

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

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Abstract.—Vetulicolians are a group of exclusively Cambrian animals characterized by an anterior section with lateral pouches and a posterior section that appears segmented. The precise phylogenetic affinity of vetulicolians is debated because there is a lack of consensus regarding the interpretation of their anatomical features. Their disparate morphology might even cause one to question whether this is a monophyletic taxon. In total, there are 15 species grouped into three families included in vetulicolians. Here we focus on new specimens of *Yuyuanozoon magnificissimi* Chen, Feng, and Zhu in Chen et al., 2003, a species that was first described from only a single specimen from the Chengjiang Biota (Cambrian Series 2, Stage 3, *Eoredlichia-Wutingaspis* trilobite Biozone), Yunnan Province, China. The species is notable in being exceptionally large (up to 20 cm long). Morphological observations on the new specimens clarify the nature of the wide circular opening at the presumed anterior end of the animal and the cowl-shaped lateral openings within this anterior section. Taphonomic observations identify wrinkles in the anterior section and twists in the posterior segmented section. In particular, the shape of the anterior opening of *Yuyuanozoon magnificissimi* suggests significant differences from other vetulicolians. Taxonomic reappraisal of *Y. magnificissimi* indicates that it belongs within the family Didazoonidae, as that is presently defined.

Introduction

As currently understood, vetulicolians are a group of exclusively marine, enigmatic, and extinct Cambrian animals represented by three families: the Vetulicolidae, the Didazoonidae, and the Banffidae (Aldridge et al., 2007). They are characterized by a bipartite body. The anterior part is covered by a structure that superficially resembles the carapace of many arthropods. This structure, here referred to as the anterior section (Fig. 1), contains five lateral pouches, some possessing a lateral groove on each side, that have been interpreted by some as possible gill slits (Shu et al., 2001). The posterior section resembles the arthropod trunk, possessing a segmented and sometimes annulated morphology. Soft-part anatomy has been reported in some vetulicolians, including structures interpreted to represent muscle fibers (Aldridge et al., 2007; Ou et al., 2012; García-Bellido et al., 2014). The vetulicolian body plan and the limited information about soft-bodied anatomical structures within the anterior section make the interpretation of these animals difficult. As a result, the phylogenetic position of vetulicolians is unclear, with proposed affinities much debated and varying from their interpretation as unusual arthropods (Hou, 1987; Caron, 2006), kinorhynchs (Aldridge et al., 2007),

or stem-group deuterostomes (Shu et al., 2001; Ou et al., 2012) or chordates (Lacalli, 2002; García-Bellido et al., 2014).

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

Yuyuanozoon magnificissimi Chen, Feng, and Zhu in Chen et al., 2003 is exceptionally large, being up to 20 cm in length, compared with other vetulicolian species, which are generally 5–14 cm long. Thus far, it has been described from a single complete specimen, but here we show by reference to new material that some of the characteristics of this original specimen have been modified postmortem, and as such its current

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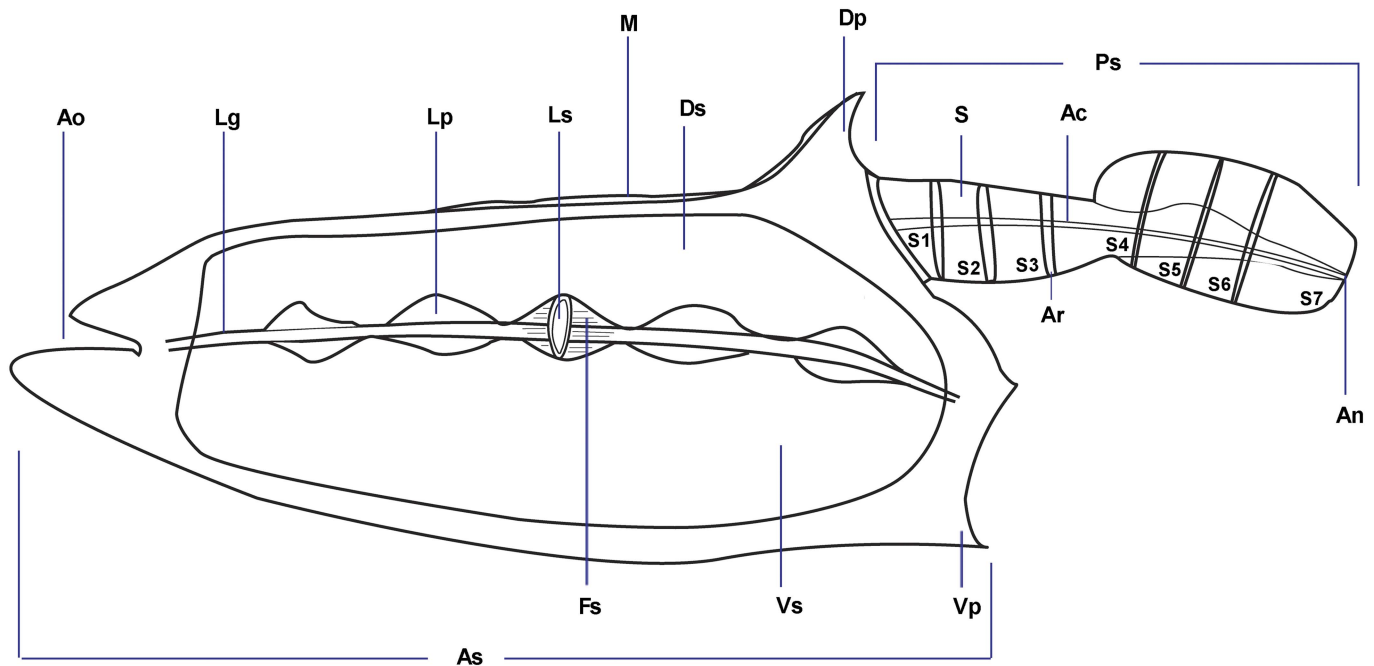


Figure 1. A hypothetical vetulicolian, showing detailed morphological characters. Abbreviations are as follows (terms used by other authors are in parentheses). Ac = alimentary canal (gut); An = anus; Ao = anterior opening (oral opening, oral, mouth, head); Ar = articulation; As = anterior section (anterior body, carapace, head +trunk), 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, abdomen), posterior part of the body; S = segment; S1–S7 = first through seventh segment of posterior section; Vp = posteroventral projection of anterior section (fin-like structure, ventral fin); Vs = ventral section.

appearance does not accurately represent *in vivo* morphology. Here we describe new specimens, provide a new interpretation for the opening at the presumed anterior end of the animal, and reassign this taxon to the vetulicolian family Didazoonidae.

Geologic setting

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

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

Materials and methods

The specimens were prepared using steel needles and examined with a Nikon SMZ–10A binocular microscope. We used a

camera lucida attached to a Wild Heerbrug M10 microscope to elucidate and record the anatomy. The digital images of the specimens were captured with Nikon D3X and Canon 500D digital cameras and a Leica DFC5000 camera attached to a Leica M205C photomicroscope and were processed in Adobe Photoshop CC. All measurements were processed with ImageJ version 1.49.

Repository and institutional abbreviation.—The three new specimens documented here are preserved with part and counterpart and are deposited in the Yunnan Key Laboratory for Palaeobiology, Yunnan University (abbreviated YKLP), Kunming, China, with numbers YKLP 13070, YKLP 13071, and YKLP 13072.

Morphology and terminology of the vetulicolian body

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

Here we use descriptive terms carefully, to avoid inference about evolutionary significance, thus avoiding the potential for circular reasoning regarding phylogenetic interpretation. For example, we do not use the term ‘carapace’ to denote the anterior section of the animal. Our morphological terms are

Table 1. Vetulicolian species and their major morphological characters. *Vetulicola* sp. from the Shipai Formation of South China (Zhang and Hua, 2005), *Didazoon* 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 because their full systematic relationships have not been discerned.

Class Vetulicolida	Order Vetulicolata	Family Vetulicolidae	Genus	Species	Occurrence	Anterior opening	Anterior section	Lateral pouches	Posterior section	Anus	Additional comments	
Chen and Zhou, 1997	Hou and Bergström, 1997	Hou and Bergström, 1997	Genus <i>Vetulicola</i> Hou, 1987	<i>Vetulicola cuneata</i> Hou, 1987	Chengjiang; Mural Formation	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 in Luo et al., 1999	Chengjiang	Anterior edge nearly vertical	Subrectangular 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	Subrectangular 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	Subrectangular 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 3rd and 4th lateral pouches	Terminal	Holotype up to 80 mm in length	
			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	Subrectangular, covered with a dense ornament of tubercles except for the marginal zone; no posterodorsal projection preserved	Five pouches; weakly developed	Last segment subquadrate	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		
			Family Didazoonidae Shu and Han in Shu et al., 2001	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	Subquadrate 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 in Luo et al., 1999 (= <i>Xidazoon</i> Shu et al., 1999)	<i>Pomatrum ventralis</i> Luo and Hu in Luo et al., 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	

Table 1. (Continued)

			Genus	Species	Occurrence	Anterior opening	Anterior section	Lateral pouches	Posterior section	Anus	Additional comments
Class Heteromorphida Shu, 2005	Order Banffiata Aldridge et al., 2007	Family Banffidae Caron, 2006	Genus <i>Nesonektris</i> García-Bellido et al., 2014	<i>Nesonektris aldridgei</i> García-Bellido et al., 2014	Emu Bay Shale	Anterior edge vertical	Subquadrate 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>Yuyuanozoon</i> Chen, Feng, and Zhu in Chen et al., 2003	<i>Yuyuanozoon 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
			Genus <i>Banffia</i> Walcott, 1911	<i>Banffia constricta</i> Walcott, 1911	Burgess Shale	Crown-like structure around the antero- ventral anterior opening is 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 in Luo et al., 1999	<i>Heteromorphus confusus</i> Chen and Zhou, 1997 (= <i>Banffia confusa</i> Chen and Zhou 1997; <i>Heteromorphus longicaudatus</i> Luo and Hu in Luo et al., 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	Pierson Cove Formation	Described as 'Head shield-like,' that is divided longitudinally and with a straight dorsal margin	Lateral groove developed, nine segments; 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		

summarized in Figures 1 and 2, which also denote how terms such as ‘ventral’ and ‘dorsal’ are applied to vetulicolians.

Preservation and taphonomy

Specimen YKLP 13071 (Fig. 3) is, like most vetulicolians, laterally compressed and retains some three-dimensional (3-D) relief. The majority of the anterior section is preserved as a thin film that does not appear to have been biomineralized though the areas adjacent to the anterior opening and the posterior end show patches of dark color. The texture and composition of this material is identical to the iron oxide coatings typical in Chengjiang fossils (Gabbott et al., 2004; Forchielli et al., 2014) and is not consistent with in vivo mineralization. The anterior section appears to comprise six subdivisions that are demarcated by five lines that circumvent the entire structure and are coincident with the five lateral cowl-shaped pouches. At the mid-point between the boundaries of these subdivisions on the dorsal side a shorter parallel line occurs, which was termed second-order annulation by Aldridge et al. (2007). There are clear wrinkles along the ventral side of the anterior section, which appear to suggest an element of twisting and/or compression postmortem.

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

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

Systematic paleontology

Class Vetulicolida Chen and Zhou, 1997
Order Vetulicolata Hou and Berström, 1997
Family Didazoonidae Shu and Han in Shu et al., 2001

Type Genus.—*Didazoon* Shu and Han in Shu et al., 2001.
Other genera.—*Pomatrum* Luo and Hu in Luo et al., 1999; *Yuyuanozoon* Chen, Feng, and Zhu in Chen et al., 2003; *Nesonektris* García-Bellido et al. 2014.

Diagnosis.—(Modified from Shu et al., 2001, Aldridge et al., 2007) Bilaterally symmetrical animal with clear subdivision of body into presumed anterior and posterior sections. Neither the subquadrate to ovoid anterior section nor the posterior section is biomineralized. The anterior section has a large, circular opening at the presumed anterior end of the animal, posterior of which are six subdivisions demarcated by five lines; five, presumed laterally positioned, oval openings on both sides of the anterior section coincide with the lines of subdivision. Segments of posterior section may bear up to six annulations.

Remarks.—In addition to characters listed by Shu et al. (2001), in well-preserved specimens of *Yuyuanozoon* (herein) and

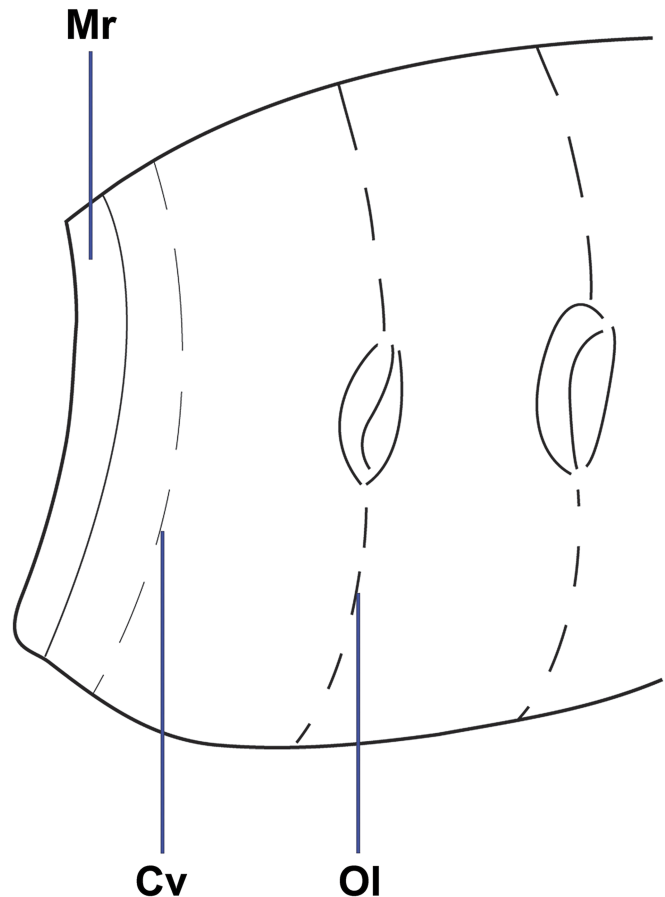


Figure 2. Additional morphological features for *Yuyuanozoon*. Abbreviations are as follows (terms used by other authors are in parentheses). Cv = circumventing feature behind the anterior opening (oral disc.); Mr = marginal region at the anterior opening (mouth plate); Ol = ordering lines (putative segments, anterior segments), lines circumventing the anterior section coalescing with lateral pouches and long axis perpendicular to the body axis.

Didazoon (YJL’s personal observations), the posterior section displays annulation within each segment.

Morphological features, including the circumventing feature behind the anterior opening of the anterior section, the posterodorsal (‘fin-like’) prolongations on the anterior section, the shape of the lateral pouches, and the segmented posterior section with annulations, place *Yuyuanozoon* in the Didazoonidae rather than in the Vetulicolidae (see also Table 1).

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

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

Diagnosis.—(Modified from Chen et al., 2003, Aldridge et al., 2007) Didazoonid with nonbiomineralized, elongate ovoid anterior section. A narrow, raised rim circumvents the entire perimeter of the anterior section, some 5 mm posterior of the anterior opening. Marginal projections and lateral groove absent from anterior section. Posterior section has seven segments, within each of which are five to six annulations; terminal segment longest.

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

Remarks.—Analysis of the body shape of *Didazoon*, *Pomatrum*, and *Yuyuanozoon* distinguishes *Yuyuanozoon* as a separate genus based on its overall size and the proportions of the anterior and posterior sections, which were fully described by Chen et al. (2003). *Yuyuanozoon* is also clearly distinct from other vetulicolians, with the exception of *Didazoon*, in possessing annulations within each segment of its posterior section.

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

Figures 3, 4, 5, 6

- 2003 *Yuyuanozoon magnificissimi* Chen, Feng, and Zhu in Chen et al., p. 282, pl. 1, figs. a–d.
 2004 *Yuyuanozoon magnificissimi*; Chen, p. 318, fig. 509.
 2007 *Yuyuanozoon magnificissimi*; Aldridge et al., p. 142, pl. 5, figs. 3, 5, text-fig. 6.
 2012 *Yuyuanozoon magnificissimi*; Ou et al., p. 81, fig. 5.
 2017 *Yuyuanozoon magnificissimi*; Hou et al., p. 276, fig. 26.3.

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

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

Diagnosis.—Monotypic, as for the genus.

Description.—The anterior section forms an elongated ellipsoid in lateral view, with five lateral pouches on each side; the anterior opening is broad (Fig. 3). The posterior section is about one-third of the width of the anterior section, elongate, segmented and annulated throughout. Narrow gut situated medially (Fig. 4.6, 4.8).

Body.—All specimens are laterally preserved. The most complete specimen YKLP 13071 (Fig. 3) has a length of at least 17.2 cm (the last two segments of the posterior section are not preserved). The anterior section is 11.8 cm long and up to 5.4 cm wide; the posterior section is more than 4.5 cm in length and has a maximum width of 2.0 cm. The dorsal surface of the anterior

section from the anterior opening to the posterior section is coincident along the dorsal side but has a concave outline on the ventral side (Fig. 3). The length of the posterior section measures 11 mm for the first segment and then posteriorly 9 mm, 9 mm, 9 mm, and at least 7 mm for the incomplete fifth segment.

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

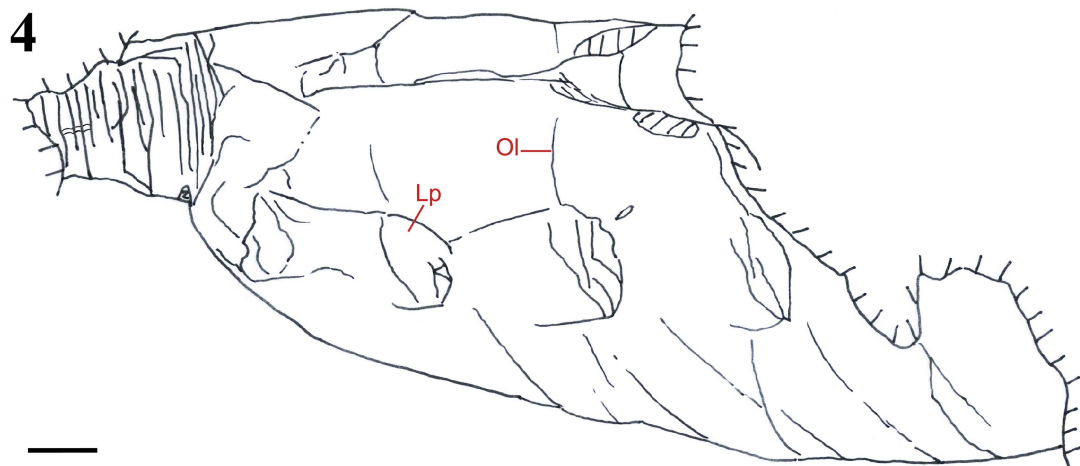
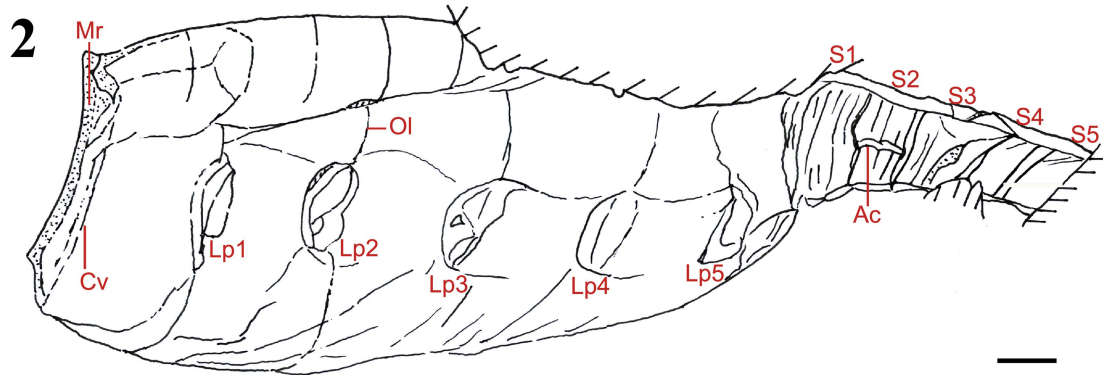
Anterior circumventing feature.—Raised rim, a narrow structure circumventing the entire perimeter of the anterior section, some 5 mm posterior of the anterior opening.

Ordering lines.—Lines circumventing the anterior section and perpendicular to the body axis are displayed best in the anterodorsal area, and here they comprise two orders. The most prominent lines traverse the entire body. These delineate six subdivisions of the anterior section, and their boundaries are coincident with five lateral pouches on each side of the animal (Figs. 3, 5.1, 5.2). There are faint lines between these boundaries that are less continuous in the dorsal section. This pattern is similar to *Vetulicola cuneata* Hou, 1987 (Chen and Zhou, 1997, fig. 135) and *V. rectangulata* Luo and Hu in Luo et al., 1999 (Aldridge et al., 2007, pl. 1, fig. 9; text-fig. 2) and is known in *Pomatrum* (Aldridge et al., 2007, pl. 5, fig. 1, text-fig. 8).

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

Posterior segmentation.—Only five of up to seven segments in the posterior part are present in YKLP 13071, and within each of these segments are five to six annulations. Only a few

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 mold) with low-angle lighting; (2) camera lucida drawing of the same specimen. The six 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 = first through fifth 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 right, 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.



annulations are apparent in the holotype of *Y. magnificissimi* possibly due to poorer preservation (Fig. 4.6). The posterior section of YKLP 13071 is twisted and deformed (Fig. 4.7, 4.8). Each segment of the posterior section has five to six annulations; junctions between segments are distinguished according to a slight change in relief, and these boundaries are one annulation in width. Both the holotype and the new specimens have annulations. Annulations are apparent in YKLP 13070 (Fig. 5.3) and YKLP 13072 (Fig. 5.2). In the holotype, annulations are clearly present on the first segment of the posterior section and the ventral area of the sixth (Fig. 4.6).

Possible alimentary tract.—The alimentary tract is preserved in the medial part of the posterior section of YKLP 13071 (Fig. 4.7–4.8). This is irregular and curved, narrow, and apparently filled with fine sediment. This structure is incomplete and only preserved at the second segment of the posterior section.

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

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

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

Contrary to the comment by Chen et al. (2003, p. 282) that *Yuyuanozoon* is distinct from other vetulicolians in the number of anterior and posterior segments, the possession of six anterior section subdivisions and seven posterior segments is

characteristic of both Vetulicolidae and Didazonidae. The anterior opening of *Y. magnificissimi* was described as ‘long-ellipsoidal’ by Chen et al. (2003). Our new material shows that the anterior end of *Yuyuanozoon* is widely open, with a circumventing feature. Reinvestigation of the holotype indicates that the anterior section of that specimen is distorted, as evidenced by a series of wrinkles, and the morphology of the anterior opening is obscured by compression.

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

Inferences about mode of life

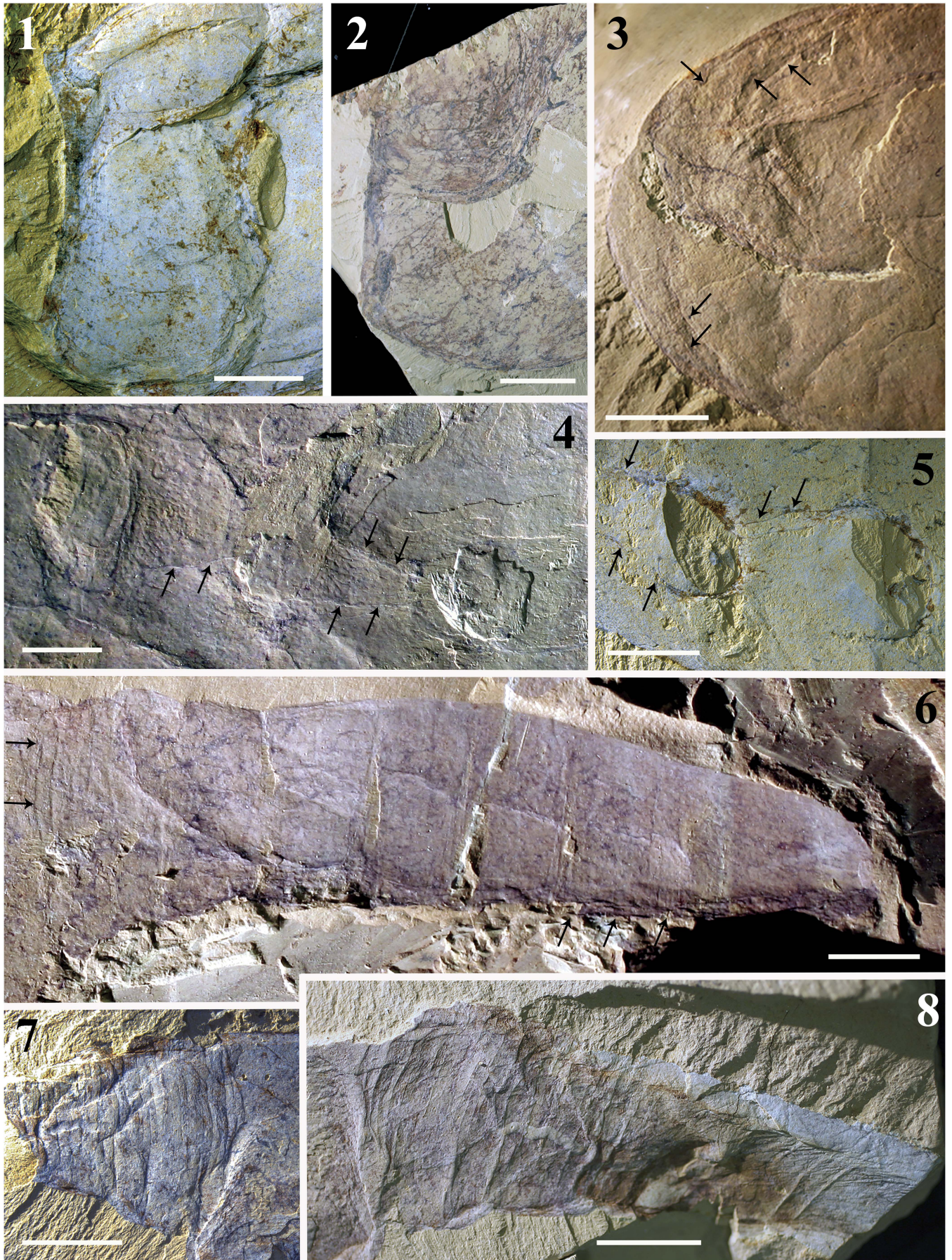
By analogy with other vetulicolids, the segmented posterior section of *Yuyuanozoon* might be interpreted as an adaptation for propulsion. However, *Yuyuanozoon* has a relatively small posterior section countered by a bulky anterior section without fin-like projections that seems ill adapted for protracted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

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

Conclusions

In this paper we have described new material of *Yuyuanozoon magnificissimi*. We have attempted to develop a unified terminology for the description of vetulicolians that avoids inferring animal relationships or functional morphology. Therefore, terms such as ‘carapace’ (suggesting an arthropod affinity) or ‘oral end’ (suggesting functionality for feeding) have been replaced with purely descriptive terms. We believe that much of the existing terminology applied to vetulicolians cannot be sustained. There is no convincing evidence to show the homology of the anterior part of vetulicolians with the carapace or head shield of arthropods. Furthermore, there is no evidence in *Y. magnificissimi* to sustain the notion that the anterior opening was ‘oral’ or even that it functioned in food collection. In deconstructing this taxonomically ‘loaded’

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 first segment. (7) Posterior section view of YKLP 13071 (counterpart); (8) posterior section view of YKLP 13071 (part). Scale bars = 10 mm.



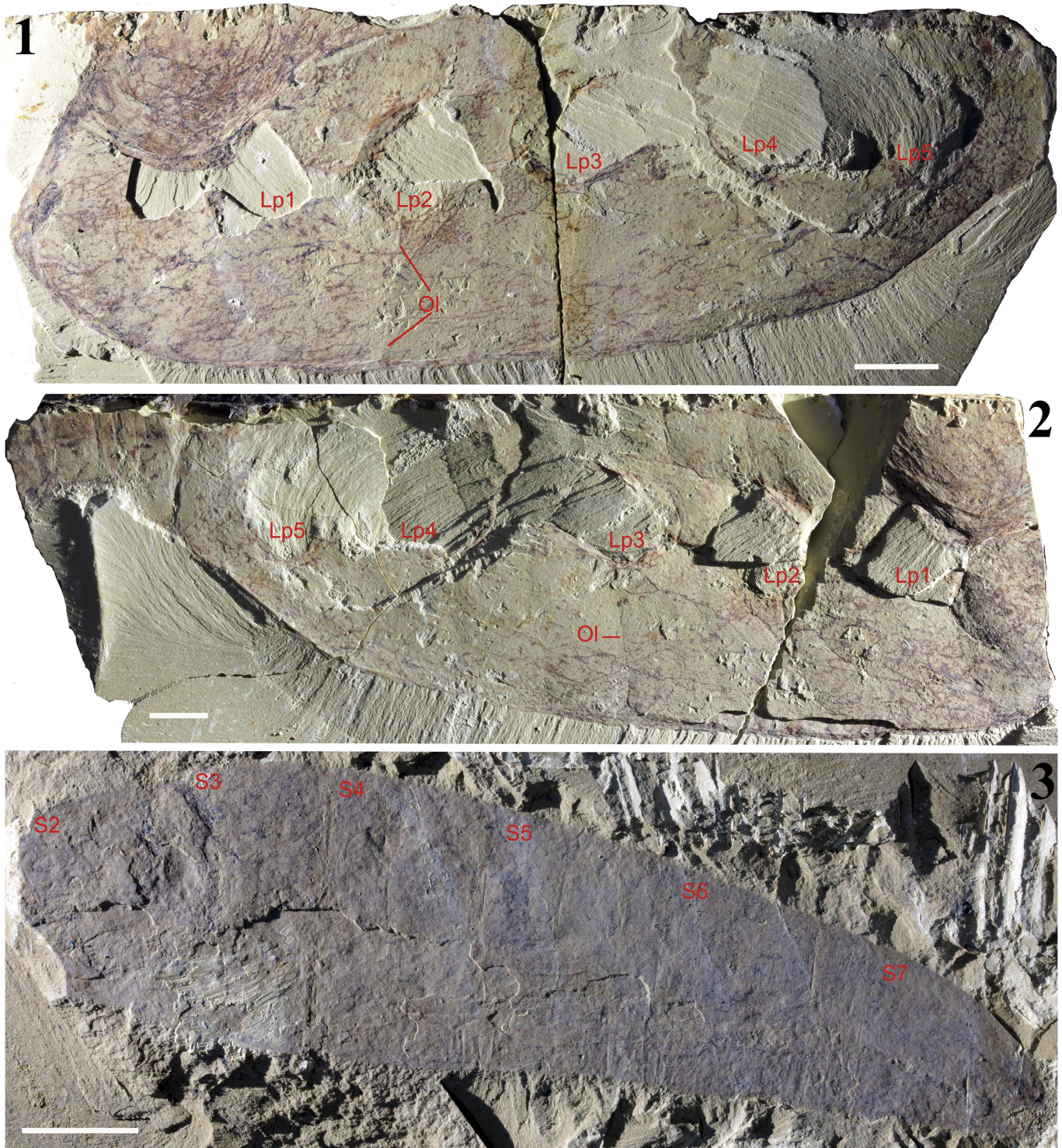


Figure 5. Overall views of *Yuyuanozoon magnificissimi*. (1) YKLP 13072 (part) anterior to left; (2) YKLP 13072 (counterpart) anterior to right; (3) YKLP 13070, posterior section with numbered segments, S2 to S7. Lp = lateral pouch; Ol = ordering lines; S = segment. Scale bars = 10 mm.

terminology we now propose a ‘ground-up’ approach to interpreting these animals that examines their full range of morphological characteristics, without preconception. New analyses should determine: (1) whether any features are homologous with extant groups of organisms, and (2) whether any features can be accorded a true function

according to basic observations of their likely adaptation for different functions. From this deconstructed database we hope that a more realistic picture of the interspecific variation of vetulicolians can be assessed, which will lead to a greater understanding of their wider animal affinities.

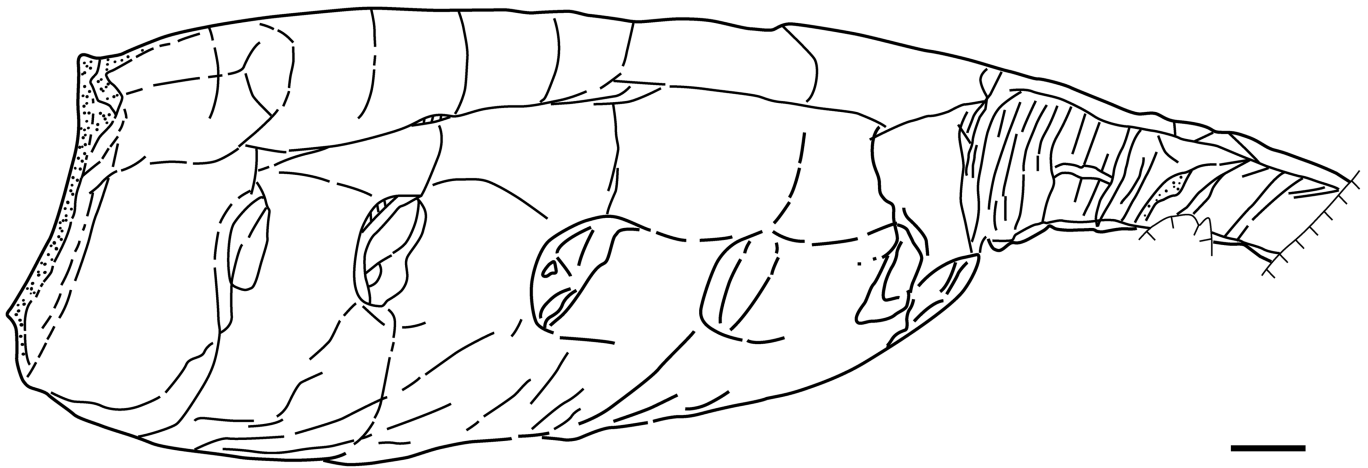


Figure 6. Composite camera lucida drawing of specimen YKLP 13071, superimposing part and counterpart, anterior to left, dorsal to top. Scale bar = 10 mm.

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