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**The enigmatic metazoan *Yuyuanozoon magnificissimi* from
the early Cambrian Chengjiang Biota, Yunnan Province,
South China**

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Manuscripts

1 **The enigmatic metazoan *Yuyuanozoon magnificissimi* from the early**
2 **Cambrian Chengjiang Biota, Yunnan Province, South China**

3

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14

15 **Abstract.**—Vetulicolians are a group of exclusively Cambrian animals characterized by an
16 anterior section with lateral pouches and a posterior section that appears segmented. The precise
17 phylogenetic affinity of vetulicolians is debated because there is a lack of consensus regarding
18 the interpretation of their anatomical features. Their disparate morphology might even question
19 whether this is a monophyletic taxon. In total, there are 15 species grouped into three families
20 included in vetulicolians. Here we focus on new specimens of *Yuyuanozoon magnificissimi*, a
21 species that was first described in 2003 based on a single specimen from the Chengjiang Biota
22 (Cambrian Series 2, Stage 3, *Eoredlichia-Wutingaspis* trilobite Biozone), Yunnan Province,
23 China. Although placed in the family Vetulicolidae, this species is notable in being exceptionally

24 large (up to 20 cm long). Morphological observations on the new specimens clarify the nature of
25 the wide circular opening at the presumed anterior end of the animal, and the ovoid shape of
26 lateral openings within this anterior section. Taphonomic observations identify wrinkles in the
27 anterior section, and twists in the posterior segmented section. In particular, the shape of the
28 anterior opening of *Yuyuanozoon magnificissimi* suggests significant differences from other
29 vetulicolians. Taxonomic re-appraisal of *Y. magnificissimi* indicates that it likely belongs within
30 the family Didazonidae, as that is presently defined.

31

32 **Introduction**

33

34 As currently understood, vetulicolians are a group of exclusively marine, enigmatic and extinct
35 Cambrian animals, represented by three families: the Vetulicolidae, the Didazonidae and the
36 Banffidae (Aldridge et al., 2007). They are characterised by a bipartite body. The anterior part is
37 covered by a structure that superficially resembles the carapace of many arthropods: this
38 structure, here referred to as the anterior section (Fig. 1), preserves five lateral pouches, some
39 possessing a lateral groove on each side, that have been interpreted by some as possible gill slits
40 (Shu et al., 2001). The posterior section resembles the arthropod trunk, possessing a segmented
41 and sometimes annulated morphology. Soft-part anatomy has been reported in some
42 vetulicolians, including structures interpreted to represent muscle fibres (Aldridge et al., 2007; Ou
43 et al., 2012; García-Bellido et al., 2014). The vetulicolian body plan and the limited information
44 about soft-bodied anatomical structures within the anterior section make the interpretation of
45 these animals difficult. As a result, the phylogenetic position of vetulicolians is unclear, with
46 proposed affinities much debated and varying from their interpretation as unusual arthropods

47 (Hou, 1987; Caron, 2006), kinorhynchs (Aldridge et al., 2007), or stem-group deuterostomes
48 (Shu et al., 2001; Ou et al., 2012) or chordates (Lacalli, 2002; García-Bellido et al., 2014).

49 Vetulicolians, as currently understood, are represented by 15 species, which occur
50 worldwide, but only in Cambrian Lagerstätten, including: Chengjiang (Hou, 1987; Luo et al.,
51 1999; Shu et al., 2001; Chen et al., 2003; Shu et al., 2005; Aldridge et al., 2007), Guanshan (Luo
52 et al., 2005; Yang et al., 2010; Li et al., 2015), and the Shipai Formation of South China (Zhang
53 & Hua, 2005); the Burgess Shale (Walcott, 1911), and the Mural Formation, both in Canada
54 (Butterfield, 2005); the Sirius Passet biota of Greenland (Vinther et al., 2011); the Emu Bay
55 Shale of Australia (García-Bellido et al., 2014); and the Spence Shale in Utah, USA (Briggs et al.,
56 2005; Conway Morris et al., 2015). They are known almost exclusively from their characteristic
57 anterior section that possesses lateral pouches, and segmented posterior section. Despite being
58 widespread and common animals throughout Cambrian Lagerstätten, the affinity of vetulicolians
59 remains controversial.

60 *Yuyuanozoon magnificissimi* is exceptionally large, being up to 20 cm in length, compared
61 with other vetulicolian species that are generally 5-14 cm long. Thus far, it has been described
62 from a single complete specimen, but here we show by reference to new material that some of
63 the characteristics of this original specimen have been modified post-mortem, and as such its
64 current appearance does not accurately represent in vivo morphology. Here we describe new
65 specimens, provide a new interpretation for the opening at the presumed anterior end of the
66 animal, and reassign this taxon to the vetulicolian family Didazonidae.

67

68 **Geological setting**

69

70 The early Cambrian Chengjiang Lagerstätte (Cambrian Series 2, Stage 3, *Eoredlichia-*
71 *Wutingaspis* trilobite Biozone of Eastern Yunnan, a biostratigraphical interval equivalent to part
72 of the *Ushbaspis* trilobite Zone of South China), occurs through a 30–50 m thick succession of
73 claystones that have been celebrated for yielding about 250 species of soft-bodied and weakly
74 biomineralized organisms (Hou et al., 2017). The dominant component of the biota, both in
75 numerical abundance and species diversity, are arthropods, but lobopodians, sponges,
76 brachiopods, some enigmatic animals and chordates are also represented (Hou et al., 2017).
77 Other significant animals are the vetulicolians of which the Chengjiang Biota contains the
78 greatest diversity and numbers from the Cambrian System worldwide.

79 The three new specimens of the vetulicolian *Yuyuanozoon magnificissimi* described here are
80 from the Ercaicun section at Haikou, Kunming area, Yunnan Province, about 30 km south of
81 Kunming city, and about 50 km northwest of Maotianshan, the original locality from which
82 Chengjiang fossils were discovered (see Hou et al., 2017 for the history of the Chengjiang Biota).

83

84 **Materials and methods**

85

86 The specimens were prepared using steel needles and examined with a Nikon SMZ–10A
87 binocular microscope. We used a camera lucida attached to a Wild Heerbrug M10 microscope in
88 order to elucidate and record the anatomy. The digital images of the specimens were captured
89 with Nikon D3X and Canon 500D digital cameras and a Leica DFC5000 camera attached to a
90 Leica M205C photo-microscope, and were processed in Adobe Photoshop CC. All
91 measurements were processed with ImageJ version 1.49.

92 *Repositories and institutional abbreviations.*—The three new specimens documented here are all
93 preserved with part and counterpart, and are deposited in the Yunnan Key Laboratory for
94 Palaeobiology, Yunnan University (abbreviated YKLP), Kunming, China with numbers YKLP
95 13070, YKLP 13071 and YKLP 13072.

96

97 **Morphology and terminology of the vetulicolian body**

98

99 The anatomical terms applied to vetulicolians are complicated because there is no consensus on a
100 common nomenclature in different publications. Vetulicolian taxonomy sometimes uses a range
101 of standard morphological terms such as ‘carapace’ and ‘gill slits’ (see Table 1), though there is
102 no certainty of the homology of such structures between taxa, or even whether these terms, some
103 for example borrowed from arthropod terminology (e.g., for the genus *Skeemella*), are actually
104 appropriate.

105 Here we use descriptive terms carefully, to avoid inference about evolutionary significance,
106 thus avoiding the potential for circular reasoning regarding phylogenetic interpretation. For
107 example, we do not use the term ‘carapace’ to denote the anterior section of the animal. Our
108 morphological terms are summarized in Figure 1, which also denotes how terms such as ‘ventral’
109 and ‘dorsal’ are applied to vetulicolians.

110

111 **Preservation and taphonomy**

112

113 Specimen YKLP 13071 (Fig. 3) is, like most vetulicolians, laterally compressed and retains some
114 3-D relief. The majority of the anterior section is preserved as a thin film that does not appear to

115 have been biomineralised, though the areas adjacent to the anterior opening and the posterior end
116 show patches of dark color. The texture and composition of this material is identical to the iron
117 oxide coatings typical in Chengjiang fossils (Gabbott et al., 2004; Forchielli et al., 2014) and is
118 not consistent with in vivo mineralization. The anterior section appears to comprise six
119 subdivisions that are marked by furrows that circumvent the entire structure and are coincident
120 with the five lateral vertical ovoid pouches. At the mid-point between the boundaries of these
121 subdivisions on the dorsal side a shorter parallel line occurs which was termed second order
122 annulation by Aldridge et al. (2007). There are clear wrinkles along the ventral side of the
123 anterior section, which appear to suggest an element of twisting and/or compression post-mortem.

124 The boundary between anterior subdivisions five and six also coincides with a marked
125 change in relief, with the sediment fill within the anterior section thicker anteriorly, and the color
126 darker posteriorly.

127 The posterior section of the holotype (CFM00059) possesses seven segments; within each
128 segment there are five, or possibly six, less well-defined lines that appear to circumvent the
129 whole structure and thus resemble annulation. Other specimens, which are incomplete, preserve
130 five (YKLP 13071) or six (YKLP 13070) posterior segments.

131

132 **Systematic paleontology**

133

134 Family Didazonidae Shu and Han (in Shu et al. 2001)

135

136 *Type Genus.*—*Didazon* Shu and Han, in Shu et al. 2001. *Pomatrum*, *Xidazon*, and
137 *Yuyuanozoon*, are also referred to this family, but *Xidazon* is regarded as a junior synonym of
138 *Pomatrum* (Chen et al., 2002; Aldridge et al., 2007).

139
140 *Diagnosis.*—(Modified from Shu et al., 2001) Bilaterally symmetrical animal with clear
141 subdivision of body into presumed anterior and posterior sections. Neither the sub-quadrate to
142 ovoid anterior section, nor the posterior section, is biomineralised. The anterior section has a
143 large, circular opening at the presumed anterior end of the animal, posterior of which there are
144 six subdivisions demarcated by five lines; five, presumed laterally positioned, oval openings on
145 both sides of the anterior section coincide with the lines of subdivision. Posterior section bears
146 seven segments, and each segment may bear up to 6 annulae.

147
148 *Remarks.*—In addition to characters listed by Shu et al. (2001), in well-preserved specimens the
149 posterior section displays annulation within each segment.

150 In vetulicolian families, a range of morphological features, including the circumventing
151 feature behind the anterior opening of the anterior section, the lack of a lateral groove in the
152 middle of the anterior section, the posterodorsal ('fin-like') prolongations on the anterior section,
153 the shape of the lateral pouches, and the segmented posterior section with annulations place
154 *Yuyuanozoon* in the Didazonidae rather than in the Vetulicolidae (see also Table 1).

155

156 Genus *Yuyuanozoon* Chen, Feng and Zhu in Chen et al., 2003

157

158 *Type species.*—*Yuyuanozoon magnificissimi* Chen, Feng and Zhu, in Chen et al. 2003, by
159 monotypy.

160

161 *Diagnosis.*—(Modified from Chen et al., 2003) Vetulicolian with non-biom mineralised, elongate
162 ovoid anterior section. A narrow raised rim circumvents the entire perimeter of the anterior
163 section, some 5 mm posterior of the anterior opening. Marginal projections and lateral groove
164 absent from anterior section. Anterior section may have six divisions and five pairs of lateral
165 pouches. Posterior section has seven segments, within each of which are five to six annulations;
166 terminal segment longest.

167

168 *Occurrence.*—Early Cambrian, Yu'an shan Member, Chiungchussu Formation, *Eoredlichia-*
169 *Wutingaspis* Biozone, Yunnan Province, South China (Chen et al., 2003).

170

171 *Remarks.*—Analysis of the body shape of *Didazon*, *Pomatrum* and *Yuyuanozoon* distinguishes
172 *Yuyuanozoon* as a separate genus based on its overall size and the proportions of the anterior and
173 posterior sections, which were fully described by Chen et al. (2003). *Yuyuanozoon* is also clearly
174 distinct from other vetulicolians in having five to six annulations within each segment of its
175 posterior section.

176

177 *Yuyuanozoon magnificissimi* Chen, Feng and Zhu in Chen et al., 2003

178

Figures 3, 4, 5, 6

179

180 2003 *Yuyuanozoon magnificissimi* Chen, Feng and Zhu, in Chen et al., pp. 282–284, pl. 1, figs a–
181 d.

182 2004 *Yuyuanozoon magnificissimi* Chen, Feng and Zhu; Chen, p. 318, fig. 509.

183 2007 *Yuyuanozoon magnificissimi* Chen, Feng and Zhu; Aldridge et al., pp. 142–145, pl. 5, figs 3,
184 5; text-fig. 6.

185 2012 *Yuyuanozoon magnificissimi* Chen, Feng and Zhu; Ou et al., p. 81, fig. 5.

186 2017 *Yuyuanozoon magnificissimi* Chen, Feng and Zhu; Hou et al., pp. 276–277, fig.26.3.

187
188 *Holotype*.—CFM00059, deposited in the Chengjiang Fauna Museum, Chengjiang National
189 Geological Park, Yunnan. The holotype was found on the northern slope of Maotianshan,
190 Chengjiang (Chen et al., 2003).

191
192 *Other material*.—Three additional specimens from Ercaicun (see Hou et al., 2017, fig. 4.3):
193 YKLP 13071, a nearly complete laterally-preserved specimen; YKLP 13072, preserving most of
194 the anterior section and part of the posterior section; and YKLP 13070, preserving most of the
195 posterior section.

196
197 *Diagnosis*.—Monotypic, as for the genus.

198
199 *Description*.—The anterior section forms an elongated ellipsoid in lateral view, with five lateral
200 pouches on each side; the anterior opening is broad (Fig. 3). The posterior section is about 1/3rd
201 of the width of the anterior section, elongate, segmented and annulated throughout. Narrow gut
202 situated medially (Fig. 4.6, 4.8).

203 Body.—All specimens are laterally preserved. The most complete specimen YKLP 13071
204 (Fig. 3) has a length of at least 17.2 cm (the last two segments of the posterior section are not
205 preserved). The anterior section is 11.8 cm long and up to 5.4 cm wide, and the posterior section
206 is more than 4.5 cm in length and has a maximum width of 2.0 cm. The dorsal surface of the
207 anterior section from the anterior opening to the posterior section is coincident along the dorsal
208 side, but has a concave outline on the ventral side (Fig. 3). The length of the posterior section
209 measures 11 mm for the first segment, and then posteriorly 9 mm, 9 mm, 9 mm and at least 7
210 mm for the incomplete fifth segment.

211 Anterior opening.—YKLP 13071 possesses a wide anterior opening (Figs. 3.1, 4.1) with a
212 circumventing rim situated 5 mm posterior of this. In YKLP 13072, the anterior section has a
213 more quadrate shape than is typical, and the anterior opening is broad but the circumventing
214 feature is less well developed (Figs. 4.2, 5.1). No anterior opening has been detected in the
215 holotype, but strongly developed wrinkles approximately parallel to the dorsal and ventral edge
216 provide a hint that the anterior opening is not observable, owing to distortion through
217 compression (Fig. 4.3).

218 Anterior circumventing feature.—Raised rim, a narrow structure circumventing the entire
219 perimeter of the anterior section, some 5 mm posterior of the anterior opening.

220 Ordering lines.—Lines circumventing the anterior section and perpendicular to the body axis
221 are displayed best in the anterodorsal area, and here they comprise two orders. The most
222 prominent lines traverse the entire body. These delineate six subdivisions of the anterior section,
223 and their boundaries are coincident with five lateral internal pouches on each side of the animal
224 (Figs. 3, 5.1, 5.2). There are faint lines between these boundaries that are less continuous in the
225 dorsal section. This pattern is similar to *Vetulicola cuneata* (Chen et al., 1997, fig. 135) and *V.*

226 *rectangulata* (Aldridge et al., 2007, pl.1, fig. 9; text-fig. 2) and is also known in *Pomatrum*
227 (Aldridge et al., 2007, pl. 5, fig. 1, text-fig. 8).

228 Lateral pouches.—The lateral pouches are one of the most prominent features of all
229 vetulicolians and number five on each side of the anterior section. In the new specimens of *Y.*
230 *magnificissimi* the five pouches are cowl-shaped and form a series of lateral openings (Fig. 4.5).
231 These pouches occur in the middle region of the dorsal and ventral sections of the anterior
232 section, and are very similar to those in the holotype (Fig. 4.4). The lateral groove is absent in all
233 of the specimens of *Y. magnificissimi*. The pouches show an orientation that may have allowed
234 water to exit the anterior section in a posteriorly flowing direction. No filaments are preserved in
235 the new material.

236 Posterior segmentation.—Only five of up to seven segments in the posterior part are present
237 in YKLP 13071, and within each of these segments there are five to six annulations— only a few
238 annulations are apparent in the holotype of *Y. magnificissimi* possibly due to poorer preservation
239 (Fig. 4.6). The posterior section of YKLP 13071 is twisted and deformed (Fig. 4.7, 4.8). Each
240 segment of the posterior section has five to six annulations; junctions between segments are
241 distinguished based on a slight change in relief and these boundaries are one annulation in width.
242 Both the holotype and the new specimens share annulations. Annulations are apparent in YKLP
243 13070 (Fig. 5.3) and YKLP 13072 (Fig. 5.2). In the holotype, annulations are clearly present on
244 the first segment of the posterior section and the ventral area of the sixth (Fig. 4.6).

245 Possible alimentary tract.—The alimentary tract is preserved in the medial part of the
246 posterior section of YKLP 13071 (Fig. 4.7-8). This is irregular and curved, narrow, and
247 apparently filled with fine sediment. This structure is incomplete and only preserved at the
248 second segment of the posterior section.

249

250 *Remarks.*—The last sub-division of the anterior section and first few segments of the posterior
251 section are marked by a wrinkled zone with dark coloration and lower relief than the other part
252 of the anterior section (Fig. 3). This may be a preservation feature of the split through the part
253 and counterpart.

254 The holotype was described by Chen et al. (2003), in which the anterior end of the anterior
255 section was considered as smooth and round without any extensions or margin. However,
256 observations on the holotype indicate that there is a visible fold that starts from the beginning of
257 the arched anterior end, surrounded by narrow wrinkles. This provides evidence that the anterior
258 end was compressed and this morphology is an artifact of decay and/or preservation. That the
259 walls of the anterior section in members of the family Didazonidae are generally thinner than in
260 Vetulicolidae, lends support to this interpretation of a distorted anterior opening. The anatomical
261 differences of the lateral filamentous pouches possessed by the holotype, and the absence of
262 these structures in the new specimens is most likely due to differences of preservation and to the
263 level at which the rock has split through these structures in different specimens.

264 *Yuyuanozoon* differs from other vetulicolians in the morphology of its bulky, ovoid anterior
265 section, the shape of its anterior opening, and possession of a posterior section with seven
266 segments that are annulated. These features suggest that *Yuyuanozoon* is closest in general form
267 to *Pomatrum* and *Didazon*.

268 Contrary to the comment by Chen et al. (2003, p. 282) that *Yuyuanozoon* is distinct from
269 other vetulicolians in the number of anterior and posterior segments, the possession of six
270 anterior section subdivisions and seven posterior segments is characteristic of both Vetulicolidae
271 and Didazonidae. The anterior opening of *Y. magnificissimi* was described as ‘long-ellipsoidal’

272 by Chen et al. (2003). Our new material shows that the anterior end of *Yuyuanozoon* is widely
273 open, with a circumventing feature. Reinvestigation of the holotype indicates that the anterior
274 section of that specimen is distorted, as evidenced by a series of wrinkles, and the morphology of
275 the anterior opening is obscured by compression.

276 In the holotype the lateral pouches and associated wrinkles have been interpreted as gill sacs
277 and external gill filaments (Chen et al., 2003), or as a possible vascular system (Ou et al., 2012).
278 Filaments have not been recognized in the new specimens of *Yuyuanozoon*, and it is possible that
279 the filaments described by Chen et al. (2003) and Ou et al. (2012) are a product of decay-induced
280 collapse forming wrinkles or the split of the fine-layered sediment, or an expression of internal
281 anatomy.

282

283 **Inferences about mode of life**

284

285 By analogy with other vetulicolids, the segmented posterior section of *Yuyuanozoon* might be
286 interpreted as an adaptation for propulsion. However, *Yuyuanozoon* has a relatively small
287 posterior section, countered by a bulky anterior section without fin-like projections that seems ill
288 adapted for protracted forward motion.

289 Vetulicolians were globally widespread in early and middle Cambrian seas and are known
290 from strata that originated in various environmental settings. All share some common features
291 such as a lateral collapse orientation retaining a degree of three-dimensional preservation,
292 suggesting that the body was made of a material with a degree of robustness, even if it was non-
293 biomineralized. How *Yuyuanozoon* fed is a matter of conjecture, as currently no feeding
294 apparatus has been preserved.

295

296 **Conclusions**

297

298 In this paper we have described new material of *Yuyuanozoon magnificissimi*. We have
299 attempted to develop a unified terminology for the description of vetulicolians that avoids
300 inferring animal relationships or functional morphology. Therefore, terms such as 'carapace' -
301 suggesting an arthropod affinity - or 'oral end' - suggesting functionality for feeding - have been
302 replaced with purely descriptive terms. We believe that much of the existing terminology applied
303 to vetulicolians cannot be sustained. There is no convincing evidence to show the homology of
304 the anterior part of vetulicolians with the carapace or head shield of arthropods. Furthermore,
305 there is no evidence in *Y. magnificissimi* to sustain that the anterior opening was 'oral', or even
306 that it functioned in food collection. In deconstructing this taxonomically 'loaded' terminology
307 we now propose a 'ground-up' approach to interpreting these animals that examines their full
308 range of morphological characteristics, without preconception. New analyses should determine:
309 1) whether any features are homologous with extant groups of organisms; 2) whether any
310 features can be accorded a true function, based on basic observations of their likely adaptation
311 for different functions. From this deconstructed database we hope that a more realistic picture of
312 the interspecific variation of vetulicolians can be assessed, that will lead to a greater
313 understanding of their wider animal affinities.

314

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316

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323

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325

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393

394 **Figures and Figure Captions**

395

396 **Figure 1.** A hypothetical vetulicolian, showing detailed morphological characters. Abbreviations
397 used for our nomenclature are given as following, with terms used by other authors presented in
398 the parentheses. Ac. Alimentary canal (Gut). An. Anus. Ao. Anterior opening (Oral opening,
399 Oral, Mouth.). Ar. Articulation. As. Anterior section (Anterior body, carapace) - presumed cover
400 of the anterior part of the body. Dp. Posterodorsal projection (Fin-like structure, Dorsal fin, Fin).
401 Ds. Dorsal section. Fs. Filamentous structures (Gill filaments). Lg. Lateral groove. - A lateral
402 midline that consists of a longitudinal groove associated with five openings at each side of the
403 anterior section. Lp. Lateral pouches/openings (Gill pouches, Serial lateral opening structure). Ls.
404 Lateral slit (Gill slit). M. Membrane. Ps. Posterior section (Posterior body, Tail) - Posterior part
405 of the body. S. Segment. S1 - S7. 1st - 7th segment of posterior section. Vp. Posteroventral
406 projection of anterior section (Fin-like structure, Ventral fin). Vs. Ventral section.

407

408 **Figure 2.** Additional features on *Yuyuanozoons*. Abbreviations used for our nomenclature are
409 given as following, with terms used by other authors presented in the parentheses. Cv.
410 Circumventing feature behind the anterior opening (Oral disc.). Mr. Marginal region at the
411 anterior opening (Mouth plate). Ol. Ordering lines (Putative segments, anterior segments) - Lines
412 circumventing the anterior section coalescing with lateral pouches, and long-axis perpendicular
413 to the body axis.

414
415 **Figure 3. (1)(2)** Lateral view of *Yuyuanozoon magnificissimi* YKLP 13071, anterior to left,
416 dorsal to top. **(1)** photograph of the fossil (largely the internal mould) with low angle lighting; **(2)**
417 camera lucida drawing of the same specimen. The 6 subdivisions of the anterior section are
418 evident, as are the occurrence of secondary lines between these subdivisions. The ‘segmentation’
419 and ‘annulation’ of the posterior part of the body (which is incomplete posteriorly) are also
420 evident. Ac, alimentary canal. Cv, circumventing feature behind the anterior opening. Lp1 – Lp5,
421 1st – 5th lateral pouch. Mr, marginal region at the anterior opening. Ol, ordering lines. S1 – S5,
422 putative segments. **(3) (4)** Lateral view of anteriorly incomplete *Yuyuanozoon magnificissimi*
423 YKLP 13071, anterior to left, dorsal to top. **(3)** photograph of counterpart YKLP 13071 with low
424 angle lighting; **(4)** camera lucida drawing of counterpart. Lp, lateral pouches. Ol, the ordering
425 lines. Scale bars=10 mm.

426
427 **Figure 4.** Detailed views of *Yuyuanozoon magnificissimi*. **(1)** anterior end of *Y. magnificissimi*
428 YKLP 13071; **(2)** anterior end of *Y. magnificissimi* YKLP 13072; **(3)** anterior end of *Y.*
429 *magnificissimi* CFM00059. Arrows show wrinkles, providing a hint that the anterior opening is
430 not observable due to distortion through compression; **(4)** anterior section view of CFM00059.

431 Arrows show the outlines of the pouches and possible underlying narrow grooves; **(5)** anterior
432 section view of YKLP 13071. Arrows show the outlines of the pouches; **(6)** posterior section
433 view of CFM00059. Arrows show the annulations within the 1st segment; **(7)** posterior section
434 view of YKLP 13071 (counterpart); **(8)** posterior section view of YKLP 13071 (part). Scale
435 bars=10 mm.

436

437 **Figure 5.** Overall views of *Yuyuanozoon magnificissimi*. **(1)** YKLP 13072 (part); **(2)** YKLP
438 13072 (counterpart); **(3)** YKLP 13070. Lp, lateral pouch. Ol, the ordering lines. S. Segment.
439 Scale bars=10 mm.

440

441 **Figure 6.** Composite camera lucida drawing of specimen YKLP 13071, superimposing part and
442 counterpart, anterior to left, dorsal to top. Scale bar=10 mm.

443

444 **Tables**

445

446 **Table 1.** Vetulicolian species and their major morphological characters. *Vetulicola* sp. from the
447 Shipai Formation of South China (Zhang & Hua, 2005), *Didazoon* sp. From the Chengjiang biota
448 (Aldridge et al., 2007), and *Vetulicola* sp. from the Guanshan biota (Li et al., 2015) are not
449 included in the Table, until their full systematic relationships are discerned.

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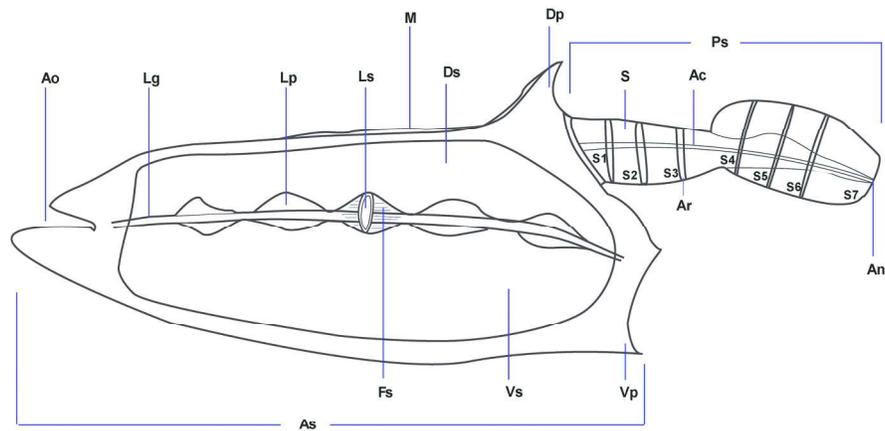


Figure 1. A hypothetical vetulicolian, showing detailed morphological characters. Abbreviations used for our nomenclature are given as following, with terms used by other authors presented in the parentheses. Ac. Alimentary canal (Gut). An. Anus. Ao. Anterior opening (Oral opening, Oral, Mouth.). Ar. Articulation. As. Anterior section (Anterior body, carapace) - presumed cover of the anterior part of the body. Dp. Posterodorsal projection (Fin-like structure, Dorsal fin, Fin). Ds. Dorsal section. Fs. Filamentous structures (Gill filaments). Lg. Lateral groove. - A lateral midline that consists of a longitudinal groove associated with five openings at each side of the anterior section. Lp. Lateral pouches/openings (Gill pouches, Serial lateral opening structure). Ls. Lateral slit (Gill slit). M. Membrane. Ps. Posterior section (Posterior body, Tail) - Posterior part of the body. S. Segment. S1 - S7. 1st - 7th segment of posterior section. Vp. Posteroventral projection of anterior section (Fin-like structure, Ventral fin). Vs. Ventral section

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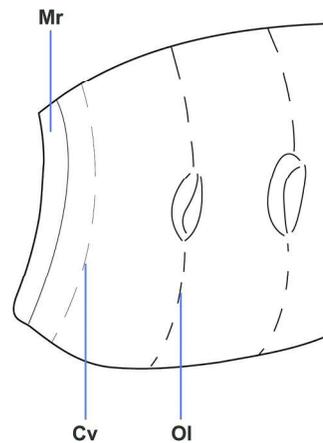


Figure 2. Additional features on Yuyuanozoos. Abbreviations used for our nomenclature are given as following, with terms used by other authors presented in the parentheses. Cv. Circumventing feature behind the anterior opening (Oral disc.). Mr. Marginal region at the anterior opening (Mouth plate). Ol. Ordering lines (Putative segments, anterior segments) - Lines circumventing the anterior section coalescing with lateral pouches, and long-axis perpendicular to the body axis.

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Figure 3. (1)(2) Lateral view of *Yuyuanozoon magnificissimi* YKLP 13071, anterior to left, dorsal to top. (1) photograph of the fossil (largely the internal mould) with low angle lighting; (2) camera lucida drawing of the same specimen. The 6 subdivisions of the anterior section are evident, as are the occurrence of secondary lines between these subdivisions. The 'segmentation' and 'annulation' of the posterior part of the body (which is incomplete posteriorly) are also evident. Ac, alimentary canal. Cv, circumventing feature behind the anterior opening. Lp1 - Lp5, 1st - 5th lateral pouch. Mr, marginal region at the anterior opening. Ol, ordering lines. S1 - S5, putative segments. (3) (4) Lateral view of anteriorly incomplete *Yuyuanozoon magnificissimi* YKLP 13071, anterior to left, dorsal to top. (3) photograph of counterpart YKLP 13071 with low angle lighting; (4) camera lucida drawing of counterpart. Lp, lateral pouches. Ol, the ordering lines. Scale bars=10 mm.

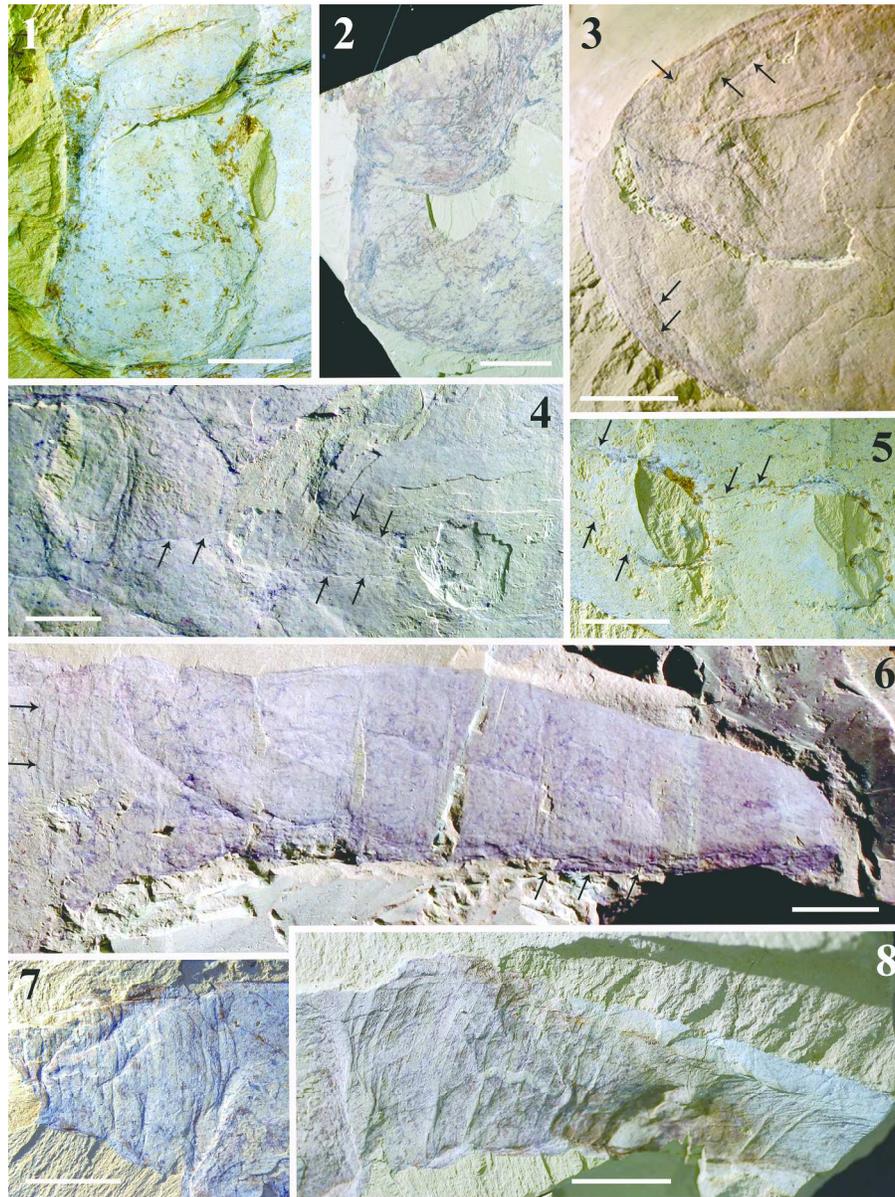


Figure 4. Detailed views of *Yuyuanozoon magnificissimi*. (1) anterior end of *Y. magnificissimi* YKLP 13071; (2) anterior end of *Y. magnificissimi* YKLP 13072; (3) anterior end of *Y. magnificissimi* CFM00059. Arrows show wrinkles, providing a hint that the anterior opening is not observable due to distortion through compression; (4) anterior section view of CFM00059. Arrows show the outlines of the pouches and possible underlying narrow grooves; (5) anterior section view of YKLP 13071. Arrows show the outlines of the pouches; (6) posterior section view of CFM00059. Arrows show the annulations within the 1st segment; (7) posterior section view of YKLP 13071 (counterpart); (8) posterior section view of YKLP 13071 (part). Scale bars=10 mm.

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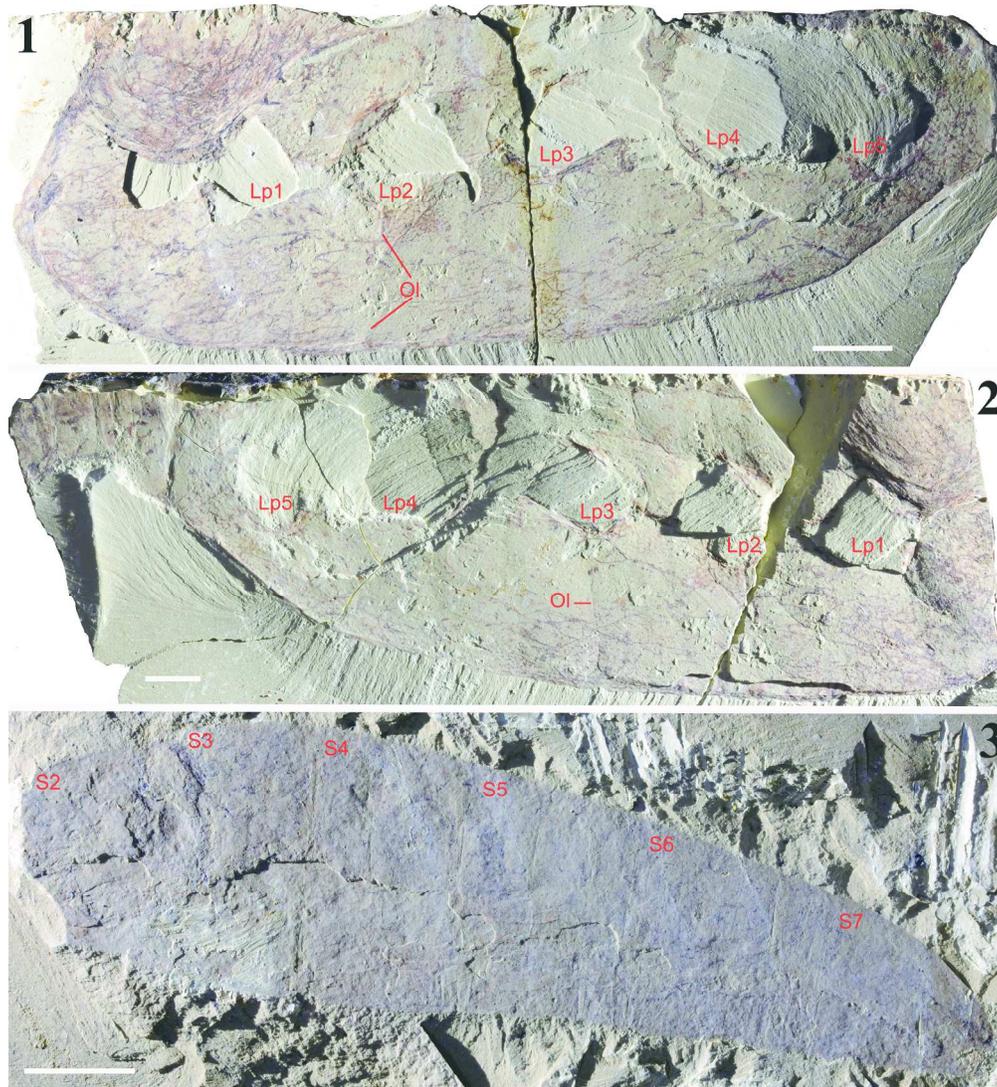


Figure 5. Overall views of *Yuyuanozoon magnificissimi*. (1) YKLP 13072 (part); (2) YKLP 13072 (counterpart); (3) YKLP 13070. Scale bars=10 mm.

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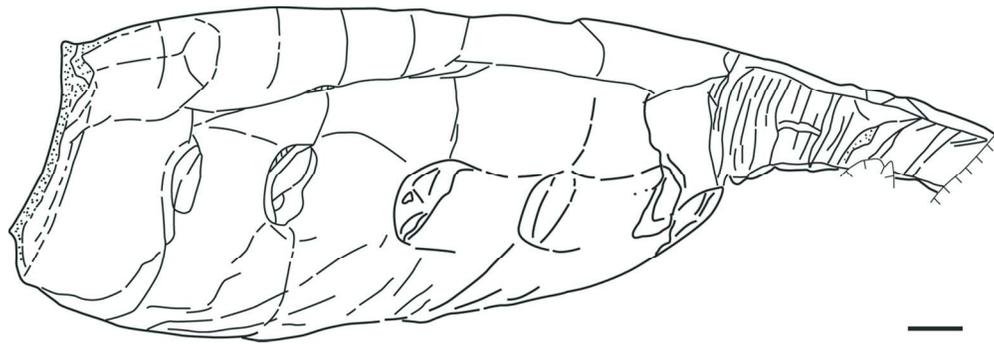


Figure 6. Composite camera lucida drawing of specimen YKLP 13071, superimposing part and counterpart, anterior to left, dorsal to top. Scale bar=10 mm.

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		Genus	Species	Occurrence	Anterior opening	Anterior section	Lateral pouches	Posterior section	Anus	Additional Comments	
Class Vetulicolida Chen and Zhou 1997	Order Vetulicolata Hou and Bergström, 1997	Family Vetulicolidae Hou and Bergström, 1997	Genus <i>Vetulicola</i> Hou, 1987	<i>Vetulicola cuneata</i> Hou, 1987	Chengjiang; Burgess Shale	Lip-like, V-shaped in lateral view	Elongate with anterior termination tapered	Five pouches; diamond- to rounded-diamond shape	Seven segments. Last 3 to 4 segments sometimes expanded to paddle-like	Terminal	
			<i>Vetulicola monile</i> Aldridge et al., 2007	Chengjiang	Anterior edge nearly vertical	Two longitudinal rows of nodes on each side of anterior section.	Five pouches; diamond- to rounded-diamond shape	Not preserved	Not preserved	Only one specimen (which is 60 mm long)	
			<i>Vetulicola rectangulata</i> Luo and Hu, 1999	Chengjiang	Anterior edge nearly vertical	Sub-rectangular in lateral view	Five pouches; diamond- to rounded-diamond shape	Seven segments. Last 3 to 4 segments sometimes expanded to paddle-like	Terminal		
			<i>Vetulicola gangtoucunensis</i> Luo et al., 2005	Guanshan	Anterior edge nearly vertical	Sub-rectangular in lateral view	Five pouches; diamond- to rounded-diamond shape; with slits and filaments	Seven segments, each being oval-shaped	Terminal	Holotype up to 95 mm in length	
			<i>Vetulicola longbaoshanensis</i> Yang et al., 2010	Guanshan	Anterior edge nearly vertical	Sub-rectangular in lateral view	Five pouches; diamond- to rounded-diamond shape	Seven segments, oar-like. Posterior section originates from the dorsal margin of the anterior section at a position between the 3 rd and 4 th lateral pouch	Terminal	Holotype up to 80 mm in length	
	Family Didazoonidae Shu and Han, 2001	Genus <i>Beidazoon</i> Shu, 2005 (= <i>Bullivetula</i> Aldridge et al., 2007)	<i>Beidazoon venustum</i> Shu, 2005 (= <i>Bullivetula variola</i> Aldridge et al., 2007)	Chengjiang	Anterior edge nearly vertical	Sub-rectangular, covered with a dense ornament of tubercles except for the marginal zone. No posterodorsal projection preserved.	Five pouches; weakly developed	Last segment sub-quadrate	Terminal	8-14 mm in length. Note that Shu (2005) originally characterized this taxon in a separate family, Beidazoonidae. Aldridge et al. (2007) reassigned this to Vetulicolidae, which we follow here	
		Genus <i>Ooedigera</i> Vinther et al., 2011	<i>Ooedigera peeli</i> Vinther et al., 2011	Sirius Passet	Anterior edge nearly vertical	Ovoid in lateral view, characterized by a delicate reticulate or anastomosing pattern	Five pouches; diamond- to rounded-diamond shape	Asymmetrically flattened broader area in the distal part	Terminal		
		Genus <i>Didazoon</i> Shu and Han, 2001	<i>Didazoon haoae</i> , Shu et al., 2001	Chengjiang	Circumventing feature behind the anterior opening narrow and indistinct, marked by short radiating lines	Sub-quadrate in lateral view, lacking marginal projections, lacking lateral groove	Five pouches; cowl-shaped	Tapering anteriorly and posteriorly	Terminal		
		Genus <i>Pomatrum</i> Luo and Hu, 1999 (= <i>Xidazoon</i> Shu et al., 1999)	<i>Pomatrum ventralis</i> Luo and Hu, 1999 (= <i>Xidazoon</i> Shu et al., 1999)	Chengjiang	Circumventing feature behind the anterior opening divided into inner and outer regions	Ovoid in lateral view, lacking lateral groove	Five pouches; cowl-shaped	Tapering anteriorly and posteriorly, with multiple segments	Terminal		
		Genus <i>Nesonektris</i> García-Bellido et al., 2014	<i>Nesonektris aldridgei</i> García-Bellido et al., 2014	Emu Bay Shale	Anterior edge vertical	Sub-quadrate in lateral view, lateral groove narrow	No pouches preserved	Internal rod-like structure extends along axis of posterior section.	Terminal	Most complete specimen is 125 mm	
	Genus <i>Yiyuanozoon</i> Chen, Feng and Zhu (in Chen et al., 2003)	<i>Yiyuanozoon magnificissimi</i> Chen, Feng and Zhu (in Chen et al., 2003)	Chengjiang	circumventing feature narrow	Elongate ovoid in lateral view, lacking lateral groove	Five pouches; Cowl-like	Seven segments, annulations within each segment	Terminal	Up to 200 mm		

Class <i>Heteromorphida</i> Shu, 2005	Order <i>Banffata</i> Aldridge et al., 2007	Family <i>Banffidae</i> Caron, 2006	Genus <i>Banffia</i> Walcott, 1911	<i>Banffia constricta</i> Walcott, 1911	Burgess shale	Crown-like structure around the antero-ventral anterior opening composed of three circlets. Frontal antenniform (?) outgrowth	Not segmented, lacking lateral groove	No pouches preserved	Flexible posterior section composed of 40 to 50 lightly sclerotized, and faintly defined segments	Terminal	Simple and narrow alimentary canal. Quadrate jointing between anterior and posterior section may reflect twisting
				<i>Banffia episoma</i> Conway Morris and Selden, 2015	Spence Shale	Circular	Shorter, narrower than posterior	No pouches preserved	Variable in shape	Terminal	Constriction with cross-over such that dorsal and ventral sides of posterior and anterior are transposed
			Genus <i>Heteromorphus</i> Luo and Hu, 1999	<i>Heteromorphus confusus</i> Chen and Zhou, 1997 (= <i>Banffia confusa</i> Chen and Zhou 1997; <i>Heteromorphus longicaudatus</i> Luo and Hu, 1999)	Chengjiang	Anterior edge nearly vertical	Lateral groove developed	Five pouches; weakly preserved	Terminal segment semicircular	Terminal	
			Genus <i>Skeemella</i> Briggs et al., 2005	<i>Skeemella clavula</i> Briggs et al., 2005	Utah, Middle Cambrian	Described as 'Head shield-like', that is divided longitudinally and with a straight dorsal margin	Lateral groove developed, nine segments separated; anterior section resembles a 'head shield'	No pouches preserved	Narrow vermiform, 43 segments; posterior section terminates in an arthropod-like unsegmented 'tail-piece' like structure	Terminal with two spines	Possible vetulicolian

Table 1. Vetulicolian species and their major morphological characters. *Vetulicola* sp. from the Shipai Formation of South China (Zhang & Hua, 2005), *Didazon* sp. From the Chengjiang biota (Aldridge et al., 2007), and *Vetulicola* sp. from the Guanshan biota (Li et al., 2015) are not included in the Table, until their full systematic relationships are discerned.