

681 **Fig. S5** “Fan” shaped phyloscan output for *Platydiscus peltatus*.

682 **Fig. S6** “Long” shaped phyloscan output for *Platydiscus peltatus*.

683

684 **Methods S1** Phyloscan scoring justifications for *Ceratopetalum gummiferum*, *C. suciensis*,
685 *Platydiscus peltatus*, and *Tropidogyne pentaptera*.

686

687 **Notes S1** Tree file used in phyloscan.

688 **Notes S2** Character matrix used for phyloscan.

689 **Notes S3** MrBayes tree files.

690

691 **Table S1** List of scanned fruits and herbarium accession numbers.

692 **Table S2** List of scan parameters.

693 **Table S3** List of taxa and GenBank accession numbers.

694 **Table S4** Floral characters for fossil species of *Ceratopetalum*.

695 **Table S5** Floral characters for extant species of *Ceratopetalum*.

696

697 **Video S1** Digital cross sections of *C. suciensis*.

698 **Video S2** Digital longitudinal sections of *C. suciensis*.

699 **Video S3** 3D model of *C. suciensis*.

700 **Video S4** 3D model of *C. succirubrum*.

701 **Video S5** *C. suciensis* and *C. succirubrum* in comparison.

702

703

704 **Figure legends**

705

706 **Figure 1. Structure of *Ceratopetalum suciensis* Tang & Atkinson sp. nov. (a-c) and extant**

707 ***Ceratopetalum succirubrum* (in d).** (a) Exposed rock showing top-down view of fruit with an

708 annular nectary, one entire wing, a partial wing, and three abraded wings (arrows). Note that the

709 upper (superior) portion of the ovary is abraded. KUPB 19168, scale bar = 5 mm. (b) Exposed

710 specimen in oblique longitudinal view of fruit body and a wing. KUPB 19169, scale bar = 5 mm

711 (image courtesy S.R. Manchester, University of Florida). (c) Three-dimensional reconstruction

712 of specimen in (b) showing general morphology of the fruit including two styles, diplostemonous

713 stamens, and four wings are present. KUPB 19169, scale bar = 5 mm. (d) Three-dimensional

714 reconstruction of extant fruit of *C. succirubrum* showing general morphology including two

715 styles, diplostemonous stamens, and four wings (apices are cropped). BH 95696, scale bar = 5

716 mm. White = calyx/wings; Orange = styles and nectary disk; Green = stamen; Blue =

717 hypanthium.

718

719 **Figure 2. Detailed view of wings, nectary lobes, and stamens of *Ceratopetalum suciensis***

720 **Tang & Atkinson sp. nov.** (a) Detailed view of wing with five primary veins (arrowheads) and

721 secondary veins that diverge from the primary veins at 45-90°. KUPB 19168, scale bar = 2 mm.

722 (b) Top-down view of tissue just outside of nectary lobe and between the wings showing an

723 inter-wing vein (arrow). KUPB 19168, scale bar = 0.3 mm. (c) Top-down view of annular

724 nectary disk (arrow). KUPB 19168, scale bar = 0.6 mm. (d) Three-dimensional reconstruction of
725 the fossil fruit showing nectary lobes (arrows) bordering stamens. KUPB 19169, scale bar = 1
726 mm. White = calyx/wings; Orange = styles and nectary disk; Green = stamen; Blue =
727 hypanthium. (e) Digital longitudinal section of micro-CT scanned fruit showing persistent
728 stamens and nectary lobes. KUPB 19169, scale bar = 4 mm. (f) Longitudinal section of the fruit
729 showing persistent stamens and nectary lobes. KUPB 19169, scale bar = 4 mm. w = wings; n =
730 nectary lobe; st = stamen; fb = fruit body.

731
732 **Figure 3. Detailed view of two styles of *Ceratopetalum suciensis* Tang & Atkinson sp. nov.,**
733 **KUPB 19169.** (a) Three-dimensional reconstruction of the fossil fruit showing persistent
734 stamens and two styles. Scale bar = 1 mm. (b) Digital longitudinal section showing the two
735 styles. Scale bar = 4 mm. (c-d) Longitudinal sections of fruit, each section shows one of two
736 styles. Scale bar = 5 mm. (e) Top-down view of the three-dimensional reconstruction. Scale bar
737 = 1mm. (f) Digital cross section showing the two styles. Scale bar = 4 mm. White = calyx/wings;
738 Orange = styles and nectary disk; Green = stamen; Blue = hypanthium. w = wings; n = nectary
739 lobe; st = stamen; s = styles; fb = fruit body.

740
741 **Figure 4. Three-dimensional reconstructions of extant fruits of *Ceratopetalum gummiferum*,**
742 ***C. apetalum*, and *C. corymbosum*.** White = calyx/wings; Pink = petals; Orange = styles and
743 nectary disk; Green = stamens; Blue = hypanthium. (a) *C. gummiferum* with persistent petals.
744 A00969696, scale bar = 4 mm. (b) *C. apetalum* showing two styles, diplostemonous stamens,
745 and five wings. A00969698, scale bar = 4mm (c) *C. corymbosum* with five calyx lobes.
746 A00969697, scale bar = 2mm.

747
748 **Figure 5. Detailed view of *Ceratopetalum gummiferum* (A00969696) and *C. corymbosum***
749 **(A00969697) fruits with the wings removed for a better view of the androecium and**
750 **gynoecium.** White = calyx/wings; Pink = petals; Orange = styles and nectary disk; Green =
751 stamens; Blue = hypanthium. (a) *C. gummiferum* fruit with persistent petals on the fruit. Scale
752 bar = 1.0 mm (b) *C. corymbosum* fruit with persistent stamens and two styles. Scale bar = 0.68

753 mm. (c) *C. gummiferum* fruit with persistent stamens and three styles present. Scale bar = 0.8
754 mm. (d) A magnified view of *C. corymbosum*. Scale bar = 0.57 mm.

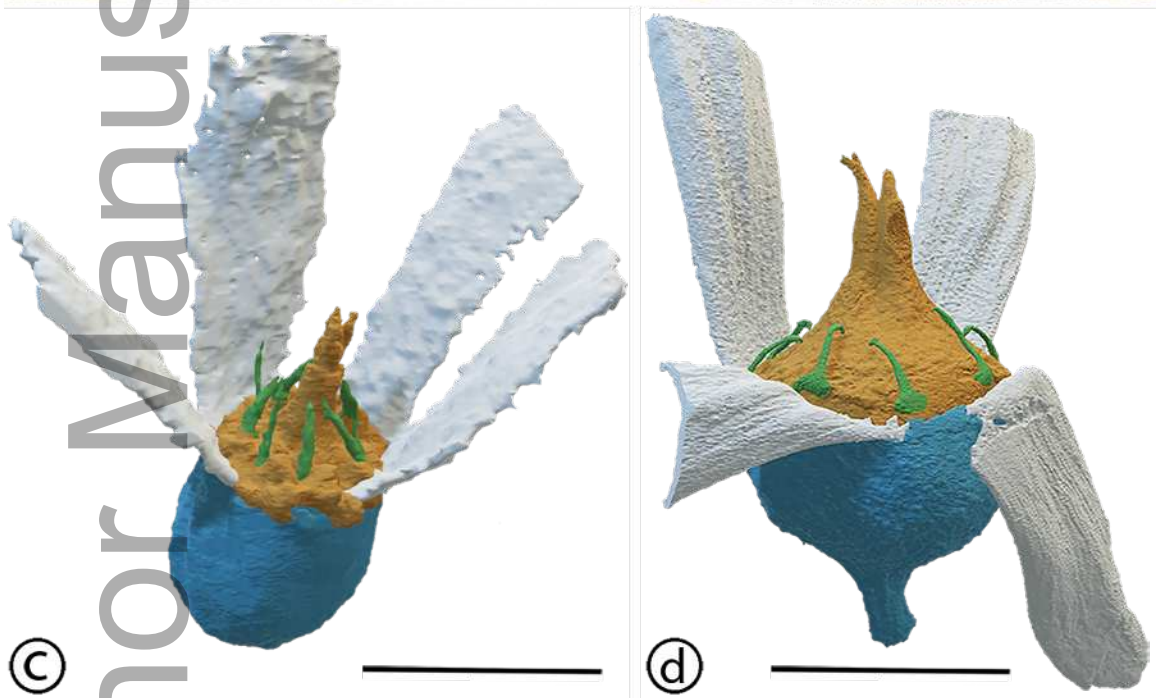
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756 **Figure 6. Majority rules consensus tree from Bayesian phylogenetic analysis showing**
757 **position of *Ceratopetalum suciaensis* (arrow) within Cunoniaceae.** Numbers above the
758 branches are posterior probability values. † indicates fossil taxon. Tribes are indicated by the
759 grey shading.

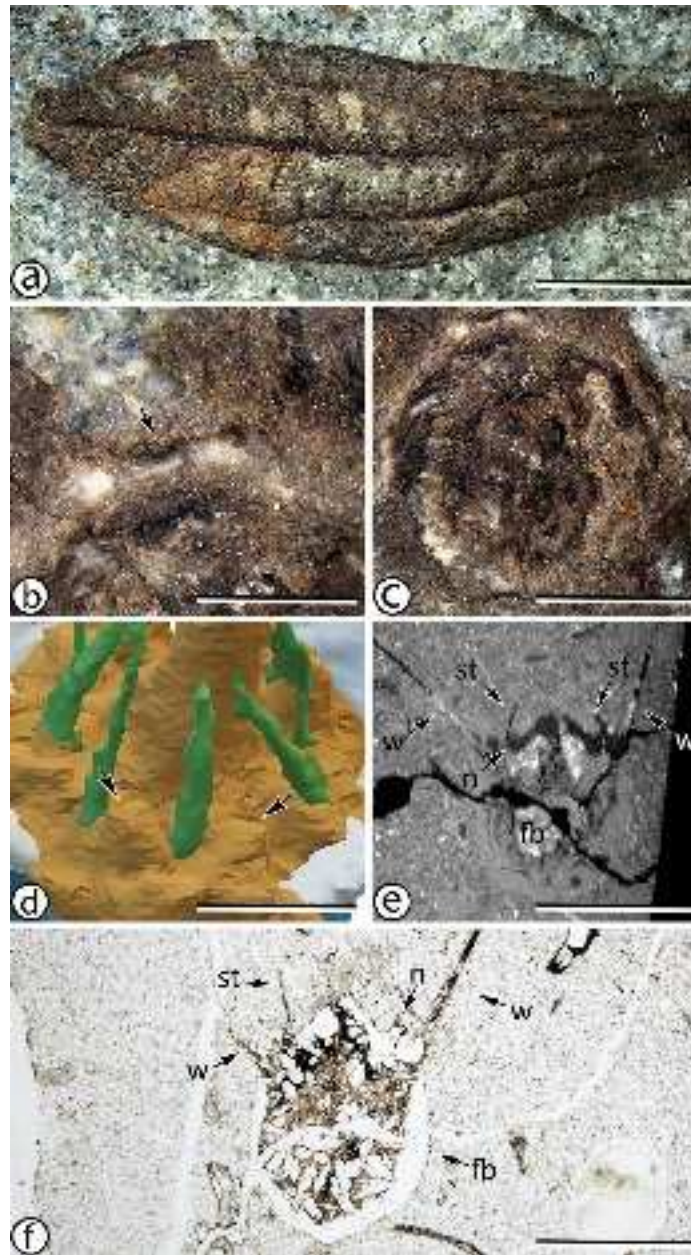
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761 **Figure 7. Majority rules consensus tree from Bayesian phylogenetic analysis including ten**
762 **additional fossils.** Arrow indicates position of *Ceratopetalum suciensis*. Numbers above
763 branches are posterior probability values. † indicates fossil taxon. Tribes are indicated by the
764 grey shading.

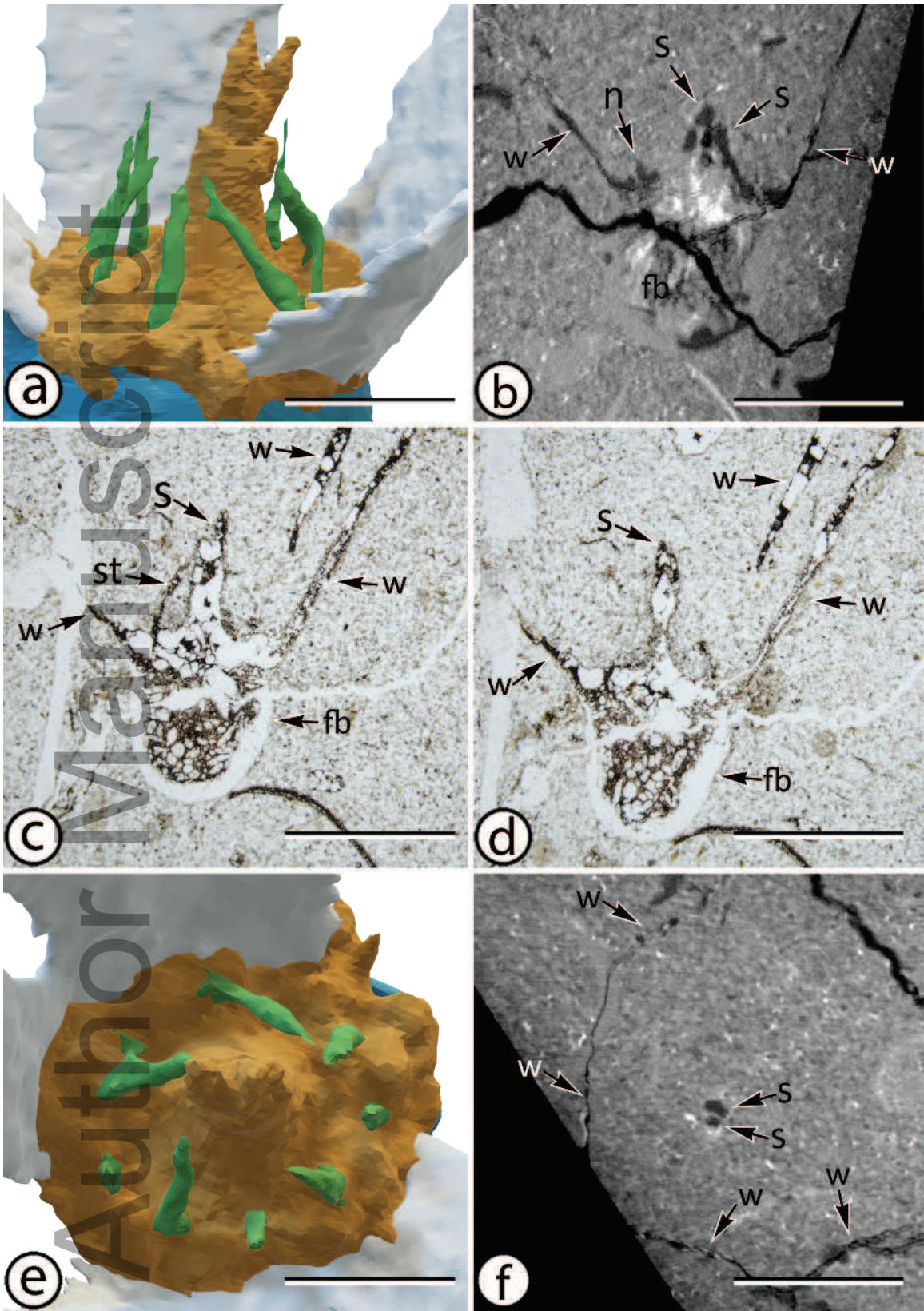
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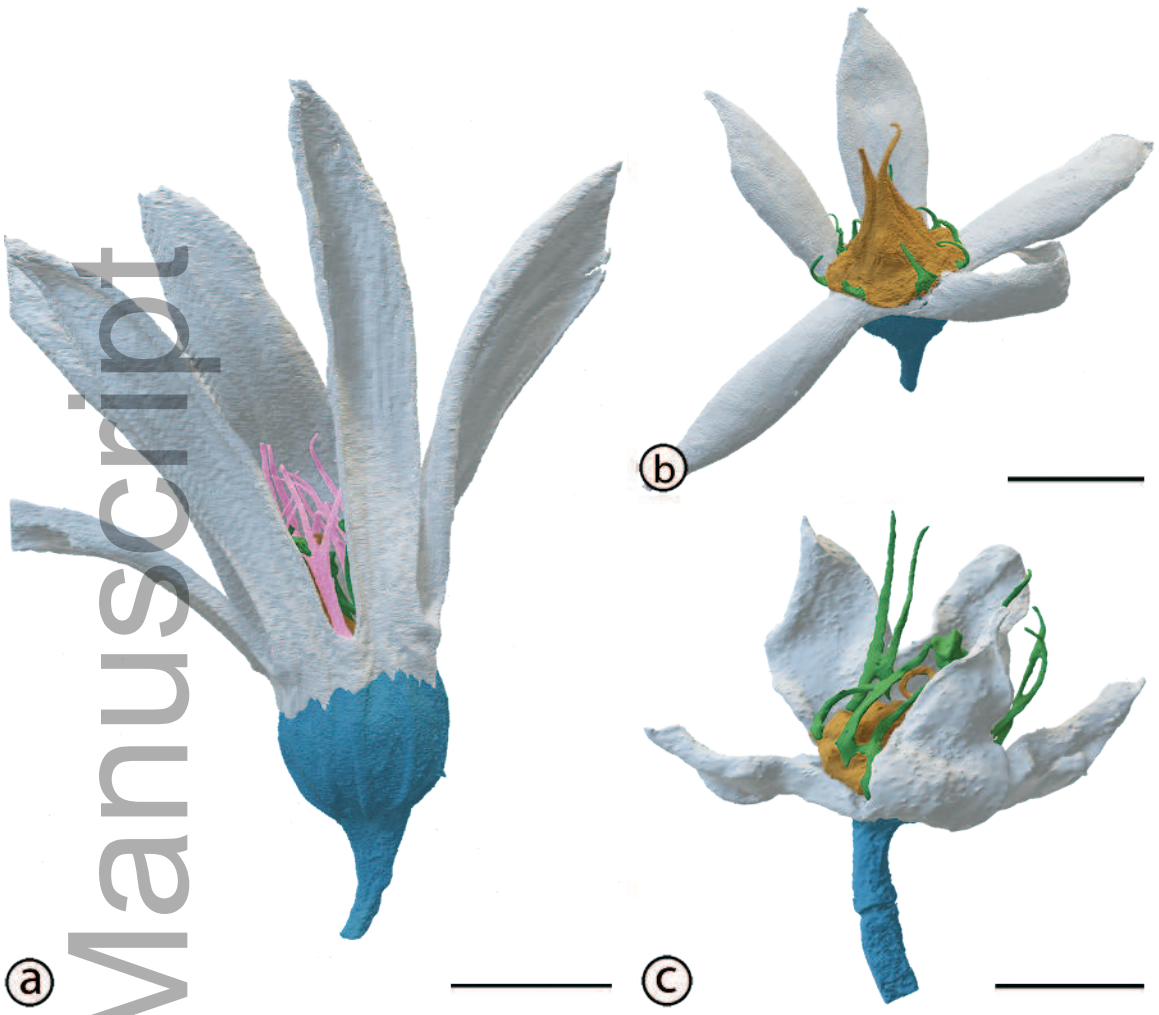
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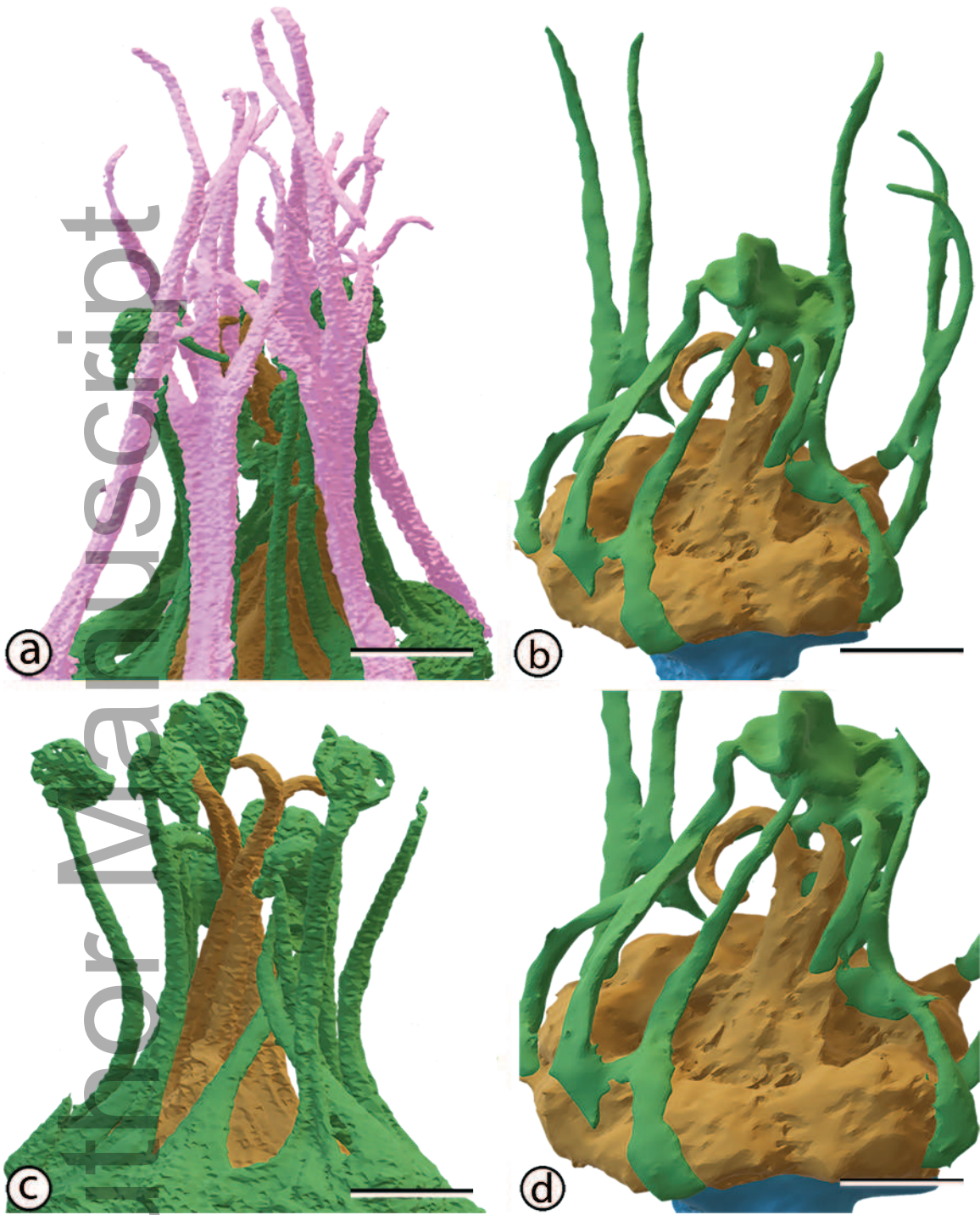
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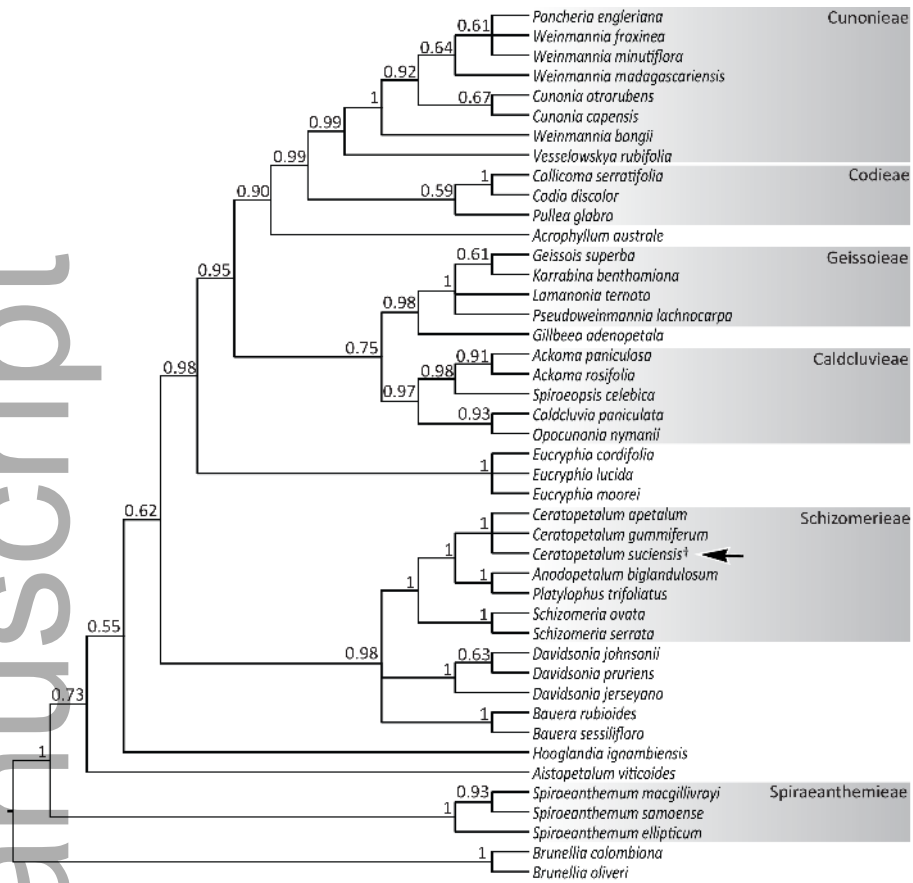
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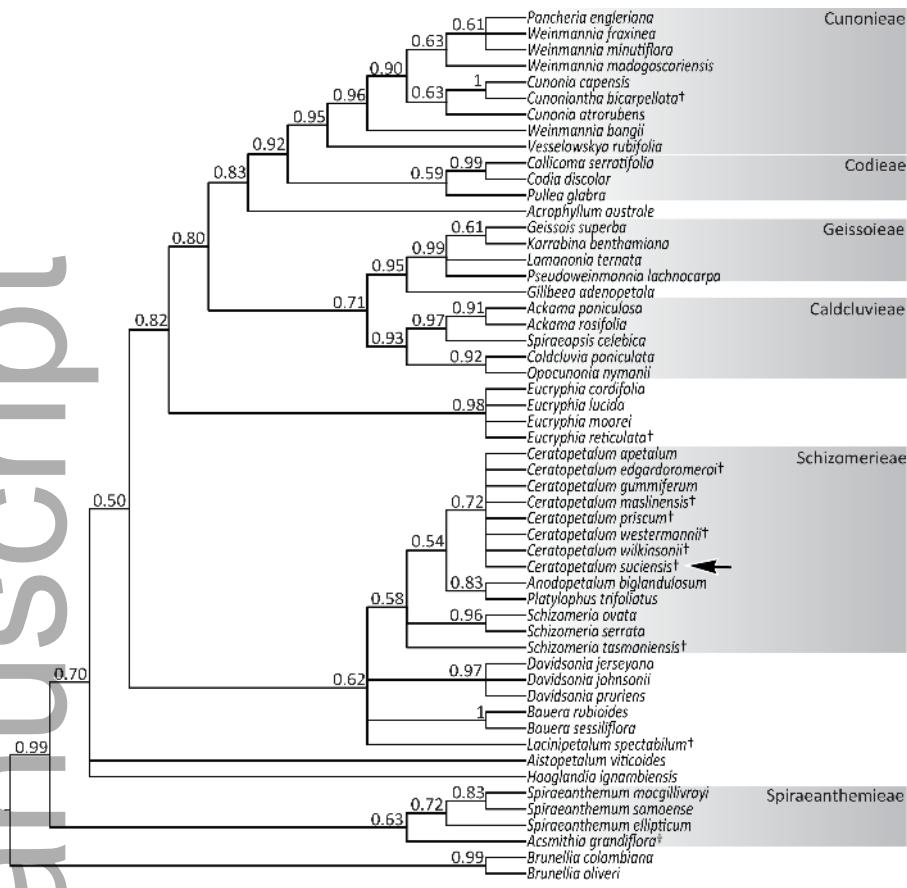
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