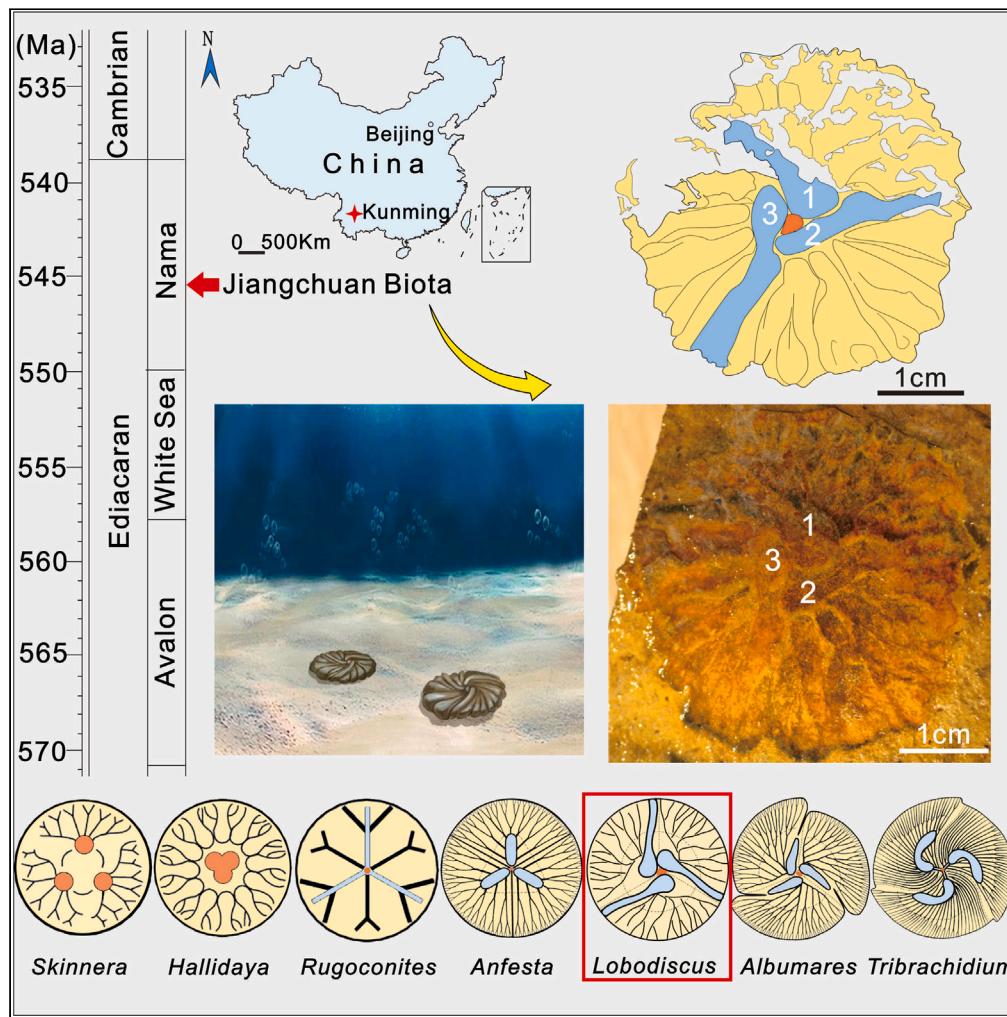


## Article

## A putative triradial macrofossil from the Ediacaran Jiangchuan Biota



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**Highlights**  
The Jiangchuan biota of  
Yunnan preserves a late-  
Ediacaran eukaryotic  
assemblage

We describe the first  
potential animal fossil from  
the Jiangchuan biota

This new triradial fossil  
might represent the  
youngest known  
trilobozoan

Our finding may  
strengthen taxonomic  
overlap among late-  
Ediacaran faunas

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## Article

# A putative triradial macrofossil from the Ediacaran Jiangchuan Biota

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## SUMMARY

The late Ediacaran Jiangchuan biota, from the Dengying Formation in eastern Yunnan, is well-known for its diverse macroalgal fossils, opening a window onto eukaryotic-dominated ecosystems from the late Neoproterozoic of South China. Although multiple lines of evidence suggest that metazoans had already evolved by the late Ediacaran, animal fossils have not yet been formally described from this locality. Here, we report a putative disc-shaped macrofossil from the Jiangchuan biota, *Lobodiscus tribrachialis* gen. et sp. nov. This specimen shows the triradial symmetry characteristic of trilobozoans, a group of Ediacaran macrofossils previously documented in Australia and Russia. *Lobodiscus* could record the youngest known occurrence of trilobozoans, strengthening taxonomic and ecological continuities between the Ediacaran "White Sea" and "Nama" assemblages. Our findings may expand the known paleogeographical distribution of trilobozoans and provide data for Ediacaran biostratigraphic correlations across the Yangtze block and globally, helping to track the diversification of early metazoan-grade organisms.

## INTRODUCTION

At the end of the last century, a taxonomically diverse assemblage of carbonaceous compression macrofossils was discovered in the Jiucheng Member of the upper Ediacaran Dengying Formation, in the Jiangchuan area of eastern Yunnan, China (Figures 1A and 1B). This fossil assemblage came to be known as the Jiangchuan Biota,<sup>1,2</sup> and has tentatively been assigned a ~546 Ma age based on U-Pb dating.<sup>3</sup> The described macrofossil record of the Jiangchuan Biota is limited to macroalgae,<sup>1,4–6</sup> and convincing metazoan fossils have so far been conspicuously absent from this locality.

However, over the past decades Ediacaran soft-bodied macrofossils of probable animal affinities<sup>14,15</sup> have increasingly been reported from most continents, spanning a succession of three biotic assemblages ranging from about 571 to 539 million years ago (Ma): the deepwater "Avalon" (~571–558 Ma), the diverse, shallow-water "White Sea" (~558–550 Ma), and the relatively depauperate shallow-water "Nama" (~550–539 Ma)<sup>16–21</sup> (Figure 1C). Faunas from these assemblages have illuminated the tempo and mode of early animal evolution, contributing to reconcile molecular clock chronologies with the fossil record<sup>22</sup> and shedding light on the early assembly of metazoan developmental programs<sup>14,15</sup> and animal-dominated ecologies.<sup>9,23,24</sup>

Among putative Ediacaran animals are a group of macrofossils with a distinctive triradial, discoidal bodyplan, known from the White Sea assemblage of Australia and Russia<sup>25–31</sup> and potentially from late Ediacaran sections of the Doushantuo Formation from Guizhou, China.<sup>32</sup> This group comprises the genera *Tribrachidium*, *Anfesta*, *Albumares*, *Hallidaya*, *Skinnera*, and *Rugoconites*,<sup>25,33–37</sup> and might also include several other problematica in need of restudy (see<sup>16</sup>).

Fedonkin assigned this group of soft-bodied triradial organisms to the newly erected class Trilobozoa together with the tube-dwelling, biomineralized anabaritids,<sup>38,39</sup> and suggested that they were related to cnidarians. However, the triradial symmetry and discoidal, lobate bodyplan of the soft-bodied trilobozoans, such as *Tribrachidium*, differ from those of cnidarians or any other extant phylum.<sup>37,40</sup> For this reason, these Ediacaran organisms are now considered to fall outside of crown-group Cnidaria,<sup>40,41</sup> and are alternatively referred to as "Tribrachiomorpha"<sup>42,43</sup> or "Triradiolomorpha".<sup>18,37</sup> Their taxonomy<sup>31</sup> and broader placement within Metazoa are unclear,<sup>9,41,44</sup> and the group remains one of the most enigmatic among Ediacaran macrofossils due to its rarity and poorly understood anatomy.<sup>31,40</sup> Nonetheless, a total-group metazoan affinity for triradiolomorphs is strongly supported by the evidence for developmentally constrained symmetry, tissue-grade

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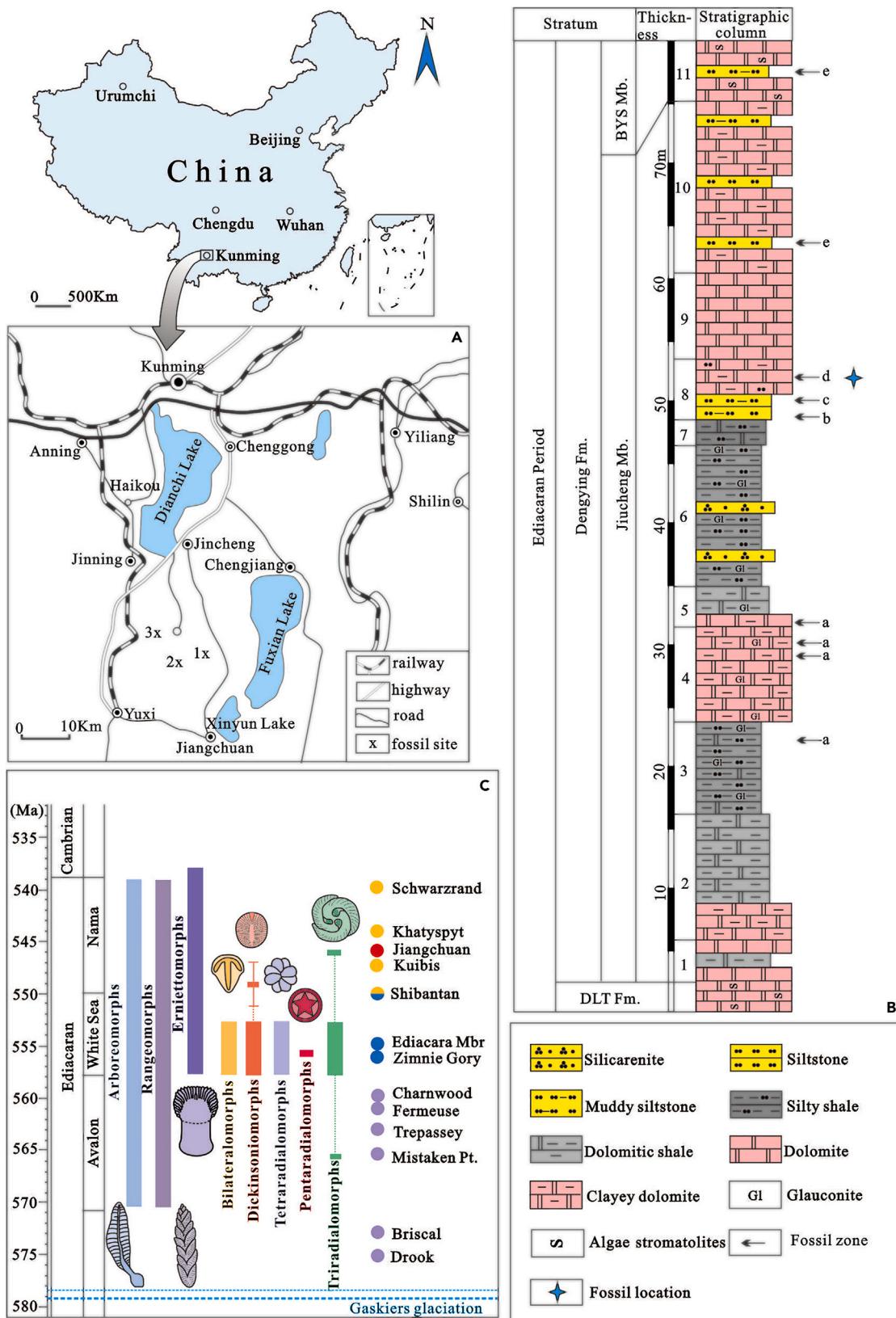
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**Figure 1. Locations, stratigraphic column of the macrofossil sections, Jiangchuan Biota in Yuxi area, Eastern Yunnan, and Schematic of Ediacaran assemblages**

(A) Geographical location of the fossil-bearing sections of the Jiangchuan Biota.<sup>7</sup> 1X: Houjiashan, 2X: Gugeng Village, 3X: Wangjiawan, Lujie; (B) stratigraphic column of the Dengying Formation, East Yunnan.<sup>7</sup> DTL Fm: Donglongtan Formation, BYS Mb: Baiyanshao Member; Zone a—*Shaanxilithes*, zone b—*Chuaria-Tawuia-Pumilibaxa*, zone c—*Shouhsienia-Vendotaenia-Houjiashanaria*, zone d—*Longfengshani-Cyclomedusa-Lobodiscus*, and zone e—*Vendotaenia-Tyrasotaenia*. (C) Schematic of Ediacaran assemblages showing major deposits of each and the temporal ranges of key taxonomic constituents of the Ediacaran Biota; yellow denotes Nama assemblage localities, blue White Sea, and purple Avalon. The Jiangchuan Biota is highlighted in red. Age and faunal data after Mussini and Dunn,<sup>8</sup> and references therein, and Xiao and Laflamme,<sup>9</sup> Xiao et al.,<sup>10</sup> Bowyer et al.,<sup>11,12</sup> and Uahengo et al.<sup>13</sup>

differentiation,<sup>37,45</sup> and possible motility<sup>40</sup> in this group. At the same time, their unique extinct bodyplan strengthens the hypothesis that Ediacaran and early Phanerozoic animal evolution was defined by early morphospace expansion followed by taxonomic diversification, with major implications for our understanding of the developmental and macroevolutionary assembly of living phyla.<sup>9,44</sup>

Here, we report a putative triradial macrofossil from the Jiangchuan Biota, *Lobodiscus tribrachialis* gen. et sp. nov., from the Houjiashan section of the Dengying Formation. *Lobodiscus*, the first trilobozoan-type fossil to be reported in the Dengying Formation, may expand the known diversity, disparity, and paleogeographical distribution of Ediacaran triradial animals, suggesting possible scenarios for the evolution of their distinctive bodyplan and pointing to a previously undocumented presence of metazoan-grade organisms in the Jiangchuan Biota. *Lobodiscus* may represent the youngest documented occurrence of trilobozoans globally, pointing to their survival into the “Nama” interval<sup>20</sup> and suggesting that the Jiucheng Member may record a transitional biota intermediate between classic White Sea and Nama-type localities.

## RESULTS

### Systematic palaeontology

Genus *Lobodiscus* gen. nov.

Type species *Lobodiscus tribrachialis* sp. nov.

*Parainaria jiangchengensis* Tang In Tang et al.,<sup>46</sup> (nom. nud.), p. 2154, figs. 3a , 3b.

### Etymology

*Lobo*-from the Latin *lobus*, meaning lobe, -*discus* from the Latin *discus*, meaning disk, denoting the disc-like main body with radiating lobes; the species name combines the prefix *tri-* (from the Latin *tres*, three) and *brachium*, the Latin for “arm”, with reference to its 3-fold symmetry.

### Diagnosis

Macroscopic, triradially symmetric discoidal fossil characterized by three raised branches radiating outward from the center of the upper body surface and meeting at approximately 120° angles. The bases of the branches are slightly offset, resulting in a weak helical arrangement. The branches partition the disc into three lobes, each comprising a series of densely spaced finger-like ridges radiating outwards from the center of the disc.

### Holotype

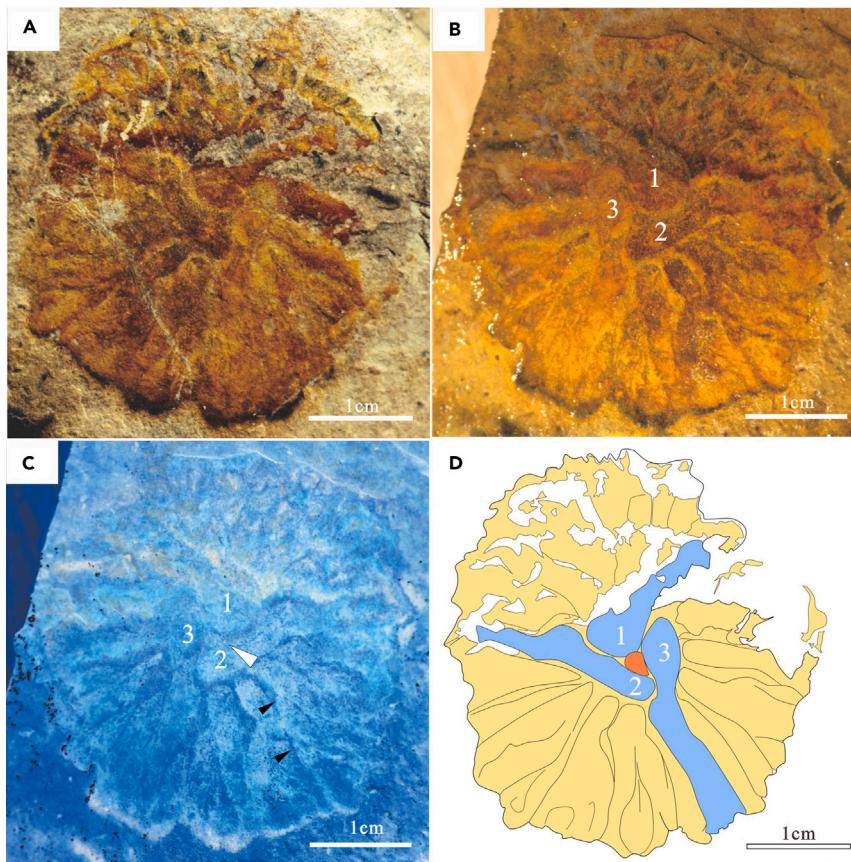
No. KGS00228 (part and counterpart; Figure 2).

### Type locality and geologic setting

Jiucheng Member, Dengying Formation, cropping out in the Houjiashan, Jiangchuan area, Yuxi City, Yunnan Province, Southern China.

### Description

The holotype of *L. tribrachialis* (Figure 2) measures approximately 37 mm in diameter. The body takes the shape of an approximately circular disc, preserved as part (in positive epirelief) and counterpart and showing faint overlying reddish-colored iron films and dark, potentially carbonaceous films (Figures 2A and 2B). The disc shows a shield-like profile, with the center slightly raised. Its three main radiating branches (“main ridges” sensu Ivantsov and Zakrevskaya<sup>40</sup>) are characterized by more prominent relief than the rest of the disc surface and meet at approximately 120° angles around its center (Figure 2). Their bases are rounded and somewhat thicker than the rest of the branch, and surround a small, circular depression that may represent an apical pit (Figures 2B–2D). The three lobes defined by the branches have a distinctive surface morphology, characterized by a dense mesh of digitiform ridges radiating outwards from the center of the disc. The ridges differ in length and show occasional bifurcations, with at least two visible branching orders (Figure 2C). Their occasional bending suggests the same degree of rigidity as the branches, but they are thinner, less distinct, and characterized by lower relief. Unlike in *Albumares* and *Tribrachidium* (e.g.<sup>40</sup>), the lobes show no signs of distal separation. However, the distal extensions of the ridges yield an irregular body margin (Figure 2). No tentacles fringe the body margin, consistent with the notion that reports of these structures in other trilobozoans<sup>47</sup> stem from anatomical misinterpretation.<sup>40</sup>



**Figure 2.** *Lobodiscus tribrachialis* (KGS00228)

(A) part, (B) counterpart, (C) inverse color photograph of b; white arrow indicates the position of the apical pit, black arrows consecutive branching orders; (D) Interpretative drawing. Red denotes the central depression, blue the main branches (numbered), yellow the disc surface with thinner branching ridges.

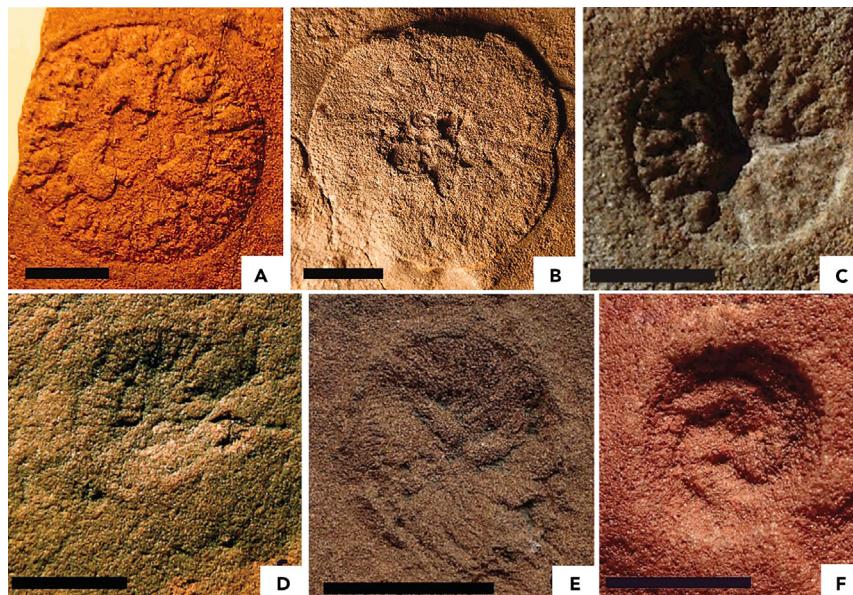
## DISCUSSION

### *Lobodiscus* and the evolution of the trilobozoan bodyplan

The *Lobodiscus* holotype (Figure 2) can be interpreted as a macroorganismal fossil based on standard biogenicity criteria, including shape, degree of morphological differentiation, biologically plausible size range, and topological correspondence to well-established biogenic counterparts.<sup>48,49</sup> The degree of morphological differentiation of *Lobodiscus*, which shows at least two orders of bifurcating surface ridges, regularly spaced branches, and a potential apical pit in addition to well-defined lobes, contrasts with that of simpler radially symmetric sedimentary concretions erroneously interpreted as macrofossils.<sup>50</sup> Lobate discs with undulate outer edges may occur in pyrite concretions forming in fluid mixtures with different viscosities,<sup>51</sup> but the preservation of the specimen as siltstone is at odds with the physical and mineralogical demands of this process. Similarly, septarian concretions may present radial or concentric features, but these consist of cracks in a clay matrix typically infilled with crystallized quartz or calcite, rather than curved lobes or ridges, and differ in mineralogical composition to the *Lobodiscus* specimen.<sup>52</sup> *Lobodiscus* also shows chromatic and textural differences from the surrounding matrix, reflected in the presence of overlying reddish-colored iron and dark, potentially carbonaceous films suggestive of an originally organic structure (Figures 2A and 2B). In the absence of a more compelling alternative explanation for its morphology, these characteristics argue against interpretations of the specimen as an abiotic sedimentary structure.

In contrast, *L. tribrachialis* shows a morphology reminiscent of better-characterized Ediacaran trilobozoans from Australia and Russia,<sup>31,34,37,40</sup> and at about 37 mm of diameter it falls neatly within the upper size range of these organisms.<sup>40</sup> Like *Lobodiscus*, all trilobozoans share a discoidal shield-like body often partitioned into three equal lobes, radial branches and/or bifurcating ridges, and three-radial or rotational symmetry.<sup>16,17,40</sup> These distinctive shared features tentatively suggest that trilobozoans form a monophyletic group.<sup>37</sup> However, trilobozoan taxa differ with respect to the shape, geometric arrangement, prominence, and degree of twisting of the lobes and branches, as well as their degree of integration into the disc's structure.

*Lobodiscus*'s prominent main branches differ from their subdued or morphologically indistinct counterparts in *Hallidaya* and *Skinneria* (Figures 3A, 3B, 4A, and 4B) linking the new taxon to the trilobozoan morphogroup comprising *Rugoconites*, *Anfesta*, *Albumares*, and *Trirachidium*<sup>37,40</sup> (Figures 3C–3F, 4C, 4D, 4F, and 4G). In *Lobodiscus*, the branches radiate from the center at 120-degree angles in a clockwise



**Figure 3. Representative Ediacaran trilobozoans from the White Sea assemblage of South Australia**

After Hall et al.<sup>37</sup>

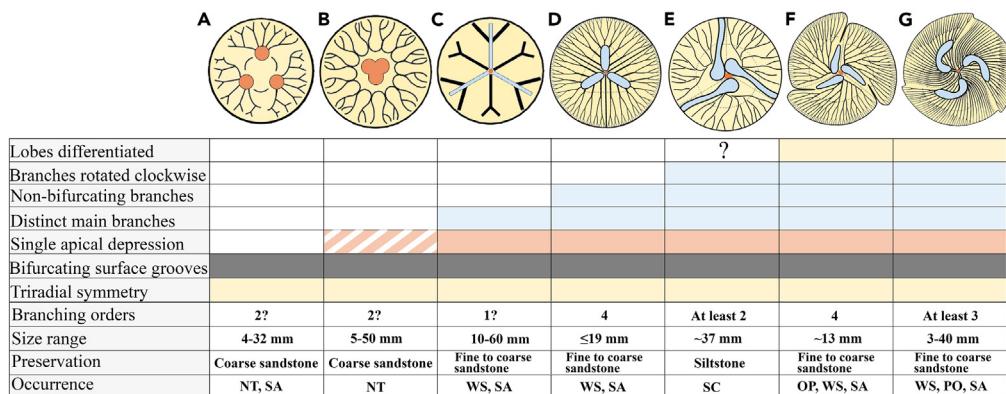
(A) *Skinnera* (SAM F16473); (B) *Hallidaya* (SAM F16464a); (C) *Rugoconites enigmaticus* (STC-J 560/493); (D) *Anfesta* (SAM P36588c); (E) *Albumares* (SAM P42554); (F) *Tribrachidium* (SAM P42662). All scale bars represent 1 cm.

direction, surrounding the rounded central depression and reaching the outer edge of the disc (Figure 2). The branches are morphologically similar to those of *Anfesta*<sup>38,40</sup> (Figure 3D), known from the White Sea of Russia<sup>38</sup> and South Australia,<sup>17</sup> that also shows three approximately straight, elongated branches with rounded ends, radiating from the center of the body at 120-degree angles. As in *Anfesta*, the branches of *Lobodiscus* are also surrounded by regions of thinner bifurcating ridges and grooves extending to the disc's outer margin (Figure 2C). Similar branching grooves also occur in *Albumares* (Figures 3E and 4F), where they radiate from the center of the shield and bifurcate at least four times toward the periphery.<sup>40,47</sup> However, unlike those of *Lobodiscus* the branches of both *Anfesta* and *Albumares* do not reach the edge of the discoidal body.<sup>27,40</sup>

*Lobodiscus* also differs from *Anfesta* in the geometry of its three putative body lobes. In *Anfesta* (Figures 3D and 4D), each represents a 120° sector of a circle, with the branches meeting apically to define a clear Y-shape.<sup>40</sup> This results in a simple radially symmetrical configuration of the lobes. In contrast, in *Lobodiscus* the basal offset between branches confers glide symmetry to the lobes (Figure 2). Glide symmetry is also clearly observed in *Albumares* and *Tribrachidium*. In these taxa, each lobe is elongated and bent clockwise, giving the body a helical aspect. As a consequence, the lobes are separated distally by asymmetrical notches.<sup>31,37,40</sup> However, it is worth noting that the asymmetrical marginal notches are less pronounced in *Tribrachidium*, where they are occasionally not preserved, compared to *Albumares*.<sup>37,40</sup> Likewise, distal notches are not observed in the *Lobodiscus* holotype, where the helical arrangement seems confined to the radiating branches and the lobes do not appear bent and twisted clockwise (Figure 2). However, the lack of additional specimens leaves open the possibility that the absence of notches may be taphonomic.

While *Tribrachidium* (Figures 3F and 4G) has been characterized as most distantly related to other trilobozoans,<sup>37</sup> this hypothesis is contradicted by morphological comparisons with *Lobodiscus* and previously described taxa. The hypotheses that *Tribrachidium* is the only trilobozoans with features that bend instead of extending straight out, and that it lacks branching structures<sup>37</sup> are contradicted by the evidence from Russian White Sea specimens.<sup>40</sup> Grooves with multiple orders of branching, akin to those of *Anfesta*, *Albumares*, and most likely *Lobodiscus* (Figure 2C) occur distally on the shield of *Tribrachidium* (Ivantsov and Zakrevskaya,<sup>40</sup> plates 3–4). Moreover, the recurved, helically arranged branches of *Tribrachidium* are reminiscent of those of *Lobodiscus* (Figure 2) and *Albumares*, although the lobes of *Tribrachidium* display the most extreme asymmetric bending.

Comparisons of lobe shapes, branching patterns, and symmetry across trilobozoans (Figure 4) suggest possible scenarios for the evolution of their bodyplan. If trilobozoans are monophyletic, with their rotational glide symmetry not observed in any other known group,<sup>31,41</sup> we tentatively suggest that their common ancestor possessed simple radial symmetry and a discoidal body shape. Hypothetically, this condition may be exemplified by *Rugoconites*, that lacks separate lobes and possesses inconspicuous branches meeting apically to define a Y-shape, or by *Hallidaya* and *Skinnera*. The latter two taxa lack distinct main branches altogether and are united by the presence of rings of multiple central depressions, that are apparently absent in other trilobozoans (Figure 4).<sup>37,40</sup> In contrast, *Anfesta*, *Lobodiscus*, *Albumares*, and *Tribrachidium*<sup>40</sup> seemingly possessed main branches surrounding a single apical pit. In lieu of simple radial symmetry, *Albumares* and *Tribrachidium* also show a clear helical arrangement not found in any living phylum,<sup>40</sup> and which might thus represent a derived condition.



**Figure 4. Summary table with proposed homology scheme, morphological features, size range, preservational mode and geographical occurrence of trilobozoans**

(A) *Skinneria*; (B) *Hallidaya*; (C) *Rugoconites*; (D) *Anfesta*; (E) *Lobodiscus*; (F) *Albumares*; (G) *Tribrachidium*. Central depressions or pits are noted in red, hypothetical digestive cavities in blue, and disc surface with branching ridges or grooves in yellow. Colored cells denote the presence of morphological features listed in the first column to the left. Differentiated lobes are scored as a question mark in *Lobodiscus* to account for the possibility of taphonomic absence. White bars in the cell denoting “Single apical depression” in *Hallidaya* reflect the presence of three fused apical pits (B), potentially intermediate between a single pit (C–G) and the condition in *Skinneria* (A). NT, Northern Territories (Australia); OP, Onega Peninsula, Russia; PO, Podolia (Ukraine); SA, South Australia; SC, southern China; WS, White Sea region (Russia). Schematic drawings, size ranges, and sedimentological and occurrence data after Ivantsov and Zakrevskaya,<sup>40</sup> for D, F, and G, Hall et al.<sup>37</sup> and references therein for a–c.

Speculatively, over the course of trilobozoan evolution the main branches of a *Rugoconites*-like ancestor may have become increasingly prominent and the bifurcating patterns of the radial grooves increasingly complex, possibly to maximize the ciliary surface and enhance feeding efficiency.<sup>40</sup> This would have yielded a configuration akin to that of *Anfesta* (Figure 4). Under this scenario, this morphology may have been further elaborated upon in *Lobodiscus*, where the beginnings of a helical bodyplan may manifest in the offset between the three main radiating branches (Figure 4). From this baseline condition, increased clockwise torsion of the branches and distal separation of the lobes to varying degrees might have resulted in the configurations observed in *Albumares* and *Tribrachidium* (Figures 4F and 4G). However, it remains possible that the non-helical, radially symmetrical bodyplans of *Rugoconites*, *Hallidaya*, and *Skinneria* reflect secondary simplification of an originally helical morphology. Alternatively, the distinct branching patterns and bodyplan symmetries of different trilobozoans might record an exclusively ecological rather than phylogenetic signal. For instance, these morphological features may have been shaped to optimize feeding efficiency under distinct local hydrodynamic flow regimes (e.g., Rahman et al.<sup>41</sup>). A conclusive test of these alternatives, which remain speculative, will require at once disentangling the placement of trilobozoans among other Ediacaran macrobionts and extant phyla<sup>31,40</sup> and systematic comparative analyses of their paleoenvironmental settings of occurrence.

### Feeding process

Although most metazoans exhibit some form of symmetry defining the whole body or some of its parts, trilobozoans are characterized by triradial symmetry, which is not present in living phyla. By comparison, most extant echinoderms exhibit pentameral symmetry, with the extinct Edrioasteroidea showing superimposed twisting distantly reminiscent of the trilobozoan condition.<sup>53</sup> Edrioasteroids and other fossil echinoderms were most likely filter feeders, and their twisted ambulacra may have helped to enhance feeding efficiency.<sup>54</sup> However, the fundamentally distinct bodyplan and putative epibenthic habits of trilobozoans suggest that this resemblance is superficial, and that their lifestyle may lack any clear Phanerozoic analog.

No direct evidence for motility is observed in *Lobodiscus*. However, putative fossil trackways suggest that at least some trilobozoans, including *Tribrachidium*, may have had modest mobility, presumably allowing the organism to evade negative stimuli and track suitable feeding spots.<sup>40</sup> Based on their rigidity, reflected by the well-delineated contours of putative trackways and their consistent trajectory in body fossils, it seems likely that the lobes of trilobozoans could not fold or bend to assist food capture. Instead, food capture may have been achieved mainly through the system of bifurcating grooves covering the disc surface. As suggested by Ivantsov and Zakrevskaya,<sup>40</sup> the grooves may have been covered by a ciliary epithelium, with food particles carried to a digestive cavity located in the middle of the disc by ciliary activity. This active feeding mode would have enabled transport of nutrients from organic-rich benthic detritus to the apical depression, where the putative mouth was located. Moreover, it would have helped to prevent wastage caused by food particles sliding down over the shield-like body. Hypothetically, this active feeding mode may have contributed to the evolution of trilobozoans with more complex surface ornamentation, which would have increased the surface area of the ciliary epithelium for more efficient feeding.<sup>40</sup> Selective pressures to maximize the surface area of this ciliary “conveyor belt” may conceivably have driven a trend toward increasingly twisted and elongated body lobes in trilobozoans, as tentatively suggested by the morphology of *Lobodiscus* (Figures 2 and 4). Instead, cilia on the underside of the trilobozoan body might have played an important role in aiding movement, as in placozoans<sup>55</sup> and many living aquatic



**Figure 5. Artistic reconstruction of *L. tribrahialis* as a benthic metazoan-grade organism**

invertebrate larvae.<sup>40</sup> While the absence of preserved cilia in *Lobodiscus* makes this hypothesis speculative, its probable branching ridges and grooves (Figure 2) tentatively suggest that the feeding strategy proposed by Ivantsov and Zakrevskaya<sup>40</sup> may have been universal across trilobozoans.

#### Sedimentary environment and ecology

*Lobodiscus* (Figure 2) occurs in dolomitic siltstones recording a warm, low-energy shallow-marine environment. In line with the limited or absent motility, benthic habits, and low-energy depositional context proposed for *Lobodiscus*, the fossil shows no signs of transport. The discovery of *Longfengshania*<sup>5</sup> and *Cyclomedusa*<sup>7</sup> in the same facies of the Jiangchuan Biota suggest considerable potential for the discovery of additional Ediacaran macrofossils, and may reflect high levels of local primary productivity supplying *Lobodiscus* with abundant food sources, including organic particulate from co-occurring algae.<sup>5</sup>

Our findings suggest that *Lobodiscus* may be reconstructed as a benthic suspension or filter-feeding organism (Figure 5) akin to other triradial animals,<sup>40,41</sup> that it was benthic, sessile to slow-moving,<sup>40</sup> and likely of a more complex grade of anatomical organization than poriferans: by comparison with Russian White Sea specimens, its branches tentatively point to the presence of internal digestive cavities.<sup>40</sup>

Globally, trilobozoans occur in depositionally and paleoenvironmentally diverse facies, suggesting that they represented a highly adaptable group thriving in varied benthic habitats.<sup>37</sup> These triradial animals probably became extinct by the beginning of the Paleozoic leaving no extant descendants, but in the late Ediacaran they show a wide distribution and considerable diversity relative to other contemporary metazoan-grade groups.<sup>37,40</sup> For the first time, our findings from the Jiangchuan Biota tentatively extend their paleogeographical record to South China, suggesting stratigraphic correlations between the Jiucheng Member of the Ediacaran Dengying Formation and late Ediacaran assemblages in South Australia<sup>37</sup> and globally. In particular, the absence of trilobozoans and a relative scarcity of other benthic, prostrate Ediacaran macrobionts from known Nama-aged intervals worldwide, which may reflect their extinction due to the escalating effects of bilaterian ecosystem engineering,<sup>20,56</sup> would suggest an age equivalent to that of the White Sea assemblage (~558–550 Ma) for the middle

Jiucheng Member. Alternatively, like the Shibantan Lagerstätte<sup>10</sup> the Jiangchuan Biota may record a “transitional” biota temporally and ecologically intermediate between White Sea and Nama communities, in accord with U-Pb dating of ash beds suggesting a ~546 Ma age for the middle Jiucheng Member.<sup>3</sup> Under this scenario, which appears most likely given the available geochronological evidence, *Lobodiscus* could represent the youngest recorded occurrence of trilobozoans globally, strengthening the taxonomic overlap between White Sea and Nama communities (e.g.<sup>20</sup>). Therefore, the occurrence of a trilobozoan in the Jiangchuan Biota may corroborate the hypothesis of a gradual, protracted phase-out of White Sea-type communities (e.g.<sup>8,24</sup>), contradicting scenarios centered on geologically rapid, environmentally driven mass extinctions between the White Sea and Nama assemblages.<sup>57</sup> Testing these hypotheses will require, crucially, enhanced sampling of the Jiucheng Member across the full spectrum of its macrofossil and trace fossil records.

### Conclusions

We describe the first putative triradial animal (Trilobozoa) from the late Ediacaran Jiucheng Member of the Dengying Formation in Yunnan province, southwest China. This specimen records the first plausible occurrence of soft-bodied, metazoan-grade macroorganisms in the Jiangchuan Biota, and might be morphologically intermediate between simple discoidal triradial forms and trilobozoans with a helical bodyplan. Its occurrence suggests a productive late Ediacaran ecosystem hosting an undocumented fauna in the Jiangchuan Biota. Moreover, it may contribute to expand the known record of trilobozoans beyond the Ediacaran fossil localities of Australia and Russia to South China, elucidating Ediacaran metazoan evolution and paleobiogeography in the southwest Yangtze margin and globally. Its occurrence in the Jiangchuan Biota, a probable Nama-interval locality, suggests that *Lobodiscus* could represent the youngest known trilobozoan, and by implication that ecological communities in the Jiangchuan Biota may have retained taxa typical of earlier White Sea-type faunas.

### Limitations of the study

Our diagnosis, description, and assessment of the biogenicity and putative biological affinities of *Lobodiscus* are based on a single specimen preserving part and counterpart. Pending the discovery of additional fossil material, our conclusions must be regarded as tentative. In the absence of more convincing abiotic or biotic explanations for the morphology of the *Lobodiscus* holotype, we provisionally regard the hypothesis of a close affinity to other Ediacaran trilobozoans as the most plausible.

### STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

- KEY RESOURCES TABLE
- RESOURCE AVAILABILITY
  - Lead contact
  - Materials availability
  - Data and code availability
- EXPERIMENTAL MODEL AND SUBJECT DETAILS
- METHOD DETAILS
  - Geological setting
  - Fossil materials and imaging methods

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### AUTHOR CONTRIBUTIONS

M.Z. performed data analysis and wrote this manuscript; G.M. proposed substantial edits and made modifications to the manuscript; Y.L. and M.L. carried out data analysis and drew relevant maps; F.T. and P.V.-R. proposed some suggestions for the manuscript; F.T. and A.C. collected specimens and geological data through fieldwork. All authors read and approved the final manuscript.

### DECLARATION OF INTERESTS

The authors declare no competing interests.

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## REFERENCES

1. Luo, H.L., Wu, X.C., Ou, Y.L., Jiang, Z.W., and Song, X.L. (1988). New correlation opinions on the sections of Sinian-Cambrian Boundary in the Yangtze Platform. *Yunnan Geol.* 7, 13–27.
2. Luo, H.L., Tao, Y.H., and Gao, S.M. (1994). Early Cambrian trace fossils near Kunming, Yunnan. *Acta Palaeontol. Sin.* 33, 676–685.
3. Yang, C., Li, X.H., Zhu, M., and Condon, D.J. (2017). SIMS U-Pb zircon geochronological constraints on upper Ediacaran stratigraphic correlations, South China. *Geol. Mag.* 154, 1202–1216.
4. Xing, Y.S., Duan, C.H., Liang, Y.Z., and Cao, R.G. (1985). Pre-Cambrian Paleontology of China (Geological Publishing House), pp. 1–243.
5. Tang, F., Song, X., Yin, C., Liu, P., Awramik, S.M., Wang, Z., and Gao, L. (2007a). Discoveries of new Longfengshaniae from the uppermost Ediacaran in eastern Yunnan, South China and the significance. *Front. Earth Sci. China* 1, 142–149.
6. Tang, F., Yin, C.Y., Liu, P.J., Gao, L.Z., and Zhang, W.Y. (2008). A New Diverse Macrofossil Lagerstätte from the Uppermost Ediacaran of Southwestern China. *Acta Geol. Sin.* 82, 1095–1103.
7. Li, Y.L., Wang, H., Liu, A.R., Li, M., Liang, Y.Z., Zhou, Y., Tang, F., and Ren, L.D. (2022). Sausage-like macrofossils from the Ediacaran Jiangchuan Biota in eastern Yunnan—New phylogenetic interpretation of Tawuia. *Geol. Rev.* 68, 1585–1603.
8. Mussini, G., and Dunn, F.S. (2024). Decline and fall of the Ediacarans: late-Neoproterozoic extinctions and the rise of the modern biosphere. *Biol. Rev.* 99, 110–130.
9. Xiao, S., and Laflamme, M. (2009). On the eve of animal radiation: phylogeny, ecology and evolution of the Ediacara biota. *Trends Ecol. Evol.* 24, 31–40.
10. Xiao, S., Chen, Z., Pang, K., Zhou, C., and Yuan, X. (2021). The Shibanian Lagerstätte: insights into the Proterozoic–Phanerozoic transition. *J. Geol. Soc.* 178, jgs2020-j2135.
11. Bowyer, F.T., Uahengo, C.I., Kaputuaza, K., Ndeuyemba, J., Yilales, M., Alexander, R.D., Curtis, A., and Wood, R.A. (2023). Constraining the onset and environmental setting of metazoan biomineralization: The Ediacaran Nama Group of the Tsau Mountains, Namibia. *Earth Planet Sci. Lett.* 620, 118336.
12. Bowyer, F.T., Zhuravlev, A.Y., Wood, R., Shields, G.A., Zhou, Y., Curtis, A., Poulton, S.W., Condon, D.J., Yang, C., and Zhu, M. (2022). Calibrating the temporal and spatial dynamics of the Ediacaran-Cambrian radiation of animals. *Earth Sci. Rev.* 225, 103913.
13. Uahengo, C.I., and Bowyer, F. (2023). In The oldest Nama Group exposed: Insights from the Tsau Mountains (Tsau Khaeb National Park) (EGU General Assembly), p. EGU-3841.
14. Dunn, F.S., Liu, A.G., Grazhdankin, D.V., Vixseboxse, P., Flannery-Sutherland, J., Green, E., Harris, S., Wilby, P.R., and Donoghue, P.C.J. (2021). The developmental biology of Charnia and the eumetazoan affinity of the Ediacaran rangeomorphs. *Sci. Adv.* 7, eabe0291.
15. Dunn, F.S., Liu, A.G., and Donoghue, P.C.J. (2018). Ediacaran developmental biology. *Biol. Rev.* 93, 914–932.
16. Fedonkin, M.A., Gehling, J.G., Grey, K., Narbonne, G.M., and Vickers-Rich, P. (2007). *The Rise of Animals. Evolution and Diversification of the Kingdom Animalia* (Johns Hopkins University Press), p. 326.
17. Fedonkin, M.A., Ivantsov, A.Y., Leonov, M.V., and Serezhnikova, E.A. (2007). Dynamics of evolution and biodiversity in the late Vendian: a view from the White Sea. In *The Rise and Fall of the Vendian (Ediacaran) Biota. Origin of the Modern Biosphere.*, M. A. Semikhatov, ed., pp. 6–9.
18. Laflamme, M., Darroch, S.A., Tweedt, S.M., Peterson, K.J., and Erwin, D.H. (2013). The end of the Ediacara: Extinction, biotic replacement, or Cheshire Cat? *Gondwana Res.* 23, 558–573.
19. Boag, T.H., Darroch, S.A.F., and Laflamme, M. (2016). Ediacaran distributions in space and time: testing assemblage concepts of earliest macroscopic body fossils. *Paleobiology* 42, 574–594.
20. Darroch, S.A.F., Smith, E.F., Laflamme, M., and Erwin, D.H. (2018). Ediacaran extinction and Cambrian explosion. *Trends Ecol. Evol.* 33, 653–663.
21. Muscente, A.D., Bykova, N., Boag, T.H., Buatois, L.A., Mángano, M.G., Eleish, A., Prabhu, A., Pan, F., Meyer, M.B., Schiffbauer, J.D., et al. (2019). Ediacaran biozones identified with network analysis provide evidence for pulsed extinctions of early complex life. *Nat. Commun.* 10, 911.
22. Cunningham, J.A., Liu, A.G., Bengtson, S., and Donoghue, P.C.J. (2017). The origin of animals: can molecular clocks and the fossil record be reconciled? *Bioessays* 39, 1–12.
23. Mitchell, E.G., Bobkov, N., Bykova, N., Dhungana, A., Kolesnikov, A.V., Hogarth, I.R.P., Liu, A.G., Mustill, T.M.R., Sozonov, N., Rogov, V.I., et al. (2020). The influence of environmental setting on the community ecology of Ediacaran organisms. *Interface Focus* 10, 20190109.
24. Eden, R., Manica, A., and Mitchell, E.G. (2022). Metacommunity analyses show an increase in ecological specialisation throughout the Ediacaran period. *PLoS Biol.* 20, e3001289.
25. Glaessner, M.F., and Daily, B. (1959). The geology and late Precambrian fauna of the Ediacara fossil reserve. *Rec. South Austr. Mus.* 13, 369–401.
26. Glaessner, M.F. (1966). The late precambrian fossils from Ediacara, South Australia. *Palaeontology* 9, 599–628.
27. Fedonkin, M.A. (1985). Systematic description of Vendian Metazoa. In *Vendskaya Sistema*, Vol. 1. Paleontology, B.S. Sokolov and A.B. Ivanovski, eds. (Nauka), pp. 70–106.
28. Seilacher, A. (1999). Biomat-related lifestyle in the Precambrian. *Palaios* 14, 83–96.
29. Ivantsov, A.Y., and Fedonkin, M.A. (2002). Conulariid-like fossil from the Vendian of Russia: a metazoan clade across the Proterozoic/Palaeozoic boundary. *Palaeontol* 45, 1219–1229.
30. McCall, G.J.H. (2006). The Vendian (Ediacaran) in the geological record: Enigmas in geology's prelude to the Cambrian explosion. *Earth Sci. Rev.* 77, 1–229.
31. Hall, C.M., Droser, M.L., Gehling, J.G., and Dzaugis, M.E. (2015). Paleoecology of the enigmatic *Tribrachidium*: New data from the Ediacaran of South Australia. *Precambrian Res.* 269, 183–194.
32. Wang, Y., Du, W., Komiya, T., Wang, X.L., and Wang, Y. (2015). Macroorganism paleoecosystems during the Middle-Late Ediacaran Period in the Yangtze Block, South China. *Paleontol. Res.* 19, 237–250.
33. Jenkins, R.J.F. (1992). Functional and ecological aspects of Ediacaran assemblages. In *Origins and Early Evolution of Metazoa*, J.H. Lipps and P.W. Signor, eds. (Plenum Press), pp. 131–176.
34. Fedonkin, M.A., and Ivantsov, A.Y. (2007). *Ventogyrus*, a possible siphonophore-like trilobozoan coelenterate from the Vendian Sequence (late Neoproterozoic), northern Russia. *Geol. Soc. Lond. Spec. Pub.* 286, 187–194.
35. Vickers-Rich, P., Ivantsov, A.Y., Trusler, P.W., Narbonne, G.M., Hall, M., Wilson, S.A., Greentree, C., Fedonkin, M.A., Elliott, D.A., Hoffmann, K.H., and Schneider, G.I.C. (2013). Reconstructing Rangea: new discoveries from the Ediacaran of southern Namibia. *J. Paleontol.* 87, 1–15.
36. Ivantsov, A.Y., Gritsenko, V.P., Palyi, V.M., Velikanov, V.A., Konstantinenko, L.I., Menasova, A.S., Fedonkin, M.A., Zakrevskaya, M.A., and Serezhnikova, E.I. (2015). Makrofossili Verkhnego Venda Vostochnoy Yevropy. Sredneye Prid-Nestrov'ye Volyn (Upper Vendian Macrofossils of Eastern Europe. Middle Dniester Area and Volhynia) (Russian Academy of Sciences), pp. 1–143.
37. Hall, C.M.S., Droser, M.L., Clites, E.C., and Gehling, J.G. (2020). The short-lived but successful triradial body plan: a view from the Ediacaran of Australia. *Aust. J. Earth Sci.* 67, 885–895.
38. Fedonkin, M.A. (1984). Promorphology of the Vendian Radialia. In *Stratigraphy and Paleontology of the Earliest Phanerozoic*, B.S. Sokolov and A.B. Ivanovski, eds. (Nauka), pp. 30–58.
39. Fedonkin, M.A. (1987). Non-skeletal fauna of the Vendian and its place in the evolution of Metazoa: Study of the Paleontological Institute. *Akad. Nauk SSSR* 22, 1–174.
40. Ivantsov, A.Y., and Zakrevskaya, M.A. (2021). Trilobozoa, Precambrian Triradial Organisms. *Paleontol. J.* 55, 727–741.
41. Rahman, I.A., Darroch, S.A.F., Racicot, R.A., and Laflamme, M. (2015). Suspension feeding in the enigmatic Ediacaran organism *Tribrachidium* demonstrates complexity of Neoproterozoic ecosystems. *Sci. Adv.* 1, e1500800.
42. Grazhdankin, D.V. (2011). Ediacaran biota. In *Encyclopedia of Geobiology*, J. Reitner, V. Thiel, A. Kappler, K.O. Konhauser, A.E. Nunez, P. Reid, and X.L. Zhang, eds. (Springer Science), pp. 342–348.
43. Grazhdankin, D. (2014). Patterns of evolution of the Ediacaran soft-bodied Biota. *J. Paleontol.* 88, 269–283.
44. Erwin, D.H., Laflamme, M., Tweedt, S.M., Sperling, E.A., Pisani, D., and Peterson, K.J. (2011). The Cambrian conundrum: early divergence and later ecological success in the early history of animals. *Sci* 334, 1091–1097.
45. Evans, S.D., Droser, M.L., and Erwin, D.H. (2021). Developmental processes in Ediacara macrofossils. *Proc. Biol. Sci.* 288, 20203055.
46. Tang, F., Gao, L.Z., Yin, C.Y., Wan, Y., and Gu, P. (2015). Macrofossil biotas in the Late Ediacaran-Cambrian boundary interval of

- South China and stratotype correlation. *Geol. Bull. China* 34, 2150–2162.
47. Keller, B.M., and Fedonkin, M.A. (1977). New organic finds in the Precambrian Valday series along the Syuz'ma River. *Int. Geol. Rev.* 19, 924–930.
  48. Baucon, A., Neto De Carvalho, C., Felletti, F., and Cabella, R. (2020). Ichnofossils, cracks or crystals? A test for biogenicity of stick-like structures from Vera Rubin Ridge, Mars. *Geosciences* 10, 39.
  49. Rouillard, J., van Zuilen, M., Pisapia, C., and Garcia-Ruiz, J.M. (2021). An alternative approach for assessing biogenicity. *Astrobiology* 21, 151–164.
  50. Nolan, M.R., Walker, S.E., Selly, T., and Schiffbauer, J. (2023). Is the middle Cambrian Brooksella a hexactinellid sponge, trace fossil or pseudofossil? *PeerJ* 11, e14796.
  51. Garcia-Ruiz, J. (1993). Natural viscous fingering. In *Growth Patterns in Physical Sciences and Biology*. NATO ASI Series, 304, J. Garcia-Ruiz, E. Louis, P. Meakin, and L. Sander, eds. (Springer US), pp. 183–189.
  52. Potter, P.E., Maynard, J.B., and Pryor, W.A. (1980). *Sedimentology of Shale : Study Guide and Reference Source* (Springer-Verlag), pp. 23–36.
  53. Rozhnov, S.V. (2012). Development of symmetry and asymmetry in the early evolution of the echinoderms. *Paleontol. J.* 46, 780–792.
  54. Dudit, L., Rahman, I., and Cunningham, J. (2018). Investigating the Evolution of Symmetry in Cambrian Echinoderms. *Progressive Palaeontology Conference*.
  55. Smith, C.L., Pivovarova, N., and Reese, T.S. (2015). Coordinated feeding behavior in Trichoplax, an animal without synapses. *PLoS One* 10, e0136098.
  56. Darroch, S.A., Cribb, A.T., Buatois, L.A., Germs, G.J., Kenchington, C.G., Smith, E.F., Mocke, H., O'Neil, G.R., Schiffbauer, J.D., Maloney, K.M., et al. (2021). The trace fossil record of the Nama Group, Namibia: exploring the terminal Ediacaran roots of the Cambrian explosion. *Earth Sci. Rev.* 212, 103435.
  57. Evans, S.D., Tu, C., Rizzo, A., Surprenant, R.L., Boan, P.C., McCandless, H., Marshall, N., Xiao, S., and Droser, M.L. (2022). Environmental drivers of the first major animal extinction across the Ediacaran White Sea-Nama transition. *Proc. Natl. Acad. Sci.* 119, e2207475119.
  58. Gao, Y., Qin, Y., Lin, S., and Ling, W. (2020). Nd isotopic stratigraphy of Paleoproterozoic to late Paleozoic sedimentary strata of the southwestern Yangtze Block and implications for its tectonic evolution. *Int. Geol. Rev.* 62, 740–753.
  59. Liu, P., Yin, C., and Tang, F. (2022). Research Progress of Ediacaran (Sinian) Biostratigraphy in South China. In *Meso-Neoproterozoic Geology and Petroleum Resources in China*, T. Wang, ed. (Springer Nature), pp. 155–179.
  60. Luo, H.L., Jiang, Z.W., Wu, X.C., Song, X.L., and Ou, Y.L. (1982). *The Sinian-Cambrian Boundary in Eastern Yunnan, China* (Kunming: Yunnan People's Publishing House), pp. 1–265.
  61. Xing, Y.S., Ding, Q.X., Luo, H.L., He, T.G., and Wang, Y.G. (1984). The Sinian-Cambrian boundary of China. *Bull. Chin. Acad. Geol. Sci.* 10, 1–262.
  62. Tang, F., Yin, C.Y., Liu, P.J., Wang, Z.Q., and Gao, L.Z. (2007b). Discovery of diverse macrofossil assemblages from the Jiucheng Member of uppermost Ediacaran in eastern Yunnan. *J. Palaeogeogr.* 9, 533–540.
  63. Tang, F., Chen, J.S., Ren, L.D., Gao, L.Z., and Hua, H. (2020). *The Trailblazer of Animals—The Fossil Documents and Comparative Study of the First Candidate GSSP Meishucun Section in China* (Yunnan Science and Technology Press), pp. 1–498.
  64. Gu, P., Zhong, L., Zhang, G.D., Song, S.C., Tang, F., Ling, M.Q., and Gao, L.Z. (2018). The division of the Late Ediacaran-Cambrian boundary interval stratigraphy and new options of Index Fossil FAD in South China. *Acta Geol. Sin.* 92, 449–465.

## STAR★METHODS

## KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Biological samples		
<i>Lobodiscus tribrachialis</i>	Kunming General Survey of Natural Resources Center, China Geological Survey	KGS00228

## RESOURCE AVAILABILITY

## Lead contact

Further information and requests for materials should be directed to and will be fulfilled by the lead contacts, Feng Tang ([tangfeng65@qq.com](mailto:tangfeng65@qq.com)).

## Materials availability

All materials examined in this study, including part and counterpart of the *Lobodiscus* holotype (KGS00228), are deposited in the Kunming General Survey of Natural Resources Center, China Geological Survey.

## Data and code availability

This paper analyzed a fossil specimen. The repository and accession number of this specimen are listed in the [key resources table](#).

This paper does not report original code.

Any additional information required to reanalyze the data reported in this paper is available from the [lead contact](#) upon request.

## EXPERIMENTAL MODEL AND SUBJECT DETAILS

No experimental model organism was used in this study.

## METHOD DETAILS

## Geological setting

The study region is in Jiangchuan, Yuxi City of eastern Yunnan, in the Neoproterozoic-Mesozoic fracture belt on the upper Yangtze block. It belongs to the Kunming district of Kangdian in the upper Yangtze sequence area of South China. Neoproterozoic to Paleozoic strata are widely exposed in the region, comprising (from oldest to youngest) the Sinian Dengying Formation, the Cambrian Yuhucun Formation, Qiongzhusi Formation, Canglangpu Formation, Longwangmiao Formation, Xiwangmiao Formation, and Loushanguan Formation, and the Permian Yangxin Formation.<sup>3,58,59</sup>

The fossil-bearing stratigraphic sequences comprising the Jiangchuan Biota are mainly located in the middle and upper parts of the Dengying Formation, which crops out from Houjiashan to the north side of the mine road in the town of Jiangcheng, Jiangchuan District, Yuxi City, Yunnan Province (Figure 1A), and from Taoxi Village to Gugeng Village (Figure 1A), as well as in the continuous outcrop section of the Dengying Formation adjacent to the county road from Liujie to Wangjiawan in the Jinning District, Kunming City (Figure 1A). Locally, the Dengying Formation is subdivided into the Algal Dolomite (the original Donglongtan Formation), Jiucheng, and Baiyanshao members in ascending order.<sup>1,60,61</sup> Its sequence of fossil-rich exposures is well zoned, and after intensive excavation over recent years, five macrofossil assemblages have been identified from the base upward.<sup>6,46,62–64</sup> These comprise assemblages A-D in the Jiucheng Member of the middle Dengying Formation, characterized by layers of fine-grained dolomite interbedded with muddy siltstone and shale, and assemblage E in the Baiyanshao Member in the upper part of the Dengying Formation: Zone a-Shaanxilithes, zone b-Chuaria-Tawuia-Pumilibaxa, zone c-Shouhsienia-Vendotaenia-Houjiashania, zone d-Longfengshani-Cyclomedusa-Lobodiscus, and zone e-Vendotaenia-Tyrasotaenia (Figure 1B).

## Fossil materials and imaging methods

The fossil described in this study was preserved *in situ* in thin layers of grey-black dolomite-bearing siltstone in the central part (D assemblage) of the Jiucheng Member (Figure 1B), and it was exposed by mechanical cleaving of the bedding planes without further preparation. The outcrop in the fossil pit preserving the B-D assemblages (Figure 1B) is located approximately 900 meters southwest of Houjiashan Village, at an elevation of H = 2106 m, latitude N: 24°27'39.3", longitude E: 102°46'48.4" (data sourced from the Beidou Navigation Satellite System). Due to weathering, the fossil-bearing layers are often yellowish-grey with a flat lying microstratigraphy, deposited in an intertidal sandy and muddy environment.<sup>1</sup> Carbonaceous compression fossils from this site are exposed at the weathered levels and easy to identify.

The fossil examined for this study was visualized using a stereomicroscope (JSZ6D) both under normal light and using a cold light illuminator (XZ-150W) to enhance the visibility of low-relief features and better characterize its morphology in detail. All photographs were taken using a Canon EOS-50D camera. All images were made in CorelDRAW 2018 and Adobe Photoshop 2022.