

1 First non-destructive internal imaging of *Rangea*, an icon of complex

2 Ediacaran life

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4 Alana C. Sharp^{a,b,*}, Alistair R. Evans^{c,d}, Siobhan A. Wilson^b, Patricia Vickers-Rich^{b,e,f}

5

6 ^aSchool of Science and Technology, University of New England, NSW 2351, Australia

7 ^bSchool of Earth, Atmosphere and Environment, Monash University, Clayton, VIC 3800,

8 Australia

9 ^cSchool of Biological Sciences, Monash University, Clayton VIC 3800, Australia

10 ^dGeosciences, Museums Victoria, Melbourne VIC 3001, Australia

11 ^eFaculty of Science, Engineering and Technology, Swinburne University, VIC Australia

12 ^fSchool of Life and Environmental Sciences, Deakin University, Burwood VIC Australia

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14 * Corresponding author. Email: alana.c.sharp@gmail.com

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16 Keywords: Ediacaran, Precambrian, computed tomography, *Rangea*, Aar Member, Namibia

17 **Abstract**

18 The origins of multicellular life have remained enigmatic due to the paucity of high-quality,
19 three-dimensionally preserved fossils. *Rangea* was a centimetre- to decimetre-scale frond
20 characterised by a repetitive pattern of self-similar branches and a sessile benthic lifestyle.
21 Fossils are typically preserved as moulds and casts exposing only a leafy petalodium, and the
22 rarity and incompleteness of specimens has made it difficult to reconstruct the three-
23 dimensional (3D) morphology of the entire organism. This, in turn, has led to many differing
24 interpretations of its morphology and phylogenetic affinities. Here we use high resolution X-
25 ray micro-computed tomography (microCT) to investigate the 3D internal morphology of rare,
26 exceptionally preserved ironstone fossils of *Rangea* from the Nama Group in southern
27 Namibia. Our investigation reveals a series of structures that represent boundaries between
28 individual fronds or structural elements that divide into smaller secondary and tertiary
29 elements, leading to a repetitive pattern of branches. These elements surround an internal core
30 of a distinctly different texture and internal appearance. There is no distortion of the walls of
31 the primary elements, thus we conclude that *Rangea* likely had a rigid or semi-rigid skeleton-
32 like structure that prevented buckling or compression and maintained integrity during life. We
33 compare these findings with previous interpretations of *Rangea* morphology and present new
34 insights on the architecture of internal structures, such as the central core, and the overall
35 appearance of this complex Ediacaran life form. Our insights based on microCT scans of these
36 rare, uniquely-preserved specimens provide a more accurate interpretation of the 3D
37 morphology essential for determining the true affinities and modes of life of the Ediacaran
38 biota during this early stage in the evolution of complex macroscopic life.

39

40 **1. Introduction**

41 *Rangaea* was the first complex Precambrian macrofossil named and described anywhere in the
42 world, and to this day is an iconic representative of Ediacaran biota (580–541 million years
43 ago) (Gürich, 1933; Hoyal Cuthill and Conway Morris, 2014; Narbonne, 2004; Richter, 1955).
44 Early interpretations of the morphology of *Rangaea*, the type genus of rangeomorphs, regarded
45 it as a primitive representative of living radial phyla, either Ctenophora (Gürich, 1929; Gürich,
46 1933) or Cnidaria (Richter, 1955). Most modern interpretations regard *Rangaea*, and other
47 rangeomorphs, as members of an extinct clade of the oldest large and complex organisms in
48 Earth history (Brasier and Antcliffe, 2004; Erwin et al., 2011; Gehling and Narbonne, 2007;
49 Narbonne, 2004; Seilacher, 1992, 2007; Xiao and Laflamme, 2009). The most common
50 reconstructions of rangeomorph morphology are as fronds, elevated above the sea floor by a
51 stalk attached to a holdfast or alternatively lying flat on the seabed, as in Newfoundland
52 (Narbonne, 2004). However, a wide range of morphologies are preserved, including long-
53 stemmed rangeomorph fronds with overlapping frondlets, short-stemmed fronds with pendant
54 frondlets that hang from a thin central stalk, bush-shaped and spindle-shaped forms, and
55 rangeomorphs with a quilted array of major and minor branches that overlay an internal organic
56 skeleton (Narbonne, 2004).

57 Specimens of *Rangaea* are rare and sometimes quite fragile, making it difficult to
58 determine its three-dimensional morphology. This has led to many different interpretations.
59 *Rangaea* is normally reconstructed as a multifoliate, epibenthic frond consisting of several
60 ‘vanes’ or ‘petaloids’ with a repetitive pattern of self-similar branches (Brasier et al., 2012;
61 Jenkins, 1985; Laflamme and Narbonne, 2008a, b; Laflamme et al., 2009; Richter, 1955).
62 These vanes are reconstructed as joining length-wise along their inner edge and radiate
63 outwards from a central axis. Estimates of the number of vanes, or elements, in the *Rangaea*
64 petalodium have ranged from two to six (Dzik, 2002; Grazhdankin and Seilacher, 2005;
65 Gürich, 1933; Jenkins, 1985; Pflüg, 1972; Richter, 1955; Vickers-Rich et al., 2013). Several

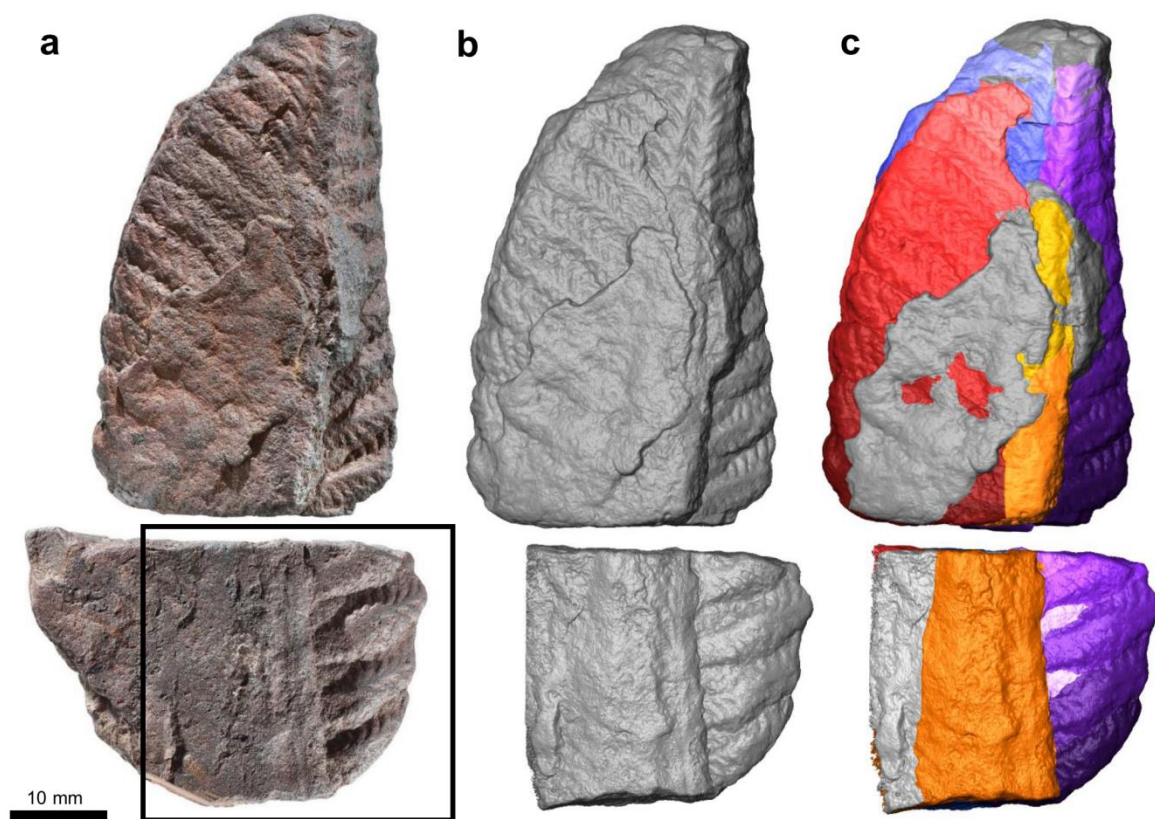
66 authors challenge this generally accepted view of *Rangaea* morphology. Based on their
67 horizontal orientation in preserving beds, Grazhdankin and Seilacher (2005) argued that
68 *Rangaea* must have been infaunal rather than an epibenthic frondose (Jenkins, 1985) or ovoid
69 (Dzik, 2002) organism. Such orientation, however, as noted by Ivantsov et al. (2013), is simply
70 an artefact of current flow during deposition of transported material. Grazhdankin and
71 Seilacher (2005) described each element as a frond with a foliate shape consisting of a series
72 of chevron-like units called ‘quilts’. They also described a double-layered structure of the frond
73 consisting of two membranes with the space between these membranes inflated and fractally
74 quilted. Dzik (2002) described *Rangaea* as tetradially symmetrical with a possible sand-filled
75 rachis and bulb, and argued for *Rangaea*’s affinity with ctenophores. Dzik (2002) also argued
76 that the fossilisation process did not reproduce the original external morphology but rather the
77 inner surface of collapsed organs, describing *Rangaea* as having complex internal anatomy, a
78 smooth external surface of the body and radial membranes.

79 Recently, Ediacaran fossils recovered from Farm Aar in southern Namibia have greatly
80 increased the number of known *Rangaea* fossils with more than 100 specimens discovered
81 (Vickers-Rich et al., 2013). The majority of these were recovered from small storm-induced
82 channel deposits and preserved in siliciclastic rocks. Many exhibit three-dimensional
83 preservation, which has revealed previously unrecorded morphology (Vickers-Rich et al.,
84 2013) that supports a six-fold symmetry, at least in this assemblage. The two specimens
85 reported on here are extremely rare and uniquely preserved as ironstone petrifications (Fig. 1a).
86 These were found on a deflation surface near the base of the late Neoproterozoic Aar Member
87 of the Dabis Formation, Nama Group, and are likely fragments of one individual organism.

88 This unique form of three-dimensional preservation as ironstone allowed us to examine
89 the structure of *Rangaea* in more detail using non-destructive methods such as X-ray

90 microcomputed tomography (microCT). Here we use microCT to compare these specimens
 91 with previous interpretations of *Rangaea* morphology to clarify the number and arrangement of
 92 fronds, and the presence or absence of a cone-shaped central core and external tubes as
 93 presented in the description in Vickers-Rich et al. (2013). Our interpretation of *Rangaea*
 94 morphology supports the classic interpretations of frond morphology in some instances, and in
 95 turn raises further questions, yet unresolved.

96



97

98 **Fig. 1.** Unique ironstone preservation of *Rangaea* fossils shows fine details of frond elements
 99 and internal structures. (A) Photographs of the two specimens of *Rangaea* with NESMF649
 100 (top) and NESMF650 (bottom). The box represents the area scanned in specimen NESMF650.
 101 (B) Surface rendered 3D models showing the pattern produced by the second- and third-order
 102 elements. Note the lack of distortion of these elements. (C) Segmented volume model of
 103 *Rangaea* showing each primary element (red, blue, purple) with different shades of colour

104 representing the secondary elements, and the axial core (orange and yellow). Grey areas are
105 matrix or areas that could not be assigned to one of the three primary elements or axial core.

106

107 **2. Methods**

108 *2.1. Specimens*

109 Fossils were recovered from surface exposures under permit from the National Heritage
110 Council of Namibia (Permit number 6 of 2011, to P.V-R.). Specimens are deposited with the
111 Geological Survey of Namibia, National Earth Science Museum (NESM) in Windhoek. Two
112 of these specimens, NESM F649 and NESMF650 (Fig. 1a), are reported on here.

113

114 *2.2. Thin sectioning*

115 A thin section of NESMF650 was produced to obtain textual and compositional information
116 about the mineralogy, and thus the mode of preservation, of this specimen. The section was
117 trimmed to size with a diamond saw, and the glass "face" was lapped flat on diamond laps and
118 hand lapped on glass with 10 micron aluminium oxide. The sample was dried and vacuum
119 impregnated with 2 part epoxy, allowed to dry and lapped flat again. Using the same epoxy,
120 the sample was glued to the slide, and excess sample cut off with a Diam saw and machine
121 lapped down to a thickness of approximately 40 μm . The sample was then hand lapped to 30
122 μm and a coverslip attached with UV resin.

123

124 *2.3. Scanning Electron Microscopy*

125 Back Scattered Electron (BSE) images and Energy Dispersive X-ray Spectra (EDS) were
126 collected from the carbon-coated polished thin section of NESMF650 using a JEOL 7001F
127 FEG-SEM at the Monash Centre for Electron Microscopy. The microscope was operated at an
128 accelerating voltage of 15 kV with a working distance of 10 mm.

129

130 *2.4. Powder X-ray Diffraction*

131 Powder X-ray diffraction (XRD) data were collected to better understand the mineralogy, and
132 thus the taphonomy, of the *Rangea* specimens. A small subsample of the fossil specimen
133 NESMF650 was removed with a Dremel tool and pulverised by hand under ethanol using an
134 agate mortar and pestle. The subsample was mounted as an ethanol slurry onto a zero-
135 background quartz plate for collection of powder XRD data. An XRD pattern was collected at
136 the Monash X-ray Platform using a Bruker D8 Advance Eco X-ray Diffractometer. The pattern
137 was obtained using a Cu X-ray tube (operated at 40 kV and 25 mA) over the range from 3–70°
138 2θ using a step size of 0.02° 2θ and a dwell time of 2.8 s/step.

139 Mineral phases were identified with reference to the Powder Diffraction File 2 (PDF-
140 2) database available from the International Center for Diffraction Data (ICDD) using the
141 DIFFRAC^{plus} EVA v.4 software program (Bruker AXS). An estimate of phase abundances was
142 obtained by Rietveld refinement (Bish and Howard, 1988; Hill and Howard, 1987; Rietveld,
143 1969) using the program Topas v.4.2 (Bruker AXS). This estimate is semi-quantitative owing
144 to data collection from a thin film of hand-pulverised material on a zero-background quartz
145 plate.

146

147 *2.5. X-ray micro-computed tomography*

148 Specimens NESM F649 and NESMF650 (Fig 1a) were scanned separately at the Monash
149 University X-ray Microscope Facility for Imaging Geomaterials (XMFIG) using an Xradia
150 XRM Versa 520 microCT scanner at 160 kV and 62 μ A for 1601 projections at 3 s exposure,
151 resulting in 35 μ m isometric voxels. NESMF649 was scanned in two parts owing to its larger
152 size. The data were converted to 8 bit TIFF image stacks (2×1004 for NESMF649 and 1004
153 for NESMF650) and imported into Avizo 9.0 for visualisation and segmentation.

154 The internal detail of each specimen was visualised as orthoslices and the volumes were
155 segmented into individual components using manual selection tools. The clarity of divisions
156 between elements was more visible in some axes than others, so segmentation was performed
157 in all three axes using a systematic approach; the structures were first selected in the transverse
158 axis and later edited in the remaining axes where other structures were more visible. Each major
159 element was assigned a different colour (red, blue or purple), and divisions within these
160 elements were graded from light to dark. A 3D surface was produced for each element for easy
161 visualisation. Our use of these methodologies and analytical techniques maximised recovery
162 of the morphological details of these uniquely preserved specimens. The microCT data will be
163 made available at Figshare.com.

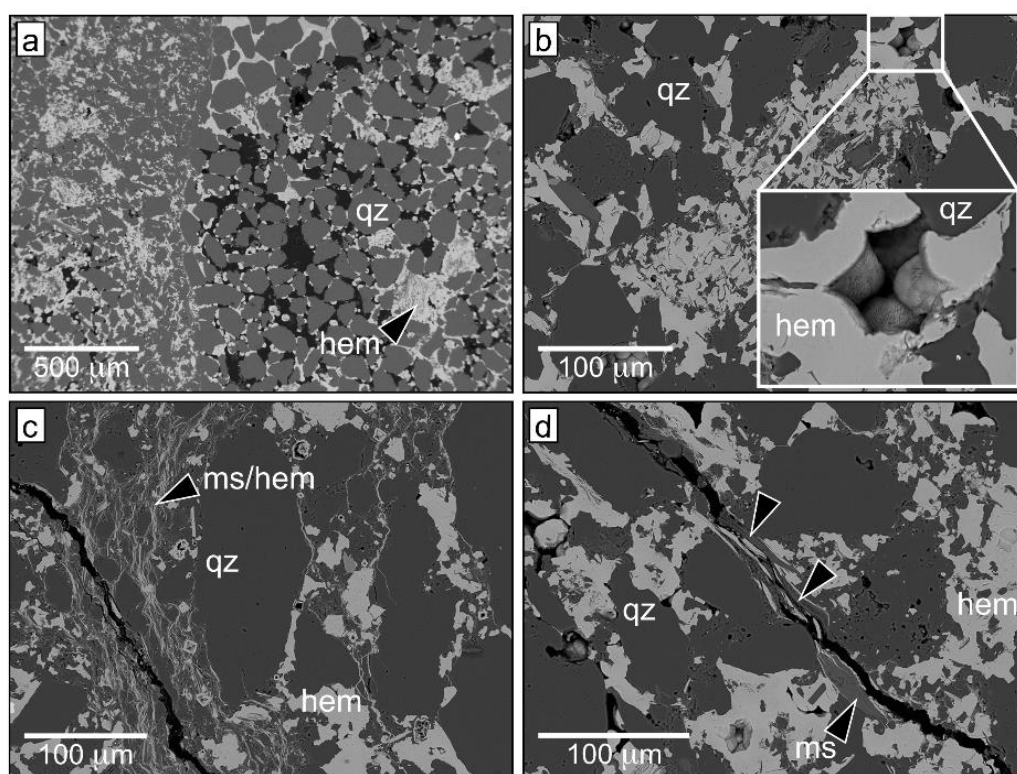
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165 **3. Results**

166 *3.1. Mineralogical Composition*

167 *Rangaea* specimens are commonly preserved by jarosite $[(K,Na,H_3O)Fe_3(SO_4)_2(OH)_6]$ as
168 moulds or casts that show only a leafy petalodium (e.g., Vickers-Rich et al., 2013). The
169 mineralogical composition of the smaller specimen in this study (NESMF650) is dominated by
170 quartz (76.7 wt.%; see Fig. S1 for the Rietveld refinement plot). Less abundant phases are

171 hematite (20.9 wt.%), goethite (1.7 wt.%), muscovite (0.5 wt.%) and Mg-calcite (0.2 wt.%).
 172 The size of quartz grains is larger within the axial core (Fig. 2a), but all grains exhibit high
 173 intragranular porosity visible using scanning electron microscopy (Fig. 2a–d). Hematite and
 174 goethite occur as micrometre-scale rosettes of platy crystals within the intergranular spaces in
 175 the specimen (Fig. 2b). Altered detrital muscovite occurs in the intergranular spaces between
 176 quartz crystals and it is commonly intermixed with platelets of hematite (Fig. 2c and d) to form
 177 anastomosing veins that fill the pore network. Muscovite grains within these veins are
 178 consistently split along the basal cleavage where hematite has grown. The low abundance of
 179 Mg-calcite is likely a component of intergranular cement.



180

181 **Fig. 2.** Backscattered electron micrographs of a thin section through sample NESMF650. (A)
 182 Detrital grains of quartz (qz) at the interface between the axial core (at the right half of the
 183 image) and an adjoining primary element. There is notably more intergranular porosity in the
 184 fossilised core than in the surrounding primary elements. Rosettes of hematite can be seen
 185 infilling this pore space, which is mostly consumed by hematite in the left half of the image

186 (within the primary element). (B) Some parts of the specimen have been heavily altered during
187 dissolution–precipitation of quartz and hematite, giving rise to complex textures. The inset in
188 B shows detail of hematite rosettes, which are composed of fine platelets of this mineral. (C,
189 D) Intermixed muscovite and micrometre-scale platelets of hematite form anastomosing veins
190 around quartz grains. The arrows in D point to relatively unaltered veins of muscovite, sheets
191 of which are commonly split along the basal cleavage where hematite has grown. Intragranular
192 porosity in quartz crystals is high and grain boundaries are irregular, features that are consistent
193 with dissolution–precipitation of quartz during diagenesis.

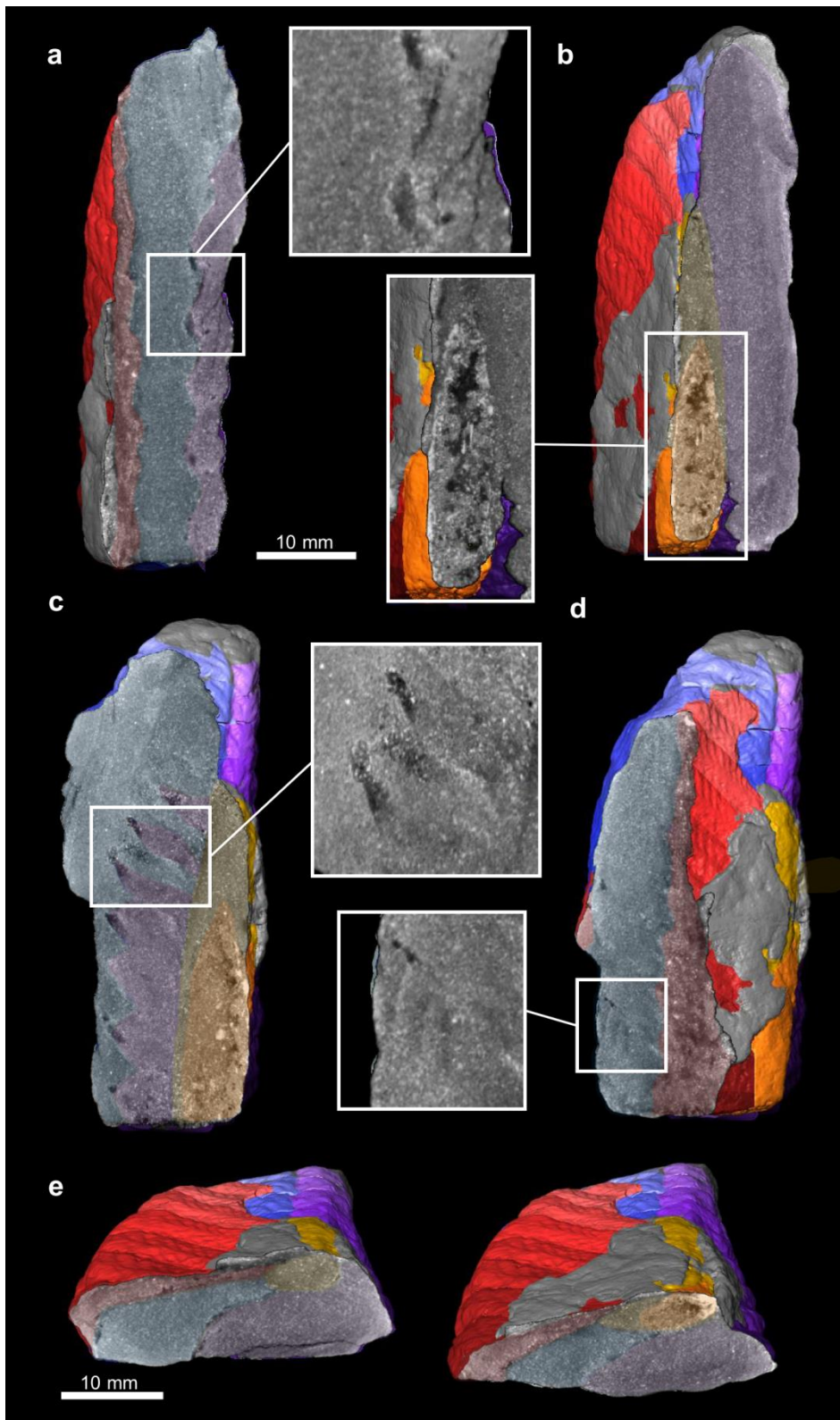
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195 *3.2. MicroCT Analysis*

196 MicroCT images (Fig. 3, Fig. S2-S5, and Supplementary Videos 1 and 2) reveal the
197 arrangement of fronds, or elements, within the fossil and show three orders of self-similar
198 branching, or divisions of complexity, plus the internal features of an axial core. Three elements
199 (of the hypothesised six) are connected to the core along its longitudinal extent (presented here
200 in Fig. 1c in three different colours). In cross-sections of the larger specimen (NESMF649),
201 two of these primary elements (red and blue) have been compressed in the transverse plane,
202 red more so than blue, whereas the third element (purple) appears relatively uncompressed
203 (Fig. 3e). There does not appear to be any compression along the longitudinal axis of the
204 specimen, suggesting a structural rigidity that prevented distortion during life and even during
205 preservation.

206 The three primary elements are divided into a second order of complexity, presented as
207 shades from light to dark within each of the primary elements (Fig. 1c). These secondary
208 elements radiate upwards at an angle of approximately 60 degrees from the longitudinal axis
209 of the central core, producing a series of stacked sections within each primary element. The
210 secondary elements gradually decrease in height from the base of the specimen towards its
211 apex. The boundary between each of the primary elements is characterised by an oscillating,

212 zig-zag pattern produced by the offset nature of secondary elements – one set of secondary
213 elements is offset by one half the length of the secondary elements in the neighbouring primary
214 element (Fig. 3a). The third order of complexity is visible within the secondary elements as
215 small, tertiary branches radiating from the midline of each secondary element (Fig. 1). The
216 architecture of these tertiary elements is visible only on the external face of the specimen;
217 however, we hypothesise that this pattern was replicated on both sides of the primary elements
218 (between red and blue, and blue and purple) during life, as supported by the preservation of the
219 structure of the second-order elements.



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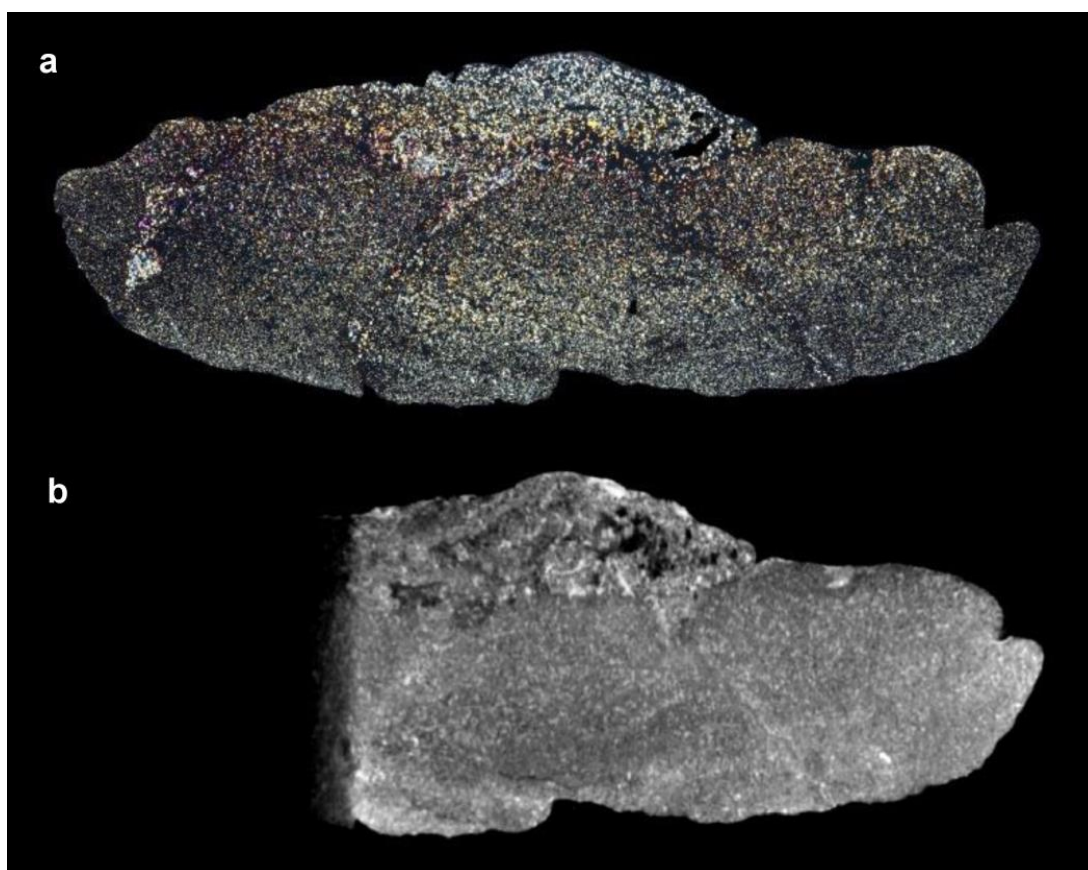
221 **Fig. 3.** Detailed internal structures of *Rangea* NESMF649 revealed by microCT imaging. (A)
 222 Zig-zag boundary between primary elements produced by the offset nature of the secondary
 223 elements; (B) internal cone-shaped axial core; (C) internal boundary between the blue and
 224 purple primary elements to the left of the axial core; (D) detail of tertiary element structure;

225 (E) cross sections showing relative compression of the frond elements. Transparent colour
226 overlays have been added to show the regions of each structure; see Fig. S2 for uncoloured
227 versions.

228

229 The internal structure revealed by microCT was confirmed during analysis of the thin
230 section through NESMF650, including the presence of boundaries between elements and the
231 internal axial core. Spatial variation in mineralogical composition of the specimen (Fig. 4a)
232 corresponds to differences in electron density revealed by the X-ray microCT (Fig. 4b).

233



234

235 **Fig. 4.** Confirmation of internal structure of *Rangea* NESMF650 through microCT, and thin
236 section. (A) Thin section photographed under cross-polar light. (B) Equivalent section in
237 microCT volume.

238 4. Discussion

239 4.1. Mechanism of preservation

240 The soft-bodied Ediacaran biota are typically preserved as moulds or cast in sandstones, and
241 are rarely preserved with the 3D morphology of the entire organism intact. Ediacaran-style
242 preservation is thought to have been aided by microbial mats that covered the sea floor,
243 producing Fe-sulfide “death masks” of the external morphology (Gehling, 1999; Laflamme et
244 al., 2011). These death masks were produced by heterotrophic sulfate-reducing bacteria that
245 mediated precipitation of Fe-sulfide minerals during decomposition of the organic matter of
246 the organism. This would have produced a mineralised layer around the outside of the
247 organism. This mode of preservation, however, does not provide detail of the internal
248 morphology of the organism, which we see in these ironstone specimens. The high abundance
249 of quartz found within these specimens is consistent with infilling of the organism by detrital
250 quartz in a marine environment and preservation in sandstone. Some of this quartz may have
251 been associated with precipitation of a silica cement (Tarhan et al., 2016), but the presence of
252 discrete grains as well as the high intragranular porosity suggests dissolution–precipitation of
253 detrital quartz (Putnis, 2015), possibly via pressure solution originating at quartz–mica grain
254 boundaries post-burial as observed by Oelkers et al., (1996). This analysis cannot be used to
255 identify multiple generations of quartz; however, cathodoluminescence microscopy could be
256 employed to distinguish between primary detrital quartz and recrystallised quartz cements (e.g.,
257 Oelkers et al., 1996).

258 Hematite, the second most abundant mineral phase in the specimen, is a common
259 dehydration product of goethite in sediments and gives the sample its dark maroon colour.
260 Goethite, which is present at low abundance in the specimen, commonly forms under
261 circumneutral to alkaline pH conditions via precursor phases including jarosite,

262 schwertmannite, or ferrihydrite, which are oxidative weathering products of iron sulfides such
263 as pyrite (Davidson et al., 2008; Zolotov and Shock, 2005; Schieber, 2011; Schweitzer et al.,
264 2013). The high abundance of Fe-oxyhydroxide minerals in the sample implies interaction with
265 an iron-bearing fluid during diagenesis. The source of this iron could have been oxidation of
266 sulfide precursor minerals, which have been shown to play a role in preservation of *Rangaea*
267 previously (Vickers-Rich et al., 2013), or alteration of Fe-rich clay minerals or micas under
268 acidic and oxidising conditions (Webb et al., 2003). The combination of infilling of the internal
269 structures by detrital quartz and diagenetic cementation by silica and hematite may have played
270 a role in the exceptional preservation of these fossils. Infilling by detrital quartz would have
271 afforded a rigidity to the structure while still providing sufficient pore space for formation of
272 hydrated Fe-bearing alteration phases without inducing deformation via reaction-driven
273 cracking.

274

275 *4.2. Morphological interpretation*

276 There have been numerous interpretations of the morphology of *Rangaea* from an epibenthic
277 frondose (Jenkins, 1985) or ovoid (Dzik, 2002) organism, to an infaunal rather than epibenthic
278 organism (Grazhdankin and Seilacher, 2005), and with the number of vanes, or elements,
279 ranging from two to six (Dzik, 2002; Grazhdankin and Seilacher, 2005; Gürich, 1933; Jenkins,
280 1985; Pflüg, 1972; Richter, 1955; Vickers-Rich et al., 2013). The uniquely preserved ironstone
281 specimens of *Rangaea* described here allowed us to examine the morphology using 3D microCT
282 which revealed the internal arrangement of structures, including a cone-shaped axial core. The
283 interpretation presented here in part supports, and in part challenges, previous reconstructions
284 of *Rangaea* as having a more inflated, bulb-like morphology of six elements surrounding a
285 central core, rather than thin lobes or sheets (Gehling, 1999). The model provided in Vickers-

286 Rich et al. (2013), with the removal of the tubes at the end of the petaloids and a marked
287 inflation of the primary elements would perhaps provide a description of what we have
288 observed in these ironstone specimens.

289 Grazhdankin and Seilacher (2005) described the primary “quilts” (a series of chevron-
290 like units; analogous to the secondary elements here) of each frond as having two rows – long
291 primary quilts and short subsidiary quilts. They suggested that these subsidiary quilts
292 terminated a short distance from the central axis and the primary quilts continued to the edge
293 of the frond. The presence of these subsidiary structures was also noted by Vickers-Rich et al.
294 (2013); however, they did not speculate on the terminal morphology of the subsidiary quilts.
295 Here, we are able to identify the subsidiary branches and describe their 3D structure (Fig 1c).
296 These structures do indeed taper out a short distance from the axis core (~7 mm) without
297 reaching the length of the primary quilts. There is no evidence for a marginal tube running
298 along the length of each vane distally as reconstructed in Vickers-Rich et al. (2013). Instead,
299 the rounded ends of each secondary branch on one side (as observed on the red element) are
300 closely stacked along the external longitudinal axis.

301 Dzik (2002) suggested that the fossilisation process did not reproduce the original
302 external morphology but rather the inner surface of collapsed organs, describing *Rangea* as
303 having complex internal anatomy, a smooth external surface, and radial membranes. We partly
304 agree with this interpretation; however, we disagree that these structures are analogous to
305 organs. We interpret the boundary between the primary, secondary and tertiary elemental
306 structures preserved on our *Rangea* specimens as a semi-rigid supporting layer, or structures,
307 for the internal tissues of the organism. In the scans, these structures separate the primary
308 elements like sheets that appear to be tightly compressed together.

309 We put forward two hypotheses for this observation. In the first hypothesis, the primary
310 elements may have been tightly connected during life, with the sheet-like supporting structures
311 separating the elements at the primary, secondary and tertiary level. For this hypothesis, an
312 external membrane or sheath would encase the entire organism producing a smooth external
313 appearance in agreement with Dzik (2002). Based on this hypothesis, the specimens we have
314 studied would have had six primary elements, three of which have not been preserved, and the
315 smooth side of the specimens would in fact be the external face of the organism. The outer
316 membrane would have provided flexibility to the structure and allowed the elements to
317 compress during fossilisation (as observed in the red and blue elements), while the rigid sheets
318 prevent compression in the longitudinal axis.

319 Alternatively, the primary elements may have been separate from one another in life,
320 and compressed together during fossilisation, with the semi-rigid structures surrounding the
321 internal content at the primary, secondary and tertiary levels like an infolded sheet. In this
322 interpretation there would be no membrane or sheath surrounding the organism but rather a
323 semi-rigid casing surrounding each element. This hypothesis is also supported by the
324 observation that one element (the red element) has more tertiary elements preserved than the
325 other externally visible element (the purple element). This suggests that the purple element was
326 damaged or torn and potentially filled with external fluid during fossilisation.

327 The nature of the base of *Rangea* has remained largely unknown and quite controversial
328 owing to typically poor preservation as moulds that only reveal a leafy petalodium. The
329 discovery and subsequent description of the base and axial core of *Rangea* was illustrated in
330 the recent reconstruction by Vickers-Rich et al. (2013) as a hexaradial, bulb-like structure
331 running up the centre of the organism, and tapering to the tip like a cone. Our microCT scans
332 confirm this observation that the axial core has a cone-shaped internal region with a tapered tip

333 dorsally (Fig. 3b) and a superior portion that has a convex end toward the apex of the specimen.
334 The internal cone is distinguished by an obvious difference in tone (which reflects electron
335 density contrast in microCT data) and grain size from the superior portion of the core, and the
336 surrounding structures (elements), representing a different mineralogical composition to the
337 rest of the specimen. In order to remain rigid, un-collapsible and upright in the water column,
338 the lower part may have been sediment-filled, as suggested by Dzik (2002), and the upper part
339 may have been liquid or gel-filled as with the surrounding elements. The nature of the base
340 cannot be determined based on the two ironstone specimens available because this region was
341 not preserved.

342 In conclusion, the 3D interpretation of *Rangea* morphology presented here in part
343 supports and in part challenges aspects of previous reconstructions. Rather than a series of
344 relatively thin lobes or sheets of elements radiating out from a central stalk, we have identified
345 structures that resemble thick wedges (the primary elements), which in preservation lie closely
346 associated with their neighbours on either side. The structures bounding the elements were
347 likely rigid, or semi-rigid, to provide stability and resistance to mechanical stress during life.
348 The determination of the true affinities and modes of life of the Ediacaran biota relies on
349 accurate interpretation of 3D morphology. Our findings represent a significant advance in this
350 direction, and the application of our methods to similarly well-preserved material of other
351 Ediacaran organisms will aid in resolving the mysteries of the earliest complex life.

352

353 **Acknowledgments** Sincere thanks to Barbara Bohem-Erni, Farm Aar, for her continued
354 support for our work in southern Namibia, the Namibian Geological Survey (especially Gabi
355 Schneider and Helke Moeke), the National Geographic Society (Grant 9208-12 to P. V-R.) and
356 the International Geosciences Program and the Australian Committee of UNESCO IGCP for

357 our projects IGCP493 and 587 for funding. We thank Robert Smith and Mary Gilroy of
358 Federation University for the thin section, Andy Tomkins and Alastair Tait of Monash
359 University for advice on mineral textures, Steven Morton for photography and Peter Trusler
360 for constructive feedback throughout. We also thank two anonymous reviewers for their valued
361 feedback and Professor Parrish for editorial handling of this manuscript.

362

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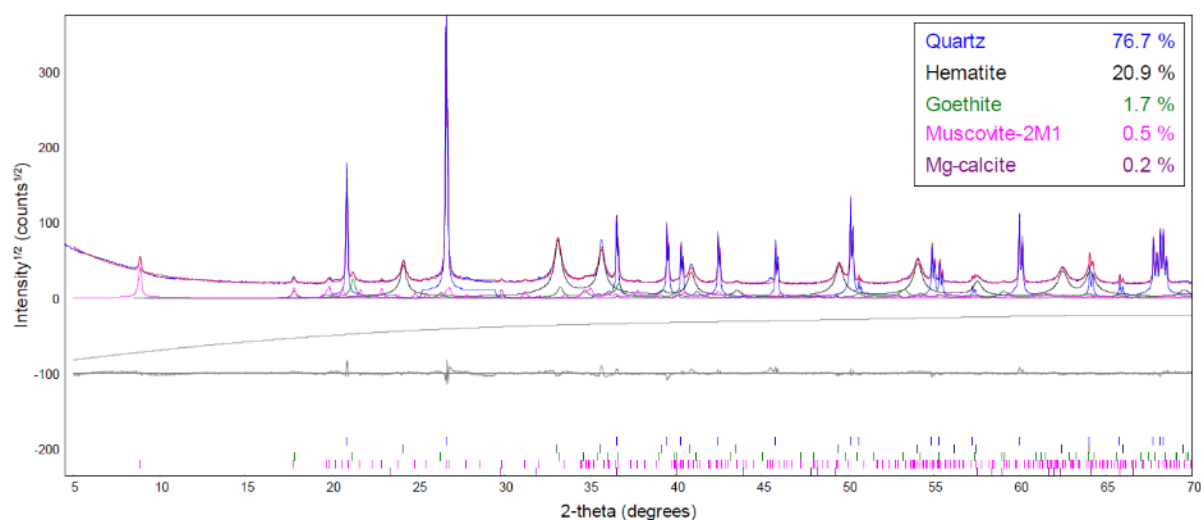
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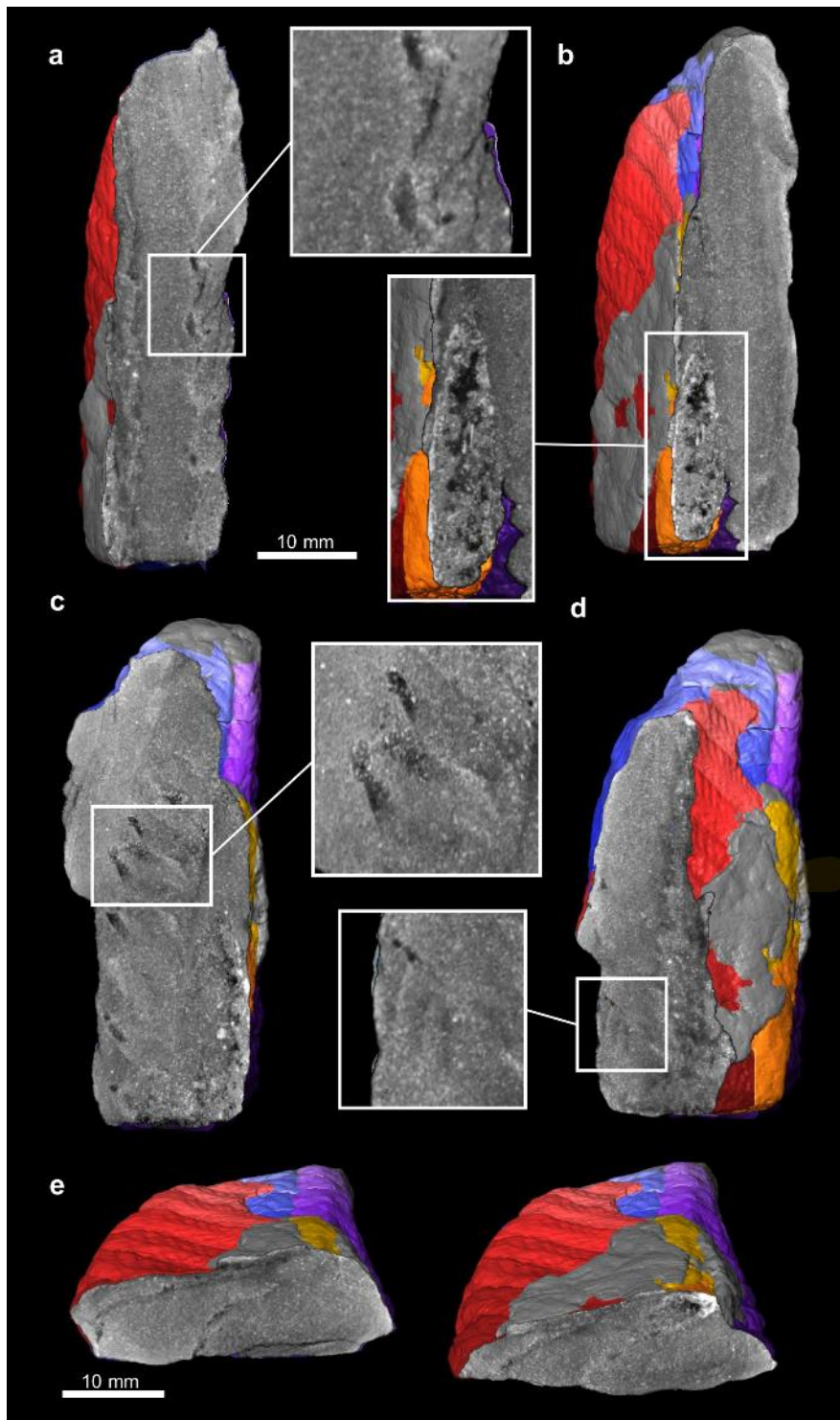
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440 **Supplementary Figures**



441

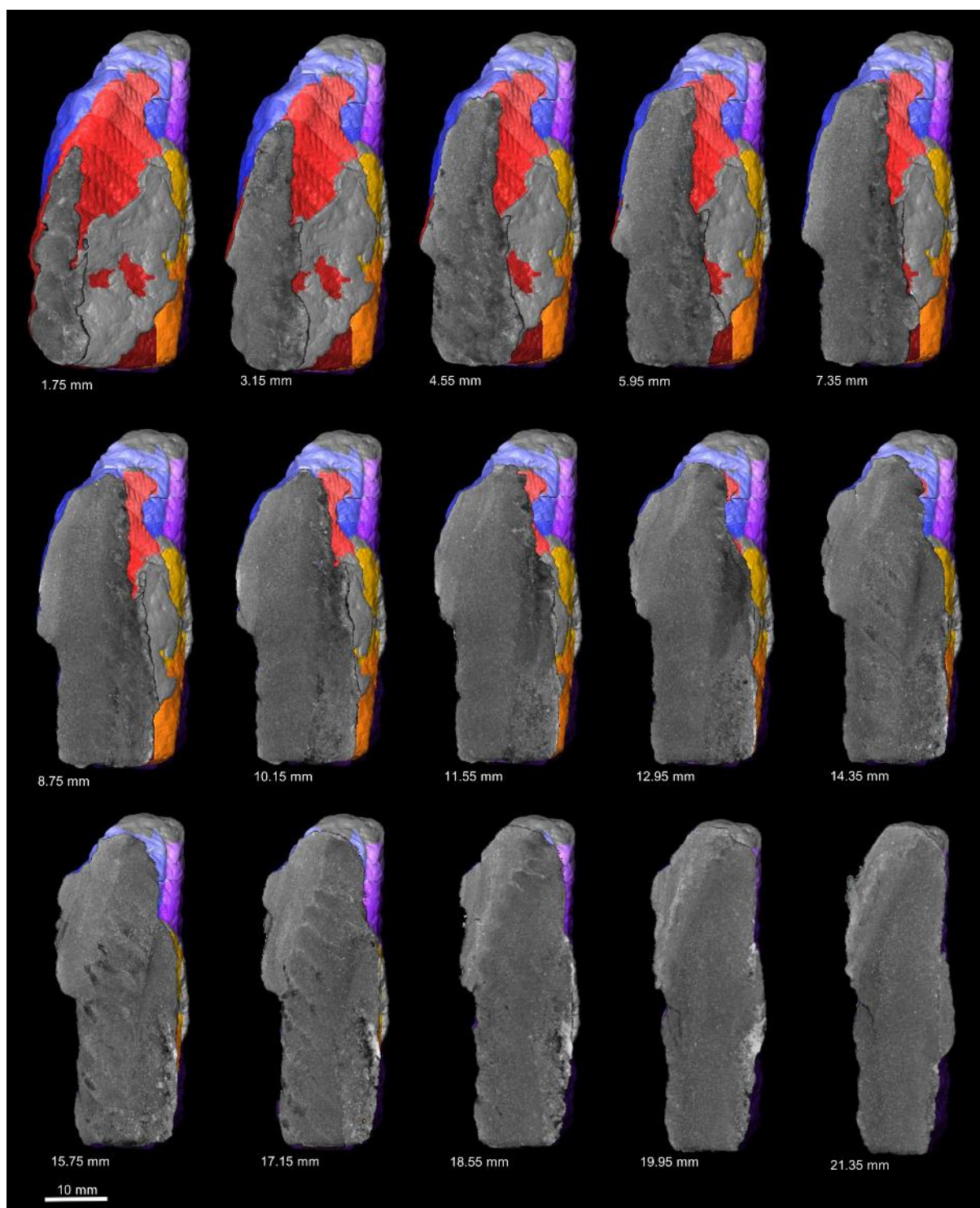
442 **Fig. S1.** Rietveld refinement results for sample NESMF650. Uppermost lines = observed data
 443 (in black) overlain by calculated pattern (in red); curves under the observed and calculated
 444 patterns = calculated patterns of each phase, colour coded by mineral. Grey curve below =
 445 background function; lowermost black line = residual pattern showing misfit between data and
 446 model; vertical lines = positions of Bragg reflections for each phase. Axes are intensity
 447 (in square root counts) versus 2θ (degrees) for Cu $K\alpha$ radiation. The weighted pattern index,
 448 R_{wp} , for the refinement is 9.6%.



449

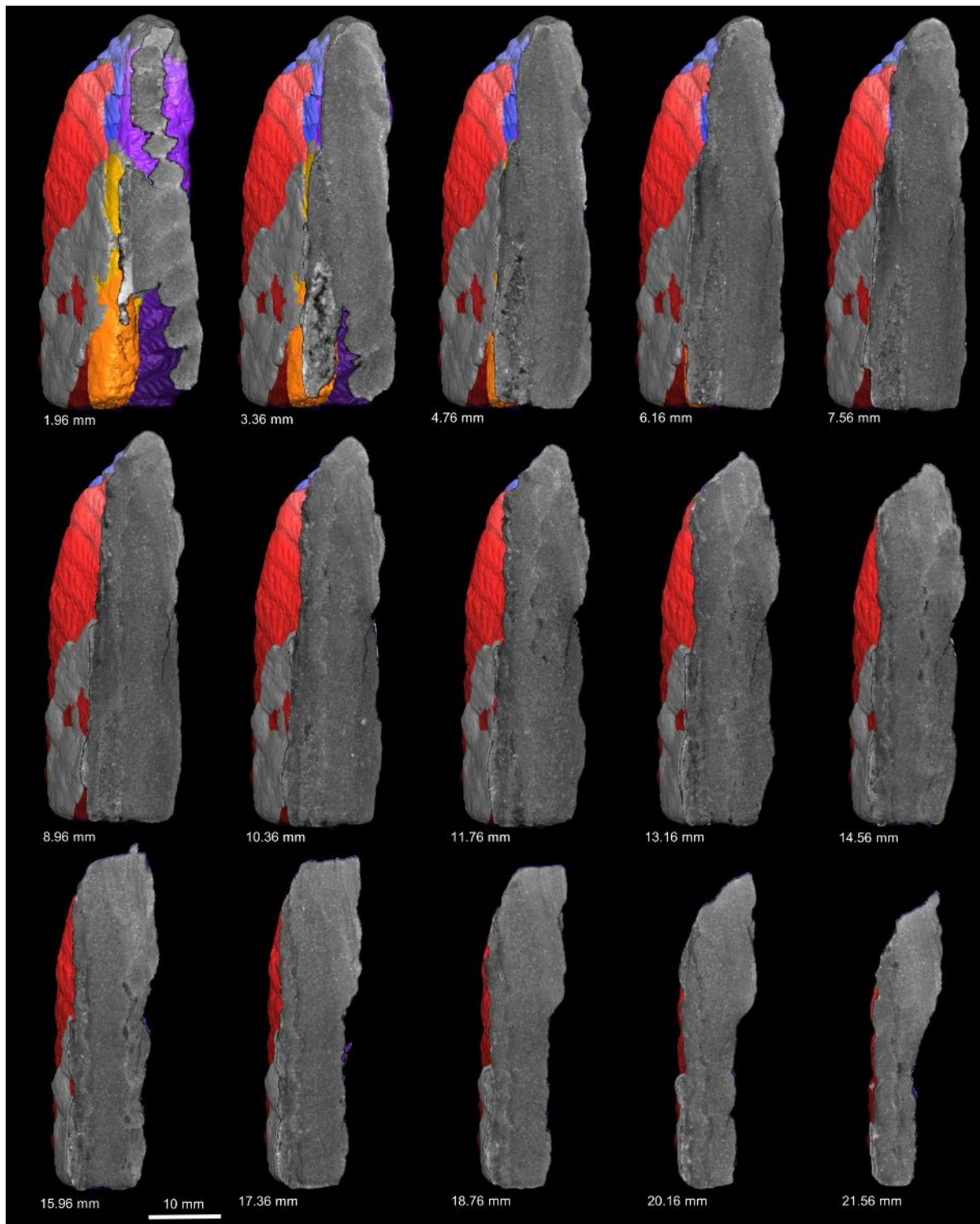
450 **Fig. S2.** Uncoloured CT sections through *Rangea* NESMF649 showing key internal structure.
 451 (A) zig-zag boundary between primary elements produced by the offset nature of the secondary
 452 elements; (B) internal cone-shaped axial core; (C) internal boundary between the blue and
 453 purple primary elements to the left of the axial core; (D) detail of tertiary element structure;
 454 (E) cross sections showing relative compression of the frond elements.

455



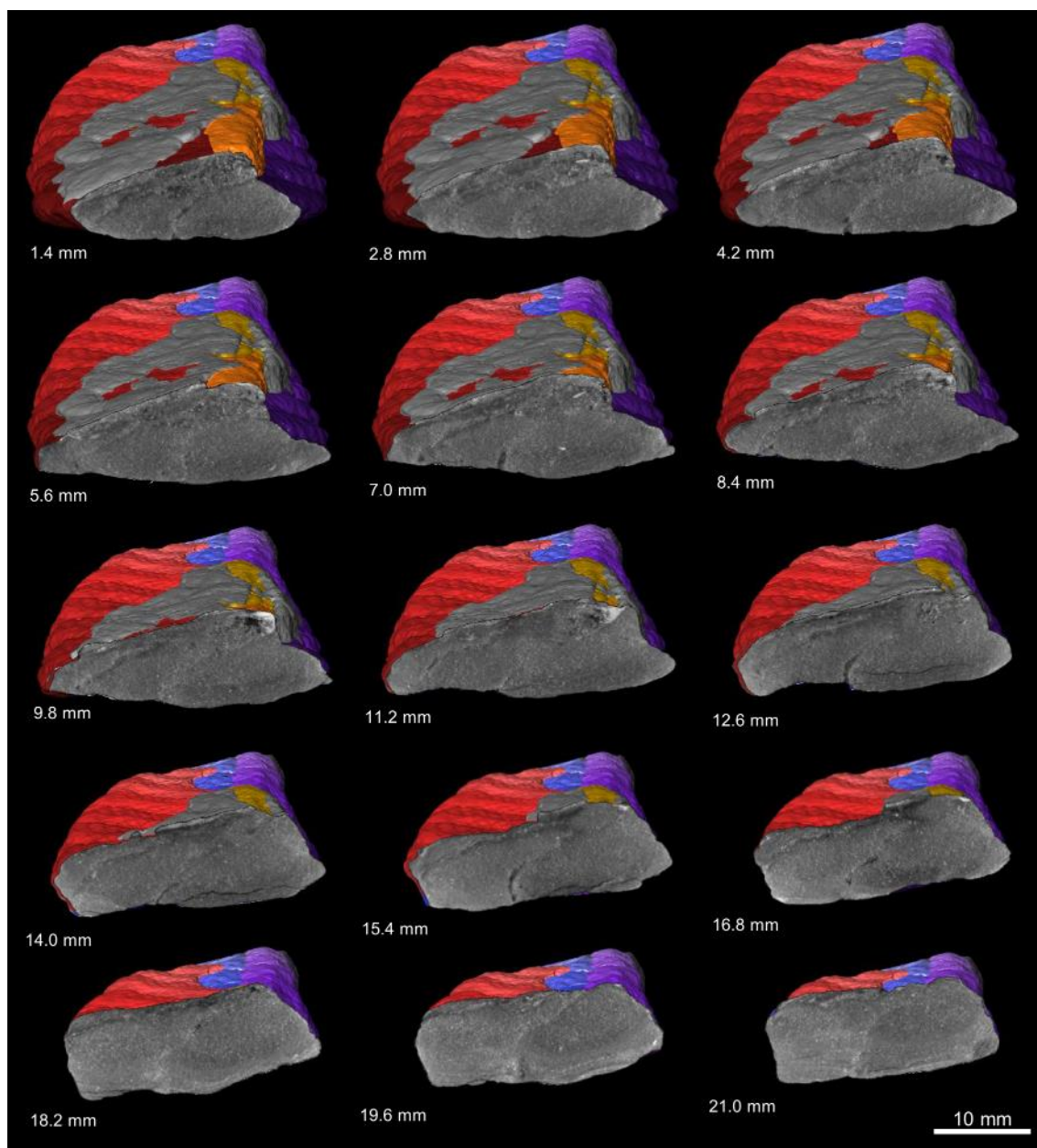
456

457 **Fig. S3.** CT sections through *Rangea* NESMF649 in the longitudinal axis. The location of each
458 section (numbered) is 1.40 mm from the previous section in the series.



459

460 **Fig. S4.** CT sections through *Rangea* NESMF649 in the second longitudinal axis. The location
 461 of each section (numbered) is 1.40 mm from the previous section in the series.



462

463 **Fig. S5.** CT cross sections through *Rangea* NESMF649. The location of each section
464 (numbered) is 1.40 mm from the previous section in the series.