

1 **A primitive starfish ancestor from the Early Ordovician of**
2 **Morocco reveals the origin of crown group Echinodermata**

3

4 **Short title:** Starfish ancestor illuminates echinoderm evolution

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23 The authors declare no competing interests.

24 **Abstract**

25 The somasteroids are Ordovician star-shaped animals widely regarded as ancestors of Asterozoa, the
26 group of extant echinoderms that includes brittle stars and starfish. The phylogenetic position of
27 somasteroids makes them critical for understanding the origin and early evolution of crown group
28 Echinodermata. However, the early evolution of asterozoans, the origin of their distinctive body
29 organization and their relationships with other Cambrian and Ordovician echinoderms, such as
30 edrioasteroids, blastozoans, crinoids, and other asterozoans, remain problematic due to the difficulties of
31 comparing the calcitic endoskeleton of these disparate groups. Here we describe the new somasteroid
32 *Cantabrigiaster fezouataensis* from the Early Ordovician (Tremadocian) Fezouata Lagerstätte in
33 Morocco. *Cantabrigiaster* shares with other somasteroids the presence of rod-like virgal ossicles that
34 articulate with the ambulacrals, but differs from all other known asterozoans in the absence of
35 adambulacral ossicles defining the arm margins. The unique arm construction evokes parallels with
36 non-asterozoan echinoderms. Developmentally informed Bayesian and parsimony based phylogenetic
37 analyses, which reflect the homology of the biserial ambulacral ossicles in Paleozoic echinoderms
38 according to the Extraxial-Axial Theory, recover *Cantabrigiaster* as basal within stem group Asterozoa.
39 Our results indicate that *Cantabrigiaster* is the earliest diverging stem group asterozoan, revealing the
40 ancestral morphology of this major clade and clarifying the affinities of problematic Ordovician taxa.
41 Somasteroids are resolved as a paraphyletic grade within stem and crown group Asterozoa (starfishes),
42 whereas stenuroids are paraphyletic within stem group Ophiuroidea (brittle stars). *Cantabrigiaster* also
43 illuminates the relationship between Ordovician crown group Echinodermata and its Cambrian stem
44 lineage, which includes sessile forms with incipient radial symmetry such as edrioasteroids and
45 blastozoans. The contentious Pelmatozoa hypothesis (i.e. monophyly of blastozoans and crinoids) is not
46 supported; instead, blastozoans represent the most likely sister-taxon of crown group Echinodermata.

47 **Author summary**

48 Starfish and brittle stars, collectively known as asterozoans, constitute a diverse and ecologically
49 successful group of echinoderms that first appear in the fossil record some 480Ma. However, the early
50 evolution of asterozoans, the origin of their distinctive body organization, and their phylogenetic
51 relationships with Cambrian echinoderms remain largely unresolved. We describe *Cantabrigiaster*
52 *fezouataensis* gen. et sp. nov., a primitive asterozoan from the Fezouata Lagerstätte, Morocco, with a
53 unique endoskeletal arm organization that reveals the ancestral morphology of this major clade.
54 Bayesian and parsimony based phylogenetic analyses indicate that *Cantabrigiaster* is the earliest
55 diverging stem group asterozoan, and resolve the phylogenetic position of Ordovician asterozoans such
56 as somasteroids. Our analyses clarify the origin of crown group echinoderms relative to their
57 problematic Cambrian stem group representatives.

58

59 **Introduction**

60 Asterozoans – whose most familiar members include starfish and brittle stars – are the
61 dominant group of extant echinoderms based on their diversity, abundance, and biogeographic
62 distribution [1]. Despite their ecological success and a fossil record spanning more than 480
63 million years [2-4], the origin and early evolution of asterozoans, and that of crown group
64 echinoderms more generally, remains uncertain given the difficulty of comparing the
65 organization of the calcified endoskeleton in diverse groups of Lower Paleozoic ancestors,
66 such as the edrioasteroids and blastozoans [5-13]. The Extraxial-Axial Theory (EAT), which
67 supports the homology of the biserial ambulacral ossicles of pentarradial echinoderms based
68 on embryonic and ontogenetic data [14-16], has been proposed as a
69 developmentally-informed model that would facilitate making comparisons among groups

70 with disparate morphologies. Although the EAT can potentially clarify the early evolution of
71 crown group Echinodermata, the broad implications of this hypothesis have never been
72 examined under a comprehensive phylogenetic framework. Consequently, the main
73 phylogenetic predictions of the EAT pertaining to the evolutionary relationships of Cambrian
74 and Ordovician echinoderms, such as the origin of the crown group from edrioasteroid-like
75 ancestors [14-16, 17], have yet to be critically tested.

76 Here, we describe the new somasteroid *Cantabrigiaster fezouataensis* gen. et sp. nov.
77 from the Early Ordovician (Tremadocian) Fezouata Shale in Zagora, central Anti-Atlas,
78 Morocco [4] (Fig S1 and SI text). The exceptionally preserved morphology of *Cantabrigiaster*
79 reveals a unique organization among somasteroids, and allows us to test the phylogenetic
80 implications of this taxon for the origin of Asterozoa and crown group Echinodermata.

81

82 **Results**

83 **Systematic Paleontology**

84 (crown group) Echinodermata Bruguière, 1791

85 (stem group) Asterozoa Zittel, 1895

86 Somasteroidea Spencer, 1951

87 *Cantabrigiaster fezouataensis* gen. et sp. nov.

88 **Etymology.**

89 Genus name derived from ‘*Cantabrigia*’, after the cities of Cambridge in the UK and USA,
90 which were home to the influential asterozoan workers John William Salter (University of
91 Cambridge), Juliet Shackleton (néé Dean) (University of Cambridge), and Howard
92 Barraclough ‘Barry’ Fell (Harvard University).

93 Holotype.

94 FSL, VOMN 424 961 (Fig 1).

95 Referred material.

96 YPM IP 535545-535559 (Fig S2 and Fig S3).

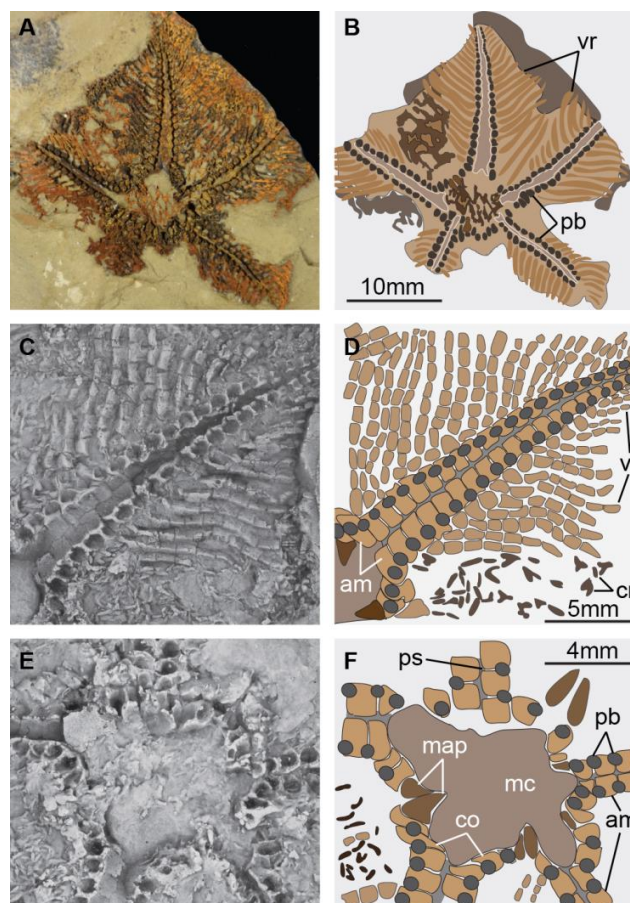
97 Diagnosis for genus and species.

98 Somasteroid typified by biserial and offset ambulacrals with thin transverse bar, wide

99 perradial groove, multiple interconnected virgal ossicles, and aboral carinal region with

100 network of spicule-like ossicles. Adambulacrals lacking along abaxial body

101 margins.



102

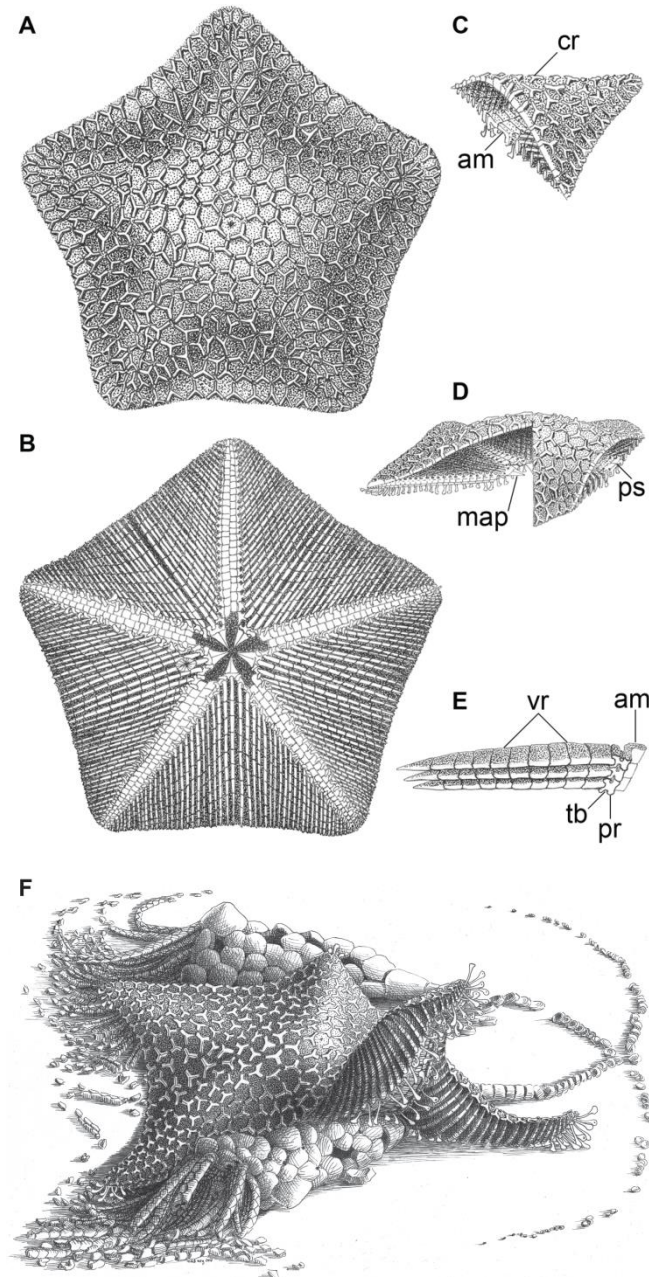
103 **Fig 1. *Cantabrigiaster fezouataensis* from the Lower Ordovician (Tremadocian) of**
104 **Morocco.** Holotype FSL-VOMN-424961. (A) Oral view (body fossil). (B) Interpretative
105 diagram of A. (C) Close-up of extended arm (latex mould). (D) Interpretative diagram of C.
106 (E) Close-up of oral region (latex mould). (F) Interpretative diagram of E. Abbreviations: am,
107 ambulacrals; co, circummorals; cr, carinal region ossicles; map, mouth angle
108 plates; mc, mouth cavity; pb, podial basins; ps, podial suture; vr, virgal ossicles.

109 **Description.**

110 The arms are broad, petaloid, and arranged in a pentagonal outline (Figs 1A, 1B, S3A, S3C
111 and S3D). The aboral skeleton (carinal region) is composed of randomly scattered spicule-like
112 ossicles arranged into an irregular network (Figs 1A, 1B, S2D, S3E and S3G). On the oral
113 side, the ambulacrals consist of flattened ossicles with a subquadrate outline. These ossicles
114 abut each other following the orientation of the perradial axis (Figs 1C, 1D, S2A, S2C, S2F
115 and S2G). The perradial suture is straight, and the ambulacrals at either side are stepped out of
116 phase by approximately half an ossicle. The abaxial organization of the ambulacrals consists
117 of an elevated perradial ridge, less than a quarter in width relative to the ambulacral, and bears
118 a thin transverse bar that occupies a central position conferring a T-shape in oral view (Figs
119 1C, 1D, S2A, S2E and S2G). The perradial ridges of the ambulacral ossicles at either side of
120 the perradial suture are substantially separated from each other, forming a wide oral groove
121 (Figs 1C-E, S2A-C and S2G). The podial basins are shared equally between adjacent
122 ambulacrals. Abaxially, the following ossicle series consist of the perpendiculars, also known
123 as virgals in somasteroids [2, 5, 6]. The perpendicular series is composed of interconnected
124 and robust rod-like virgal ossicles without spines. These ossicles follow a perpendicular
125 orientation relative to the perradial suture (Figs 1A-D and S2). The virgal ossicles close to the
126 ambulacrals are the largest, and become smaller in length and width towards the abaxial body
127 margins. Likewise, adjacent perpendicular series are in direct contact with each other
128 adaxially relative to the perradial suture, whereas it is possible to observe open gaps between
129 them towards the abaxial body margins. Proximal (relative to the mouth) perpendiculars series
130 consist of up to nine virgal ossicles, that gradually decrease in number towards the tips of the
131 arms (Figs 1A-D and 2). The circumoral ossicles are enlarged relative to ambulacral ossicles,

132 and the first podial pore is shared equally with the small and sub-triangular mouth angle
133 plates (Figs 1E and 1F). The madreporite is not preserved.

134



135

136

137 **Fig 2. Morphological reconstruction of *Cantabrigiaster fezouataensis*.** (A) Aboral view. (B)
138 Oral view. (C) Cross section of isolated arm in oblique view. (D) Cross section of main body
139 cavity lateral view. (E) Isolated virginal ossicle series and ambulacrals in oral view. (F) Life
140 reconstruction of *Cantabrigiaster fezouataensis*. Artwork by Marguerite Lardanchet.

141 Abbreviations: am, ambulacral ossicles; cr, carinal region ossicles; map, mouth angle plates;
142 pr, perradial ridge; ps, podial suture; tb, transverse bar; vr, virginal ossicles.

143

144 **Discussion**

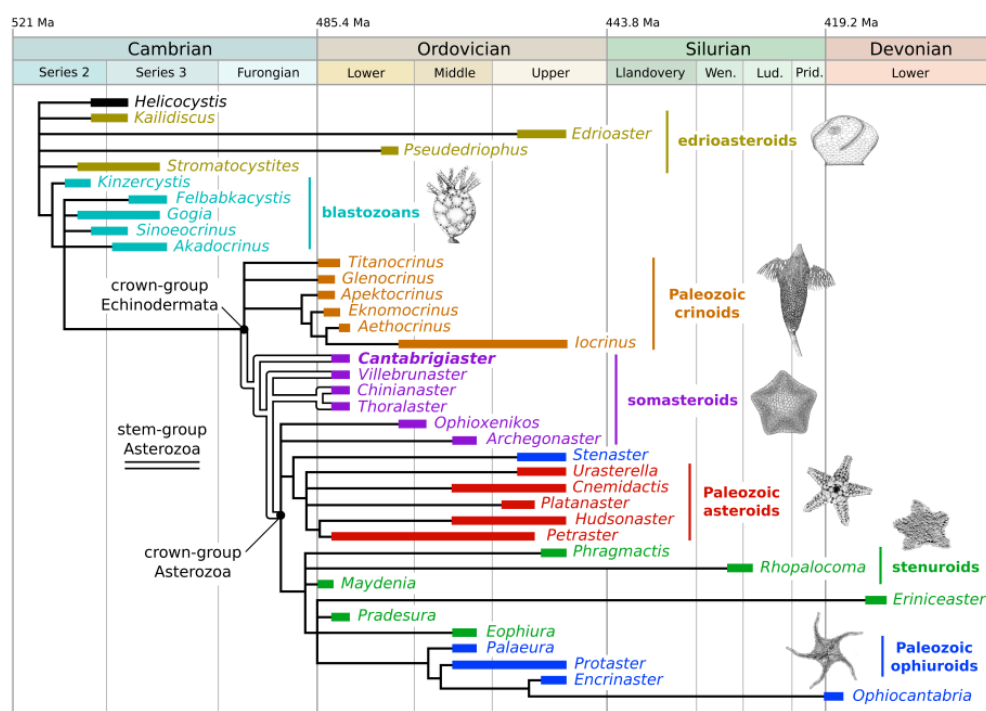
145 The presence of virgal ossicles in *Cantabrigiaster* strongly supports its affinities with
146 somasteroids [2, 5-9, 14, 21]. *Cantabrigiaster* bears the greatest similarity to the Tremadocian
147 taxa *Chinianaster*, *Thoralaster*, and *Villebrunaster* (Fig S4), but is unique among
148 somasteroids in lacking ossicles along the abaxial lateral margins of the arms (Figs 1A and
149 1D). The arm construction of *Cantabrigiaster* consists of flattened and offset biserial
150 ambulacrals, each of which articulates with an abaxially-oriented (i.e. perpendicular)
151 perpendicular series composed of simple virgal ossicles (Fig 2). In addition to these features,
152 the arms of all other somasteroids also possess a series of axially-oriented ossicles along the
153 lateral margins that vary from small and bead-like – albeit with occasional spikes – in
154 Tremadocian taxa [2, 5, 6] (Fig S4), to robust and block-like in the stratigraphically younger
155 (Floian) *Ophioxenikos* [10] and *Arhegonaster* [9]. These comparisons suggest a selective
156 pressure towards the addition of new ossicle series among early asterozoans (Fig S5).
157 *Cantabrigiaster* embodies the ancestral condition by virtue of lacking ossicles defining the
158 lateral arm margins (Figs 1 and 2), whereas other somasteroids record the first appearance of
159 these structures along the edges of the arms, and their subsequent changes in size and shape.
160 Based on this sequence, we propose that the origin of new axially-oriented ossicle series in
161 early asterozoans required their formation on the abaxial edges of the arms. Our hypothesis
162 implies that the proximity of axially-oriented ossicle series relative to the perradial axis
163 reflects the order of their evolutionary appearance (Fig S5 and SI text); since virgals are
164 abaxially-oriented, they are not directly comparable with any of the axially-oriented ossicle
165 series observed in Paleozoic asterozoans. In this context, *Cantabrigiaster* specifically lacks
166 the adambulacral ossicle series present in more derived somasteroids, stenuroids, ophiuroids

167 and asteroids, highlighting its profound significance for understanding the evolution of the
168 asterozoan body plan.

169 The Extraxial-Axial Theory (EAT) supports the homology of the ambulacrals
170 across pentaradial total-group echinoderms based on their developmental origin and
171 postembryonic ontogeny [14-17], and allows comparison of the skeletal organization of
172 *Cantabrigiaster* in a broader phylogenetic scale. Outside Asterozoa, the absence of
173 adambulacrals in *Cantabrigiaster* draws parallels with Tremadocian crinoids (e.g.
174 protocrinoids, *Apektocrinus*, *Eknomocrinus*), whose arm construction incorporates flattened
175 and offset biserial ambulacrals articulated to an abaxially-oriented series of simple ossicles,
176 here expressed as the cover plates [13, 16-18] (Fig S5 and SI text). A similar axial skeletal
177 organization is also observed among Cambrian forms, most notably edrioasteroids – which
178 also possess flattened and offset biserial ambulacrals but lack free appendages [9, 11, 19], and
179 to a lesser extent blastozoans, which have free appendages formed by modified ambulacrals
180 known as brachioles [12, 20, 21]. The widespread occurrence of these characters among
181 non-asterozoan groups suggests that their presence in *Cantabrigiaster* is symplesiomorphic.

182 We designed a comprehensive phylogenetic analysis of Lower Paleozoic
183 total-group echinoderms in order to test the significance of *Cantabrigiaster* for the origin of
184 Asterozoa. The dataset reflects the ambulacral homology proposed by the EAT [14-18], the
185 oral symmetry model proposed by Universal Element Homology [22-24], and our hypothesis
186 for the correspondence of axially-oriented ossicle series in early asterozoans (Fig S5 and SI
187 text). Bayesian and parsimony-based analyses recover practically identical topologies (Figs 3,
188 S6 and S7), despite a modest loss in tree resolution that can be expected from the former
189 methodology, indicating a robust phylogenetic signal [25]. *Cantabrigiaster* occupies a basal

190 position within total-group Asterozoa, supporting our hypothesis that the absence of
 191 adambulacrals is ancestral. Tremadocian somasteroids are resolved as a paraphyletic grade
 192 of stem group asterozoans (per refs [2, 26]; *contra* ref. [5]), whereas the Floian *Ophioxenikos*
 193 [10] and *Archegonaster* [9] consistently occupy a more derived position as members of crown
 194 group Asterozoa. The analyses argue against the monophyly of stenuroids [6], but corroborate
 195 their close phylogenetic relationship to ophiuroids, specifically as their earliest diverging stem
 196 group representatives [2, 5, 7, 26]. These findings indicate that the evolution of a
 197 well-developed adambulacral ossicle series constitutes a critical step in the origin of crown
 198 group Asterozoa, and demonstrate that the abaxially-oriented virgals of somasteroids became
 199 independently reduced – and ultimately lost – within the stem lineages of Ophiuroidea and
 200 Asteroidea [6] (Fig S5).



201
 202 **Fig 3. Evolution of crown group Echinodermata.** Consensus topology based on the
 203 Bayesian-inference analysis of 38 taxa and 73 morphological characters informed by the EAT
 204 [14, 15] (SI text). See Fig S6 for support values and comparison with the results of the
 205 parsimony-based phylogenetic analyses. Stratigraphic ranges of taxa based on refs [3, 6, 12,
 206 18, 27].

207 Our results also clarify the heated debate over the phylogenetic placement of
208 Cambrian edrioasteroids and blastozoans relative to Ordovician crinoids and asterozoans [9,
209 11, 13-18, 20, 22-24, 27] (Figs 3, S6 and S7). Edrioasteroids and blastozoans are resolved as
210 stem group echinoderms. Contrary to previous hypotheses [8, 9, 11] and predictions from EAT
211 proponents [13, 16-18], blastozoans – rather than edrioasteroids – are the most derived stem
212 group representatives, making them strong candidates for the sister-taxon of crown group
213 Echinodermata. This position confirms that blastozoans are ancestral relative to crinoids, and
214 simultaneously falsifies the monophyly of these taxa according to the Pelmatozoa hypothesis
215 [11, 20, 22-24, 27]. Character mapping indicates that most of the features that Tremadocian
216 crinoids share with edrioasteroids (e.g. flattened and offset biserial ambulacrals, cover plates
217 [15-18]) and blastozoans (e.g. irregular thecal plating, extended perforate region, 2-1-2
218 symmetry [22, 23]) are symplesiomorphic (Fig S5). The consensus topology suggests a single
219 origin for the free appendages of blastozoans and crown group echinoderms, albeit with
220 fundamental differences in their endoskeletal construction [14,16,17]. Brachioles are
221 exclusive – and most likely autapomorphic – to blastozoans [12, 20, 21]. The presence of a
222 straight perradial suture, and the aboral extension of the body wall over the arms forming
223 coelomic cavities, represent fundamental synapomorphies uniting total-group Crinoidea and
224 total-group Asterozoa [15-17], despite rare examples of convergence within the echinoderm
225 stem group [22, 27]. Ultimately, our findings reconcile the evidence supporting the homology
226 of ambulacral and oral ossicle organization in edrioasteroids, blastozoans, crinoids and
227 asterozoans, into a robust phylogenetic hypothesis that informs the origin of crown group
228 Echinodermata and the gradual early evolution of the archetypical asterozoan body plan (Figs
229 3 and S5).

230 **Materials and Methods**

231 **Specimen analysis**

232 Studied material is deposited at the Faculty of Science, Claude Bernard University of Lyon 1
233 (FSL-VOMN), Natural History Museum of Nantes (MHNN), National Museum, Prague
234 (NM-P), and Yale Peabody Museum, Yale University (YPM). Latex molds were made of all
235 the material with the exception of that of the YPM. The material was photographed with a
236 Nikon D5500 SLR fitted with Micro Nikkor 40mm.

237

238 **Phylogenetic analysis**

239 The character matrix for the phylogenetic analyses includes 38 taxa and 73 characters (see
240 Dataset S1 and S2); detailed discussion of character scoring and applicability are provided
241 below. The Bayesian analysis was run in MrBayes 3.2 using the Monte Carlo Markov-chain
242 model for discrete morphological characters [28, 29] for 10 million generations (four chains),
243 with every 1000th sample stored (resulting in 10,000 samples), and 25% burn-in (resulting in
244 7,500 retained samples). The parsimony analyses were run in TNT [30] under New
245 Technology Search, using Driven Search with Sectorial Search, Ratchet, Drift, and Tree
246 fusing options activated with standard settings [31, 32]. The analysis was set to find the
247 minimum tree length 100 times and to collapse trees after each search. All characters were
248 treated as unordered. For comparative purposes, analyses were performed under equal and
249 implied weights ($k=3$) to test the effect of homoplasy penalization on the position of
250 *Cantabrigiaster* and the robustness of the dataset [33]. Comparisons between results of the
251 phylogenetic analyses are presented in figures S6 and S7. Parsimony-based analysis under
252 Traditional Search with 10,000 replicates produced identical results as those obtained under
253 New Technology Search.

254 **Acknowledgements**

255 We acknowledge support from a Herchel Smith Research Fellowship in Biological Sciences, a
256 Bye-Fellowship at Emmanuel College (both JO-H) and visiting fellowship at Clare Hall
257 (AWH). National Geographic for funded the collection of the holotype. Dr. Emmanuel Robert
258 (FSL) is thanked for assisting access to the holotype and other figured material. Additional
259 thanks go to Dr. Martin Valent (NM-P) for access to types of *Archegonaster*. Dr. Fred
260 Hotchkiss (MPRI) and the Yale Peabody Museum assisted in securing the lectotypes.

261

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