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## Enigmatic ribbon-like fossil from Early Cambrian of Yunnan, China

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### ABSTRACT

During the Late Neoproterozoic and Early Cambrian, a series of paleogeographic and paleoecological events occurred associated with deglaciations and the evolution of life. The appearance of fossils representing diverse phyla, novel body plans and complex ecologies in Ediacaran and Cambrian sedimentary successions has sparked diverse hypotheses about potential drivers for the radiation of early animals during this interval. Recently, new macroscopic fossils of carbonaceous compressions with unique features have been found in Anning, Yunnan, China. The fossils' bodies are ribbon-shaped and bilaterally symmetric, with dense longitudinal features and transversal features. The fossils occur 0.68 m below a bentonite interlayer which has been dated  $535.2 \pm 1.7$  Ma by Ri-xiang Zhu and his team in 2009. The relatively simply morphology of these fossils, coupled with a lack of preserved internal structures challenge efforts taxonomically identify the precursor organism and definitively ally it to a living group. However, the symmetry and unusual features of the body are analogous to members of Platyzoa. The presence of ribbon-shaped fossils in the Zhongyicun Member in Anning indicates that these organisms were at least a locally significant component of Cambrian seafloor ecosystems, and may hold important implications for our understanding of the early evolution of Bilateria.

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## 1. Introduction

The Cambrian Explosion—recorded by a major increase in the size, diversity and apparent ecological complexity of skeletonized animal body fossils, as well as trace fossils—was a remarkable episode in Earth history. Although recent years have witnessed debate as to whether the Cambrian radiation was truly “explosive” in nature, or whether its roots extended back into the Ediacaran (Wood R et al., 2019; Paterson JR et al., 2019; Parry LA et al., 2017), the Cambrian fossil record nonetheless provides critical insights into the radiation of diverse animal lineages, the widespread emergence of biomineralization in both macroorganisms and small shelly faunas, and the extensive colonization by animals of both the upper surface of the seafloor and seafloor sediments.

Although bilaterian-produced trace fossils occur in Ediacaran and Terreneuvian successions, a paucity of macrofaunal body fossils from this interval has, historically, hampered efforts to identify potential tracemakers.

With prompt evidenced delivered by the abrupt appearances of diverse animal lineages in the fossil record during the Early Cambrian (about 541–509 Ma), the Cambrian explosion was an astonishing evolutionary event of great magnitude. The Terreneuvian Epoch (about 541–521 Ma) (Landing E et al., 2007) are characterized by fossils of tubes, shells, and sclerites of small shelly faunas and trace fossils as large burrows and trails implying that soft-bodied elongate animals evolved instantly before the dawn of Cambrian. However, no confirmed body fossils that could have produced these trace fossils have been found before or during the Terreneuvian Epoch (Zhang XL et al., 2017), which might due to the absence of macroscopic soft-bodied faunas during this period.

Here the authors reported a soft-bodied, ribbon-shaped, macro fossil, *Rugosusivitta orthogonia* gen. et. sp. from Early

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Cambrian phosphorite of Anning City, Yunnan Province, China (Fig. 1). These fossils appear to be a Fortunian in age and appear 0.68 m below an 80 cm thick bentonite horizon dated to  $535.2 \pm 1.7$  Ma (Zhu RX et al., 2009). This bentonite layer is commonly found in between two series of phosphorite in Huanan (South China) Block and has been considered to mark an isochronous surface. The fossils' light brown bodies are ribbon-shaped and bilaterally symmetric with dense longitudinal and transversal features and the length always exceeds its width. The widest part is approximately 1 cm and has preserved more than 34 cm in maximum length. In rough morphology, the fossil is similar to macro-algae or vermiform animals of the Bilateria. Due to the paucity of well-preserved anatomical details, the taxa affinity of *Rugosusivitta* is still very enigmatic. However, the unique combination of repeated longitudinal and transversal striations are more characteristic of bilaterian groups. In addition, *Rugosusivitta* may potentially provide a record of not only large, soft-bodied life during the Early Cambrian, but also a potential progenitor for Early Cambrian large trace fossils. If *Rugosusivitta* is flat-bodied animals, this ontological fossil preservation might provide a vital record of the large soft-bodied organism during the Early Cambrian that could be the producer of those large trace fossils from Early Cambrian in Yunnan and imply a great significance to the earliest evolution of macroscopic soft-bodied faunas.

## 2. Geological setting

All specimens are collected from the Zhongyicun Member of the Yuhucun Formation. General geology, stratigraphy, and palaeontology of eastern Yunnan Province, China, have been discussed in a number of publications (Luo HL et al., 1994; Zhu MY et al., 2001, 2019; Li DA et al., 2009).

In the Meishucun section of eastern Yunnan Province,

South China, The Zhongyicun Member is subdivided into Lower Phosphate, White Clay, Upper Phosphate and Dahai members (Zhu MY et al., 1997). The Zhongyicun Member ranges around 12 m in Anning City, and consists of light colored thin to medium thick layer phosphorite with bentonite intervals. Abundant fossils including small shelly fossils *Circotheca*, *Turcutheca*, trace fossils *Sellaulichmus* and *Chondrites* were reported in the Lower Zhongyicun Member (Hua H et al., 2001). The fossils first occur 0.68 m below the  $535.2 \pm 1.7$  Ma bentonite and are found very abundant in an enrich interval of 0.8 m height (Fig. 2) in dolomitic phosphorite. The GSSP of Precambrian–Cambrian boundary is marked by the first appearance datum (FAD) of the trace fossil *Treptichnus pedum* (Crimes TP et al., 1986; Buatois LA, 2018). In the Zhongyicun Member, the FAD of *Treptichnus pedum* is in layer 5 and 6.4 m above the bottom of Zhongyicun Member (Zhang ZL et al., 2015). The first occurrence of *Rugosusivitta* is very close to the defined Precambrian–Cambrian boundary in Yunnan Province.

## 3. Systematic paleontology

**Phylum** Platyhelminthes

**Class** Uncertain

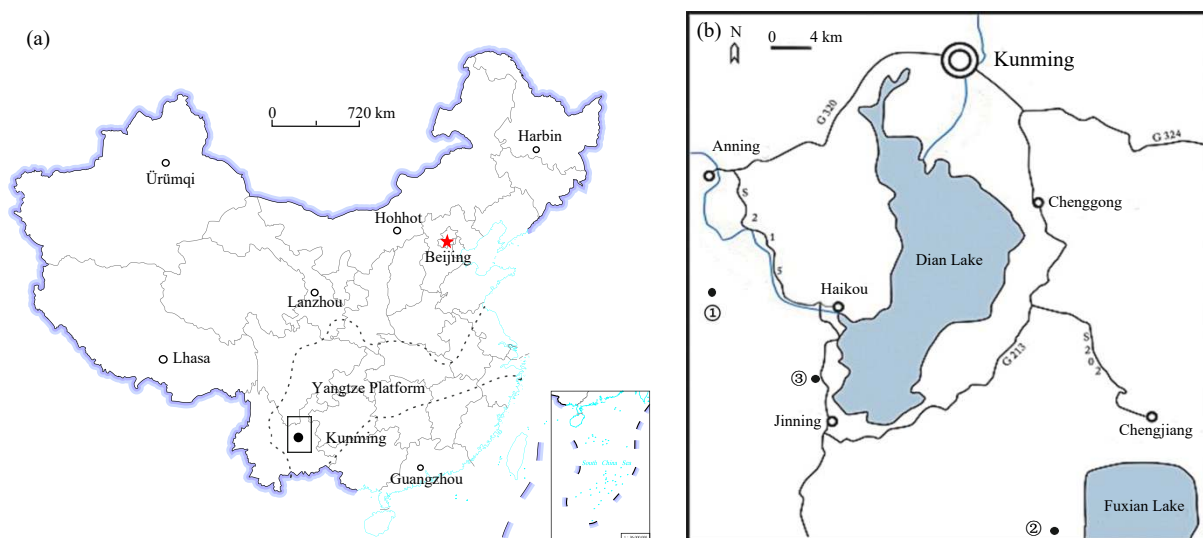
**Family** Uncertain

**Genus** *Rugosusivitta* gen nov. Figs. 3a–e; Figs. 4a–d

**Type**—A specimen with no counter part: IG-170922. The specimen is deposit at present in Key Laboratory of Stratigraphy and Palaeontology, Ministry of Natural Resources, Beijing, China.

**Etymology**—The Latin “vitta” (band) indicates the elongated ribbon-like body of the fossils and “*Rugosus*” (densly folded) indicates the dense pleat ornamentation on the body.

**Diagnosis**—The macrofossil compressions generally



**Fig. 1.** Map showing the locations of the studied sections of the Anning fossils *Rugosusivitta*. ①—the Mingyihe section. It is in a phosphorite quarry owned by Yunnan Phosphate Chemical Group where the fossils were collected. The quarry is 62 km from Kunming, Yunnan. The specimens were collected from Yuhucun Formation, Zhongyicun Member. ②—the locality of the Qingshuigou section. ③—the locality of the well-known Meishucun section.

present a banding outline. No distinct segmentation features nor head or tail structures. The body is elongate and flat. Dense pleat wrinkles is on the whole body.

***Rugosusivitta orthogonia*** sp. nov. Figs. 3a–e;

**Holotype**—Referred to specimen IG-170922 (Fig. 3e), deposit at present in Key Laboratory of Stratigraphy and Palaeontology, Ministry of Natural Resources of China, Beijing, China.

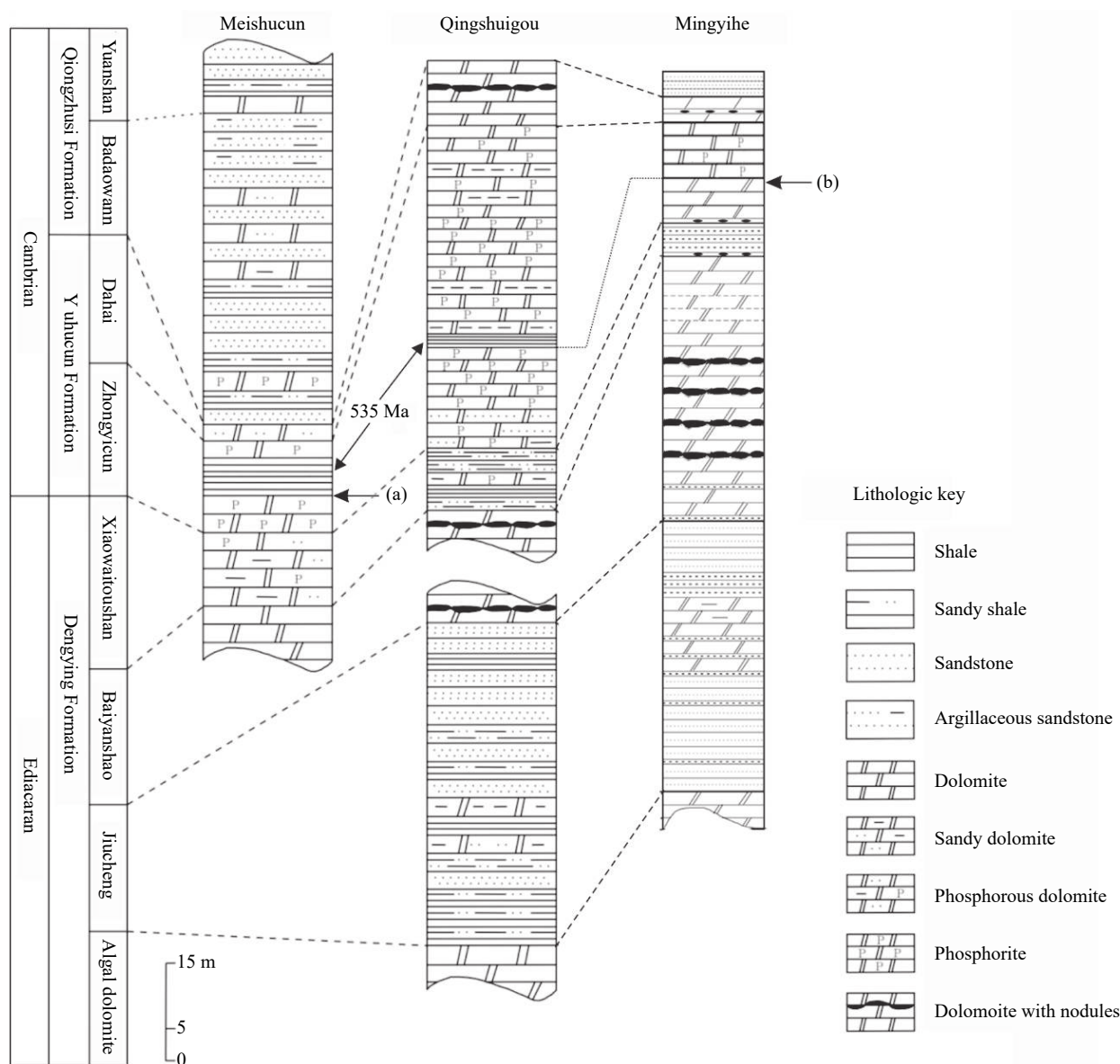
**Type horizon and locality** - Yuhucun Formation, Zhongyicun Member, near Wangjiawan, Yuxi, Yunnan Province, China. The GPS is 24°48'00"N, 102°28'12"E.

**Etymology**—"vitta" indicates the elongated ribbon-like body of the fossils and "*Rugosus*" indicates the dense pleat ornamentation on the body. "*orthogonia*" (orthogonal) refers to the two sets of orthogonal dense and parallel line textures on the body.

**Paratype**—IG170915-2, IG190818 deposit at present in Key Laboratory of Stratigraphy and Palaeontology, Ministry of Natural Resources of China, Beijing, China.

**Other materials**—An additional 66 specimens are preserved on the same surface in Anning City and preserved in Key Laboratory of Stratigraphy and Palaeontology, Ministry of Natural Resources of China, Beijing, China after measured and photographed.

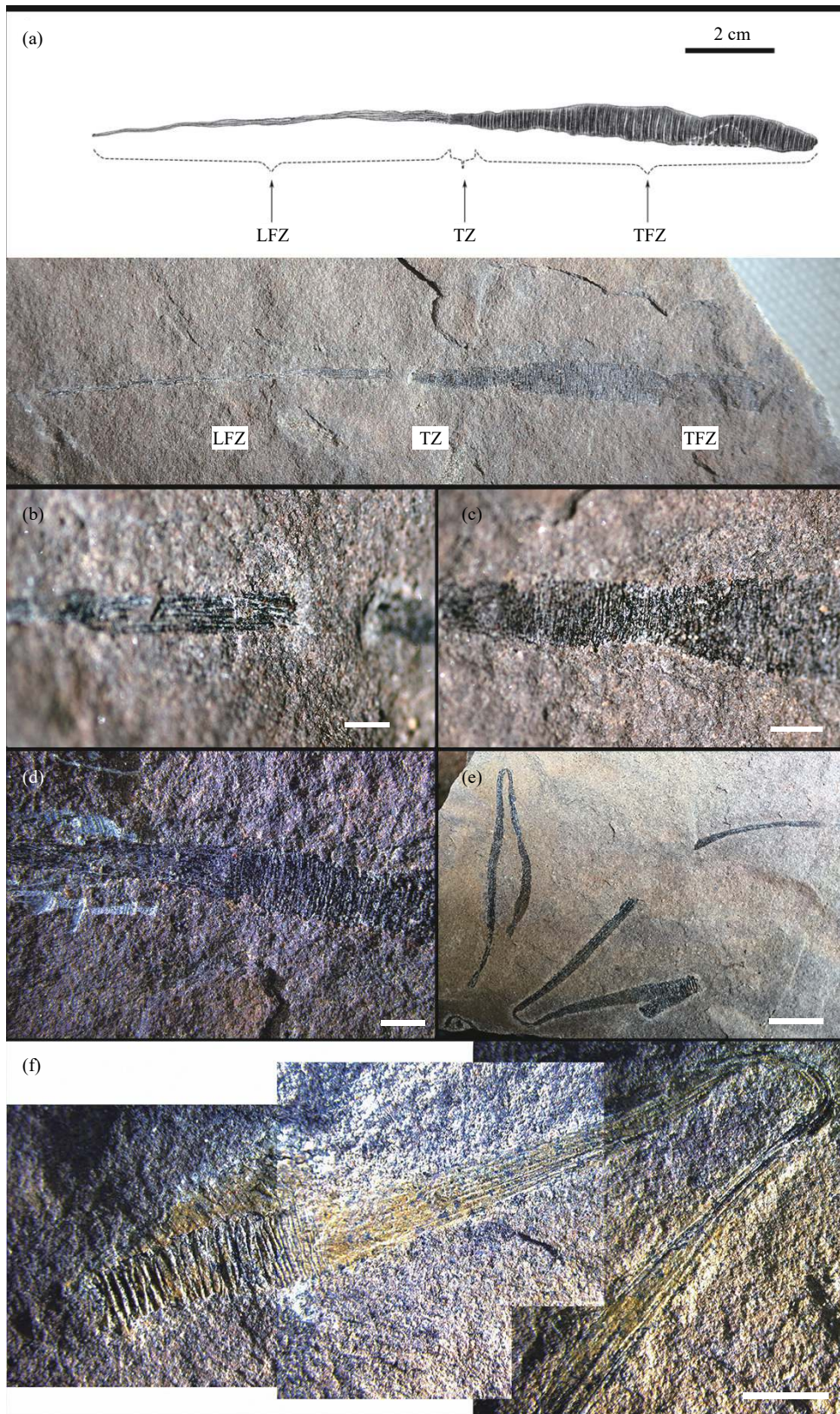
**Diagnosis**—The macrofossil compressions generally present a banding outline. No distinct segmentation features nor head or tail structures. The light brown ribbon-like flat body usually presents "U" shape curves, "Z" shape folds and "X" shape twists in the rock (Figs. 4a–d). Body length ranges from 50 to 150 mm and body width ranges from 2 to 5 mm. The body consists of three distinct units or zones, defined by (1) longitudinal features, (2) transverse features and (3) a



**Fig. 2.** Stratigraphic column of Dengying and Yuhucun Formations, Anning City, South China. Position of the interbed yielding fossils is indicated in the column with an arrow. The 535 Ma old bentonite layer is marked and correlated between the columns. a—the FAD of *Treptichnus pedum* in Meishucun section is at the top of the Lower Phosphate unit (Zhu MY et al., 1997). b—the first occurrence of *Rugosusivitta orthogonia* is 0.68 m below the bentonite layer. All specimens were collected from the Zhongyicun Member.

transitional zone intermediate between the zones associated with longitudinal and transverse features. The longitudinal

zone bears elongate, narrow longitudinal features parallel to the body margin, typically consisting of 10–14 distinct ridges.



**Fig. 3.** a—specimen No. IG-170915-2: the body divided into three zones: transversal features zone (TFZ), transition zone (TZ) and longitudinal features zone (LFZ). b—details of the longitudinal features zone. c— details of the transversal features zone. d—details of the transition zone. e—specimen No. IG-170922: the preservation of *Rugosusivitta*, the fossils come out separately. f—spliced image of the up left folded specimen of IG-170922. The black scale is 2 cm and the white scale is 1 cm. The specimens are housed in the Institute of Geology, Chinese Academy of Geological Sciences.

The so-called transition zone is short, and contains both longitudinal and transverse features. The transverse zone bears dense transverss features perpendicular to the body margin and typically contains 6 to 8 lines per mm. Most of these macrofossils are preserved linearly. However, occasionally these macrofossils are bent or folded.

**Description**—The body is relatively elongate (total length 16.8 cm and maximum width 1.3 cm), and can be divided into three zones: Transversal features zone, transition zone and longitudinal features zone according to the features on the body (Fig. 3a). The longitudinal features zone is the narrow part of the body and the full width is about 1–5 mm (Fig. 3c). The narrowest part occurs in bending and folding areas. The length of the longitudinal zone is slightly more than a half of the whole body. Longitudinal features, oriented parallel to the body axis, occur throughout this zone, without branching and spaced less than 1 mm apart. The transversal features zone commonly occurs in the widest section of the body, where maximum width is about 5–8 mm. This broader interval usually constitutes approximately half of the whole body (Fig. 3d). Transversal zone bears dense parallel transversal textures which is fine and closely woven. The transition zone is connecting the transversal zone and the longitudinal zone. It is the shortest section on the body and the total length is below 1 cm (Fig. 3e). In this section, the body width narrows from the transversal zone to the longitudinal zone. In the transition

zone, the pattern of the longitudinal textures changes slightly. While approaching the transverse textures, the longitudinal features begin to bend inward and intersect with adjacent lines. However, this variation appears to largely define exterior or distal longitudinal features; in the middle of this zone, the lines remain straight and parallel. The transverse textures in the transition zone hold the same pattern as transition zone which are dense and parallel and cut off crisply at the junction with longitudinal textures. Considering the transverse zone always exceeds the longitudinal zone in width and the transition between two textures are abrupt, the transverse zone is likely to be a sheath covering the longitudinal feature zone outside. Disc-shaped structure was found attached to the end of the longitudinal feature zone in 3 specimens (Fig. 3a–c). In most specimens, no origination or terminal was preserved.

**Occurrence**—Lower Cambrian, Southwest China.

#### 4. Discussion

The fossils were first reported in 1986 by Hui-ling Luo as *Sabellidites yunnanensis* Luo et Zhang 1986 and *Sabellidites badaowanensis* Luo et Zhang 1986 in upper Yuanshan Section in Jinning, Yunnan Province (Luo HL and Zhang SS, 1986). The transversal features on the ribbon like body is similar to the *Sabellidites* Yanichevsky, 1926 (Sokolov BS et al., 1965) discovered in Baltic Stage in Russia. Later, the



**Fig. 4.** Ribbon-like fossils from Qingshuigou, Jiangchuan, Yunnan Province. a—dense transversal features similar to *Rugosusivitta*; b, c—abundant in the lowermost Zhongyicun Member; d—directional alignment of the ribbon-like fossils. Scale bar for all specimens is 1 cm.

*Sabellidites yunnanensis* and *Sabellidites badaowanensis* was considered to be a synonym of *Mafangscoclex sinensis* Hu 2005 due to the same microstructure of plates on the body. The same bone plate with 5 rows of papillae structure was the key evidence that those fossils were synonyms. And the discovery of introverts and a pair at the tail characteristics of hook-like spines on *Mafangscoclex sinensis* suggest that those fossils belong to Palaeoscolecidae Whittard, 1953 instead of Palpitaria (Luo HL et al., 2014).

Due to their ribbon-shaped, longitudinally ornamented elongate bodies and the chronostratigraphic position of this material, the authors compared the Anning fossils to that of other Upper Neoproterozoic and Lower Cambrian taxa with broadly similar morphologies. Some of these features are shared by a wide range of organisms, including algae, cnidarians, bilaterians and some uncertain phylogenetic metazoans. Despite from the paucity of discrete characters among the Anning fossils, the apparent bilateral symmetry of its flat and elongate body and the dense linear ornamentation on its surface suggest closer affinity to members of Platyzoa, as well as macroalgae. The bending, folding and twisting of the body of taphonomically deformed Zhongyicun fossils suggest that this organism contained a soft, relatively flat body, perhaps most similar to the plesiomorphic characters of Platyzoa (Figs. 3e–f, 4a–d).

#### 4.1. Taxonomic affinities and the ribbon-like preservation

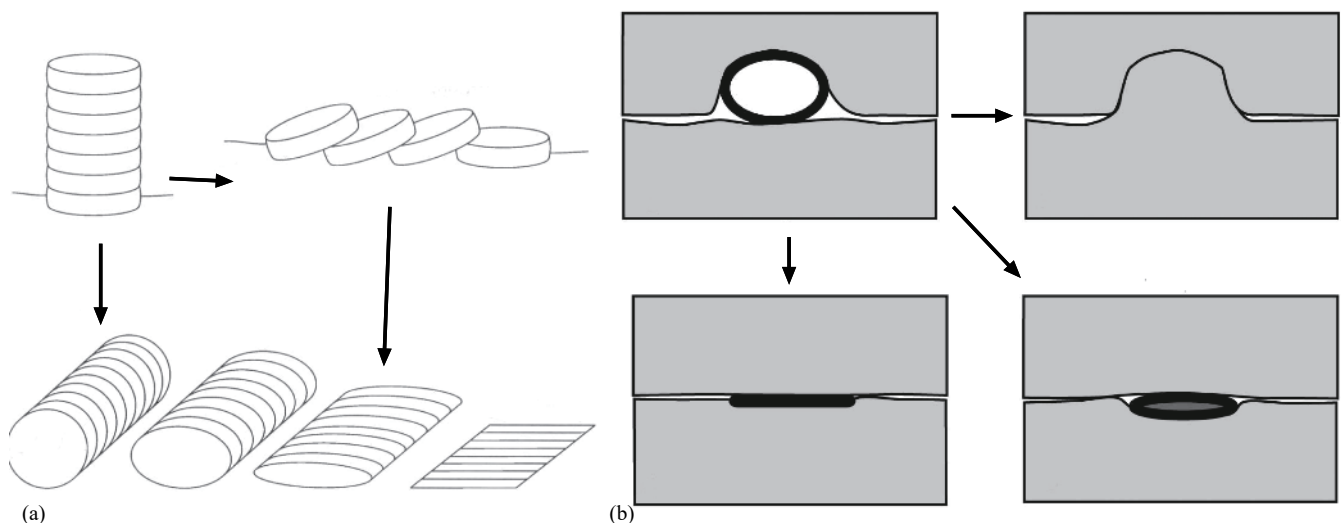
The affinities of this worm are obscure due to its relatively simple morphology. *Rugosusivitta orthogonia* stands out from the matrix sharply because of their strong color contrast to the surrounding. The so-called ribbon-like outline with its body ornamentation morphology is enigmatic. The lacks of both internal and out-attached structures of the body make it difficult to define its taxonomic categorization. Compared with the Early Cambrian fossil species with similar morphological features, it is found that these newly

discovered fossils have similar characteristics with algae, Palaeoscolecidae and trace fossils of the same period.

The fossils discovered in Anning were identified as belonging within Palaeoscolecidae, due to similarities in overall, elongate morphology and the presence of transverse features. The specimens from Anning do share some resemblance to a putative palaeoscolecid fossil in Jinning, Yunnan Province. The lack of evidence of plates and pailla associated with the transverse-feature zone were interpreted to be taphonomic rather than anatomical; the strong contraction of the body renders identification of distinct plates challenging. The strong contraction could secondarily make the irregular or staggered arrangement of the large bone plates appear more regular than they were during the organism's lifetime (Luo HL et al., 2014), but these parallel surface ornamentations will show a visible fluctuation on every single line during the secondary contraction. *Rugosusivitta orthogonia* have straight-line ornamentation and these parallel surface features are much denser than the ones on Palaeoscolecidae.

At same time, the new fossil records found in Anning present not only transversal ornamentation as micro ridges on the body but also longitudinal features on half of the body that *Mafangscoclex sinensis* and other Palaeoscolecidae fossils would not preserve. Due to this morphological difference on the body, there would be no reason to consider the ribbon-like fossils in Anning as Palaeoscolecidae.

According to the morphological characteristics of *Rugosusivitta*, there could be many interpretations of its taxa. Another interpretation from the earliest interpretation is that these fossils could be an alternative form of *Shaanxilithes* as they were reported in 1982 (Bureau of Geology and Mineral Resources Exploration of Yunnan Province, 1990). *Shaanxilithes ningqiangensis* was originally described as a ribbon-shaped trace fossil, composed of transverse, parallel annulations and was first assigned these enigmatic structures to *Sabellidites* (Xing YS et al., 1984). Subsequent research



**Fig. 5.** The preservation of the ribbon-like fossils. a—compression of the *Shaanxilithes*, the disk-like units might deform during the compression. b—the compression of the tubular algae fossils. Various forms would appear as ridges, bands and filled minerals.

has found that *Shaanxilithes ningqiangensis* is a body fossil consisting of compressed organic tubes characterized by transverse ornamentation, and which are also preserved as fragments, as well as in the form of disarticulated units (Fig. 5a; Tarhan LG et al., 2014). *Shaanxilithes* have a long-debated problem of its ecology and taphonomy. *Shaanxilithes* are found in Jiucheng Member in Houjiashan Formation which is quite near the occurrence of the specimen (Gu P et al., 2018). The annulated structure of *Shaanxilithes*, with dense transverse features, is readily recognizable from hand samples. However, longitudinal features analogous to those observed in the Anning specimen, are not known for *Shaanxilithes*.

*Shaanxilithes ningqiangensis* is often preserved along bedding planes of phosphate-rich silty and calcareous shale, containing little to no carbonaceous material and have disc-like units (Meyer MB, 2012). If *Rugosusivitta* were a putatively related form of *Shaanxilithes* in a different taphonomic process, the original sub-disc shape should be preserved as well and the outline would be waved, while *Rugosusivitta* preserved mainly intact in a ribbon-like form and no fluctuation on the edges was found in the fossil record.

Morphologically analogous fossils—including forms characterized by multiple styles of surface ornamentation—include priapulid fossils in Chengjiang fauna. For instance, *Ottoia* in the Maotianshan Shale are commonly preserved as carbonaceous compressions bearing longitudinal textures. Vermicular priapulids in Chengjiang fauna are cylindrical and elongate, and many species of Chengjiang priapulids have both longitudinal and transversal ornamentation, analogous to that characterizing the specimen from Anning (Ma XY et al., 2010).

However, there is no any distinguishable sign of head or tail on the body of *Rugosusivitta orthogonia*, which indicates that nothing on the specimen can correspond to a structure related to its proboscis or holdfast as small claws. It would be unlikely that all the specimens are preserved without any sign of introverts or its fragments assuming they were priapulids. One is that the fossil is at least quite similar to macroalgae fossils such as *Vendotaenia*.

Macroalgae fossils occur massively in Jiucheng Member (which underlies the Xiaowaitoushan Member) including *Vendotaenia*, *Chuarua*, *Tawuia*, *Shouhsenia*, *Longfengshaniaceae*, etc (Tang F et al., 2015). *Vendotaenia antiqua* Gnilovskaya, 1971 are ribbon-shaped, carbonaceous, Precambrian macrofossils. The *Vendotaenia* fossils are preserved as carbonaceous compressions which stand out clearly from the surrounding matrix with no branch and elongate longitudinal textures across the whole body. If the features on the body were created through taphonomy process, it is unlikely that all the specimens have the same pattern of clear features on their bodies. In addition, the "transition zone" containing both longitudinal and transverse features appears to be distinctive to the Anning fossils; this has not been described from *Vendotaenia* or any of its putatively related forms. It is less probable that the taphonomy process would create two perpendicular linear features on the same body of each specimen of Anning fossils.

Therefore, fossils from Anning are not particularly similar to the macroalgae described from other units in the Yunnan region.

*Rugosusivitta* is bilateral symmetry and its inflated side of the body with features leading to the hypothesis that *Rugosusivitta* could be a stem group to the Platyhelminthes. Comparing to present Platyhelminthes, the fossil has common ground in ribbon-like and segmented body. Modern cestodes would be an analogue of *Rugosusivitta*.

The cestode ribbon-like body consists of many similar units, known as proglottids, that are similar to the ridges and intervals in the transverse zone of *Rugosusivitta* when the vertical and strong contraction of the body occurred during the preservation. Cestodes have no gut or mouth that might be an explanation that no clear structures have been found inside or outside the body of *Rugosusivitta*. Circular and longitudinal muscles lie under the neodermis of modern cestodes, beneath which further longitudinal, dorso-ventral and transverse muscles surround the central parenchyma (Ruppert EE et al., 2004). This muscle framework of cestodes could lead to both transversal and longitudinal features on the different parts of the body for example like some species from Tetrephyllidea. These perpendicular features on the body of Anning fossils occur rarely on other bilaterally symmetrical fossils and modern species.

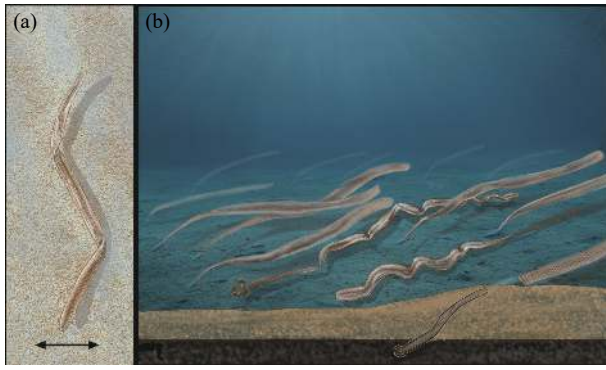
Even though *Rugosusivitta* shares much common ground to modern cestodes, it is arbitrary to define *Rugosusivitta* as tapeworms. Unlike its modern analogues, *Rugosusivitta* fossils were found in abundance and in isolation from other fossils, without any evidence for parasitism. Therefore, *Rugosusivitta* might be the free-living ancestor of *Platyhelminthes* and have significant implication to the early evolution of *Platyzoa*.

#### 4.2. Paleoecology and phylogenetic interpretation

*Rugosusivitta* is most likely to be interpreted as a worm with a soft and flat body. The majority of the *Rugosusivitta* fossils were found straight or folding like bands. Fossils from Chengjiang biota show that cylindrical-shaped soft long body was usually preserved curling or twisting (Ma XY et al., 2010). A tubular body is less likely to be preserved as a "Z" shaped folding or an "X" shaped twisting body (Cohen PA et al., 2009). Tubular fossils might be preserved as carbon compressions but might also be preserved as ridges or infilled with sediments (Fig. 5b) which has not been found in *Rugosusivitta* fossils

Since the ribbon-like compressions are so dense in the sediments (about 6–10 individuals within a 5 cm × 5 cm matrix) (Figs. 4b–d), *Rugosusivitta* fossils were possibly transported on the surface of the sea floor before being buried and compressed by the loading later. Hydrodynamic reworking by waves might be the cause of the bending and folding of these fossils (Fig. 6). The wave dragged the flat body back and forth and created the folding at all angles. The helical "X" twisting might be due to the shrinking of the worms after its death.

There are many Ediacaran and lower Cambrian strata in

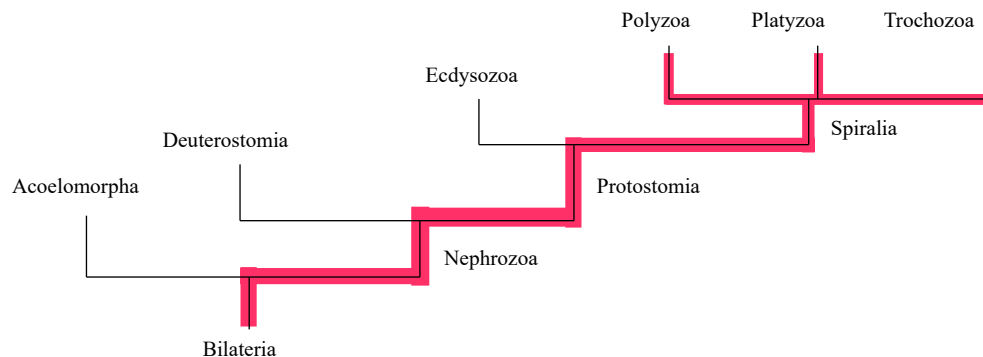


**Fig. 6.** a, b—imaginary photographs of *Rugosusivitta*. Wave-induced currents can be the cause of the folding of *Rugosusivitta* fossils. The black arrows in (a) represent the direction of the currents. The original ribbon-like bodies of *Rugosusivitta* fossils lived on the sea floor and were transported after death. The dynamic of the waves can fold the dead worms back and forth and in the end buried in sediments.

the central Yunnan Province of China, including the famous lower Cambrian “Chengjiang biota” and Meishucun small shelly fauna. The former provides us with precious data on the diversity of biological evolution during the Cambrian explosion as viewed through the lens of exceptionally preserved soft-bodied organisms and the latter records some of the earliest stages in the radiation of biomineralizing organisms, one of the hallmarks of the Cambrian explosion, finds out a large number of soft body preserved as fossils, and the latter is the “first act of the Cambrian explosion”, which proves that on the eve of the Cambrian explosion, abundant evidence of large-scale reproduction of life with shell also indicates the coming of Phanerozoic (Knoll AH et al., 1999). Trace fossils in this period have shown a prosperous ecosystem on the seafloor with large soft body worm-like species.

Many phylogenetic hypotheses have been published in the past decade alone, and the most dedicated systematic researcher may from time to time fail to see the consensus in this dark forest of phylogenetic trees for these early evolved taxa (Narbonne GM, 2005). Some former phylogenomic studies explore the current consensus in metazoan phylogeny by pointing out congruence and discrepancies between various hypotheses (Fig. 7).

*Rugosusivitta* have bilateral symmetry body and feature



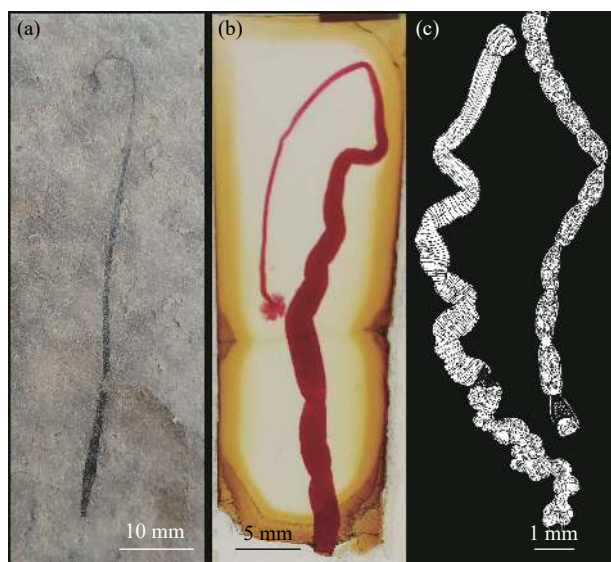
**Fig. 7.** Sketched from the figure of summary of relationships within Bilateria by Edgecombe GD et al. (2011) page 153. The possible taxonomy of *Rugosusivitta* is marked as red.

similar to modern Cestodes. The unique orthogonal dense and parallel line textures on the flat body are similar to modern species *Taciniatum* Linton, *Rhinebothrium himanturi* etc. in Tetraphyllidea (Figs. 8b–c). The three *Rugosusivitta* specimens found with terminal attachments might show the preserved holdfasts (Fig. 8a). Since the fossils cannot live audaciously, the holdfasts can be used to attach the body into the sediments. If the holdfasts decayed at a different rate than the rest of the organism’s body, or simply remained immersed in sediment, it might not be transported with the rest of the body. This might explain why only several specimens were found with holdfast-like structures. Molecular clock predictions and trace fossil evidence indicate that bilaterians emerged prior to the Cambrian (Peterson KJ et al., 2008; Erwin DH et al., 2011; Parry LA et al., 2017; Jensen S, 2003; Tarhan LG et al., 2020). A maximum of over 600 Ma was set for Bilateria in former studies (Baguña J et al., 2004; Peterson KJ et al., 2008). This date was used by as a maximum for Eumetazoa based on paleoecological changes because subsequently published studies have provided strong evidence for crown-group sponged by Love GD et al. (2009). Considering the first occurrence of *Rugosusivitta* is below the  $535.2 \pm 1.7$  Ma bentonite layer in Anning, it might be the early member in Platyzoa clade. Unfortunately, the authors did not find any evidence of the inter structures of *Rugosusivitta*, so that the authors roughly put it in Platyzoa. More evidence of its morphological and molecular features need to be analyzed to provide a clearer position on the tree.

Many clades of Bilateria show no fossil evidence until about 520 Ma (Edgecombe GD et al., 2011). The time between the dawn of Bilateria and the fast explosion of the clades is enigmatic due to the lack of fossil records. The occurrence of *Rugosusivitta* is in this period of low biodiversity. It might be a key to the early evolution of Bilateria and physical evidence related to the abundant trace fossil record near the Precambrian–Cambrian boundary.

## 5. Conclusion

Here the authors report the occurrence of a new body fossil, *Rugosusivitta*, from the Ediacaran–Cambrian boundary interval of the Zhongyicun Member in Yunnan Province, China. This fossil is, unusually, characterized by both longitudinal and transverse ornamentation, and is commonly



**Fig. 8.** a—specimen No. IG-190818: *Rugosusivitta* with a elliptical attachment at the end of the longitudinal feature zone and look very similar to modern *Cesdote*. b—Tetraphyllidea *Anthobothrium laciniatum* Linton, 1890 is collected from Fiddler ray in Zoo lab UCL. c—*Pedibothrium mounseyi* sketched by Ruhnke TR et al. (2009).

preserved in assemblages of folded and twisted specimens, indicative of hydrodynamic reworking. The simplicity in morphologic and the lack of internal structures of the body make definitive taxonomic categorization of *Rugosusivitta* difficult. However, its bilateral symmetry and body features indicate that *Rugosusivitta* can be interpreted as Platyhelminthes and an early prototype of Bilateria. The consistent presence of ribbon-shaped fossils in Zhongyicun Member in Anning City and in other distributed localities in southern China indicates that these organisms were a significant component of Ediacaran biomass and may prove to be the oldest species of Platyhelminthes.

In Meishucun section the *Treptichnus pedum* occurs in strata near the top of the Lower Phosphate Member (Zhu MY et al., 1997). The Ediacaran–Cambrian boundary is based on the first appearance of the ichnofossil *Treptichnus pedum*. However, it has been a focus of criticism that the authors put the investment in an ichnotaxon fossil. The utility of *Treptichnus pedum* as a biostratigraphic marker, the ichnotaxonomical and behavioural objections are the ones that can be regarded as less significant of its unneglectable issues of ichnotaxonomy, behavioural significance, facies controls and stratigraphic occurrence (Buatois LA, 2018).

The first occurrence of *Treptichnus pedum* in this area is at 6.4 m above the bottom of the Zhongyicun Member. Small shelly fossils occur below the first occurrence of *Treptichnus pedum* and, therefore, the Ediacaran–Cambrian boundary has been placed at the contact between the Xiaowaitoushan Member and the Meishucun Formation (Qian Y et al., 2001). Therefore, the Zhongyicun Member might be a lithostratigraphic unit across the Ediacaran–Cambrian boundary. And due to these compromises to the accuracy of compiling vertical distribution of trace fossils with a reasonable stratigraphic framework, defining the Ediacaran–Cambrian boundary could not strictly rely on the

occurrence of *Treptichnus pedum*, especially in Meishucun section in Yunnan Province (Xing YS et al., 1984; Zhu MY et al., 2019). A single tool is never the most adequate strategy to solve geological problems so the discovery of *Rugosusivitta* fossils will be of help to overcome the problem of those areas like Meishucun where *Treptichnus pedum* has not been recognized or occurs significantly above the boundary (Shu DG et al., 2009). The trace fossils are abundant in siliciclastics, while small shelly fossils and *Rugosusivitta* fossils are more abundant in carbonates that illustrate the complementary of these two biostratigraphic tools to construct a sound stratigraphic framework during this critical time period of Ediacaran–Cambrian boundary.

The *Rugosusivitta* occurred before the isochronous surface of  $535.2 \pm 1.7$  Ma in Yunnan Province and was discovered in layers adjacent to the layer that *Treptichnus pedum* first occurred. The first occurrence of *Treptichnus pedum* is currently been considered as the GSSP type fossil of the Ediacaran–Cambrian boundary. *Rugosusivitta* can be taken as a biological marker of the Ediacaran–Cambrian boundary and a mark of global formation comparison.

#### CRedit authorship contribution statement

Si-cun Song and Feng Tang came up with the conception of the project and designed the study, organized the field trips and collected the specimens with the assistant of Guang-xu Zhang. Guang-xu Zhang also assisted with the measurements of the specimens. Si-cun Song, Feng Tang and Guang-xu Zhang wrote the manuscript in consultation. Ai-lin Chen helped revising the manuscript critically for intellectual content.

#### Declaration of competing interest

The authors declare no conflicts of interest.

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