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A new primitive polychaete with eyes from the lower Cambrian Guanshan biota of Yunnan Province, China

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Annelids are abundant and speciose in the modern world but are comparatively few in the fossil record. Primitive annelids were expected to have developed eyes and nuchal organs, but until now definitive evidence is still lacking. Based on a new specimen from the Wulongqing Formation, we describe *Gaoloufangchaeta bifurcus* gen. et sp. nov. from the Guanshan biota (Cambrian Series 2, Stage 4) of Yunnan province, China. The overall profile of the body and the presence of tentacles and stout parapodia with simple chaetae establish it as a primitive polychaete. By bearing bicellular eyes and possible nuchal organs, the new form has developed relatively strong sensory abilities. Our material further confirms that polychaetes were already diverse by Cambrian Series 2, indicating a much earlier origin for the group.

KEYWORDS

Annelida, Burgess Shale-type *Lagerstätte*, South China, Cambrian explosion, soft-bodied organism

Introduction

Annelida is a highly diverse phylum that includes approximately 17,000 described species (Nanglu and Caron, 2018). The records of fossil representatives are sparse because annelids are entirely soft-bodied and decay rapidly (Briggs and Kear, 1993; Parry et al., 2014). Whole-body fossil annelids have been recovered from early Cambrian to Carboniferous strata (Conway Morris, 1979; Schram, 1979; Thompson, 1979; Briggs et al., 1996; Sutton et al., 2001; Huang et al., 2004; Farrel and Briggs, 2007; Vinther et al., 2008; Högström et al., 2009; Briggs and Bartels, 2010; Liu et al., 2015; Han et al., 2019). In particular, the Cambrian annelids are predominantly polychaetes, which are strikingly various and widely distributed, including *Burgessochaeta setigera* (Walcott, 1911), *Canadia spinosa* (Walcott, 1911), *Peronochaeta dubia* (Walcott, 1911), *Insolicorypha psygma* (Conway Morris, 1979), *Stephenscolex argutus* (Conway Morris, 1979), and *Kootenayscolex barbarensis* (Nanglu and Caron, 2018) from the Burgess Shale, *Phragmochaeta canicularis* (Conway Morris and Peel, 2008), and *Pygocirrus butyricampum* (Vinther et al., 2011) from Sirius Passet, *Ipoliknus avitus* (Han et al., 2019), and *Adelochaeta sinensis* (Han et al., 2019) from Chengjiang, *Dannychaeta tucolus* (Chen et al., 2020) from the Cambrian Canglangpu Formation of Yunnan, and *Guanshanchaeta felicia* (Liu et al., 2015) from Guanshan. Nanglu and Caron (2018) proposed that primitive annelids could have developed eyes and nuchal organs. However, of all the polychaetes documented above, none has been demonstrated to possess eyes thus far.

Here, we describe a new primitive polychaete, *Gaoloufangchaeta bifurcus* gen. et sp. nov., from the Guanshan biota, which is characterized by the presence of a possibly tripartite body profile, a pair of tentacles, bicellular eyes, possible nuchal organs, and a bifid pygidium. These are the first taxon-bearing visual organs among Cambrian annelids. Our material provides a new epibenthic soft-bodied metazoan for the Burgess Shale-type *Lagerstätte* and further confirms the diversity of polychaetes by Cambrian Series 2, demonstrating that the group originated in a deeper time.

Geological setting

The Guanshan biota occurs in the Wulongqing Formation (Cambrian Series 2, Stage 4), which is distributed widely in eastern Yunnan, southwest China, including the Kunming-Wuding and Malong-Yiliang areas. The best-studied sections include the Gaoloufang and Gangtoucun sections of Kunming, the Shijiangjun section of Wuding, the Lihuazhuang section of Yiliang, and the Wulongqing section of Malong (Hu et al., 2013; Figure 1).

The specimen described in this study was collected from the Gaoloufang section (24.95916°N, 102.80539°E), which is ∼15 km southeast of the downtown area of Kunming (Figure 1). The Cambrian succession in this section mainly consists of the Hongjingshao and Wulongqing Formations. The former is composed of dark brown sandstones and gray argillaceous siltstones, while the latter comprises grayish-yellow silty mudstones interbedded with dark brown siltstones.

Materials and methods

The single specimen (RCP-ZJ-0001), preserved in a gray-yellow mudstone, was prepared using a fine needle under a Nikon SMZ 800 N microscope, revealing parts covered by matrix. Digital photographs were taken using a Canon EOS 5D SR camera with a Canon MP-E 65 (1-5X) macro lens under cross-polarized light, with the brightness and contrast of the resulting images processed in Adobe Photoshop CS 5. The specimen was imaged using an FEI Quanta 650 FEG scanning electron microscope. Elemental mapping was undertaken using an EDAX Pegasus energy dispersive X-ray spectroscopy (EDX) system, 112×magnification, 10.3 mm working distance, and an accelerating voltage of 20 kV. The specimen is housed in the Research Center of Paleobiology, Yuxi Normal University (RCP).

The specimen is of a bizarre appearance. Behind the second pair of uniramous parapodia, there is an apparent constriction, forming a neck-like structure, which is not known for any other Cambrian polychaetes (Figure 2). Based on the overall morphology of the body, we suspect that this is a taphonomic artifact. We tentatively divide the body into three regions as follows: anterior part, trunk, and pygidium, as shown in Figure 2.

The current publication and the new species are registered in ZooBank as urn:lsid:zoobank.org: act:54120A6E-2195-478E-A924-E686FD88D633 and urn:lsid:zoobank.org:act:D0F29632-9BDC-4CF6-9299-D84279B28A46, respectively.

Systematic paleontology

Phylum Annelida (Lamarck, 1809)
Class Polychaeta (Grube, 1850)
Gaoloufangchaeta gen. nov.

Derivation of name

Gaoloufang, referring to the location where the fossil was found; *chaeta*, a diagnostic characteristic of polychaetes.

Type species

Gaoloufangchaeta bifurcus sp. nov.

Diagnosis

Body tripartite (tentative) and elongated, bearing a pair of tentacles, bicellular eyes, and possible nuchal organs; the anterior part of the body being a reversed trapezoid in outline; at least seven pairs of uniramous parapodia with simple chaetae; pygidium large and bifid.

Gaoloufangchaeta bifurcus sp. nov.
Figures 2–4.

Derivation of name

From the Latin *bifurcus*, referring to the bifid structure on the pygidium.

Holotype

RCP-ZJ-0001, a complete specimen.

Type locality

Gaoloufang section, Kunming, Yunnan, China.

Type horizon

Wulongqing Formation (Cambrian Series 2, Stage 4).

Diagnosis

As for genus.

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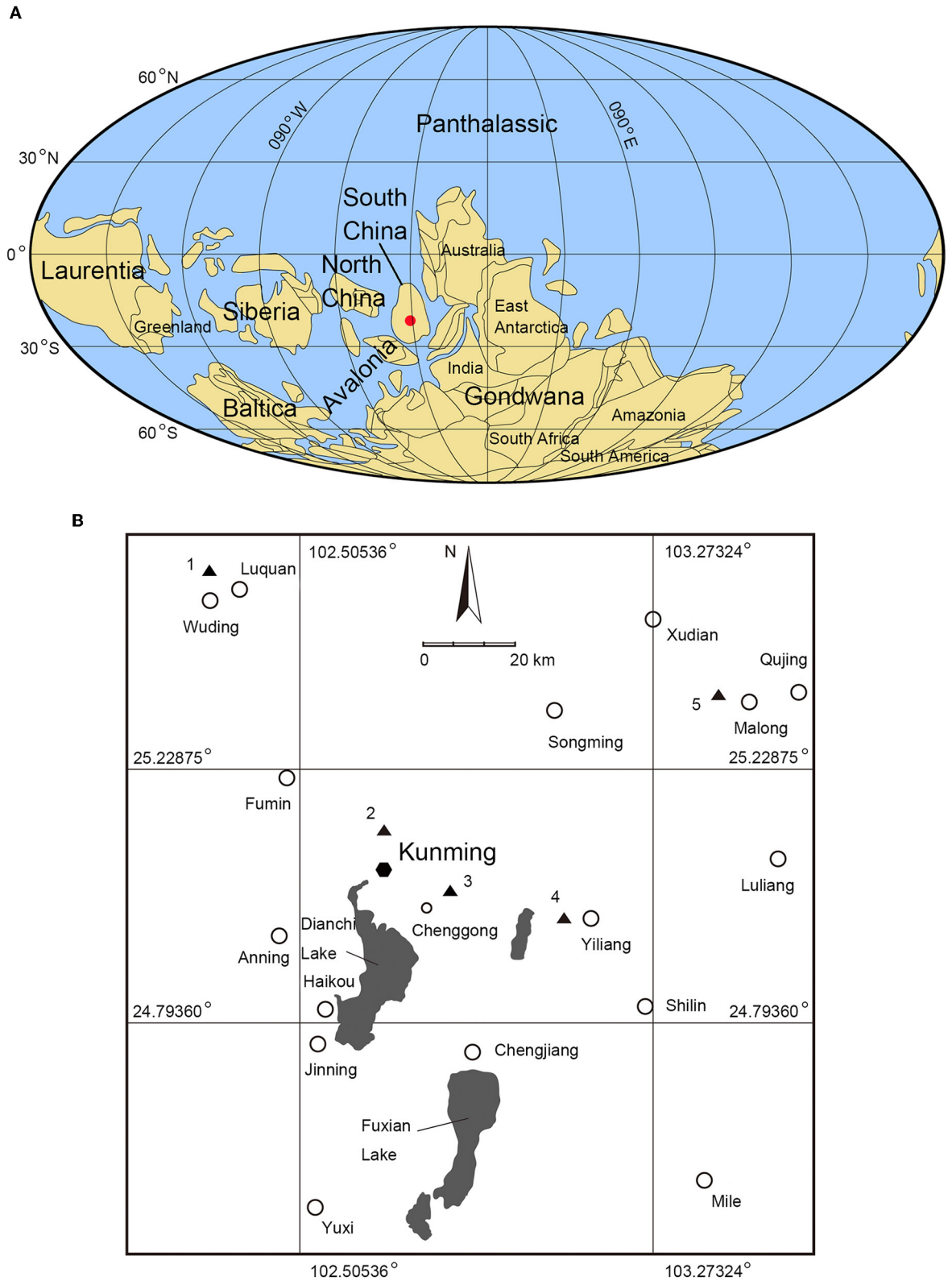

FIGURE 1
Paleogeographic and geographic maps, showing the occurrence of *Gaoloufangchaeta bifurcus* gen. et sp. nov. **(A)** paleogeographic reconstruction in early and middle Cambrian, modified from Torsvik and Cocks (2017); **(B)** the main fossil sites of the Guanshan biota in eastern Yunnan. 1, Shijiangjun; 2, Gangtoucun; 3, Gaoloufang; 4, Lihuazhang; 5, Wulongqing.

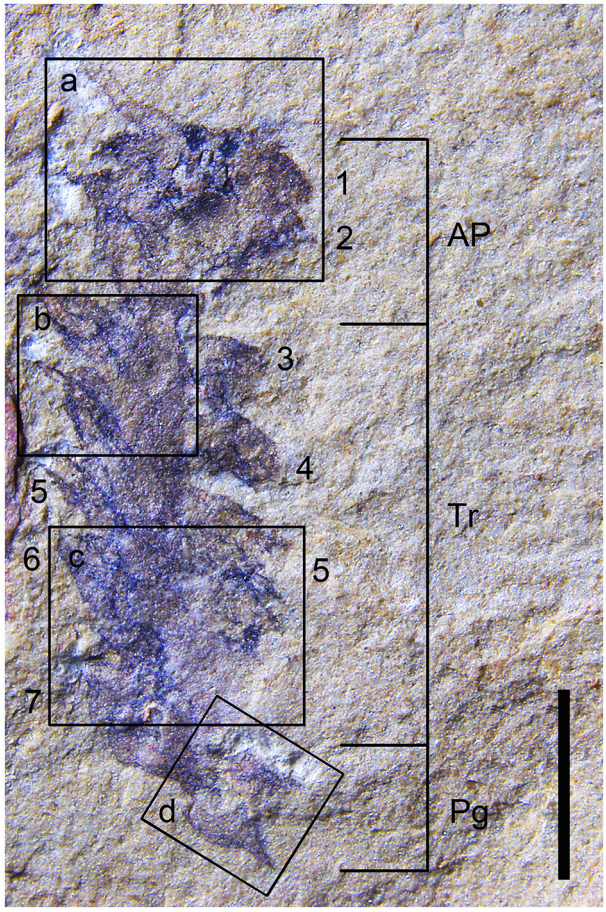

FIGURE 2
Gaoloufangchaeta bifurcus gen. et sp. nov. from the early Cambrian Guanshan biota (Yunnan Province, China). AP, anterior part; Pg, pygidium; Tr, trunk. The scale bar is 2 mm.

Description

The body is bilaterally symmetrical and possibly tripartite (composed of the anterior part, trunk, and pygidium) and preserved dorsoventrally flattened in parallel aspect, measuring 9 mm long (excluding tentacles).

The anterior part is a reversed trapezoid in the overall profile and measures 2 mm in length and 2.5 mm in maximum width (including parapodia, just above mid-length; Figures 2, 3A). A pair of tentacles stretches out anterolaterally from near the center of the anterior margin and tapers distally, with the best-preserved branch (left) measuring 1 mm long and 0.5 mm wide at the base (Figure 3). A pair of bicellular eyes is located behind the anterior margin and close to the bases of tentacles, with the diameter of each being 0.3 mm (Figure 3A). A total of two short longitudinal grooves, with each being 0.2 mm in length, are situated behind the eyes, which are interpreted here as possible nuchal organs (Figure 3A). A sub-ovoid dark patch lies behind the possible nuchal organs and may represent traces of the mouth or a partly preserved pharynx on the ventral side (Figure 3A). The posterior region of the anterior part is apparently constricted, forming a neck-like structure (Figure 2). Two pairs of uniramous parapodia are lined along both sides of the anterior part and are roughly triangular in outline (Figures 2, 3).

The trunk is elongated and tapers posteriorly, measuring 6 mm in length and approximately 3 mm in maximum width (at the first pair of parapodia). It comprises at least five homonomous segments, with each bearing a pair of uniramous parapodia that are broadly based and taper slightly distally, ending in blunt terminations (Figures 2, 4A, B). Chaetae are simple, thin, and situated at the distal ends of parapodia (Figures 4A, C). The posterior right side of the trunk is obscured, likely as a result of decay (Figure 4C). The boundaries of trunk segments are faint. The posterior part of the trunk is constricted slightly and associated with the pygidium and is devoid of any parapodia (Figure 4D). Column-like structures along the median trunk region are interpreted as traces of the gut (Figure 4A).

The pygidium is sub-rectangular in outline and measures 0.5 mm in length and 1.2 mm in width. From its posterior–lateral corners, two triangular structures arise (0.5 mm long for each), creating a more or less U-shaped morphology of the posterior margin (Figures 4D, E).

Remarks

The general shape of the body and the presence of tentacles, eyes, parapodia with chaetae, and pygidium clearly demonstrate that *Gaoloufangchaeta bifurcus* is a polychaete annelid. Chaetae are hard parts and most easily to be preserved, but they are absent in most parapodia of the new form. Decay could result in the detachment of chaetae in Cambrian polychaetes, e.g., *Canadia spinosa* (Walcott, 1911; Briggs et al., 1994; Parry et al., 2016). Traces of decay are present at the posterior right side of the trunk of *G. bifurcus* (Figure 4C), indicating that the body indeed experienced a period of decay prior to burial.

Gaoloufangchaeta bifurcus resembles *Guanshanchaeta felicia* (Liu et al., 2015) in having an elongated body, a pair of tentacles, and a bifid pygidium. However, *G. bifurcus* differs from *G. felicia* in that the body is much shorter and the trunk segments fewer; parapodia are uniramous and the first two pairs are followed by a constriction, forming a reversed trapezoid for the anterior part of the body (although this could be a taphonomic artifact; Figure 2). In addition, in *G. bifurcus,* the pygidium is strongly differentiated from the trunk and large relative to the body size (Figures 2, 4D, E), whereas it is poorly defined and rather smaller in *G. felicia* (figure 1 in Liu et al., 2015). *G. felicia* tapers both anteriorly and posteriorly, a morphological characteristic not found in *G. bifurcus*. Lastly, *G. bifurcus* differs from *G. felicia* in the presence of eyes and possible nuchal organs and the absence of a buccal tube. The differences above discriminate *G. bifurcus* from being a juvenile of *G. felicia*.

Han et al. (2019) described two polychaetes [*Ipoliknus avitus* (Han et al., 2019) and *Adelochaeta sinensis* (Han et al., 2019)] and three additional polychaete specimens from the earlier Chengjiang biota. *Gaoloufangchaeta bifurcus* differs from *Ipoliknus avitus,* in particular, in the absence of sclerites

FIGURE 3
Gaoloufangchaeta bifurcus gen. et sp. nov. **(A)** detail of Figure 2, position marked by frame a. **(B, C)** SEM-EDX maps of **(A)**, the specimen was rotated slightly to the left. Ey, eye; Mo?, possible mouth; NO?, possible nuchal organ; Pa, parapodium; Te, tentacle. The scale bars are 0.5 mm.

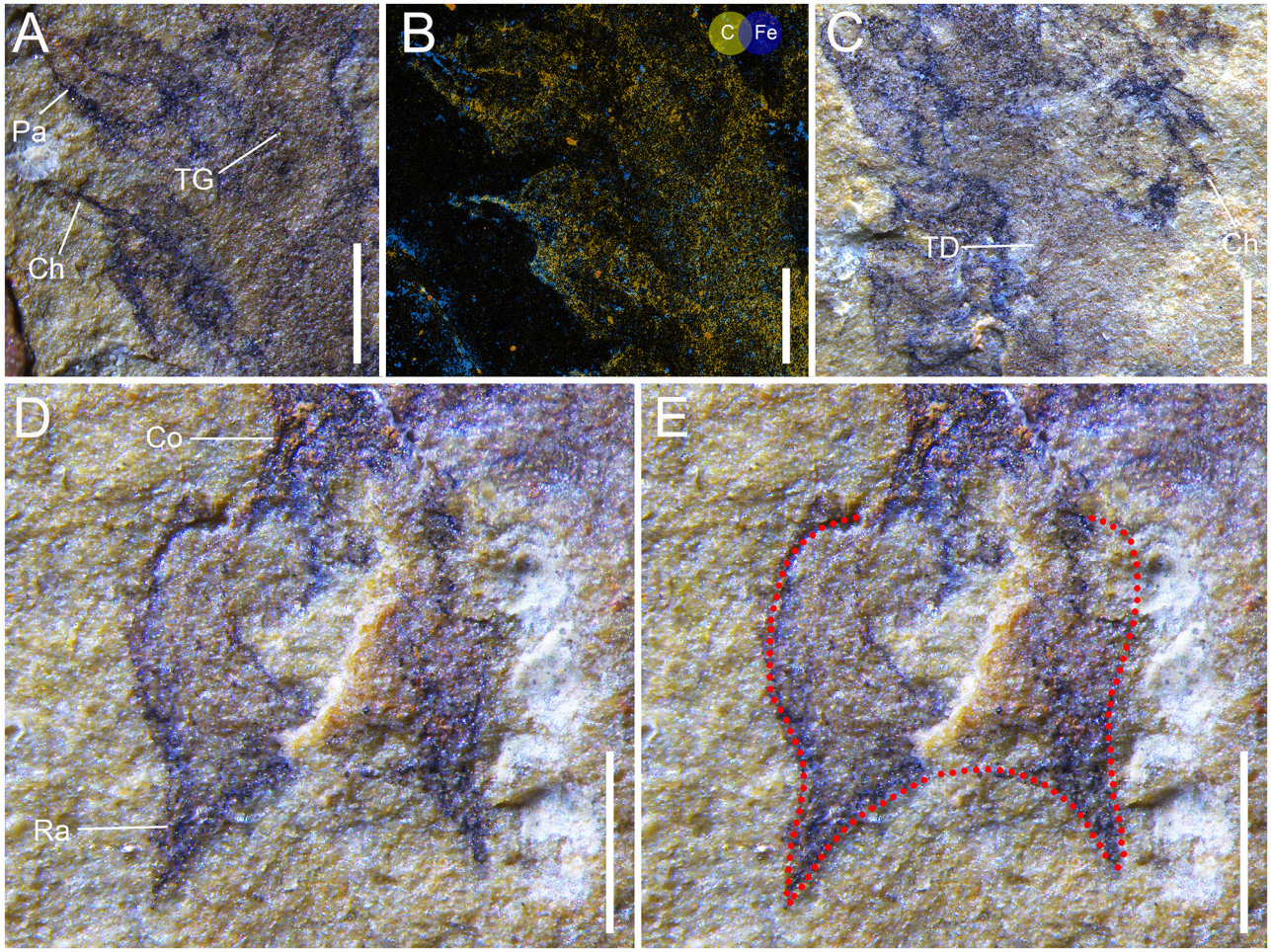

FIGURE 4
Gaoloufangchaeta bifurcus gen. et sp. nov. **(A)** detail of Figure 2, position marked by frame b. **(B)** EDX map of **(A)**, the specimen was rotated anticlockwise slightly. **(C)** Detail of Figure 2, position marked by frame c. **(D)** Detail of Figure 2, position marked by frame d; the specimen was rotated clockwise a little to show the pygidium in upright orientation. **(E)** Detail of Figure 2, position marked by frame d; the red dotted line shows the profile of the pygidium. Ch, chaeta; Co, constriction; Pa, parapodium; Ra, ramus; TD, traces of decay; TG, traces of gut. The scale bars are 0.5 mm.

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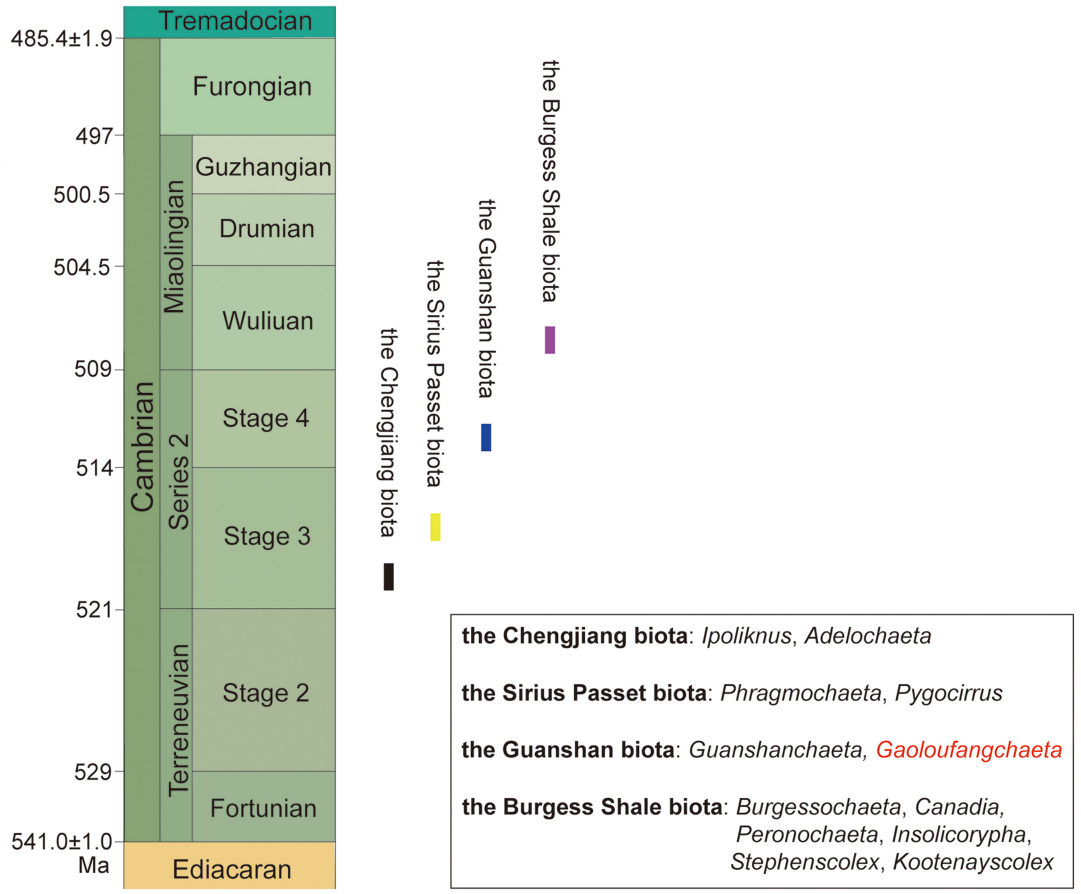

FIGURE 5
Main early and middle Cambrian fossil *Lagerstätten* yielding polychaetes.

and evident segment boundaries. *G. bifurcus* is different from *Adelochaeta sinensis* in that the latter has a clearly defined head region and aciculae, which are absent from the former. The most obvious similarity between *G. bifurcus* and the three unidentified polychaetes is the presence of chaetae; further comparisons are hard to make owing to the incomplete preservation of the three individuals. The absence of characteristics such as palps, prostomium, thorax, and parapodia with lateral lamellae discriminates *G. bifurcus* from *Dannychaeta tucolus* (Chen et al., 2020), a tube-dwelling polychaete from the Canglangpu formation (Cambrian Series 2, Stage 3) of Yunnan province.

Hitherto, the Burgess Shale has yielded the most abundant polychaetes of various morphologies in Cambrian *Lagerstätten*. *Gaoloufangchaeta bifurcus* approximates *Burgessochaeta setigera* and *Canadia spinosa* in the elongated profile of the body and by having uniramous parapodia. However, the number of body segments and the presence or absence of branchia discriminate the three taxa. *Peronochaeta dubia* and *Stephenscolex argutus* most differ from *G. bifurcus* in that they bear papillae at the anterior end of the body, instead of tentacles. *G. bifurcus* shares the same body length with *Insolicorypha psygma*, whereas the latter has a bipartite head region and more trunk segments. *Kootenayscolex barbarensis* bears a pair of large palps and a median antenna, which are absent from *G. bifurcus*.

Different from *Gaoloufangchaeta bifurcus*, *Phragmochaeta canicularis* (Conway Morris and Peel, 2008), a polychaete from the Sirius Passet *Lagerstätte*, has numerous long and thin chaetae and more trunk segments. The body terminating in a bifid structure is the most apparent similarity between *G. bifurcus* and *Pygocirrus butyricampum* (Vinther et al., 2011), another polychaete from the Sirius Passet. However, the profile of the bifid structure is different between the two taxa: V-shaped for *P. butyricampum* and more or less U-shaped for *G. bifurcus*. In addition, *P. butyricampum* has more trunk segments.

Discussion

Gaoloufangchaeta bifurcus gen. et sp. nov. is described based on a single specimen with decay traces, and thus, some of its characteristics cannot be confirmed as original. The neck-like structure (Figure 2) may be an artifact formed during burial given the soft nature of annelid bodies, and hence, the tripartite outline of the body of the new form is tentative in this study; the parapodia lined along both sides of the trunk appear to be too stout, and whether each is composed of two lobes (i.e., notopodium and neuropodium) cannot be confirmed on this comparatively poorly preserved specimen; they are

temporarily interpreted here as uniramous; the morphologies of the inferred nuchal organs and mouth are not clearly shown on the specimen, and their identities need to be confirmed by additional and better-preserved ones; decay traces obscure the morphology of the posterior part of the trunk (Figures 2, 4C).

Gaoloufangchaeta bifurcus from Cambrian Series 2 of southwest China is one of the oldest fossil annelids recovered so far. Structures such as eyes and nuchal organs have previously been expected but not found in ancestral annelids (Weigert et al., 2014; Nanglu and Caron, 2018). The specimen of *G. bifurcus* clearly shows evidence of eyes and possible nuchal organs (Figures 2, 3) for the first time in Cambrian polychaetes, demonstrating that the oldest annelids are not all devoid of these sensory organs. By having tentacles, eyes, possible nuchal organs, and stout parapodia, *G. bifurcus* clearly had comparatively strong sensory abilities and an active and epibenthic lifestyle. Although no evidence of a proboscis with jaws is found in the single specimen, the possibility of the new taxon being a predator or scavenger cannot be ruled out. Our material not only provides a new epibenthic representative for early Cambrian marine animals but also a new soft-bodied metazoan for the Guanshan biota.

Until now, fossil polychaetes are the most diversified and abundant in the Burgess Shale (Cambrian Miaolingian, Wuliuan); the earliest whole-body preserved ones date back to Cambrian Series 2, Stage 3, represented by *Phragmochaeta canicularis* and *Pygocirrus butyricampum* from Sirius Passet, and *Ipoliknus avitus* and *Adelochaeta sinensis* from Chengjiang. Together with *Gaoloufangchaeta bifurcus*, the slightly younger Guanshan biota (Figure 5) has yielded two types of polychaetes. These occurrences confirm that polychaetes were already diverse in morphology by Cambrian Series 2, indicating a much earlier origin for the group.

Gaoloufangchaeta shows the characteristics proposed for primitive annelids, i.e., errant polychaete body form, parapodia with simple chaetae, and prostomial sensory organs (Parry et al., 2014; Weigert et al., 2014), and thus, it is among the primitive representatives of Annelida. Of all the early and middle Cambrian polychaetes, only the bodies of *Pygocirrus*, *Guanshanchaeta,* and *Gaoloufangchaeta* terminate in a bifid structure, suggesting a similar phylogenetic grade in between. *Gaoloufangchaeta* bears eyes and possible nuchal organs that are absent from *Pygocirrus* and *Guanshanchaeta*, which implies that *Gaoloufangchaeta* might be comparatively more derived and/or even a representative of the last common ancestor of annelids.

Conclusion

We describe a new primitive polychaete, *Gaoloufangchaeta bifurcus* gen. et sp. nov., from the Cambrian Series 2, Stage 4 of southwest China. This is the second polychaete from the Guanshan biota and among the oldest records of fossil annelids globally. Our material not only demonstrates that relatively strong sensory organs had developed in Cambrian annelids but also further confirms that polychaetes were already diverse in morphology by Cambrian Series 2.

Data availability statement

The original contributions presented in the study are included in the article/supplementary material, further inquiries can be directed to the corresponding author.

Author contributions

JZ and YL designed the study, collected and prepared the fossil, and wrote the first draft of the manuscript with substantial input from PS. JZ photographed the specimen and prepared the figures. All authors described and interpreted the specimen. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

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