

Deep water vetulicolians from the lower Cambrian of China

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ABSTRACT

Vetulicolians are an enigmatic phylum of extinct Cambrian marine invertebrates. They are particularly diverse in the Chengjiang Biota of China, but representatives have been recovered from other Fossil-Lagerstätten (Cambrian Stage 3-Drumian). These organisms are characterized by a bipartite body, which is split into an anterior section and a posterior segmented section connected by a narrow constriction. Here we report new material of the genus *Pomatrum* from the Cambrian Balang Biota (Series 2, Stage 4) of Hunan, southern China. This is the first discovery of this vetulicolian outside of the Chengjiang Biota (Series 2, Stage 3) and the first report of vetulicolians from the Balang Biota. This finding not only suggests that this group had a wider spatial and temporal distribution than previously known, but also adds information to the overall biodiversity of the Balang Biota—one of the most important Stage 4 fossil deposits known from Gondwana.

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INTRODUCTION

Vetulicolians are a problematic group of extinct marine invertebrates found in Cambrian Fossil-Lagerstätten (*sensu Kimmig & Schiffbauer, 2024*), with 16 species amongst ten genera that have been described so far, with more awaiting description (Table 1) (*Walcott, 1911; Hou, 1987; Chen & Zhou, 1997; Luo et al., 1999; Shu et al., 2001; Chen et al., 2003; Briggs et al., 2005; Luo et al., 2005; Shu, 2005; Aldridge et al., 2007; Yang et al., 2010; Vinther, Smith & Harper, 2011; García-Bellido et al., 2014; Conway Morris et al., 2015; Fu et al., 2019; Kimmig, Leibach & Lieberman, 2020*). Vetulicolians have a peculiar body structure, divided into an anterior and posterior body. The bilaterally symmetrical anterior body is usually weakly divided by five orderly lines and preserves five lateral pouches on

Table 1 Vetulicolian species in time and space.

Family	Species	Occurrence	Cambrian stage	References
Vetulicolidae (Hou & Bergström, 1997)	<i>Vetulicola cuneata</i> Hou, 1987	Chengjiang Biota	Stage 3	Hou (1987), Aldridge et al. (2007)
	<i>Vetulicola monile</i> Aldridge et al., 2007	Chengjiang Biota	Stage 3	Aldridge et al. (2007)
	<i>Vetulicola rectangulata</i> Luo & Hu in Luo et al., 1999	Chengjiang Biota	Stage 3	Luo et al. (1999), Aldridge et al. (2007)
	<i>Vetulicola gangtoucunensis</i> Luo, Fu & Hu in Luo et al., 2005	Guanshan Biota	Stage 4	Luo et al. (2005), Hu et al. (2013)
	<i>Vetulicola longbaoshanensis</i> Yang et al., 2010	Guanshan Biota	Stage 4	Yang et al. (2010), Hu et al. (2013)
	<i>Vetulicola</i> sp.	Malong Biota	Stage 3	Luo et al. (2008)
	<i>Vetulicola</i> sp.	Xiaoshi Biota	Stage 3	S. Ma, 2024, personal observations
	<i>Vetulicola</i> sp.	Shipai Biota	Stage 4	Zhang & Hua (2005)
	<i>Vetulicola</i> sp.	Jianhe Biota	Stage 4	Yang (2019)
	<i>Vetulicola</i> sp.	Guanshan Biota	Stage 4	Li et al. (2015)
	<i>Beidazon venustum</i> Shu, 2005 (= <i>Bullivetula variola</i> Aldridge et al., 2007)	Chengjiang Biota	Stage 3	Shu (2005), Aldridge et al. (2007)
<i>Ooedigera peeli</i> Vinther, Smith & Harper, 2011	Sirius Passet	Stage 3	Vinther, Smith & Harper (2011)	
Didazonidae (Shu et al., 2001)	<i>Didazon haoae</i> Shu et al., 2001	Chengjiang Biota	Stage 3	Shu et al. (2001), Aldridge et al. (2007), Yang et al. (2023b)
	<i>Pomatrum ventralis</i> Luo & Hu in Luo et al., 1999 (= <i>Xidazon</i> Shu et al., 1999)	Chengjiang Biota, Balang Biota	Stage 3–Stage 4	Luo et al. (1999), Shu et al. (1999), Aldridge et al. (2007), Yang et al. (2023b), this study
	<i>Nesonektris aldridgei</i> García-Bellido et al., 2014	Emu Bay Shale	Stage 3	García-Bellido et al. (2014)
	<i>Yuyuanozoon magnificissimi</i> Chen, Feng & Zhu in Chen et al., 2003	Chengjiang Biota	Stage 3	Chen et al. (2003), Aldridge et al. (2007), Li et al. (2018)
Banffidae (Caron, 2006)	<i>Banffia constricta</i> Walcott, 1911	Burgess shale	Wuliuan	Caron (2006), Aldridge et al. (2007)
	<i>Banffia episoma</i> Conway Morris & Selden in Conway Morris et al., 2015	Spence Shale	Wuliuan	Conway Morris et al. (2015), Kimmig et al. (2019)
	<i>Banffia</i> sp.	Qingjiang Biota	Stage 3	Fu et al. (2019)
	<i>Heteromorphus confusus</i> Chen & Zhou, 1997 (= <i>Banffia confusa</i> Chen & Zhou, 1997)	Chengjiang Biota	Stage 3	Chen & Zhou (1997), Aldridge et al. (2007), Yang et al. (2021)
	<i>Heteromorphus longicaudatus</i> Luo & Hu, in Luo et al., 1999	Chengjiang Biota	Stage 3	Luo et al. (1999), Aldridge et al. (2007)
<i>Skeemella clavula</i> Briggs et al., 2005	Marjum Formation, Pierson Cove Formation	Drumian	Briggs et al. (2005), Aldridge et al. (2007), Kimmig, Leibach & Lieberman (2020)	
Indet.	new vetulicolian A	Qingjiang Biota	Stage 3	Fu et al. (2019)
	new vetulicolian B	Qingjiang Biota	Stage 3	Fu et al. (2019)

each side (Ou et al., 2012; Li et al., 2018). The bilaterally symmetrical posterior body is generally paddle- or broad-leaf-shaped, and clearly divided into seven or more segments. It houses the gut and has a terminal anus. Additionally, some species preserve an enigmatic structure in the ventral position of their posterior ‘tail’. Though this feature has been suggested to be a likely internal organ, its function is currently unknown with inferences related to reproduction, excretion, and digestion (Yang et al., 2023b).

The peculiar body shape of vetulicolians has led to continued conversation regarding their phylogenetic placement. Originally, vetulicolians were considered a type of large bivalved arthropod (e.g., [Hou, 1987](#); [Caron, 2001](#)). However, the consistent absence of appendages in an increasing number of vetulicolian species has swayed most away from this position, instead resulting in propositions of several other affinities, including deuterostomes (e.g., [Shu et al., 2001](#)), stem-chordates ([Gee, 2001](#)), tunicates (e.g., [Lacalli, 2002](#)), or ecdysozoans (e.g., [Briggs et al., 2005](#)). The prevailing view is that vetulicolians are a monophyletic group within the deuterostomes, perhaps closest to free-swimming tunicates, but their precise position within the Deuterostomia is still debated ([García-Bellido et al., 2014](#); [Li, Liu & Ou, 2017](#); [Li et al., 2018](#); [Zhu et al., 2019](#); [Shu & Han, 2020](#); [Yang et al., 2023b](#)). Indeed, the most recent phylogenetic analysis ([Mussini et al., 2024](#)) changes course again, suggesting a paraphyletic group amongst stem-chordates, with the Didazonids placed most closely to *Yunnanozoon*. Another hypothesis would place vetulicolians within the stem-group protostomes under a scenario of deuterostome paraphyly ([Kapli et al., 2021](#)).

Vetulicolians exhibit a relatively wide distribution in space, as they are known from Cambrian Stage 3–Stage 4 of Gondwana and the Wuliuan–Drumian of Laurentia ([Table 1](#)). However, the majority of vetulicolians come from South China, and most species are restricted to the Chiungchussu Formation of South China ([Table 1](#)). This makes the recent discovery of *Pomatrum* cf. *P. ventralis* from the Balang Formation (Cambrian, Series 2, Stage 4), Xiangxi Region, Hunan, China, significant, as it represents the first appearance of the genus outside of the Chengjiang Biota (Series 2, Stage 3). Here we describe ten new specimens of *Pomatrum*, explore the distribution of the genus in time and space, and discuss potential adaptations of vetulicolians to deeper water environments.

MATERIALS AND METHODS

The new specimens of *Pomatrum* cf. *P. ventralis* described here are repositied in the collections of the Yunnan Key Laboratory for Palaeobiology, Yunnan University, Kunming, China (YKLP), with specimen numbers YKLP 14,591–14,601. Specimens with the prefix Hz-f are repositied in the collections of the Yunnan Institute of Geological Sciences, Kunming, China.

Imaging

The specimens were photographed using a Canon EOS 5D digital SLR camera with a Canon 50 mm macro lens, cross-polarized lighting, and one-sided, low-angle lighting. Close-ups were captured using a Leica DFC 500 digital camera mounted on a Leica M205-C stereoscope. The specimens were submerged in water to increase contrast. The contrast, color space, and brightness were adjusted using Adobe Photoshop CC.

Terminology

The vetulicolian terminology in our descriptions broadly follows [Li et al. \(2018\)](#).

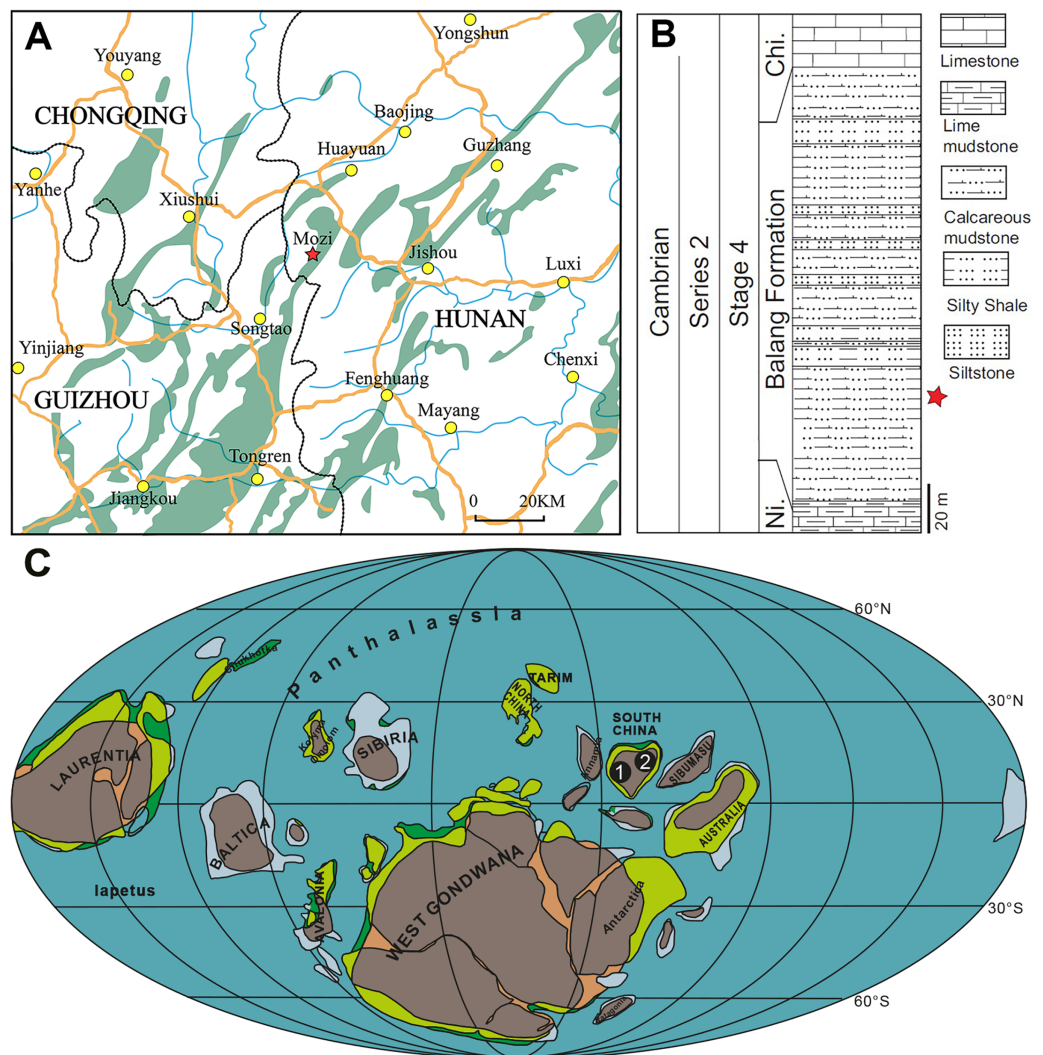


Figure 1 Location and stratigraphy. (A) Location of the studied section of the Balang Formation. It is located approximately 32 km south-west of Huayuan Town, Xiangxi Region, Hunan Province, South China. Lower Cambrian Outcrops in grey. Fossil site indicated by red star. (B) Generalized stratigraphy of the Balang Formation at this location. Modified from Yang et al. (2023a). (C) Palaeogeographical distribution of *Pomatrum* specimens during Cambrian Stages 3–4 and during the Wuliuan (map modified from Streng & Geyer (2019)). 1. Chengjiang Biota, Yunnan, China, Stage 3, 2. Balang Biota, Hunan, China, Stage 4. Full-size [DOI: 10.7717/peerj.18864/fig-1](https://doi.org/10.7717/peerj.18864/fig-1)

GEOLOGICAL SETTING

The Balang Formation is exposed in the eastern Guizhou and western Hunan Provinces of southern China (Zhou et al., 1979, 1980; Yin, 1996; Yang et al., 2023a). The thickness of the Balang Formation varies between 300 and 600 m in the Guizhou Province and is generally about 200 m in the Hunan Province. The specimens described herein come from an outcrop approximately 32 km south-west of Huayuan Town, Xiangxi Region, Hunan Province, South China (Fig. 1A). At this location, the Balang Formation conformably overlies the lower Cambrian Niutitang Formation and is in turn conformably overlain by the Chingsutung Formation. The Balang Formation itself can be divided into a lower and

an upper section. The lower part of the section contains abundant small planktonic trilobites such as Oryctocephalidae, reflecting a deeper water environment. The upper part of the section contains abundant benthic trilobites belonging to the Ptychopariida and Redlichiida (Yin, 1996).

The vetulicolian specimens here were collected from the dark grey calcareous mudstones of the lower part of the Balang Formation (Fig. 1B). The abundance of the trilobite *Oryctocarella duyunensis* in the same beds places these units within Cambrian Series 2, Stage 3–4 (Peng et al., 2017; National Commission on Stratigraphy of China, 2018; Zhao et al., 2019; Dai et al., 2021). Specimens from this location are preserved as carbonaceous compressions (Wen et al., 2019; Yang et al., 2023a).

RESULTS

Systematic Paleontology

Phylum: Vetulicolia Shu et al., 2001

Class: Vetulicolida Chen & Zhou, 1997

Order: Vetulicolata Hou & Bergström, 1997

Family: Didazonidae Shu & Han in Shu et al., 2001

Genus *Pomatrum* Luo & Hu in Luo et al., 1999

Xidazon.—Shu, Conway Morris & Zhang, 1999: 747.

Remarks. We follow Chen et al. (2002) and Aldridge et al. (2007) in considering *Xidazon* a junior synonym of *Pomatrum*.

Pomatrum cf. *P. ventralis*.—Luo & Hu in Luo et al., 1999

Pomatrum ventralis.—Luo and Hu, in Luo et al., 1999: 65–66, pl. 12, fig. 3.

Xidazon stephanus.—Shu, Conway Morris & Zhang, in Shu et al., 1999: 747–749, figs. 1a–d, 2.

Xidazon stephanus.—Shu et al., 2001: figs 2e–f, 3c–d.

Pomatrum ventralis.—Chen et al., 2002: pl. 12, fig. 4.

Xidazon stephanus.—Shu, 2003: fig. 3b.

Pomatrum ventralis.—Chen, 2004: 309, 315, figs. 493–494, 501, 505.

Pomatrum ventralis.—Aldridge et al., 2007: 146–147, pl. 4, figs. 6–8, 10–12.

Xidazon stephanus.—Yang et al., 2023b: 4, figs. 1E, H, 2, 3, S1–S7, S8C–F.

Holotype. Hz-f-7-390.

New Material. YKLP 14591–14592 (part and counterpart of a nearly complete laterally compressed specimen (Figs. 2A–2F). YKLP 14593–14601, nine laterally compressed incomplete specimens on a single slab (Figs. 3A, 3B).

Provenance. Balang Formation, lower Cambrian (Series 2, Stage 3–4), *Oryctocarella duyunensis* biozone, Mozi Village, Paiwu Township, approximately 32 km south-west of

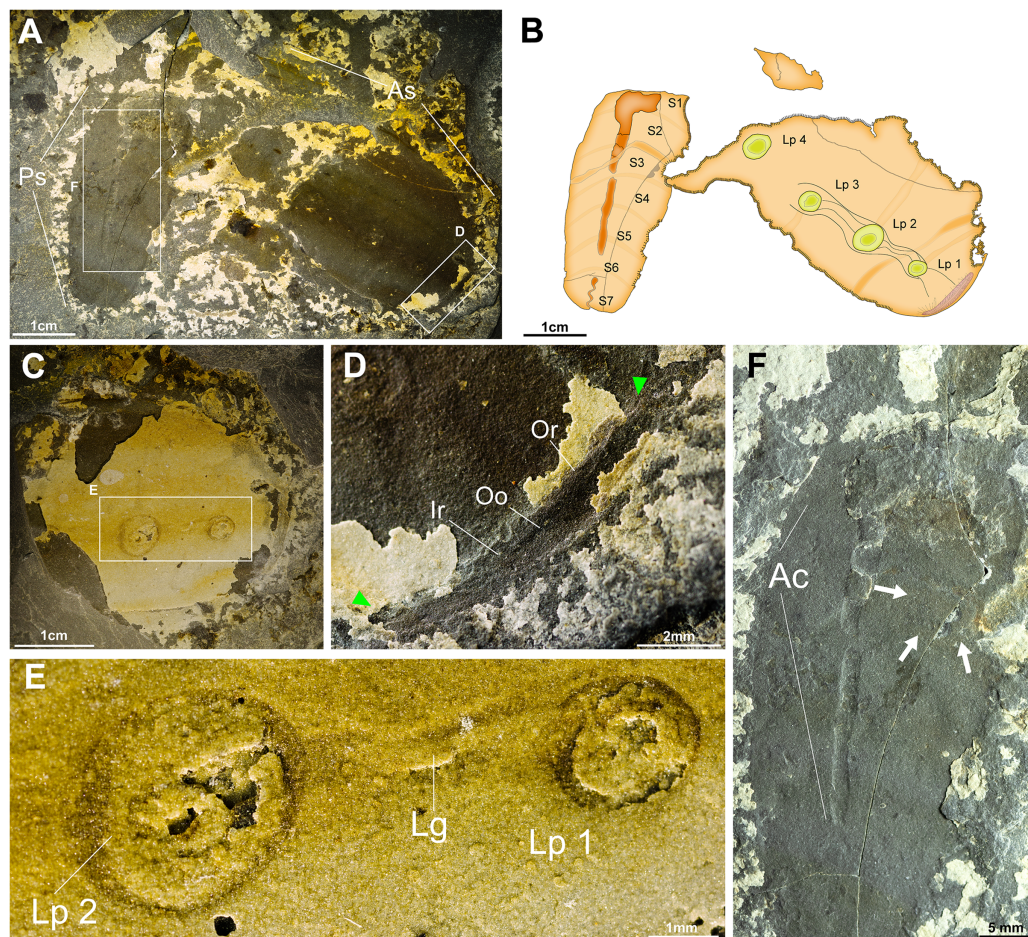


Figure 2 Nearly complete specimen of *Pomatrum* cf. *P. ventralis* Luo & Hu in Luo et al. (1999) from the Cambrian Stage 4 Balang Formation of China. (A) YKLP 14591, part, a relatively complete specimen of preserving the anterior and posterior body, lateral pouch, lateral groove and alimentary canal. (B) Explanatory drawing of (A). (C) YKLP 14592 counterpart, preserving the first three subdivisions of the anterior section, two lateral pouches, lateral groove and marginal zone. (D) Close-up of the anterior opening, indicated by arrows. (E) Close-up of the lateral pouches and lateral groove from (C). (F) Close-up of the alimentary canal and the enigmatic sub-rounded structure of the posterior section, indicated by arrows. Abbreviations: Ac, Alimentary canal; As, Anterior section; Ir, Inner region; Lg, Lateral groove; Lp, lateral pouch; Mz, Marginal zone; Oo, Oral opening; Or, Outer region; Ps, Posterior section; S, Segment.

[Full-size !\[\]\(1663bb69f307a960345edb0e712f8c02_img.jpg\) DOI: 10.7717/peerj.18864/fig-2](https://doi.org/10.7717/peerj.18864/fig-2)

Huayuan Town, Xiangxi Region, Hunan Province, China. Yu'an Shan Member, Chiungchussu Formation, lower Cambrian (Series 2, Stage 3), *Wutingaspis*-*Eoredlichia* biozone, Yunnan, China.

Emended diagnosis. Vetulicolian with a weakly sclerotized, bipartite body. Anterior body with smooth surface, ovoid with weak segmentation, most prominent anteriorly, with circular anterior opening surrounded by prominent plates divided into inner and outer regions. Either side of anterior section with a longitudinal series of five oval-shaped lateral pouches, each covered by a hood-like structure. Posterior ventral margin of anterior section with a narrow finlike structure. Posterior section, laterally flattened, tapering

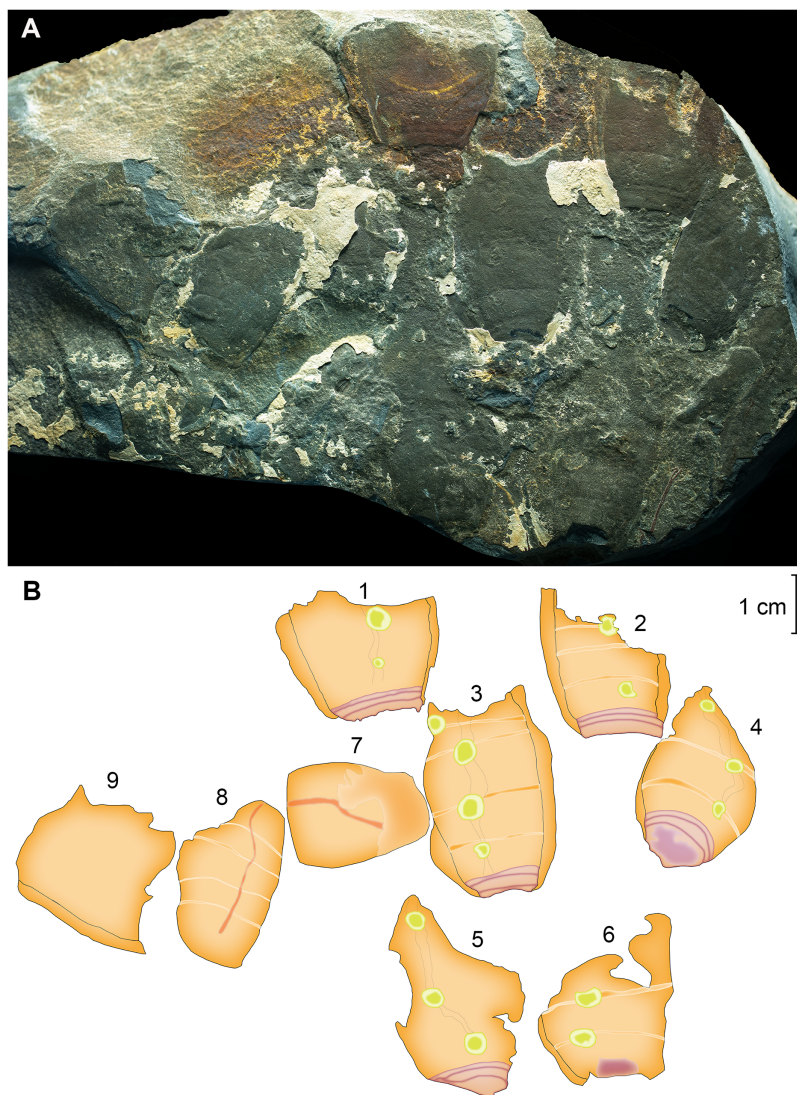


Figure 3 Clustered partial specimens of *Pomatrum* cf. *P. ventralis* Luo & Hu in Luo *et al.* (1999) from the Cambrian Stage 4 Balang Formation of China. (A) YKLP 14593-14561, six anterior specimens, one posterior specimen and two unidentifiable fragments of *Pomatrum* cf. *P. ventralis*. (B) Interpretative drawing of (A). [Full-size !\[\]\(ba1b80118482ccef74a5d718ca4d7242_img.jpg\) DOI: 10.7717/peerj.18864/fig-3](https://doi.org/10.7717/peerj.18864/fig-3)

anteriorly and posteriorly, with seven segments. Anus located near the center of the final segment of the posterior section, followed by a terminal notch. A sub-rounded, striated structure located at or between the third and fourth tail segments (modified from Aldridge *et al.*, 2007 and Yang *et al.*, 2023b).

Description. Best-preserved specimen includes part (YKLP 14591) and counterpart (YKLP 14592) (Fig. 2). Specimen bipartite, divided into anterior and posterior sections. Anterior ovoid, missing part of the dorsal margin. Weakly subdivided by ordering lines, only the anterior most subdivisions are visible (Fig. 2A). Surface smooth. Anterior section is 50 mm long and 25 mm wide at its widest point. First subdivision preserves a circular anterior opening. Inner anterior disc surrounds the opening, visible as a darkened disc,

displays some very fine lines radiating from the opening (Fig. 2D). Outer anterior disc region less well preserved, can be distinguished from the inner disc by a change in color (Fig. 2D). Lateral groove connects the opening and four ovoid lateral pouches; the fifth lateral pouch is not preserved. Anterior subdivisions preserves four ordering lines (Fig. 2B) only one crosses the whole body. Other ordering lines incomplete or missing. Diameter of the lateral pouches ranges from 2 to 5 mm.

The posterior section of YKLP 14591 appears to be detached from the anterior section. Anterior section 30 mm long and 15 mm wide at its widest point. Divided into seven segments (Fig. 2A). Alimentary canal located along the central axis, mostly complete, however, the sedimentary infill is intermittent, but locally present (Fig. 2F). Anus and notch not preserved. In segment 4, structure resembling the enigmatic sub-rounded structure preserved (Fig. 2F) described by *Yang et al. (2023b)*.

Counterpart (YKLP 14592) only preserves the first three segments of anterior section, oral opening, and two lateral pouches (maximum diameter 5 mm) (Figs. 2C, 2E).

In addition to the mostly complete specimen, nine (YKLP14593–YKLP14601) incomplete specimens are preserved on a single slab (Fig. 3). Six anterior sections, based on preserved lateral pouches. Their length varies between 22 and 34 mm, and the maximum width ranges from 18 to 25 mm. One specimen (Fig. 3B, #8) represents a posterior body. It preserves five segments, and most of the alimentary canal. This specimen is 31 mm long and 21 mm at its widest point. The other two specimens on this slab are not preserved well enough to identify them as anterior or posterior.

Remarks. The Balang Formation vetulicolians are tentatively assigned to *Pomatrum ventralis* based on the following structures they have in common with the specimens from the Chengjiang Biota (*Luo & Hu in Luo et al., 1999; Shu et al., 1999; Aldridge et al., 2007; Yang et al., 2023b*): a bipartite ovoid anterior section weakly subdivided by ordering lines, a circular anterior opening divided into inner and outer regions, the presence of oval-shaped lateral pouches connected by a lateral groove, a posterior section that is laterally flattened, tapering anteriorly and posteriorly, preserves seven segments, a medial alimentary canal and includes the presence of a sub-rounded structure located at the fourth tail segment. The tentative assignment is due to the incomplete preservation of all ten specimens. However, none of the morphological features suggest that the specimens might belong to a different species or even genus.

DISCUSSION

The oldest, and until now only known, occurrences of *Pomatrum ventralis* are from the lower Cambrian (Series 2, Stage 3) Chengjiang Biota of China, where hundreds of specimens have been recovered (*Shu et al., 1999; Aldridge et al., 2007; Hou et al., 2017; Yang et al., 2023b*). The specimens reported herein from the Balang Formation in Xiangxi Region, Hunan Province, are younger (Series 2, Stage 3–4), and preserved in dark grey calcareous mudstones. The limited distribution of the species in time and space suggests that this species might have been restricted to the lower Cambrian of Gondwana, however there are more Konservat-Lagerstätten (*sensu Kimmig & Schiffbauer, 2024*) in this time

interval in Gondwana than in Laurentia, which might lead to a biased view (*sensu Whitaker & Kimmig, 2020*) of its distribution.

This discovery of *Pomatrum* in deeper water sediments implores consideration of how broad the niche of *Pomatrum*, and vetulicolians in general, might have been as early as the lower Cambrian. Based on published data, the majority of vetulicolian species, including *Pomatrum*, are found in the Chengjiang Biota (*Shu, 2005; Aldridge et al., 2007*). This suggests that they likely preferred shallower, better oxygenated waters in the photic zone, as the Chengjiang Biota has been considered to record faunas from deltaic to inner shelf environments (*Saleh et al., 2022*). While few in number, the majority of the Balang Formation specimens (*Figs. 2, 3*) reported here are from a single slab (*Fig. 3*) and aligned in one direction, which suggests that the specimens were likely transported postmortem by currents, or represent a small die-off with clustered animals open to decomposition on the seafloor before burial. The presence of complete and exquisitely preserved *Herpetogaster collinsi* specimens in the same beds as the *Pomatrum* specimens (*Yang et al., 2023a*) suggest that transportation was probably minimal, and that the dismemberment of the *Pomatrum* specimens was more likely due to decomposition. In turn, this suggests that *Pomatrum* was living in deeper water environments.

While finding vetulicolians in deeper water environments in the lower Cambrian is unusual compared to other known Chinese specimens (*Fig. 4*), the Laurentian species of the Wuliuan and Drumian are all found in deeper water deposits (*Briggs et al., 2005; Caron, 2006; Aldridge et al., 2007; Conway Morris et al., 2015; Kimmig, Leibach & Lieberman, 2020*). This may imply an overall niche evolution for vetulicolians from shallow water environments in Cambrian Stage 3 to deeper water environments by Stage 4 (e.g., *Hou, 1987; Luo et al., 2005; Zhang & Hua, 2005; Luo et al., 2008; Yang et al., 2010; Li et al., 2015; Li, Liu & Ou, 2017; Chen et al., 2019; Fu et al., 2019; Yang, 2019*). If the signal is true and not an exposure or a taphonomic bias in different time slices—and there are currently no shallow water Konservat-Lagerstätten that offer a palaeoenvironmental counterpoint to the Chengjiang Biota known from the Wuliuan or Drumian (*Muscente et al., 2017*), a question that arises is what forces drove vetulicolians into deeper water environments? Increasing oxygenation of deeper waters and/or changes to resource availability may have been contributing factors (e.g., *Stockey et al., 2024*). A general trend to invade deeper water environments for Cambrian organisms, potentially linked to environmental pressures or biotic refuges, has been suggested (e.g., *Conway Morris, 1989* and references therein). However, this hypothesis will only be testable through shallow water Konservat-Lagerstätten from the middle and late Cambrian.

The Balang Formation preserves a relatively diverse fossil assemblage (e.g., *Liu & Lei, 2013; Yang et al., 2023a*) and the limited amount of taxonomic work it has received suggests, that the diversity is significantly higher than currently known. The lower Balang Formation deposit likely represented a depositional environment similar to the deeper water deposits of the Wulian Spence Shale in the Wellsville Mountains (*Kimmig et al., 2019*) or the Burgess Shale (*Nanglu, Caron & Gaines, 2020*). This is supported by the presence of several taxonomic groups that are usually associated with deeper water environments, like planktonic oryctocephalid trilobites (*Yin, 1996*) and *Herpetogaster*

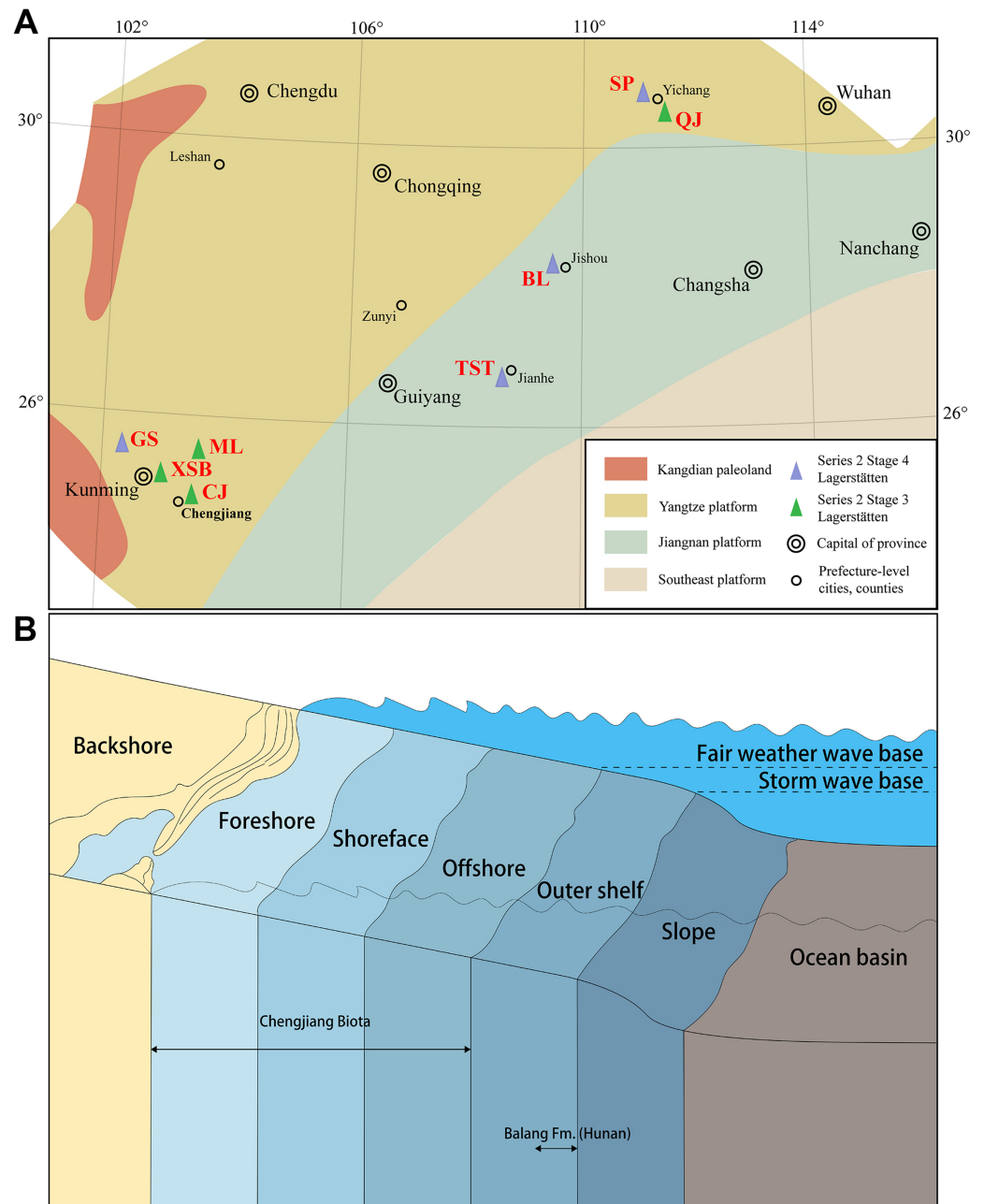


Figure 4 Distribution of vetulicolians in South China. (A) Paleogeographical distribution of vetulicolians in South China (Cambrian, Series 2, Stages 3–4). (B) Depositional environment of *Pomatrum* in South China (Cambrian, Series 2, Stages 3–4). Abbreviations: Bl, Balang Formation; Cj, Chengjiang Biota; Gs, Guanshan Biota; Ml, Malong Biota; Qj, Qingjiang Biota; Sp, Shipai Biota; Tst, Tsingshutung Formation (Jianhe Biota); Xsb, Xiaoshiba Biota. [Full-size !\[\]\(fcc3264021d438d9732560e78099f674_img.jpg\) DOI: 10.7717/peerj.18864/fig-4](https://doi.org/10.7717/peerj.18864/fig-4)

(Yang et al., 2023a), as well as the dark grey calcareous mudstones that preserve the biota. With each new discovery, it is also becoming more apparent that the taxonomic composition and species diversity of the Balang Biota are a unique window into the deeper-water Konservat-Lagerstätten of Gondwana. This deposit is currently also the most comparable Konservat-Lagerstätte to the Wuliuan and Drumian ones of Laurentia, not

only in biologic diversity and depositional environment, but also in the type of preservation of the fossils (*Wen et al., 2019; Yang et al., 2023a*). More research on this and similar deposits will provide a more complete picture of the biodiversity and paleoecology of the lower Cambrian deeper water environments and will contribute to the understanding of the early evolution of these habitats.

CONCLUSIONS

The Balang specimens of *Pomatrum* cf. *P. ventralis* represent the first report of this species from outside the Chengjiang Biota. The detailed preservation of the specimens, which includes the characteristic lateral pouches and the circular oral opening surrounded by two circular discs, makes an assignment to the genus unquestionable. This extends the range of the species into Cambrian Series 4. Additionally, the new specimens provide evidence for a wider ecological niche in early vetulicolians, exploring deeper water environments as early as late Cambrian Stage 4.

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ADDITIONAL INFORMATION AND DECLARATIONS

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Competing Interests

The authors declare that they have no competing interests.

Author Contributions

- Shuhan Ma conceived and designed the experiments, performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the article, and approved the final draft.

- Julien Kimmig analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the article, and approved the final draft.
- James D. Schiffbauer analyzed the data, authored or reviewed drafts of the article, and approved the final draft.
- Ruibo Li analyzed the data, authored or reviewed drafts of the article, and approved the final draft.
- Shanchi Peng analyzed the data, authored or reviewed drafts of the article, and approved the final draft.
- Xianfeng Yang conceived and designed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the article, and approved the final draft.

Data Availability

The following information was supplied regarding data availability:

The specimen data is available in Table 1.

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