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Article type : Original Article

Editor : George Sevastopulo

Running head: CRINOID NERVOUS AND CIRCULATORY SYSTEMS

Handling Editor: Prof. George Sevastopulo

The nervous and circulatory systems of a Cretaceous crinoid: preservation, palaeobiology and evolutionary significance

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ABSTRACT

Featherstars, comatulid crinoids that shed their stalk during their ontogeny, are the most species-rich lineage of modern crinoids and the only ones present in shallow water today. Although they are of considerable palaeontological interest as a ‘success story’ of the Mesozoic Marine Revolution, their fossil record is relatively species-poor and fragmentary. New Spanish fossils of the Cretaceous featherstar *Decameros ricordeanus* preserve the shape and configuration of

This is the author manuscript accepted for publication and has undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the [Version of Record](#). Please cite this article as [doi: 10.1111/pala.12452](https://doi.org/10.1111/pala.12452)

27 nervous and circulatory anatomy in the form of infilled cavities, which we reconstruct from CT
28 scans. The circulatory system of *D. ricordeanus* was relatively extensive and complex, implying
29 a pattern of coelomic fluid flow that is unique among crinoids, and the peripheral parts of the
30 nervous system include linkages both to the circulatory system and to the surface of the body. A
31 phylogenetic analysis – the first to include both living and fossil featherstars and which includes
32 characters from internal anatomy – recovers *D. ricordeanus* among the lineage of featherstars
33 that includes Himerometroidea, *Tropiometra* and ‘Antedonoidea’, among others. *D. ricordeanus*
34 is larger than almost any modern featherstar, and its elaborate coelomic morphology appears to
35 be a consequence of positive allometry. All featherstars with coelomic diverticula are shown to
36 belong to a single comatulid subclade, and this feature may constitute a synapomorphy of that
37 group. Some preservation of cavities corresponding to soft tissue is probably not exceptional in
38 fossil crinoids, providing an opportunity to study the diversity and evolution of extinct
39 anatomical systems typically only preserved in Lagerstätten.

40

41 *Keywords:* palaeobiology, preservation, fossil, evolution, crinoid, nervous system

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43

44 INTRODUCTION

45 DURING the Mesozoic, the rise of the major modern groups of eukaryotic phytoplankton and
46 the concurrent diversification of marine grazers and durophagous predators initiated (or
47 constituted) a broad shift in the structure of marine ecosystems known as the Mesozoic Marine
48 Revolution (MMR). Crinoids have provided an important case study as ‘victims’ of the MMR: as
49 durophagous predators such as teleost fishes and echinoids became more prevalent in shallow
50 marine ecosystems, these sessile or slow-moving, benthic passive suspension feeders are thought
51 to have been restricted to deep-water settings in which they encountered fewer predators (Meyer
52 and Macurda 1977; Bottjer and Jablonski 1988; Oji 1996; Gorzelak *et al.* 2012). Featherstars,
53 those crinoids in the order Comatulida that shed their stalk during ontogeny and live as stalkless
54 adults, constitute an important exception to this pattern: featherstars today are globally
55 distributed in shallow- and deep-water settings, and represent the majority of crinoid diversity
56 (556/665 spp. (Appeltans *et al.* 2012)). Their relative ecological and evolutionary success has
57 long been attributed to the enhanced motility afforded by a stalkless lifestyle: many featherstars

58 change position diurnally, and most groups are able to swim when stimulated by a potential
59 predator, remaining in the water column for as long as several minutes (Purens 2014). That
60 featherstars can persist in shallow water as a result of their increased motility is corroborated by
61 the fact that all living bourgueticrinids – the 2-4 comatulid lineages that probably re-acquired
62 sessility secondarily (Rouse *et al.* 2013) – are found exclusively in deep water.

63 Despite their centrality to the evolution of the modern crinoid fauna, the evolutionary
64 history of featherstars is obscured by a poor fossil record. Their fossil diversity is under-
65 represented relative to that of stalked crinoids (Purens 2016), possibly because they are most
66 diverse in areas of poor preservation potential, and most fossil species are known only from
67 fragmentary material. Furthermore, the systematics of extant featherstars is based in large part on
68 features that do not preserve in most fossil taxa – for example, the arms and pinnules (Clark
69 1967; Hess and Messing 2011). Consequently, much remains unknown about the phylogeny and
70 palaeobiology of early featherstars (Hess 2014). Here we describe new, exquisitely-preserved
71 fossil featherstars from the Lower Cretaceous of Northeastern Spain and infer their phylogenetic
72 affinities in the first explicit phylogenetic analysis of both living and fossil featherstars.
73 Surprisingly, these fossils preserve intricate traces of nervous and circulatory anatomy, shedding
74 light on anatomical innovations within this successful clade of marine invertebrates.

75

76 MATERIALS AND METHODS

77 Specimens of the featherstar *Decameros ricordeanus* (Decameridae, Comatulida, Crinoidea)
78 were recovered from the Maestrazgo Basin (Teruel, NE Spain) in loosely-consolidated marls
79 dated to the early Aptian based on ammonite biostratigraphy and inferred to have been deposited
80 in a low-energy outer ramp setting (Bover-Arnal *et al.* 2016). Detailed palaeoecological and
81 stratigraphical information is given by Zamora *et al.* (2018). Importantly, no other crinoid
82 species were recovered from the same locality. Material studied here includes six complete and
83 two fragmentary calyces, 20 articulated arm fragments, ten articulated cirrus fragments, 200
84 isolated cirrals, 400 isolated brachials, and 20 isolated radials (Fig. 1). Specimens are deposited
85 in the Museo de Ciencias Naturales de la Universidad de Zaragoza under the acronym MPZ.
86 Specimens were prepared using potassium hydroxide (KOH), and later neutralized with
87 hydrochloric acid (10%). Crinoids disarticulate rapidly upon dying, and the many partially-
88 articulated specimens described here probably died shortly before or during burial. External

89 features of specimens are preserved in fine detail, and details of stereom on the outside of fossils
90 can be visualized with microscopy for some specimens.

91 Six fossil specimens were scanned using X-ray microcomputed tomography (μ CT) with the
92 University of Michigan CTEES facility with a Nikon 62 XT H 225ST industrial μ CT system
93 using a tungsten reflection target. Fossils were scanned at 95-105 kV and 96-155 μ A, with
94 resolution 8.0-11.8 μ m. 3D images were reconstructed from 2D projections using CT Pro 3D
95 (Nikon Metrology). Scans reveal complex internal morphology visible as relatively high-density
96 infillings of cavities within the crinoid skeleton. These infillings are reddish-black to orange in
97 colour and are suggested to be iron-rich (Fig. 2A, B). In reconstructed CT datasets, they appear
98 as clusters of small (\sim 20 μ m) grains that may be either restricted to cavities within the skeleton
99 or distributed more uniformly throughout the stereom. Thus, the amount of anatomical
100 information they preserve is variable. The outline of cavities corresponding to coelomic or
101 nervous tissue is preserved in fine detail in two specimens, but in most cases these details are
102 obscured or obliterated. One fossil specimen (MPZ-2019/366) with exceptionally preserved
103 internal features, scanned at 105 kV and 155 μ A with a resolution of 10.9 μ m, was chosen for
104 further study. 3D surfaces based on reconstructed μ CT scans were generated using the medical
105 imaging software Materialise Mimics (Materialise NV, Leuven, Belgium).

106 The results of a phylogenetically broad μ CT-based survey of extant crinoids were used for
107 comparison with *D. ricordeanus* (Saulsbury and Zamora 2019). Many of these specimens were
108 used in assembling a morphological character matrix for phylogenetic inference. We used
109 molecular data and discrete and continuous morphological characters to infer the phylogenetic
110 affinities of *D. ricordeanus* and several other fossil featherstars. Several studies have estimated
111 the phylogeny of extant crinoids using molecular data (Hemery *et al.* 2013; Rouse *et al.* 2013;
112 Cohen and Pisera 2017), but because previous attempts at inferring the phylogeny of living
113 crinoids have disagreed substantially with one another and have not included many of the taxa
114 for which morphological data have been gathered in this study, we estimated the molecular
115 phylogeny of crinoids independently. We inferred the relationships among 158 species of living
116 crinoid in a maximum likelihood framework using two nuclear (*18S*, *28S*) and three
117 mitochondrial genes (*16S*, *cytb*, and *COI*). Non-protein-coding sequences (*16S*, *18S*, *28S*) were
118 aligned using PRANK ([wasabiapp.org], (Loytynoja and Goldman 2005)); the remaining
119 sequences were aligned using MAFFT ([<https://mafft.cbrc.jp/alignment/software/>]). Aligned

120 sequences were concatenated using SequenceMatrix (<http://www.ggvaidya.com/taxondna/>). We
121 used RAxML (Stamatakis 2014) to infer phylogeny using separate partitions for each gene and
122 using the GTR+ Γ model of molecular evolution. When the resulting tree is pruned to include
123 only those taxa with morphological data available, it is roughly concordant with the maximum
124 likelihood crinoid phylogenies presented by Hemery *et al.* (2013) and Rouse *et al.* (2013),
125 sharing most clades with the findings of both studies. This constraint tree is available in
126 Saulsbury & Zamora (2019).

127 We used TNT to infer the phylogeny of living and fossil featherstars with morphological
128 data while using the molecular phylogeny as a topological constraint. A matrix of 37 discrete and
129 24 continuous morphological characters was assembled and scored for 21 living and 5 extinct
130 species of comatulid crinoids. Specimens examined are listed in Saulsbury & Zamora (2019).
131 All discrete morphological characters were treated as unordered. Several discrete characters used
132 in the morphological matrix were not parsimony-informative, (i.e. they are not scored for at least
133 two states for each of at least two characters), but are included in this study as a framework for
134 future phylogenetic studies. Continuous characters included linear measurements (e.g.
135 centrodorsal radius), ratios of linear measurements (e.g. height of radial muscle fossa / height of
136 interarticular fossa), and one angle measurement (angle between radial interarticular ligament
137 fossa and fulcral ridge). Multiple measurements were averaged where possible, first across
138 repeated elements within specimens and then across multiple specimens within species.
139 Character definitions are provided in Saulsbury & Zamora (2019, data 2). Measurements were
140 taken from imagery, from 3D models generated from CT scans, or directly from specimens using
141 calipers. We used TNT to infer the phylogeny of featherstars by maximum parsimony with
142 implied weighting. Support was assessed with symmetric resampling (Goloboff *et al.* 2003),
143 implemented in TNTR (Matzke 2015). We used the paracomatulids – specifically, *Paracomatula*
144 *helvetica* – as the outgroup to Comatulida, following Hess (2014). A thorough summary of
145 TNT's treatment of continuous characters is given by Jones and Butler (2018). The analysis
146 presented here represents the first effort to explicitly infer the phylogenetic affinities of fossil and
147 living featherstars. The molecular sequence alignment, maximum likelihood molecular
148 phylogeny, morphological character matrix, TNT input file, and tree file are available in
149 Saulsbury & Zamora (2019).

150

151 **RESULTS**152 *Skeletal morphology*

153 The material described here is referred to the species *Decameros ricordeanus* (Orbigny,
154 1850), as redescribed by Rasmussen (1961, 1978), based on the following characteristics: arms
155 five, with no syzygies or synarthries; first pinnule on the first brachial; unbranched ventral side
156 of centrodorsal with radiating coelomic furrows; large, low, discoidal centrodorsal; large, stout,
157 rhombic basals; wide, shallow radial cavity; and radials with low free surface (Fig. 1). We note
158 that the proximal dozen or so brachials typically bear a single aboral spine (except the first
159 brachial, which never bears a spine); some brachials have two spines. *Decameros ricordeanus* is
160 an exceptionally large featherstar, and the material described here includes calyces above 1.5 cm
161 in diameter. Complete calyces vary in diameter by more than a factor of two, and the ontogenetic
162 changes in shape recorded in these fossils are similar to those observed in its congener
163 *Decameros wertheimi* (Peck & Watkins, 1972): larger forms have wider centrodorsals.

164 *Coelomic and nervous anatomy*

165 Background on the structure and variation of anatomical systems in crinoids is given in
166 Saulsbury and Zamora (2019). Importantly, all discussion of coelomic anatomy here refers to the
167 somatocoel, the system of spacious, fluid-filled secondary body cavities common to
168 Echinodermata. We do not refer to the haemal or water vascular systems; the former is a
169 relatively inconspicuous primary body cavity (i.e. not a coelom), and neither of the two are
170 associated with the skeleton in any modern crinoid studied (Heinzeller and Welsch 1994). Like
171 other crinoids, *Decameros* possesses an extension of the somatocoel in the radial cavity termed
172 the ‘axial sinus’ (Heinzeller and Welsch 1994), separated from the aboral nerve centre (Fig. 2C,
173 anc) by the basal circlet. In *Decameros* this coelomic feature is uniquely elaborate and extensive.
174 Skeletal canals corresponding to extensions of the somatocoel occur along all sutures between
175 plates of the calyx (Figs 1C, D; 2C, D). Canals are circular to elliptical in cross section and are
176 between 0.05 mm and 0.35 mm in diameter, usually between 0.15 and 0.3 mm. A single bundle
177 of coelomic canals occurs in the axis of the crinoid, in the centre of the basal ring (Fig. 2C, cb).
178 In each radius, some of these canals connect with a fan-shaped complex of coelomic canals
179 between the radial and centrodorsal plates (Fig. 2I). The canals that make up these fans are
180 radially-oriented and reticulate extensively toward the edges, where they form a perforate sheet
181 (Fig. 2E). Each fan is aborally embayed in the radius, conforming to the suture between the

182 radial circlet and the centrodorsal. Fans do not reach the edge of the calyx, terminating 0.5 – 1
183 mm from the lateral margin. Each fan is connected to a planar network of canals between the
184 radials and basals, and to two such networks between adjacent radials (Fig. 2I). Networks
185 between adjacent radials have a characteristic geometry, their most conspicuous feature being a
186 broad, straight canal connecting the radial fans with the canals between radials and basals. This
187 canal is visible on the surface of disarticulated radials as a diagonal groove (Fig. 2B). The entire
188 network of coelomic canals in the calyx has 11 outlets in the radial cavity. One large outlet
189 occurs in the axis, corresponding to the large axial bundle of canals mentioned earlier, and 10
190 outlets (5 radial: Fig. 2C, ro; 5 interradial: Fig. 2C, iro) occur at the junctions between the radial
191 and basal circlets.

192 Although the calyx coelom in *D. ricordeanus* is more elaborate than that of any living form,
193 *Decameros* is not the only crinoid whose coelom bears extensions in the calyx, referred to here
194 and elsewhere (Hess and Messing 2011) as coelomic diverticula. Diverticula can be oriented
195 laterally or aborally, corresponding respectively to the ‘coelomic furrows’ and ‘radial pits’
196 mentioned frequently in the taxonomic literature (Rasmussen 1961; Hess and Messing 2011).
197 Skeletal features corresponding to coelomic diverticula are reported in some or all members of
198 12 out of 29 comatulid families (Antedonidae, Aporometridae, Asterometridae, Colobometridae,
199 Decameridae, Himerometridae, Mariametridae, Notocrinidae, Ptilometridae, Solanocrinitidae,
200 Tropiometridae and Zygometridae) (Hess and Messing 2011). Moreover, unique configurations
201 of coelomic morphology appear to characterize major clades. We highlight the following axes of
202 morphological variation, which are incorporated into our phylogenetic analysis:

- 203 1. In all himerometroids surveyed here, the coelom in the calyx axis is divided into a central
204 bundle of canals and five radiolateral canals. In all other taxa, the coelom in the axis is
205 present as a single bundle of canals.
- 206 2. Notocrinidae and Asterometridae share deep aboral diverticula, but in notocrinids each
207 diverticulum is single. In asterometrids they are divided into a tight bundle of narrow
208 canals.
- 209 3. All members of Ptilometridae and Asterometridae, which have been recovered together
210 as a monophyletic clade in previous phylogenetic analyses, share both *radial* and
211 *interradial* sets of coelomic diverticula, instead of just the radial ones present in other
212 taxa.

213 4. In two antedonids surveyed, *Heliometra glacialis* and *Florometra serratissima* (the latter
214 not included in phylogenetic analysis), radial coelomic diverticula are present and are
215 oriented into the radial plate, rather than between the radial circlet and centrodorsal. In
216 our molecular phylogeny and that of Hemery *et al.* (2013), *H. glacialis* and *F.*
217 *serratissima* are closely related to one another and are nested within a clade of antedonids
218 generally lacking radial coelomic diverticula.

219 Diverticula have not been reported in stalked crinoids, nor do we observe them in any stalked
220 crinoids surveyed here.

221 The layout of the featherstar central ANS – here used to refer to the relatively thick
222 brachial nerves, pinnule nerves, cirral nerves, pentagonal nerve ring, aboral nerve centre, and the
223 nerves connecting the previous two elements – has previously been reconstructed from CT scans
224 and histology of living species (Aschauer *et al.* 2010; Engle 2012) and appears to be conserved
225 across featherstars. The layout of the central ANS in *Decameros ricordeanus* matches previous
226 descriptions given for a generalized featherstar (Moore and Teichert 1978; Heinzeller 1998),
227 differing only in the relative lengths and diameters of its constituent nerves. Here we reconstruct
228 details of the peripheral ANS, which has received far less study across Crinoidea, in *D.*
229 *ricordeanus*. Hamman (1889) has demonstrated that four pairs of nerves issue from the brachial
230 nerve cord in each arm plate of a living crinoid. Only some or occasionally none of these
231 peripheral nerves are visible in CT scans; it is not clear whether this apparent absence reflects an
232 actual lack of these nerves in some lineages or in some parts of the arm, or whether instead these
233 nerves are present but do not appear because they are finer than the resolution of the CT scans or
234 of the meshwork of the skeleton. In the arm plates (brachials) of several extant featherstars, we
235 observe aborally-directed passages that match the two pairs of putatively sensory nerves
236 indicated by Hamann (1889). We identify this same set of peripheral nerves in *Decameros*
237 *ricordeanus*. More strikingly, CT scans reveal peripheral nerves in the radial plates of extant and
238 fossil crinoids, which previously have not been demonstrated. In several extant crinoids
239 surveyed, one to two pairs of peripheral nerves issue from the brachial nerve in the radial
240 (Saulsbury and Zamora 2019, fig. S1). In some cases these peripheral nerves terminate on the
241 free surface of the radial (i.e. on the outside of the animal) and in other cases they are directed
242 orally, possibly connecting with one of the other major nervous systems. In *Decameros*, we
243 identify two pairs of peripheral nerves that originate at the junction of the pentagonal nerve ring

244 with the brachial nerve and another that originates partway along the brachial nerve (Fig. 2F, J).
245 One of the former pair connects aborally with a coelomic fan; the other two pairs extend to the
246 free surface of the radial and terminate there. These three pairs of peripheral nerves are
247 extensively linked with each other, such that the peripheral ANS within each radial forms a well-
248 connected network (Fig. 2G, J). The nerves constituting this network are relatively fine: in the
249 best preserved specimen the brachial nerves in the radials are between 0.35 and 0.4 mm in
250 diameter and the peripheral nerves are between 0.05 and 0.15 mm in diameter. We observe a
251 similar, though less well-preserved, network of canals in the centrodorsal plate. We do not
252 observe any peripheral nerves extending between the ANS and the coelom in CT scans of living
253 taxa, but because the stereom between the ANS and the coelom is very coarse in places, the
254 existence of such nerves cannot be ruled out.

255 *Phylogenetic affinities*

256 The results of our phylogenetic analysis are shown in Fig. 3. All four fossil species analyzed
257 fall within crown-group Comatulida. *Decameros ricordeanus* and both species of *Solanocrinites*
258 analyzed were recovered as a monophyletic clade. This tree topology accords with Rasmussen's
259 (1961) classification of *Decameros* as a subgenus of *Solanocrinites* and goes against more recent
260 definitions of the Decameridae and Solanocrinitidae. *Decameros ricordeanus* and *Solanocrinites*
261 are recovered as part of a clade comprising Himerometroidea, *Tropiometra* and Asterometridae +
262 Ptilometridae. Thus, *Decameros* is part of a clade whose members generally bear coelomic
263 diverticula. *Palaeocomaster* and *Archaeometra* fall outside this clade, despite being previously
264 classified together with *Solanocrinites* and *Decameros* in the Solanocrinitoidea (Hess and
265 Messing 2011). Support values are generally low throughout the tree, but the placement of
266 *Decameros ricordeanus* is relatively stable even when all morphological characters relating to
267 coelomic diverticula are excluded, when the morphological matrix includes only discrete or only
268 continuous characters, and when all other extinct taxa are removed from the analysis (Saulsbury
269 and Zamora 2019).

270

271 **DISCUSSION**

272 *Preservation*

273 The fine detail of the anatomical features preserved in *Decameros ricordeanus* is
274 unprecedented for fossilized post-Palaeozoic crinoids, but the preservation of internal anatomy in

275 fossil crinoids is probably not exceptional. The fossils described here, for example, do not come
276 from a Lagerstätte and are partly disarticulated. Small cavities in echinoderm fossils tend to be
277 obliterated by the growth of calcite during diagenesis, but the infillings documented here appear
278 to prevent obliteration of internal features. Features preserved in this way should be more
279 amenable to study with μ CT if they are infilled with material of a sufficiently different density
280 from the surrounding calcite, as in the fossils presented here. Although *D. ricordeanus* represents
281 only the third fossil crinoid species studied with μ CT to date (Zamora *et al.* 2015; Baumiller and
282 Fordyce 2018), reports of internal anatomy in fossil crinoids are fairly common (Jaekel 1891;
283 Rasmussen 1961; Haugh 1975*a, b*; Hunter *et al.* 2016), and thus computed tomography has the
284 potential to play an important role in understanding the evolution of organ systems in this taxon.
285 Moreover, a deeper understanding of crinoid internal anatomy and its diversity could help to
286 resolve the uncertain state of post-Palaeozoic crinoid systematics. Efforts to infer the phylogeny
287 of extant crinoids within the last decade have disagreed on the relationships between the four
288 living orders, and the phylogenetic affinities of most of the extinct post-Palaeozoic groups –
289 including roveacrinids, uintacrinids, the enormous driftwood crinoids *Traumatocrinus* and
290 *Seirocrinus*, and millericrinids – remain unresolved. The internal anatomy of fossil crinoids
291 represents a largely untapped source of morphological data, which might prove useful in
292 resolving these uncertainties. At least six unique configurations of the aboral nervous system
293 have been demonstrated in extant crinoids (Heinzeller 1998; Bohn and Heinzeller 1999), and the
294 results of the present study demonstrate remarkable morphological disparity in the crinoid body
295 cavity, at least among featherstars. Thus, future efforts at understanding the evolutionary history
296 and systematics of fossil Articulata can benefit from a consideration of both external and internal
297 morphology.

298

299 *Circulation of coelomic fluid in Decameros and other crinoids*

300 Although the hydrodynamics of circulation in the crinoid calyx have not been studied in
301 detail, it is possible to reconstruct possible circulatory patterns in the coelom of extinct crinoids
302 based on comparison with modern forms. Based on the coelomic layout of the extant featherstar
303 *Tropiometra carinata* (Saulsbury and Zamora 2019, fig. S1), the coelomic canals form an axial
304 bundle in the calyx, with incurrent canals fully encircled by excurrent ones. In *T. carinata*, which
305 bears diverticula, coelomic fluid probably travels down the axis through a central bundle of

306 canals, flushes into the diverticula, and then travels orally through five lateral canals and into the
307 arms. Based on this general pattern we reconstruct one possible circulatory configuration for *D.*
308 *ricordeanus* in which coelomic fluid entered the calyx through the central bundle of coelomic
309 canals and flowed out through the ten outlets at the junction between the basal and radial circlets
310 (Fig. 2C, ro, iro). Other configurations are plausible; we reconstruct a possible flow pattern here
311 only to show that, despite its complex shape, fluid probably circulated through the entire calyx
312 coelom in life.

313 Coelomic circulation in crinoids probably serves multiple important roles, including nutrient
314 and hormone transport and respiration (Grimmer and Holland 1979). Moreover, the crinoid
315 coelom within the calyx scales with positive allometry, such that all featherstars above a certain
316 size bear coelomic diverticula (Saulsbury, unpub. data). Under isometric scaling, the surface area
317 exposed to circulatory fluid and hence the maximum functional capability of the circulatory
318 system would decrease with increased size, so if a larger crinoid does not have a circulatory
319 system of correspondingly greater surface area, it risks suffocation. Thus, *Decameros*
320 *ricordeanus* bears exceptionally complex coelomic diverticula because it is exceptionally large,
321 and having an elaborate circulatory system is necessary at that size.

322

323 *Neurobiology of Decameros and other crinoids*

324 The function of the crinoid aboral nervous system (ANS) has been investigated by Hamann
325 (1889) and Nakano (2004). The peripheral parts of the ANS have not yet been investigated in
326 any detail, but some functions can be suggested based on morphology. In each arm plate of
327 living crinoids, two pairs of peripheral nerves are oriented from the brachial nerve toward the
328 aboral surface of the arm, where they terminate. Along the way they do not contact or pass near
329 any effectors like muscles, and Hamann (1889) suggests that these nerves are probably sensory,
330 based on their arrangement. Although the peripheral nerves originating in the radial plates have
331 not been documented previously, their similarity (in terms of symmetry, size relative to the
332 central ANS, and branching geometry) to the peripheral nerves in the arm plates suggests they
333 might play a similar role. Some of the peripheral nerves in the radial circlet terminate on the free
334 surface of the radial in both living crinoids and in *Decameros ricordeanus*. These peripheral
335 nerves are well-situated to sense environmental conditions. For example, crinoids are sensitive to
336 flow conditions, and will change their position and deploy or enroll their filtration fans in

337 response to changes in current (Meyer 1997). Nerve endings on the aboral surface of the arms
338 and radials are therefore ideally placed to detect such changes, although such a function is
339 speculative. In *Decameros*, we also observe peripheral nerves that terminate on coelomic
340 diverticula; we have not identified these in any extant crinoids but cannot rule out their existence.
341 We suggest that, like some other peripheral nerves, these might serve a sensory function, for
342 example by detecting changes in the composition of coelomic fluid. However, we cannot rule out
343 the possibility that these peripheral nerves innervate some previously-undetected effector – for
344 example, a feature of endocrine anatomy adjacent to the coelomic canals. No distinct anatomical
345 features have been observed in the dense stereom between the radial plates and the centrodorsal,
346 but little histological work has been done on the crinoid calyx, perhaps due to the difficulties of
347 applying traditional histological techniques to the echinoderm skeleton (Dietrich and Fontaine
348 1975). Modern immunostaining approaches have recently been used to reconstruct nervous
349 anatomy of non-crinoid echinoderms in stunning detail (Schmidt-Rhaesa *et al.* 2015; Vázquez-
350 Figueroa *et al.* 2016; Zueva *et al.* 2018), facilitating robust tests of functional hypotheses. Until
351 modern methods like these are applied to the crinoid nervous system, the functions of the
352 peripheral ANS will remain enigmatic. Nevertheless, it is clear at least that peripheral nerves
353 associated with the circulatory system either originated or became more intricate in the lineage
354 leading to *Decameros ricordeanus*. Whether and how this is associated with the increase in body
355 size and the associated increase in the complexity of the circulatory system will require
356 comparative analyses and a more complete knowledge of the diversity of the crinoid nervous
357 system.

358

359 *Decameros in crinoid phylogeny*

360 The phylogenetic affinities of fossil comatulids inferred in this study are concordant with
361 historical taxonomic work in some but not all respects. *Solanocrinites* and *Decameros* are
362 recovered as sister taxa in our analysis; likewise, Rasmussen (Rasmussen 1961) considered
363 *Decameros* to be a subgenus of *Solanocrinites*, although he later separated them into different
364 families (Rasmussen 1978). However, all fossil featherstars included in our phylogenetic
365 analysis have been assigned to the superfamily Solanocrinitoidea, which our study indicates is
366 polyphyletic. We suggest that the traits that have been used to define this superfamily – including
367 stout basal plates and a narrow centrodorsal cavity – are plesiomorphic or homoplasious. The

368 clade uniting *Decameros ricordeanus* and *Solanocrinites depressus* is recovered with strong
369 support as sister to *Tropiometra*, a nearly pantropical genus in the monotypic family
370 Tropiometridae. Monophyly of this clade is indicated primarily by continuous characters,
371 including a relatively low centrodorsal, low radials, and a broad radial cavity.

372 The soft tissue features preserved in *D. ricordeanus* provide some useful characters for
373 phylogenetic analysis. We recover *D. ricordeanus* deeply nested within an as-yet unnamed clade
374 that has nevertheless been recovered in all recent molecular phylogenetic studies: namely, the
375 clade that unites Zenometridae, ‘Antedonidae’, Himerometroidea, most of ‘Tropiometroidea’ and
376 *Notocrinus* to the exclusion of Comatulidae, Thalassometridae, Charitometridae,
377 Pentametrocrinidae, and most stalked comatulids. Coelomic diverticula are present in most
378 members of this clade that are included in our analysis and are rare or totally absent outside of
379 this clade. Other traits relating to coelomic anatomy help refine the placement of *D. ricordeanus*.
380 A distinct separation of the axial and lateral coelomic canals in the radial circlet unites
381 Himerometroidea to the exclusion of all other taxa considered, and *Decameros* is distinguished
382 from members of the Asterometridae by the presence of both radial and interradial coelomic
383 diverticula in the latter taxon. The central ANS exhibits considerable variability among major
384 crinoid taxa, encompassing at least six unique configurations (Heinzeller 1998; Bohn and
385 Heinzeller 1999). However, featherstars share an apparently uniform central ANS, so no
386 phylogenetically useful characters were sourced from this part of the body. We observe hints of
387 phylogenetically informative morphological variability in the peripheral ANS: for example, CT
388 scans of some extant members of the Comatulidae reveal pairs of thin nerves that extend orally
389 from the brachial nerve in the radial, and we do not observe these in any other taxon. However, it
390 is impossible to conclusively demonstrate the absence of peripheral nerves from CT scans alone,
391 as these nerves may be smaller than the ‘resolution’ of stereom. A thorough study of the
392 evolution of the peripheral ANS in crinoids will rely on histological research outside the scope of
393 the present study. However, if the success of ‘neurophylogeny’ for making sense of deep
394 relationships among living and fossil arthropods is any indication (Harzsch 2006; Tanaka *et al.*
395 2013; Cong *et al.* 2014), an understanding of neurobiology may be a useful tool in confronting
396 long-standing problems in crinoid systematics – for example, the relationships among the four
397 extant orders (Hemery *et al.* 2013; Rouse *et al.* 2013).

398

399 **CONCLUSIONS**

400 The potential for crinoids to preserve phylogenetically useful and biologically interesting
401 features of soft tissue in non-Lagerstätte settings is arguably underappreciated. In many crinoid
402 taxa, including all members of the crown-group, the skeleton conforms closely to soft-tissue
403 internal anatomy, so the contours of features such as the aboral nervous system and the coelomic
404 circulatory system can be visualized in fossils in which postmortem cementation or infilling of
405 stereom has not been so extensive as to obscure internal features. Notably, infilling with
406 sediment of a density that contrasts with that of stereom may preserve internal features in great
407 detail, as it does here. The openings of nerve canals are present on most fossil crinoid ossicles
408 (Hess and Messing 2011), suggesting that some preserve nervous anatomy internally. Findings
409 from sectioned or corroded specimens bear this out (Paul 1970; Žitt 1973). For example, Jaekel
410 (1891) described a silicified and partially corroded Jurassic cyrtocrinid whose aboral nervous
411 system differs strikingly from the highly derived layouts of its extant relatives *Cyathidium* and
412 *Holopus* (Grimmer and Holland 1990; Heinzeller 1998). Beyond encasing their anatomy in
413 dense skeleton, crinoids exhibit a general tendency to calcify their soft tissues to varying degrees
414 (Hyman 1955; Breimer 1978). In extreme cases this can lead to the preservation of entire suites
415 of internal organs, as in the silicified camerate crinoids of the Burlington Limestone (Haugh
416 1975*b*). Both these avenues of preservation are especially amenable to study by computed
417 tomography. Further study will likely resolve important open questions in crinoid phylogeny and
418 facilitate comparative work on the evolution of organ systems.

419 In this study we reconstruct aspects of the internal anatomy and physiology of the extinct
420 featherstar *Decameros ricordeanus*. We find several features that are novel among crinoids,
421 including a complex circulatory system linked extensively with the aboral nervous system.
422 Featherstar internal anatomy as reconstructed by CT scans provides systematically useful
423 information for a group that has to date eluded morphological phylogenetics. Furthermore, our
424 research highlights unexplored and potentially fruitful avenues for histological and functional
425 morphological research on living crinoids.

426

427

428 *Acknowledgements.* Many thanks to Mr J. Espílez, who found the locality where the fossil
429 material was recovered. Thanks also to University of Michigan undergraduate student Rebecca

430 To for her help in taking the morphological measurements used here in phylogenetic inference.
431 We appreciate the helpful comments of two anonymous referees and Sally Thomas on an earlier
432 draft of this paper. This study includes data produced in the CTEES facility at University of
433 Michigan, supported by the Department of Earth & Environmental Sciences and College of
434 Literature, Science, and the Arts. Funding was provided by the Society of Systematic Biologists
435 Graduate Student Research Award to JS, and by the project ‘Aragosaurus: recursos geológicos y
436 paleoambientales’ (ref: E18_17R), funded by the Government of Aragón, to SZ.

437 DATA ARCHIVING STATEMENT

438 Supplementary information (including character descriptions, supplementary figure and
439 morphological character descriptions), videos and digital models of the fossil crinoid *Decameros*
440 *ricordeanus* and its internal anatomy, a table with specimen information, all files needed to rerun
441 phylogenetic analyses, and several phylogenies are available in the Dryad Digital Repository:
442 <https://doi.org/10.5061/dryad.rf7c284>

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609 Figures

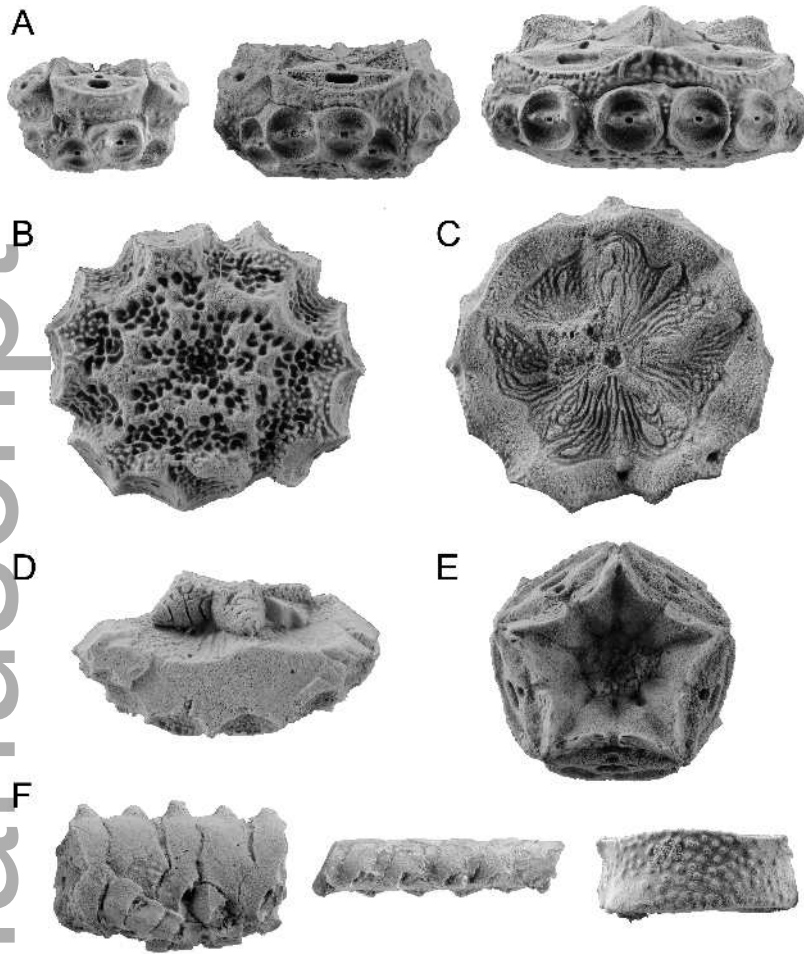
610 **Figure 1.** Skeletal morphology of *Decameros ricordeanus*. (a) Calyces, lateral view. *Left*, MPZ-
 611 2019/367. *Middle*, MPZ-2019/366. *Right*, MPZ-2018/483. Note the allometric changes in calyx
 612 shape, which mirror those of *Decameros wertheimi*. (b) MPZ-2019/368, centrodorsal, aboral
 613 view showing texturing on surface. (c) MPZ-2019/369, centrodorsal, oral view showing
 614 coelomic impressions. (d) MPZ-2019/370, fragment of centrodorsal and basal plates. Note the

615 impressions of coelomic canals on the basals and centrodorsal. (e) MPZ-2019/366, calyx, oral
 616 view. (f) Arm plates. *Left*, MPZ-2019/371, 5 proximal brachials with proximal pinnulars in place.
 617 *Middle*, MPZ-2019/372, 10 distal brachials. *Right*, MPZ-2019/373, a single proximal brachial in
 618 aboral view showing rugose texture. Scale bar represents 1 cm.

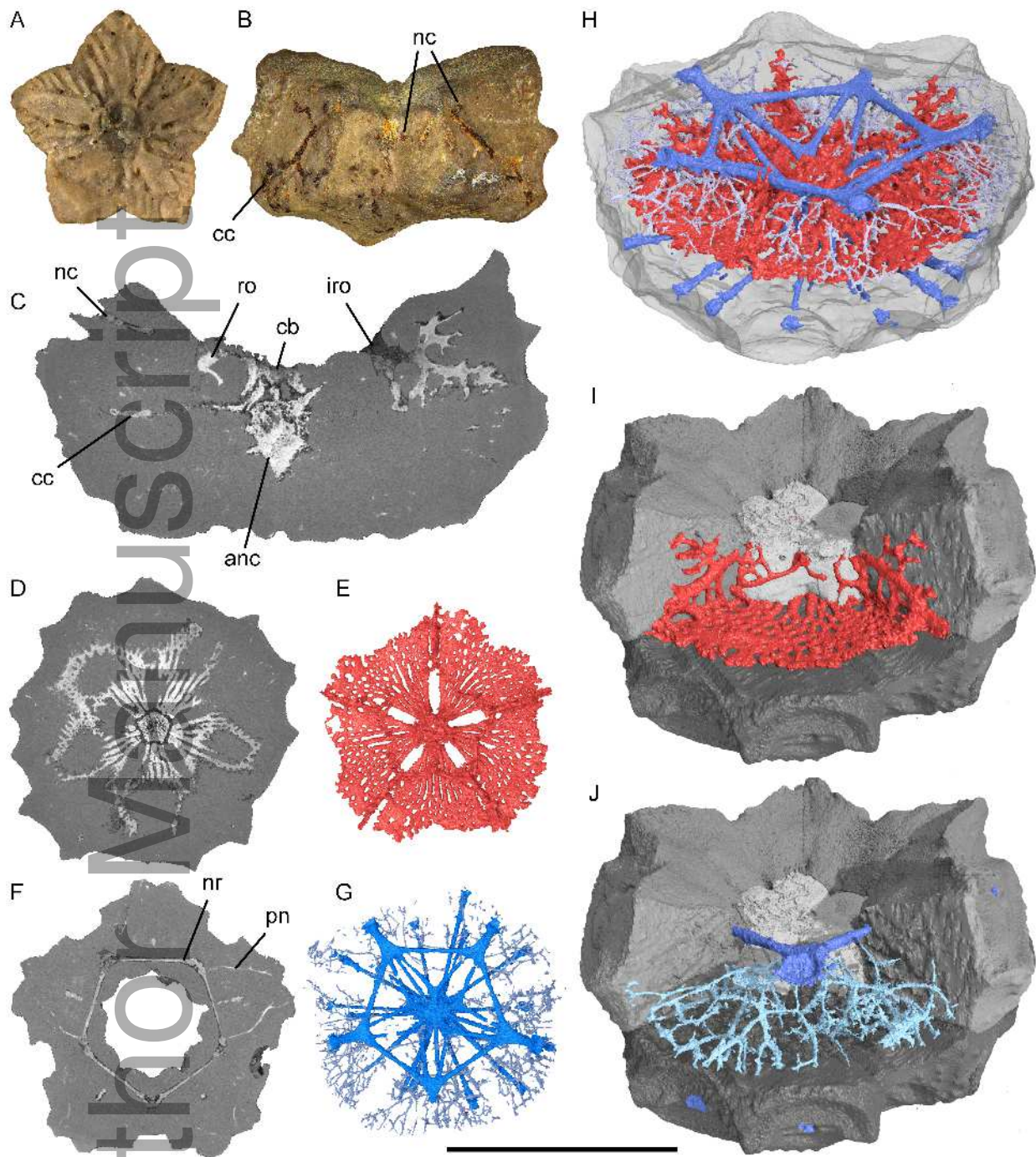
619 **Fig. 2.** Skeletal, coelomic, and nervous anatomy of *Decameros ricordeanus*. A, microphotograph
 620 of MPZ-2019/374, basal ring, aboral view. Note radially-oriented impressions of coelomic
 621 canals. B, microphotograph of MPZ-2019/375, radial plate, interior view. Internal anatomy
 622 preserved as reddish, granular infillings. C, MPZ-2019/366 (along with all subsequent
 623 subfigures), 2D slice through calyx parallel to oral-aboral axis, radius at left and interradius at
 624 right. Generated from μ CT scan. Lighter grey values correspond to higher density. D, 2D slice
 625 perpendicular to oral-aboral axis showing lateral coelomic diverticula. E, 3D model of coelomic
 626 anatomy, oral view. F, 2D slice perpendicular to oral-aboral axis showing pentagonal nerve ring,
 627 which gives rise to branches of the peripheral nervous system. G, 3D model of central (dark
 628 blue) and peripheral (light blue) nervous anatomy. H, oblique view of coelomic and nervous
 629 anatomy. Skeleton transparent, other color codings as in E and G. I, calyx with one radial plate
 630 removed, showing nervous anatomy present in a single radial plate. Basal plates light grey, radial
 631 plates grey, centrodorsal plate dark grey. J, the same view as I, showing coelomic anatomy. *anc*,
 632 aboral nerve centre. *cc*, coelomic canals; *cb*, central bundle; *nc*, nerve canal; *nr*, nerve ring; *pn*,
 633 peripheral nerve; *ro/iro*, radial/interradial openings into coelomic vasculature in the calyx. Scale
 634 bar represents 6 mm for A and B, 5 mm for C and H – J, and 9 mm for D – G.

635 **Fig. 3.** Phylogeny of living and fossil featherstars. Percentage of replicates in which each clade
 636 occurs and group present-contradicted percent differences under symmetric resampling
 637 (Goloboff *et al.* 2003) are plotted above and below each branch, respectively, except for clades
 638 recovered in all replicates. *Decameros* and *Solanocrinites* are members of an as-yet unnamed
 639 clade that includes *Notocrinus*, Antedonidae, most Tropiometroidea, and Himerometroidea, and
 640 which is recovered in all recent molecular phylogenetic analyses. 3D models of calyces (left) and
 641 coelomic cavities (right) shown for taxa with names in bold font. Extinct taxa are indicated with
 642 dagger symbols. Scale differs between taxa.

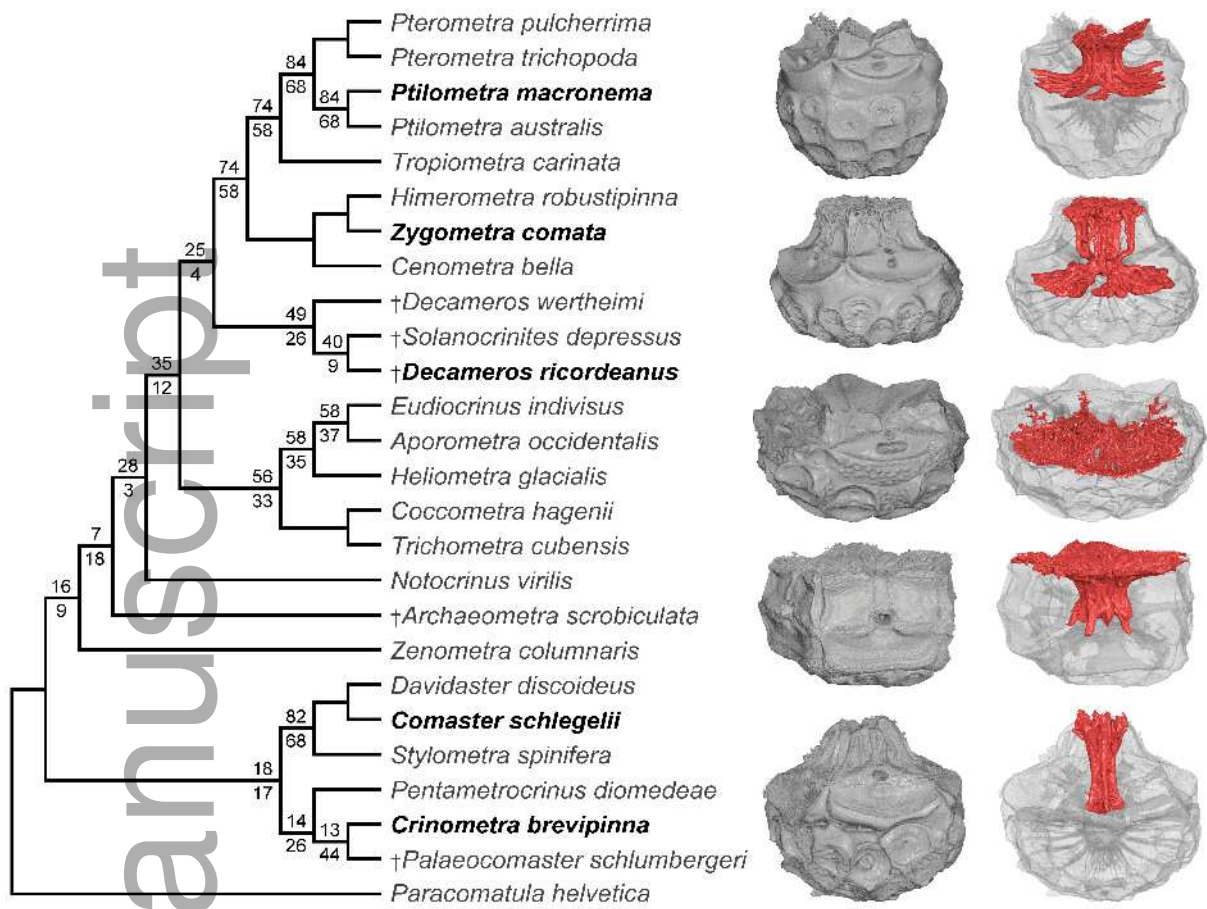
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