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Death march of a segmented and trilobate bilaterian elucidates early animal evolution

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Supplementary information

1. Geological setting and materials

The Ediacaran System is well exposed in the Yangtze Gorges area (Extended Data Fig. 1a). It includes the Doushantuo Formation and the overlying Dengying Formation. The Doushantuo Formation in the Yangtze Gorges area may have been deposited in an intrashelf basin, but the Dengying Formation in this area was likely deposited in a carbonate platform³¹. The Ediacaran System is underlain by glacial diamictite of the Cryogenian Nantuo Formation and overlain by the lower Cambrian Yanjiahe Formation that contains basal Cambrian small shelly fossils and the *Asteridium*–*Comasphaeridium*–*Heliosphaeridium* microfossil assemblage^{32–35}. A zircon TIMS U-Pb age of 551.1 ± 0.7 Ma from the uppermost Miaohu Member of the Doushantuo Formation¹⁷ and a zircon nanoSIMS U-Pb age of 526.4 ± 5.4 Ma from the base of the lower Cambrian Shuijingtuo Formation in the Yangtze Gorges area¹⁸ bracket the depositional age constraint of the Dengying Formation. Considering that the Ediacaran-Cambrian boundary is likely around 539 Ma³⁶, the Dengying Formation is probably between 551 Ma and 539 Ma.

The terminal Ediacaran Dengying Formation is well exposed in the Yangtze Gorges area (Extended Data Fig. 1). It is subdivided into three lithostratigraphic units: the Hamajing, Shibantan, and Baimatuo members. The Shibantan Member consists of dark grey, thin-bedded, microlaminated micritic limestone deposited in subtidal environments³⁷. It contains a number of soft-bodied Ediacara-type fossils³⁸, trace fossils^{3,37,39}, as well as problematic fossils^{40,41}.

A total of 48 specimens (35 body fossils and 13 trace fossils) were collected from a unit of gray-dark thin-bedded limestone about 0.5–10 m above the base of the Shibantan Member at the Wuhe village (30°47′10″–30°47′27″ N, 111°02′47″–111°03′23″ E) in Hubei Province. Specimens are most abundant at 0.5–2 m above the base of the Shibantan Member. Co-occurring fossils include *Aspidella*, *Hiemalora*, *Charnia*, and *Wutubus*; these taxa can be preserved on the same bedding surface as *Yilingia* or its trace fossils. *Yilingia* is the second most abundant taxon after *Hiemalora*. Specimens (NIGP-166252 to NIGP-166258, NIGP-169869 to NIGP-169870) are repositied in the Nanjing Institute of Geology and Palaeontology, except one specimen (NIGP-169869) that is currently left on the outcrop (30°47′9.5″ N, 111°02′57.6″ E).

2. Detailed fossil description

2.1. General description

Descriptive terminology is illustrated in Extended Data Fig. 2. *Yilingia spiciformis* is an elongate, strap-like, bilaterally symmetrical fossil with repeated segments. Segments are trilobate, each consisting of a central and two lateral lobes. Lateral lobes are obliquely attached to the central lobe, consistently directed to one end of the fossil, which is interpreted to be the posterior end. The body slightly tapers anteriorly and narrows more abruptly at the posterior end.

2.2. Measurements (Extended Data Table 1)

The fossil is straight or slight curved, with a consistent width of 5–26 mm and a preserved length up to 27 cm (Extended Data Fig. 3a). The most complete specimen is

estimated to have up to 50 segments (Extended Data Fig. 5a–b, NIGP-169869). The central lobe is rhomboidal in shape, representing about one fifth of the body width. Average segment length is positively correlated with body width (Extended Data Fig. 3b). Lateral lobes are elongate to subtriangular in shape, 5 mm in maximum width, 14 mm in maximum length, and obliquely attached to the central lobe with an angle of about 30°–60° relative to the body axis.

The holotype (Fig. 1a–c, Extended Data Fig. 4a) is an incomplete specimen, with the anterior and posterior ends missing. It is preserved with a part and a counterpart, and in combination they give a more complete picture of the fossil. The specimen is biconvex in transverse cross section, showing well-preserved dorsal structures (Fig. 1a and left part of Fig. 1b) but ventral structures are obscured (right part of Fig. 1b). The maximum width, about 23 mm, occurs in the middle of trunk, which narrows toward both ends. At least 32 segments can be counted in the preserved specimen, which is about 199 mm in length. The axial region consisting of the central lobes is about 4.7 mm in width. Lateral lobes slightly taper distally, some with putative podomere-like structures (Fig. 1c), although these may also be taphonomic artifacts. The inclination angle between the long body axis and lateral lobes is about 40° and 50° on either side.

A nearly complete but less well-preserved specimen (Extended Data Fig. 5a–b) is presently left on the outcrop. It is slight curved, 267 mm in length, and 14.9 mm in maximum width. Although its anterior and posterior ends are poorly preserved, most segments are recognizable and countable. We estimated that it has about 50 segments.

2.3. Dorso-ventral differentiation

Most specimens are preserved as concave molds in bed tops or convex casts in bed soles, thus exposing ventral features (Extended Data Fig. 4c–d). Five specimens are preserved as convex casts on bed tops, thus exposing dorsal characters (Extended Data Figs. 4a–b, 5a). The relief indicates that the fossil was biconvex in transverse cross section, as confirmed in thin section observation (Fig. 1e, g).

Based on a comparison between dorsal and ventral morphologies, it is clear that, although both sides are characterized by trilobate segments, there are some subtle differences, suggesting a degree of dorso-ventral differentiation. These differences include: (1) the lateral lobes are elongate on the dorsal side (Extended Data Fig. 4a–b) but subtriangular in ventral view (Extended Data Fig. 4c–d); (2) the lateral lobes on the dorsal side seem to consist of podomere-like structures (Fig. 1c, Extended Data Fig. 4a); podomere-like structures on dorsal side can be recognized in two other specimens, one of which is illustrated in Extended Data Figure 4b, although these structures need to be confirmed with additional and better preserved specimens; (3) the central lobes are rhomboidal and exposed wider on the dorsal side (Extended Data Fig. 4a–b) than on the ventral side, where the central lobes are narrower (Extended Data Fig. 4c–d), apparently because the lateral lobes are tucked beneath the central lobes; and (4) the ventral side appears to have a greater relief (Extended Data Fig. 4c–d) than the dorsal side (Extended Data Fig. 4a–b, 5a).

2.4. Antero-posterior differentiation

The lateral lobes are consistently directed toward one end of the strap-like body of *Yilingia spiciformis*. This end is regarded as the posterior end based on the association of

a body fossil and a mortichnium (Fig. 1f). The animal gradually tapers toward the anterior end (Extended Data Fig. 5c) and more rapidly narrows at the posterior end (Extended Data Fig. 4c–d), which seems to consist of two or more rod-like structure (Extended Data Fig. 4c). No distinctive tagmata or head structure is recognized.

3. Morphological reconstruction (Extended Data Fig. 6)

Based on our observations, *Yilingia spiciformis* is reconstructed as an elongate strap-like animal with a biconvex transverse cross section and consisting of a series of repetitive and presumably homologous segments along the long body axis. Each segment consists of two lateral lobes attached to a central lobe. The lateral lobes are directed posteriorly, with an angle of about 30°–60°. The body slightly and gradually tapers anteriorly and narrows more sharply toward the posterior end.

4. Comparisons with other Ediacaran fossils

Yilingia spiciformis is morphologically distinct from other terminal Ediacaran body fossils in the Shibantan Member and elsewhere. Frondose Ediacara-type fossils, such as *Charnia*⁴², *Arborea*⁴³, *Rangea*⁴⁴, *Swartpuntia*⁴⁵, and *Pteridinium*⁴⁶ have two or more sets of serially arranged tubular modules, but these fossils are not bilaterally symmetric in a strict sense as the modules are typically offset at the central axis, and all but the last genus are interpreted as erect benthic organisms with a holdfast attaching to the substrate.

Several slightly older Ediacaran fossils, including *Dickinsonia*, *Yorgia*, *Andiva*, *Spriggina*, *Marywadea*, *Precambrium*, *Vendia*, and *Vendomia*, have been interpreted as segmented animals with body polarity^{27,29,47–51}. Some of them—for example *Spriggina*

and *Marywadea*—may even have specialized cephalon-, trunk-, and pygidium-like tagmata⁵². *Spriggina* has a horseshoe-shaped cephalon with a smoothly curved anterior margin and posterolaterally directed projections. A medial groove runs along the trunk, which consists of up to 42 segments with parapodia-like structures⁵³. *Marywadea* is broadly similar to *Spriggina* but has a half-moon shaped head. Thus, although *Spriggina* and *Marywadea* are similar to *Yilingia* in being segmented organisms, they do not have a trilobate bodyplan as does *Yilingia spiciformis*, and they show evidence of tagmatization. Nonetheless, these Ediacaran fossils suggest that various metameric or segmented animals have already evolved by the Ediacaran Period and a systematic evaluation of these fossils can illuminate the current debate on the origin of segmentation in bilaterian animals^{22,26,27,29}, particularly the progressive evolution of serial pattern, metamerism, and segmentation²⁸.

Several late Ediacaran tubular fossils are superficially similar to *Yilingia* in having serially repeated units. These include *Plexus*⁵⁴, *Wutubus*³⁸, and *Funisia*⁵⁵. However, these Ediacaran fossils have simple repetitive units that are neither trilobate nor polarized, and at least *Wutubus* and *Funisia* are not bilaterally symmetric.

5. Phylogenetic interpretation of *Yilingia spiciformis*

Although serial repetition occurs in a number of eukaryote clades, including rhizarians, plants, and fungi²⁹, metamerism and segmentation in bilaterian animals are produced through distinct developmental programs^{27,29}. The precisely programmed bilateral symmetry and polarized repetitive units in *Yilingia* are characteristic of segmented bilaterian animals. In contrast, repetitive modules of rhizarians, plants, and

fungi are not bilaterally symmetric in a strict sense, and their symmetry is often upset by diffuse, aberrant, and indeterminate growth²⁷. These morphological features, considered together with the evidence for motility (see below), *Yilingia* is best interpreted as a bilaterian animal.

6. Mortichnium of *Yilingia spiciformis*

Specimen NIGP-166253 (Fig. 1f–g, Extended Data Fig. 7)

Observation: Both part and counterpart were collected. The specimen is best seen on the bed sole. It consists of a body fossil (blue bracket in Extended Data Fig. 7b–c) that is physically connected with a mortichnium (white bracket in Extended Data Fig. 7b–c). The body fossil is 23–25 mm in width and 179 mm in preserved length. It has a convex relief on the bed sole, a biconvex transverse profile (Fig. 1g), and at least 19 discernable segments with central and lateral lobes. The mortichnium is similar in width to the body fossil, 151 mm in length, flanked with two lateral grooves, preserved in low relief, and has poorly recognizable segments. Two poorly preserved specimens of *Yilingia spiciformis* (arrows in Extended Data Fig. 7a) and several undermat burrows, including *Helminthoidichnites*-like trace fossils (as negative hyporelief; arrowheads and *Ht* in Extended Data Fig. 7), are present on the same slab. Some of these *Helminthoidichnites*-like trace fossils are clearly truncated by the mortichnium.

Interpretation: The interpretation of the mortichnium is supported by the presence of two lateral grooves (equivalent to lateral levees on the bed top) that truncate primary bedding surface structures and *Helminthoidichnites*-like trace fossils. This interpretation is also consistent with the poor ornamentation and the lower relief of the mortichnium

relative to the attached body fossil, which preserves the diagnostic feature of *Yilingia spiciformis*, including the trilobate segments. Importantly, the posterior end of the body fossil terminates abruptly and is featured with at least two rod-like structures, similar to those shown in Extended Data Fig. 4c. Together, these observations strongly support the interpretation of the mortichnium in connection with and behind a body fossil of *Yilingia spiciformis*.

7. Other trace fossils produced by *Yilingia*

Specimen NIGP-166256 (Fig. 2a–b, Extended Data Fig. 8)

Observation: This specimen was collected as a float with unknown stratigraphic orientation but with part and counterpart. It is a long sinuous trace with prominent lateral grooves flanking a central bulge (Extended Data Fig. 8a) and corresponding levees surrounding a central trough (Extended Data Fig. 8b). The trace fossil is about 4–7 mm in width and about 168 mm in length. Chevron-like structures are present in part of the specimen (i.e., left part of Extended Data Fig. 8a, about 47 mm in length), and these structures are similar to the trilobate segments of *Yilingia spiciformis*. The rest of the trace is featureless with the exception of the lateral grooves and levees (arrows in Extended Data Fig. 8b–c), and a vaguely visible central ridge (Extended Data Fig. 8b, between two arrows to the right). In addition to the trace fossil, the slab contains another poorly preserved fossil (arrow in Extended Data Fig. 8d), which is about 5 mm in width, about 26 mm preserved length, and appears to consist of three rows of knobby structures. This poorly preserved fossil is oriented nearly perpendicular to and apparently lies atop the trace fossil.

Interpretation: Although this specimen is not stratigraphically oriented, the surface with the lateral grooves is inferred as bed sole (Extended Data Fig. 8a) and that with the lateral levees as bed top (Extended Data Fig. 8b). Thus, the central trough in Extended Data Fig. 8b represents a trail with flanking levees. The chevron-like structures are broadly similar to the trilobate segments of *Yilingia spiciformis*, indicating that this trace fossil was made by *Yilingia spiciformis*. This is further supported by the presence of a central ridge between two arrows in the right of Extended Data Fig. 8b, which is interpreted as the impression of the narrow gap between the two lateral lobes tucked beneath the central lobe. In this interpretation, the part with a central ridge (right part of Extended Data Fig. 8a–b) is a surface trail whereas the part with the chevron-like structures probably represents a resting trace.

The poorly preserved fossil (arrow in Extended Data Fig. 8d) cannot be positively identified, although it could be a body fossil of *Yilingia spiciformis*. Because it appears to lie atop of the trail (Extended Data Fig. 8d), it must have been emplaced after the trail was made.

Specimen NIGP-166255 (Fig. 2c–d, g)

Observation: This specimen is about 10 mm in width and 152 mm in observable length. It is preserved as a positive hyporelief (Fig. 2c), as confirmed by thin section observation (Fig. 2g). It has two prominent lateral grooves (arrows in Fig. 2d) surrounding a central bulge and vague chevron-like structures (Fig. 2d) that are similar to trilobate segments in *Yilingia spiciformis*. It truncates small (~2 mm wide) *Torrowangea*-like trace fossils (arrowhead in Fig. 2d) and other primary bedding surface structures

(Fig. 2d). Several other trace fossils are present on the same slab, to the right and upper right of the *Yilingia spiciformis* trace fossil in Fig. 2c.

Interpretation: The presence of lateral grooves flanking a central bulge on the bed sole, the semirelief preservation, and the truncation relationship with small trace fossils, indicate that sediment was disrupted and thus establish this specimen as a trace fossil. The preservation of chevron-like structures resembling the trilobate segments indicates that this trace was produced by *Yilingia spiciformis*.

Specimen NIGP-166257 (Fig. 2e–f, h)

Observation: This specimen has part and counterpart, with known stratigraphic orientation. It is preserved as a semirelief (Fig. 2h). Chevron-like structures are discernable on the negative epirelief (Fig. 2e), presumably representing an impression of the ventral surface of the trace maker. It has lateral levees flanking a central trough on the bed top (Fig. 2e).

Interpretation: The semirelief preservation and lateral levees suggest that this specimen is a trace fossil. The chevron-like structures, although poorly preserved, broadly resemble the trilobate segments of *Yilingia spiciformis*, which was probably the trace producer. We note that the two lateral levees are not equal in height, with the one on top of Fig. 2e broader but lower than the one at bottom. The cause of this asymmetry is unknown, but may be related to uneven cohesiveness of the substrate or an attempt by the trace maker to move sideways or to make a turn. Regardless, the prominent levees, particularly on the lower side in Fig. 2e, provide strong evidence for sediment displacement and the trace fossil interpretation.

8. Ichnotaxonomic comparison

Surface trails with lateral levees are produced when a trace maker pushes itself through the upper portion of the sediment layer and displaces sediment to either side of the organism^{19,56}. Based on neoichnological observations, such lateral levees can be produced by a variety of animals⁵⁷⁻⁵⁹ and some protists⁶⁰. The Shibantan trace fossils with lateral levees surrounding a featureless trough (e.g., right part of Fig. 2a) can be regarded as *Archaeonassa*-type trails¹. *Archaeonassa* is composed of two lateral levees separated by a flat, convex, or concave central zone. The ichnogenus *Archaeonassa* is generally interpreted as a pascichnia produced by various invertebrates, including arthropods and mollusks⁶¹⁻⁶³, and modern *Archaeonassa* is related to locomotion behavior of gastropods^{58,64}. The Ediacaran fossil *Somatohelix*, which is interpreted as a tubular body fossil⁶⁵, also appears to have levee-like and groove-like structures (figs. 3 and 7–8 of Sappenfield et al., 2011); further study is required to determine whether these levee-like and groove-like structures represent sediment disruption related to a trace fossil or sediment injection underneath a body fossil⁶⁵. Nonetheless, the ichnofossils by *Yilingia* are distinct from *Archaeonassa* and *Somatohelix* in sometimes having chevron-like structures.

Shibantan traces with chevron-like structures that clearly resemble the trilobate segments of *Yilingia spiciformis* (Fig. 2b, d; Extended Data Fig. 8c) are superficially similar to several ichnogenera, such as *Arthropycus*, *Ophiomorpha*, *Scolicia*, and *Protovirgularia*. However, *Arthropycus* commonly occurs as bundles of annulated, curved, and simple or branched burrows, which typically display bilobate median

253 longitudinal depression and strong, very regularly spaced transverse annulations.
254 *Arthropycus* is widely accepted as a feeding trace by unspecified “worms” and various
255 arthropods ^{11,61,66-69}. *Ophiomorpha* is a horizontal or subhorizontal cylindrical burrow that
256 is typically covered with dense, regularly distributed, discoid, ovoid, or irregular
257 polygonal pellets arranged perpendicularly to the long axis of the burrow. *Ophiomorpha*
258 burrows are considered to be dwelling and feeding burrow of suspension feeders ⁷⁰⁻⁷⁶.
259 *Arthropycus* and *Ophiomorpha* are burrows or burrow systems, fundamentally different
260 from the exogenic surface traces of *Yilingia spiciformis* described here. Their
261 ornamentations are also different, with *Arthropycus* characterized by discrete and
262 prominent transverse annulations, *Ophiomorpha* by dense packed pellets, whereas the
263 *Yilingia* traces are featured with trilobate chevron-like structures. *Scolicia* is a
264 meandering, trilobate trail consisting of a variably shaped medial axis with transverse
265 laminae, flanked by two lateral bands of smooth or curved laminae, and with broadly U-
266 shaped in transverse section. *Scolicia* are thought to be produced by echinoids ^{61,74,77-80}.
267 That the medial axis and lateral bands are distinctly separated by groove or sediment
268 strings in *Scolicia* is different from the traces produced by *Yilingia spiciformis*.

269 Several named trace fossils have chevron-like structures that invite comparison with
270 some of the traces described here. For example, *Protovirgularia* is a trail preserved as
271 positive semi-cylindrical hyporelief, and characterized by delicate, inclined-to-horizontal,
272 chevronate structures. Trace fossils included in *Protovirgularia* display strong
273 morphological variations ⁸¹⁻⁸³ and hence ichnotaxonomic classification is a challenge.
274 Several ichnogenera described as *Walcottia*, *Pennatulites*, *Uchirites*, *Imbrichnus*,
275 *Sustergichnus*, and *Chevronichnus* have been included in *Protovirgularia* ^{82,84-86}. In any

case, *Protovirgularia* has been interpreted as a locomotion-feeding trace of protobranch bivalves or scaphopods moving through the sediment by means of a cleft foot that employs a push-and-pull mechanism, — an interpretation supported by neoichnological observations^{81,86-88}, although Lima, et al.⁸⁹ proposed that isopods are the tracemakers of *Protovirgularia*. *Protovirgularia* typically consists of a median furrow, which is different from impression of central lobes in the trace of *Yilingia spiciformis*. Additionally, the open side of the chevrons in *Protovirgularia* faces toward the direction of locomotion^{82,85,86,90}, which is different from the *Yilingia* traces, where the open side of the chevron-like structures faces away from the direction of movement. We surmise that *Yilingia* probably adopted a locomotive strategy different from that of the cleft foot of mollusks but more akin to some arthropods^{11,91}. In addition to *Protovirgularia*, it is worth mentioning that an unnamed ichnofossil described as a chevronlike trail from Early Devonian Santa Rosa Formation in Bolivia (fig. 3.7–3.8 in Gaillard and Racheboeuf⁹²) is also broadly similar to the traces of *Yilingia spiciformis*. This Devonian chevron-like trail may have been produced by an arthropod using numerous appendages for locomotion⁹².

Finally, the *Yilingia* trace illustrated in Fig. 2e is somewhat similar to *Climactichnites* which is a trail or burrow consisting of undulating bars and furrows oriented at an angle to the direction of movement. Several paleoichnological studies and neoichnological experiments have shown that the tracemaker of *Climactichnites* was probably an elongate, bilaterally symmetrical, dorsoventrally flattened, soft-bodied, mollusk-like animal with a muscular foot⁹³⁻⁹⁵. The *Yilingia* trace has two prominent lateral levees and chevron-like structures running over one of the lateral levees, features that are not common in *Climactichnites*.

To summarize, although a number of published ichnotaxa show some intriguing similarities to the Shibantan trace fossils described here, none provide an appropriate ichnotaxonomic home for these trace fossils. The *Yilingia* traces likely represent a new ichnotaxon.

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