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1 ***Hallucigenia*'s head and the pharyngeal armature of early ecdysozoans**

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9 **Keywords:** *Hallucigenia*, Ecdysozoa, Panarthropoda, Onychophora, Lobopodia, Burgess
10 Shale, Cambrian explosion.

11 **The molecularly-defined clade Ecdysozoa¹ comprises the panarthropods**
12 **(Euarthropoda, Onychophora, and Tardigrada) and the cycloneuralian worms**
13 **(Nematoda, Nematomorpha, Priapulida, Loricifera, and Kinorhyncha). These**
14 **disparate phyla are united by their means of moulting, but otherwise share few**
15 **morphological characters – none of which has a meaningful fossilization potential. As**
16 **such, the early evolutionary history of the group as a whole is largely uncharted. Here**
17 **we redescribe the 508 million year old stem-group onychophoran *Hallucigenia sparsa*^{2–6}**
18 **from the mid-Cambrian Burgess Shale. We document an elongate head with a pair of**
19 **simple eyes, a terminal buccal chamber containing a radial array of sclerotized**
20 **elements, and a differentiated foregut that is lined with acicular teeth. The radial**
21 **elements and pharyngeal teeth resemble the sclerotized circumoral elements and**
22 **pharyngeal teeth expressed in tardigrades^{7–9}, stem-group euarthropods^{10–12}, and**

23 **cycloneuralian worms¹³. Phylogenetic results indicate that equivalent structures**
24 **characterized the ancestral panarthropod and, seemingly, the ancestral ecdysozoan –**
25 **demonstrating the deep homology of panarthropod and cycloneuralian mouthparts, and**
26 **providing an anatomical synapomorphy for the ecdysozoan supergroup.**

27 Although Cambrian ecdysozoans offer an unrivalled perspective on early ecdysozoan
28 evolution^{6,14}, significant uncertainty surrounds the morphology of the ancestral ecdysozoan.
29 One of the few areas of agreement is that this ancestor bore a pharynx lined with
30 ectodermally-derived, periodically moulted cuticle⁷ and opening at a terminal mouth¹⁵.

31 In many ecdysozoan taxa, the pharynx is lined with sclerotized teeth^{9,10,12,13,16}, and
32 the mouth is surrounded by circumoral elements. The typical cycloneuralian mouth is
33 surrounded by a ring of spines¹³; the tardigrade mouth bears circumoral lamellae^{11,14,17}; stem-
34 group euarthropods (e.g. *Hurdia*, *Kerygmachela*, *Jianshanopodia*) exhibit various lamellae
35 and plates^{10–12}; and the onychophoran mouth is enclosed by pustular lips. These elements
36 have formerly been regarded as homologous throughout Ecdysozoa^{12,15,18–21}. However, the
37 non-sclerotized lips of onychophorans are not strictly circumoral²², and onychophorans
38 conspicuously lack pharyngeal teeth¹⁶. This suggests two possibilities: (1), a foregut
39 armature of circumoral elements and pharyngeal teeth did exist in the ancestral ecdysozoan,
40 but was secondarily lost in onychophorans; or (2) homoplasious armatures arose
41 independently in Panarthropoda (either once or twice, depending on panarthropod
42 relationships^{6,23}) and Cycloneuralia.

43 The earliest history of onychophorans is pivotal to this dilemma. The first scenario
44 implies that foregut armature was present in the ancestral onychophoran, whereas under the
45 second, onychophorans never had foregut armature. To reconstruct the ancestral
46 configuration of the onychophoran foregut, we turn to the celebrated lobopodian

47 *Hallucigenia sparsa*²⁻⁴, now regarded as a stem-group onychophoran^{5,6}. Until now, this
48 taxon's potential significance for early ecdysozoan evolution has been curtailed by
49 uncertainty in its morphological interpretation: *Hallucigenia* has variously been reconstructed
50 on its side, upside down, and back to front (Extended Data Table 1). New material
51 (Supplementary Table 1) and high-resolution microscopic analysis reveals many anatomical
52 features in *Hallucigenia* for the first time. In particular, robust carbonaceous elements occur
53 around *Hallucigenia*'s mouth and along its pharynx, implying that the ancestral
54 onychophoran – and seemingly the ancestral ecdysozoan – bore circumoral elements and
55 pharyngeal teeth.

56 *Hallucigenia*'s tubular body ranges from 10 mm to more than 50 mm in length
57 (Extended Data Fig. 1a–c; Supplementary Table 2). It bears ten elongate ventrolateral
58 appendages (Fig. 1a–e); the anterior eight are of uniform length, whereas the posterior two
59 are progressively shorter (Fig. 1d–e; Extended Data Fig. 2a–c). The final pair of appendages
60 is terminal, confirming the absence of a posterior extension of the trunk⁴. The third to tenth
61 leg pairs are regularly spaced; the first, second and third leg pairs are twice as close together
62 (Fig. 1a–b, e; Extended Data Figs. 1c, 3a–b, 4e, 5a). The anterior three pairs of appendages
63 are 1.5–2.0 times narrower than the posterior seven, and lacked claws. These narrow
64 appendages were flexible and long enough to reach the mouth (Fig. 1a, e–g; Extended Data
65 Figs. 1c–d, 2d, 3a, 4a, 6e–f). The posterior seven appendages bear terminal claws: two claws
66 are present on appendages four to eight, forming an acute angle (Fig. 1a–d, Extended Data
67 Fig. 3c–d, g), whereas a single claw adorns appendages nine and ten.

68 Seven pairs of equally-spaced elongate spines occupy the dorsolateral pinnacles of the
69 trunk, situated above the third to ninth appendage pairs (Fig. 1a–e). The spines in each pair
70 are separated by 60–90° (Extended Data Figs. 1, 4, 7). Each spine is supported by a buttress
71 of soft tissue which forms a hump-like swelling of the body wall and is particularly

72 prominent in larger individuals (Fig. 1d; Extended Data Figs. 1a, c, e, 6). The spines are
73 uniform in length, width, spacing and shape: they are not quite straight but curve slightly
74 ($3.5^\circ \pm 0.9^\circ$) posteriad. The spines are centrifugally arranged in lateral view: the more
75 anterior spines tilt forwards, the rear spines tilt backwards. The construction of the spines
76 and claws from stacks of nested elements has been reported elsewhere^{5,6}.

77 The character of the trunk changes markedly at the position of the first pair of spines.
78 Behind this point, the trunk exhibits a uniform girth. (A linear relationship between trunk
79 girth and body length indicates isometric growth; see Supplementary Table 2.) In front of the
80 first spine pair, the trunk is a third narrower than the posterior trunk, with a bulbous anterior
81 expansion evident in smaller specimens (Fig. 1a–e; Extended Data Figs. 1–8). The anterior
82 trunk usually bends at its midpoint, orienting the mouth opening ventrally.

83 Approximately 500 μm from the anterior of the body and 100 μm from the sagittal
84 axis lies a dorsal pair of convex carbonaceous impressions, reaching 200 μm in diameter,
85 which we interpret as eyes (Fig. 2a–c, i–j; Extended Data Figs. 3, 5, 7, 8b–d, 8i–m). Their
86 irregular surface (Fig. 2c; Extended Data Figs. 3e, 5f, 8j, 8m) argues against the presence of
87 ommatidia; the eyes were presumably simple rather than compound. This seems to be
88 consistent with the eyes of other lobopodians (Supplementary Note 1, trans. ser. 18).

89 Reflective or darker regions occur along the axes of well-preserved appendages and
90 appear, in the manner typical of lobopod limbs²⁴, to represent extensions of the hydrostatic
91 body cavity (Fig. 1e). A large ampulla-shaped structure that opens anteriorly represents a
92 buccal chamber or ‘mouth’ (Fig. 1f–g; Extended Data Figs. 1d, 2f–g, 4b, 4f, 8f–g), and is
93 followed by a foregut that consistently occupies the central 50% of the anterior trunk (Fig. 1e;
94 Extended Data Figs. 1d, 2f–g, 4, 6, 7, 8a, 8k). The foregut is darker than the surrounding
95 tissue, conceivably indicating the presence of a cuticular lining. At the end of the head, the
96 foregut widens into a broader, poorly preserved midgut (Fig. 1e; Extended Data Figs. 2b, 4,

97 6); the gut ends in a terminal anus (Extended Data Fig. 2b), through which decay fluids –
98 represented by a darkly stained region of variable extent (Fig. 1b, e; Extended Data Figs. 2a–
99 c, 3a–b, 6a–d) – were expelled. Preservation of the hindgut is inadequate to determine
100 whether it was differentiated from the midgut.

101 From behind the buccal chamber to the first pair of appendages, the dorsal surface of
102 the foregut lumen is lined with dozens of posterior-directed aciculae (Fig. 2g–l; Extended
103 Data Fig. 4c–d). These robustly carbonaceous structures are 10 μm long and gently curved;
104 their consistent size and orientation, uniform distribution, and absence elsewhere in the gut
105 excludes the possibility that they represent gut contents; rather, they were biologically
106 associated with the gut wall.

107 At the back of the buccal chamber, around 200 μm from the anterior termination of
108 the trunk, lies a 250 μm -wide crescentic structure composed of multiple identical lamellae,
109 each around 10 μm across and 60 μm long. Lamellae are evident in every structure that is
110 preserved, and consistently display a radial arrangement (Fig. 2a–f, i–j, Extended Data Figs.
111 5c–d, 8j–m). The structure is preserved laterally; it originally constituted a ring of lamellae
112 around the opening of the foregut.

113 Like the claws and spines, the radial lamellae preserve as discrete carbonaceous films
114 – they were originally sclerotized, rather than representing soft tissue such as muscle,
115 cuticular folds, or pigmentation, and they do not represent a taphonomic artefact. The
116 lamellae are fundamentally unlike the modified pair of claws that form the jaws of modern
117 onychophorans. Insofar as they are numerous, elongate, and sclerotized, and are arranged
118 radially around the anterior opening of the foregut, the lamellae convincingly resemble the
119 circumoral elements present in other ecdysozoans (see discussion in Supplementary Note 1,
120 trans. ser. 9). To evaluate the evolutionary significance of this similarity we incorporated our

121 observations (summarized in Fig. 3 and Supplementary Videos 1–2) into an updated
122 phylogenetic matrix (Supplementary Data).

123 The reconstruction of character states through Fitch parsimony indicates that
124 sclerotized circumoral elements were present in the ancestral ecdysozoan (Fig. 4;
125 Supplementary Note 1, trans. ser. 9), supporting the homology between circumoral structures
126 in Tardigrada^{9,14} and stem-euarthropods^{10,11,14,25} and the circumoral (‘coronal’) spines of
127 cycloneuralians^{13,20,26} (see discussion in Supplementary Notes 1 & 2, trans. ser. 9).
128 Homology between the panarthropod pharynx and the cycloneuralian pharynx is corroborated
129 by the presence of robust sclerotized teeth in the anterior pharynx (Fig. 4; Supplementary
130 Note 1, trans. ser. 13), previously reported in extant cycloneuralians, euarthropods and
131 tardigrades^{9,13,16,27} and now also evident in stem-group onychophorans. The simple
132 construction of the modern onychophoran foregut therefore reflects a secondary loss of
133 cycloneuralian-like pharyngeal teeth and circumoral elements in the onychophoran stem
134 lineage, and stands in marked contrast to the complex armoured foregut of the ancestral
135 ecdysozoan.

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201 **Supplementary information** is linked to the online version of the paper at
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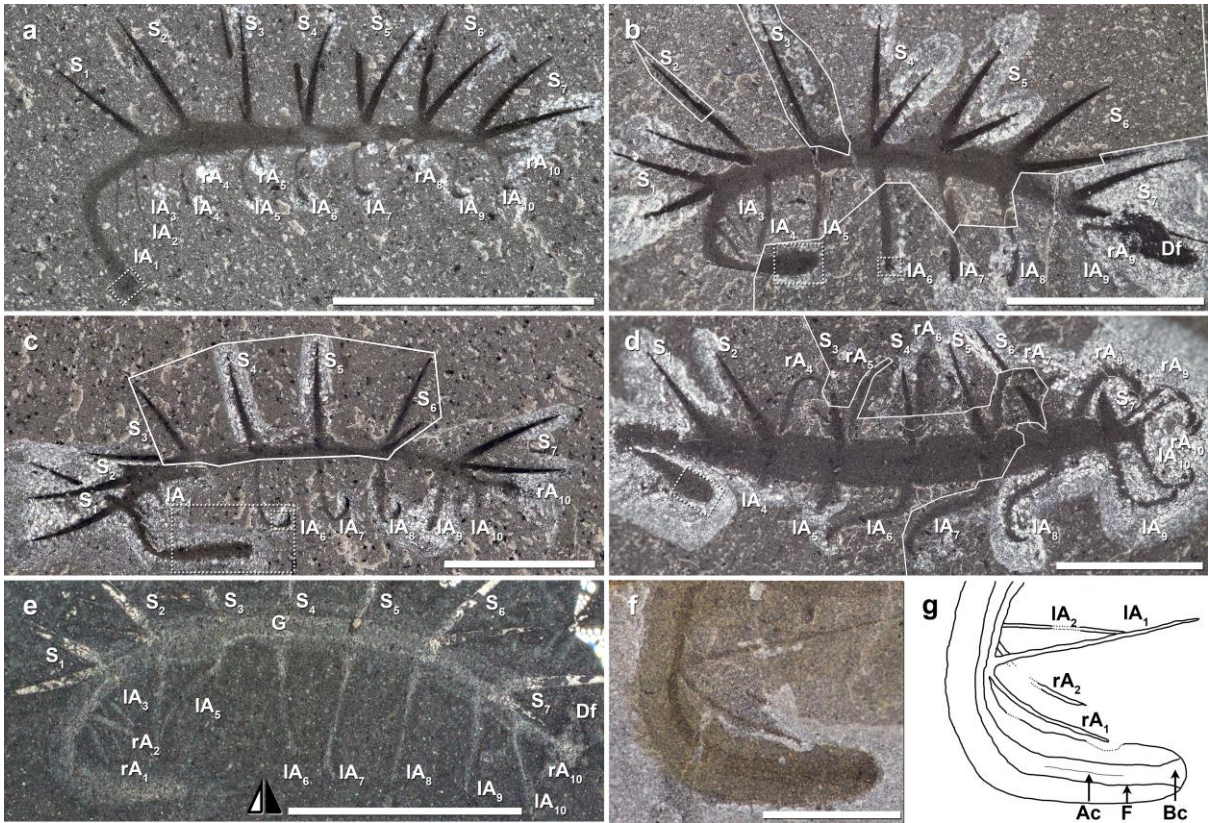
212 **Author contributions.** MRS performed data analysis; both authors examined and imaged
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214 **Author information.** The authors declare no competing financial interests.

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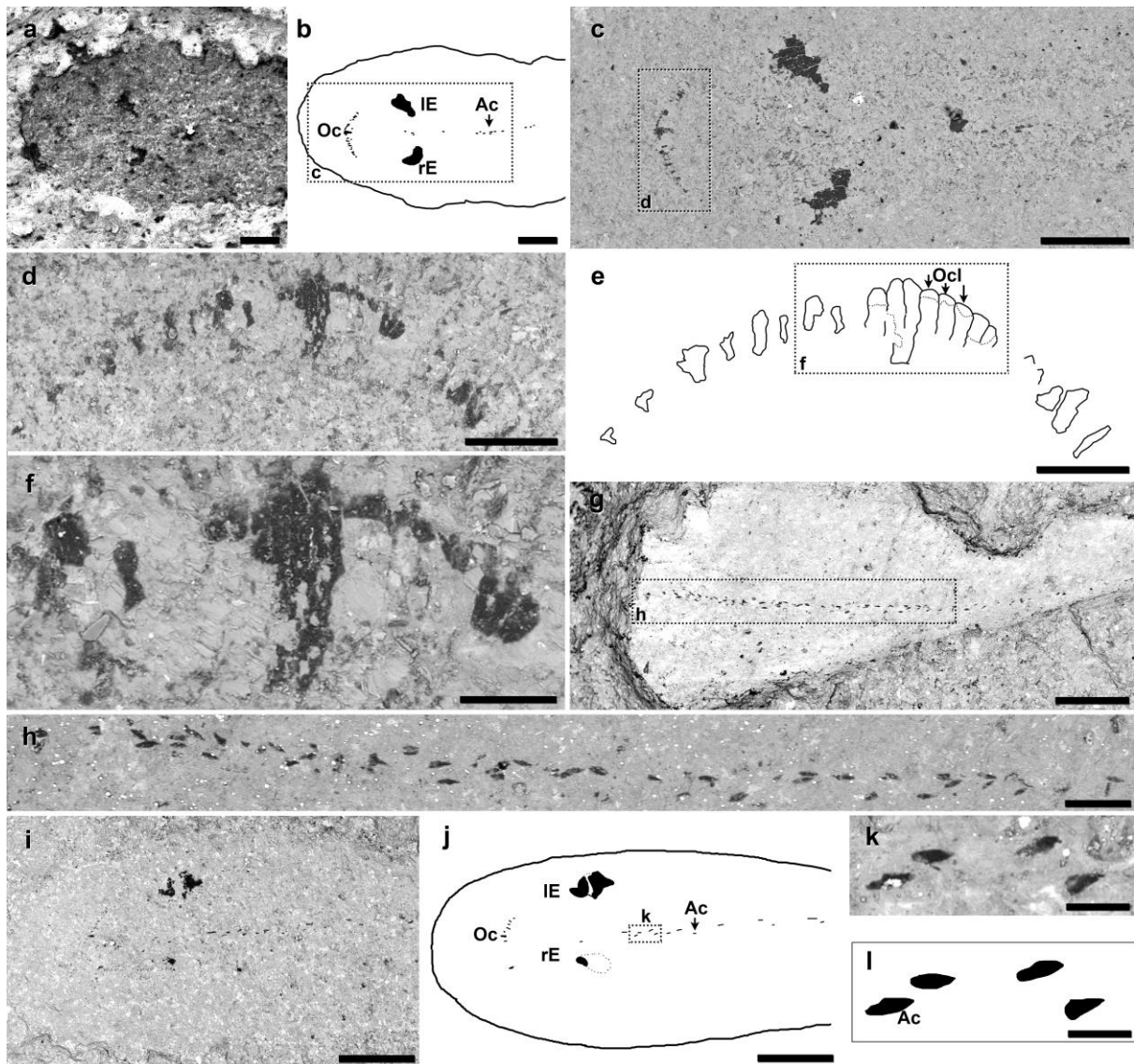
216 Correspondence should be addressed to ms609@cam.ac.uk.

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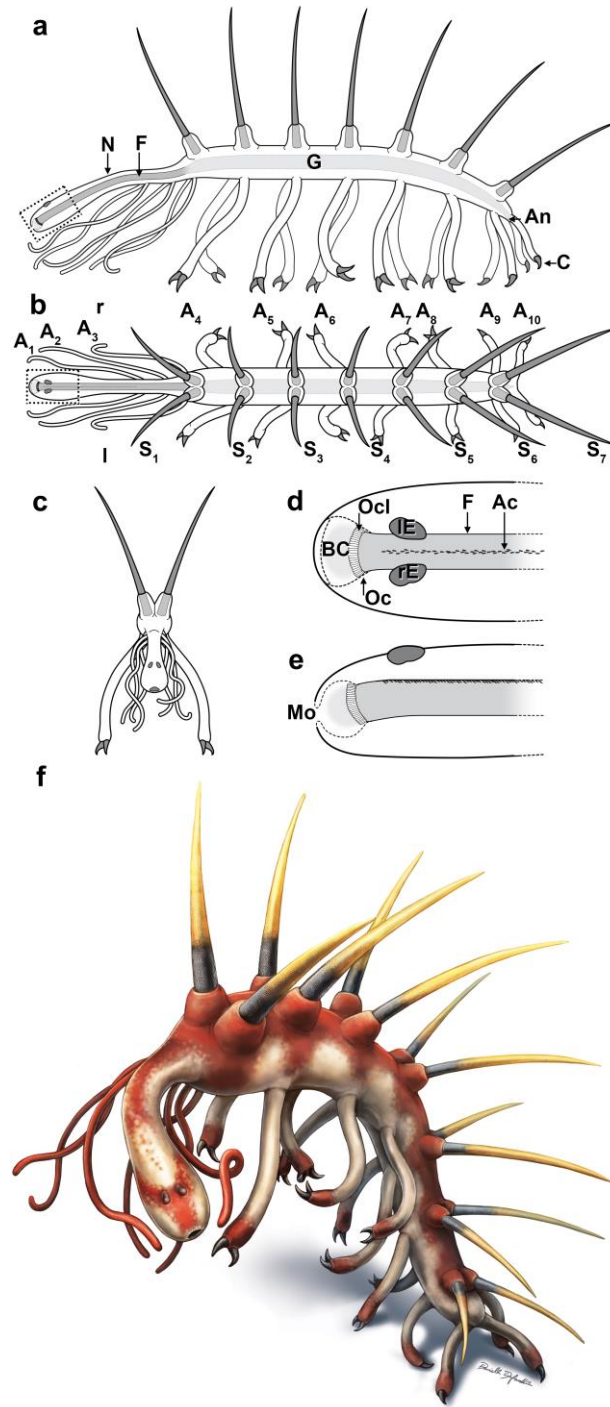
218 **Figure 1:** Optical images of *Hallucigenia sparsa* from the Burgess Shale (anterior to the
 219 left). **a**, ROM 62269 (see also Extended Data Fig. 5); **b**, ROM 63142, SEM images are
 220 provided in Fig. 2g–l and Extended Data Fig. 3c; **c**, ROM 63051; see also Extended Data Fig.
 221 3b, d–g; **d**, ROM 63146; high magnification images of the head are provided in Fig. 2a–f and
 222 Extended Data Fig. 7; **e**, NMNH 198658; see also Extended Data Fig. 2b–c; **f–g**, anterior
 223 section of ROM 57168; see also Extended Data Fig. 1c–e.

224 Acronyms for all figures: A = appendages, Ac = aciculae, An = anus, Bc = buccal chamber,
 225 C = claw, Df = decay fluids, E = eyes, F = foregut, G = gut, l = left, Mo = mouth opening,
 226 Cs = circumoral structure, Ce = circumoral elements, r = right, S = spines, A_{1–n} or S_{1–n} =
 227 order of A or S from front to back. Dotted white lines identify areas enlarged in Fig. 2 and
 228 Extended Data Figures, as denoted in captions. Unbroken white lines in b–d represent edges
 229 of the composite images of both parts and counterparts superimposed together. Black and
 230 white arrowhead denotes images flipped horizontally. Scale bars = 5 mm (a–e), 0.5 mm (f–
 231 g).

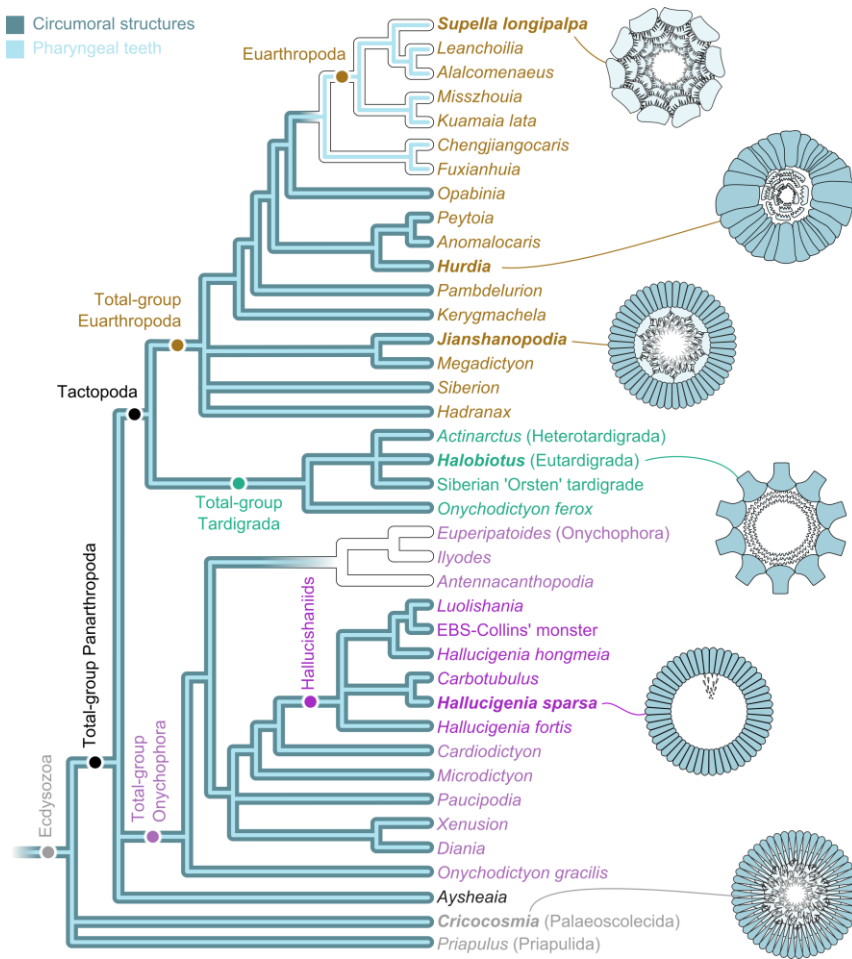


233 **Figure 2:** Scanning electron micrographs of the head region of *Hallucigenia sparsa* from the
 234 Burgess Shale. Anterior to the left except d–f, anterior to top of page. **a–f**, ROM 63146 (see
 235 Fig. 1d) with sketches of anterior region (b) and mouth plates (e); **g–l**, ROM 63142, part (g–
 236 h) and counterpart (i–l) showing aciculae. Acronyms and symbols as in Fig. 1. Detector
 237 mode: a, secondary electron; c–k, backscatter. Scale bars = 200 μm (a–c, g, i–j), 50 μm (d–e,
 238 h), 20 μm (f, k–l).

239



240 **Figure 3:** Anatomical drawings of *Hallucigenia sparsa* from the Burgess Shale. **a**, lateral
 241 profile; **b**, dorsal profile; **c**, frontal profile; **d–e**, head in dorsal (d) and lateral (e) views; **f**, full
 242 anatomical reconstruction. Drawings by Danielle Dufault. Acronyms as in Fig. 1.
 243



244 **Figure 4:** Ecdysozoan phylogeny, showing most parsimonious character distribution of
 245 circumoral structures (dark blue) and pharyngeal teeth (light blue). Fitch parsimony indicates
 246 the presence of both these structures in the ancestral ecdysozoan; a scenario positing multiple
 247 independent innovations of this armature would be less parsimonious. Topology shown
 248 denotes the strict consensus of all most parsimonious trees recovered under implied weights
 249 with concavity constant (k) between 0.46 and 211, after the removal of *Orstenotubulus*. The
 250 ‘hallucishaniid’ clade – diagnosed by a swollen head, dorsal spines, and the differentiation of
 251 the anterior trunk and trunk appendages – includes luolishaniids, *Orstenotubulus* and
 252 *Carbotubulus* within a paraphyletic ‘*Hallucigenia*’. Illustrated taxa are in bold type; see
 253 discussion of trans. ser. 9 & 13 in Supplementary Note 1. For phylogenetic data and full
 254 results see Supplementary Data.

256 **Methods**

257 **Fossil materials.** Materials are deposited at the Royal Ontario Museum, Toronto (ROM) and
258 the Smithsonian Institution National Museum of Natural History, Washington DC (NMNH).
259 Sediment covering parts of certain ROM specimens was manually removed using a tungsten-
260 tipped micro-engraving tool. Specimens were photographed under various lighting
261 conditions including dark- and bright-field illumination and polarized light, and imaged by
262 backscatter and secondary electron microscopy under variable pressure.

263 **Taphonomic considerations.** As with other Burgess Shale organisms^{28,29}, *Hallucigenia*
264 *sparsa* exhibits various degrees of pre- and post-burial decay, ranging from disarticulated
265 specimens represented only by pairs of decay-resistant spines (Extended Data Fig. 9a)
266 through partly disarticulated specimens retaining parts of the body (Extended Data Fig. 9b) to
267 complete specimens, whose curled appendages and trunks are consistent with post-mortem
268 contraction following rapid burial of live organisms (Fig. 1a–e; Extended Data Figs. 1–8).
269 Consequently, the widths of the trunk and appendages are subject to slight taphonomic
270 variation within and between specimens (e.g. Fig. 1). The full length of the body and
271 appendages, where preserved, is typically buried within the matrix and is difficult to prepare
272 mechanically.

273 **Phylogenetic analysis.** Phylogenetic analysis was conducted using the methods of Smith &
274 Ortega-Hernández⁶; in summary, parsimony analysis was performed in TNT³⁰ under a range
275 of weighting parameters, with Goloboff's concavity constant³¹ ranging from $k = 0.118$ to
276 211, and under equal weights ($k = \infty$). Code is available in the Supplementary Data.
277 *Orstenotubulus* (80% tokens 'ambiguous' or 'inapplicable') was identified as a wildcard
278 taxon with an unconstrained position within the hallucishaniids; to improve resolution it is
279 omitted from the strict consensus trees presented in the main manuscript.

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298

299 **Extended Data legends**

300 **Extended Data Table 1:** Interpretations of *Hallucigenia* through time.

301 **Extended Data Figure 1:** *Hallucigenia sparsa* from the Burgess Shale. **a–b**, largest (a, ROM
302 57169) and smallest (b, ROM 62093) specimens, to the same scale; **c**, ROM 57168, with
303 enlargements of the anterior (**d**) and mid-trunk (**e**). Acronyms as in Fig. 1. Scale bars = 5 mm

304 **Extended Data Figure 2:** *Hallucigenia sparsa* from the Burgess Shale. **a**, ROM 63139,
305 showing posterior body termination; **b–c**, NMNH 198658, showing posterior termination (see
306 also Fig. 1e); **d–g**, ROM 63143: e, enlargement of region marked in d; f–g: backscatter SEMs
307 of regions marked in e. Acronyms as in Fig. 1. Scale bars = 5 mm (a–d), 1 mm (e), 0.5 mm
308 (f), 0.1 mm (g).

309 **Extended Data Figure 3:** *Hallucigenia sparsa* from the Burgess Shale. **a, c**, ROM 63142: a,
310 composite image incorporating part and counterpart of the entire specimen; c, claw pair; **b**,
311 **d–g**, ROM 63051: b, composite image incorporating part and counterpart of the entire
312 specimen; d, anterior section; e–f, eyes; g, claw pair. c–e are backscatter electron
313 micrographs.. Acronyms as in Fig. 1. Scale bars = 5 mm (a–b), 500 μm (d), 50 μm (c, f–g),
314 20 μm (e).

315 **Extended Data Figure 4:** *Hallucigenia sparsa* from the Burgess Shale. **a–d**, ROM 61513; a,
316 entire specimen; b–d, enlargements of anterior region, showing mouth opening, aciculae and
317 eyes; mouth opening to right in b, to left in c, d; **e–f**, ROM 61143; anterior region marked in e
318 is enlarged in f. Acronyms as in Fig. 1. Scale bars = 5 mm (a, e), 1 mm (b, f), 200 μm (c),
319 20 μm (d).

320 **Extended Data Figure 5:** *Hallucigenia sparsa* (ROM 62269) from the Burgess Shale. **a**,
321 part; **b**, counterpart, anterior section, showing eyes; **c–d**, eyes and mouthparts (backscatter
322 SEM); **e–f**, detail of eyes (counterpart). Acronyms as in Fig. 1. Scale bars = 1 mm (a–b), 200
323 μm (e), 100 μm (c–d), 20 μm (f).

324 **Extended Data Figure 6:** *Hallucigenia sparsa* from the Burgess Shale. **a–d**, NMNH 83935
325 (holotype): in contrast to body tissue, decay fluids lack a sharp margin and are non-reflective;
326 **e–f**, ROM 57776, showing full length of appendage one. Acronyms as in Fig. 1. Scale bars
327 = 5 mm.

328 **Extended Data Figure 7:** *Hallucigenia sparsa* (ROM 63146), composite image of part and
329 counterpart. Acronyms as in Fig. 1. Scale bar = 5 mm.

330 **Extended Data Figure 8:** *Hallucigenia sparsa* from the Burgess Shale. **a–d**, NMNH
331 193996: **b–c**, enlargements of area boxed in **a**; **c**, secondary electron micrograph; **d**,
332 backscatter electron micrograph of region marked in **c**; **e–g**, ROM 63141, showing position
333 of mouth; **h–j**, ROM 63144; **i**, secondary electron image of region marked in **h**; **j**, backscatter
334 electron image of region marked in **i**, showing eyes and mouthparts, with interpretative
335 diagram; **k–m**, ROM 63140; **l**, backscatter SEM of head, showing right eye and mouthparts
336 (enlarged in **m**, with interpretative diagram). Acronyms as in Fig. 1. Scale bars = 10 mm (**k**),
337 5 mm (**a**, **e**, **h**), 1 mm (**b–c**, **l**), 0.5 mm (**i**), 0.1 mm (**d**, **j**, **m**).

338 **Extended Data Figure 9:** *Hallucigenia sparsa* from the Burgess Shale. **a**, ROM 43045,
339 cluster of dissociated specimens; **b**, ROM 63145, dissociated specimen showing spines in
340 close anatomical position. Acronyms as in Fig. 1. Scale bars = 10 mm.