PALEONTOLOGY

Late Ediacaran trackways produced by bilaterian animals with paired appendages

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Ediacaran trace fossils provide key paleontological evidence for the evolution of early animals and their behaviors. Thus far, however, this fossil record has been limited to simple surface trails and relatively shallow burrows. We report possible trackways, preserved in association with burrows, from the terminal Ediacaran Shibantan Member (ca. 551 to ca. 541 million years ago) in the Yangtze Gorges area of South China. These trace fossils represent the earliest known trackways. They consist of two rows of imprints arranged in poorly organized series or repeated groups. These trackways may have been produced by bilaterian animals with paired appendages, although the phylum-level phylogenetic affinity of the trace makers remains unknown. It is possible that the trackways and associated burrows were produced by the same trace maker, indicating a complex behavior involving both walking and burrowing. Together, these trackways and burrows mark the arrival of a new era characterized by an increasing geobiological footprint of bilaterian animals.

INTRODUCTION

Molecular clocks indicate that the kingdom Metazoa diverged in the Tonian Period [~1000 to 720 million years (Ma) ago], major superphyla of animals in the Cryogenian Period (~720 to 635 Ma ago), and most bilaterian animal phyla in the Ediacaran Period (635 to 541 Ma ago) (*1*). However, although molecular fossils of sponges have been reported from the Cryogenian Period (*2*), unambiguous bilaterian animals do not occur in the fossil record until the late Ediacaran Period (*3*).

Traditionally, many Ediacaran body fossils have been interpreted as representatives of living animal phyla (*4*). In this traditional view, arthropods and annelids, both of which are expected to have paired appendages, are featured prominently in the Ediacara biota. For example, *Dickinsonia* and *Spriggina* have been interpreted as polychaetes, and *Parvancorina* has been interpreted as an arthropod (*4*). However, diagnostic anatomical features supporting such interpretations—that is, parapodia that are inferred to be present in the last common ancestor of annelids (*5*) and jointed appendages in the last common ancestor of arthropods (*6*)—are either absent or not preserved in these fossils. Thus, these traditional interpretations have been questioned (*7*), and the current view is that few Ediacaran animal fossils are phylogenetically resolved at the phylum level (*8*). Thus far, no Ediacaran body fossils have been convincingly shown to bear paired appendages.

The trace fossil record provides another archive that can be explored to gain insights into the early evolution of animals and appendages (*9*). In general, most Ediacaran trace fossils are simple, horizontal, unbranched trails and burrows, representing simple behaviors of cnidarian-grade and simple worm-like animals that lived close to the sediment surface (*10*, *11*). Only a few Ediacaran trace fossils record moderately complex behaviors of trace-making animals (*12*–*15*). Trackways, which are a series of impressions left by locomotion appendages (for example, parapodia of annelids and appendages of panarthropods) and represent an important category of ichnological architecture, are hitherto unknown in the Ediacaran Period [(*9*), but see Chen *et al.* (*13*)]. This pattern is in sharp contrast to the early Cambrian ichnological record, where trackways are common and some seem to record locomotion activities of early arthropods (*10*, *16*, *17*).

Here, we report new trace fossils from the terminal Ediacaran Shibantan Member of the upper Dengying Formation (ca. 551 to ca. 541 Ma ago) in the Yangtze Gorges area of South China (Fig. 1; see the Supplementary Materials for a description of the geological and stratigraphic setting). These trace fossils include burrows and possible trackways that are preserved in close proximity and are apparently connected. They were probably made by millimeter-sized animals with bilateral appendages and can provide important insights into early bilaterian evolution and behaviors.

RESULTS

The trace fossils described in this paper are preserved in dark gray, thin-bedded, bituminous limestone of the ca. 551-Ma to ca. 541-Ma Shibantan Member deposited in a subtidal environment between fair-weather and storm wave bases (*15*, *18*). Like other trace fossils from the same locality and horizon, they exclusively occur in beds characterized by crinkled microlaminae, which are interpreted as microbial mats, suggesting intimate ecological interactions between the trace makers and the mats (*13*, *15*, *19*). These microbial mats comprised a few millimeters of sediment and may have also helped trace fossil preservation (*20*, *21*).

The material consists of co-occurring trackways (labeled TW1 and TW2 in Fig. 2) and burrows (labeled UB1 to UB3 in Fig. 2) that were excavated in situ with known stratigraphic orientation and with both parts and counterparts. Thus, there is no ambiguity with regard to the identification of epirelief versus hyporelief preservation.

Trackways

The trackways are straight or slightly curved, each consisting of two rows of shallow depressions on the top bedding surface (that is, negative epireliefs; Fig. 2A) and two rows of projections on the corresponding bottom surface (that is, positive hyporeliefs; Fig. 2B). Other than these depressions and projections, there is no discernible topographic relief or evidence for sediment disturbance between and beyond the

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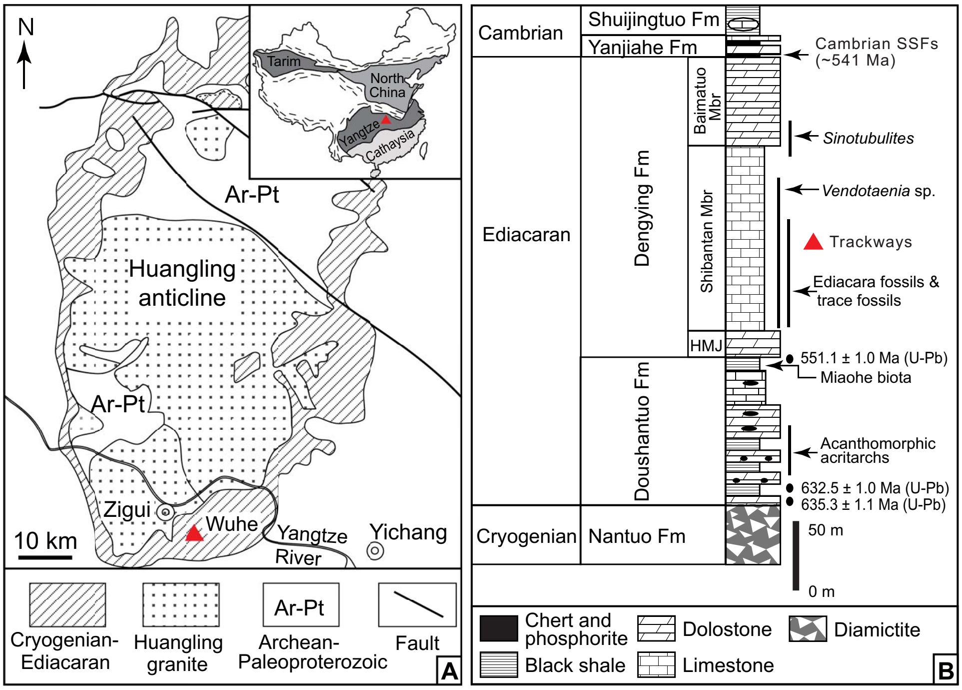

Fig. 1. Geological map and stratigraphic column. (**A**) Generalized geological map of the Yangtze Gorges area, showing the distribution of Ediacaran strata and the fossil location at Wuhe (triangle). Inset map shows the location of the Yangtze Platform in South China. (**B**) Stratigraphic column of the Ediacaran Doushantuo and Dengying formations, showing stratigraphic occurrences of fossils, including the trackways (triangle) reported in this paper. Mbr, Member; Fm, Formation; SSF, small shelly fossil; HMJ, Hamajing Formation. Zircon U-Pb ages from the work of Schmitz (*40*). Figure produced by S.X. using Adobe Illustrator.

two rows of depressions. Furthermore, TW2 crosses over but does not disrupt UB1 and UB2 (Fig. 2, A and C). Thus, TW1 and TW2 cannot be trails, partially preserved or partially excavated burrows, or collapsed burrows (fig. S2), because trails or burrows would disrupt the sediment between the two lateral walls (fig. S2, A and C), they would cut into UB1 and UB2 when crossing over the latter (fig. S2, E and F), and the lateral walls of collapsed burrows would be preserved as positive epireliefs rather than negative epireliefs (fig. S2C). For the same reasons, the depressions in TW2 cannot be outlets emerging from a horizontal burrow, for example, epichnial version of a treptichnid (*10*), as has been proposed for the Cambrian trace fossil *Bicavichnites* that was otherwise interpreted as a trackway (*22*). Instead, the most likely and parsimonious interpretation is that TW1 and TW2 represent epichnial trackways. It is possible that they are undertracks (that is, appendage imprints on sediments below a microbial mat, made by an animal walking atop the mat), considering that they are closely associated with microbial mats. Thus, the depressions are interpreted as tracks or imprints of bilateral locomotory appendages, which are preserved as negative epireliefs on the top bedding surface (Fig. 2A) or as positive hyporeliefs on the bottom bedding surface (Fig. 2B). The trackways are described below following the terminology of Trewin (*23*).

TW1 has a preserved length of about 70 mm, an external width of about 13.8 mm, and an internal width of about 4 mm. The external and internal trackway widths are consistent along the length of TW1. The tracks (that is, depressions or imprints) are ~1 to 2 mm in size and ~1 mm in epichnial depth, with an appreciable amount of size variation perhaps due to alteration in association with carbonate diagenesis. The tracks are not as regularly arranged as most Phanerozoic trackways (*23*). However, at least four sets of tracks (Fig. 3, A and B; yellow lines in Fig. 3E) can be vaguely recognized. Each set consists of two opposingly facing series that are at an acute angle (~15°) with respect to the midline. Each series is 17 to 18 mm in length and consists of four or more tracks, although the exact number of tracks is difficult to determine. The opposingly facing series are asymmetrical across the midline and are slightly staggered (or overlap) along the length. The apparent "stride" (distance between two successive series along length) is ~13.7 mm. Discontinuous impressions seem to be present along the midline and oblique scratches on one side of the trackway (Fig. 3, C and D; green color in Fig. 3E), but it is uncertain whether these are distinct features.

TW2 has a preserved trackway length of ~91 mm, an external width of ~16 mm, and an internal width of ~4 mm (Fig. 4, A to C). Track size is similar to that of TW1. Tracks are organized in two well-defined rows but do not form clearly recognizable series (Fig. 4), although repeated groups of tracks seem to be apparent (yellow circlets in Fig. 4C), with each group consisting of five imprints (labeled L2 to L6 in Fig. 4C). No medial impressions are apparent. Shallow and small dimples can be observed in the inner side of one of the two rows (red circlets in Fig. 4C, labeled L1), imparting an asymmetry of the trackway. Both the dimples and track groups (red and yellow circlets, respectively, in Fig. 4C) are spaced in similar distances of about 8 to 10 mm.

Undermat burrows

The co-occurring burrows (UB1 to UB3) have a consistent width of about 9.5 to 11.5 mm. UB2 and UB3 are relatively straight and short (42 and 21 mm in length, respectively), whereas UB1 is gently curved and longer (133 mm in length). UB1 and UB2 are preserved as positive epireliefs (Fig. 2A), whereas UB3 is preserved as a positive hyporelief (Fig. 2, B and D). This is consistent with the preservational style of undermat burrows in the Shibantan Member, where both microbial mats above and below the burrows can serve as parting surfaces [for

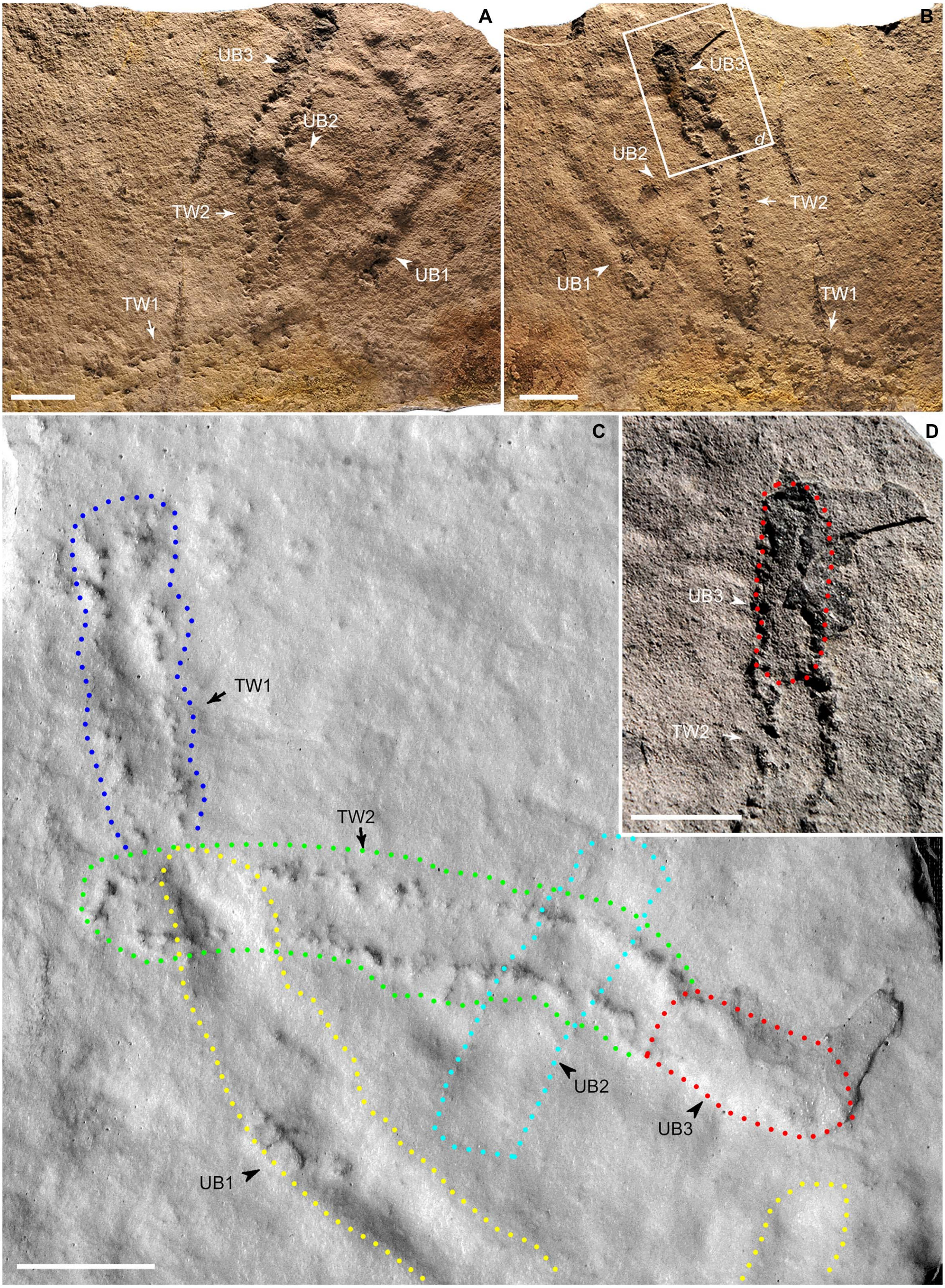

Fig. 2. Trackways and burrows excavated in situ from the Shibantan Member. (**A** and **B**) Epirelief (top bedding surface) and hyporelief (bottom bedding surface), respectively. NIGP-166148. Trackways (TW1 and TW2) and undermat burrows (UB1 to UB3) are labeled. (**C**) Latex mold of (B), with trackways and burrows marked and labeled. (**D**) Enlargement of rectangle in (B), showing connection between TW2 and UB3 (marked). All photographs were taken with lighting from upper right. Scale bars, 2 cm. Figure produced by Z.C. and S.X. using Adobe Photoshop.

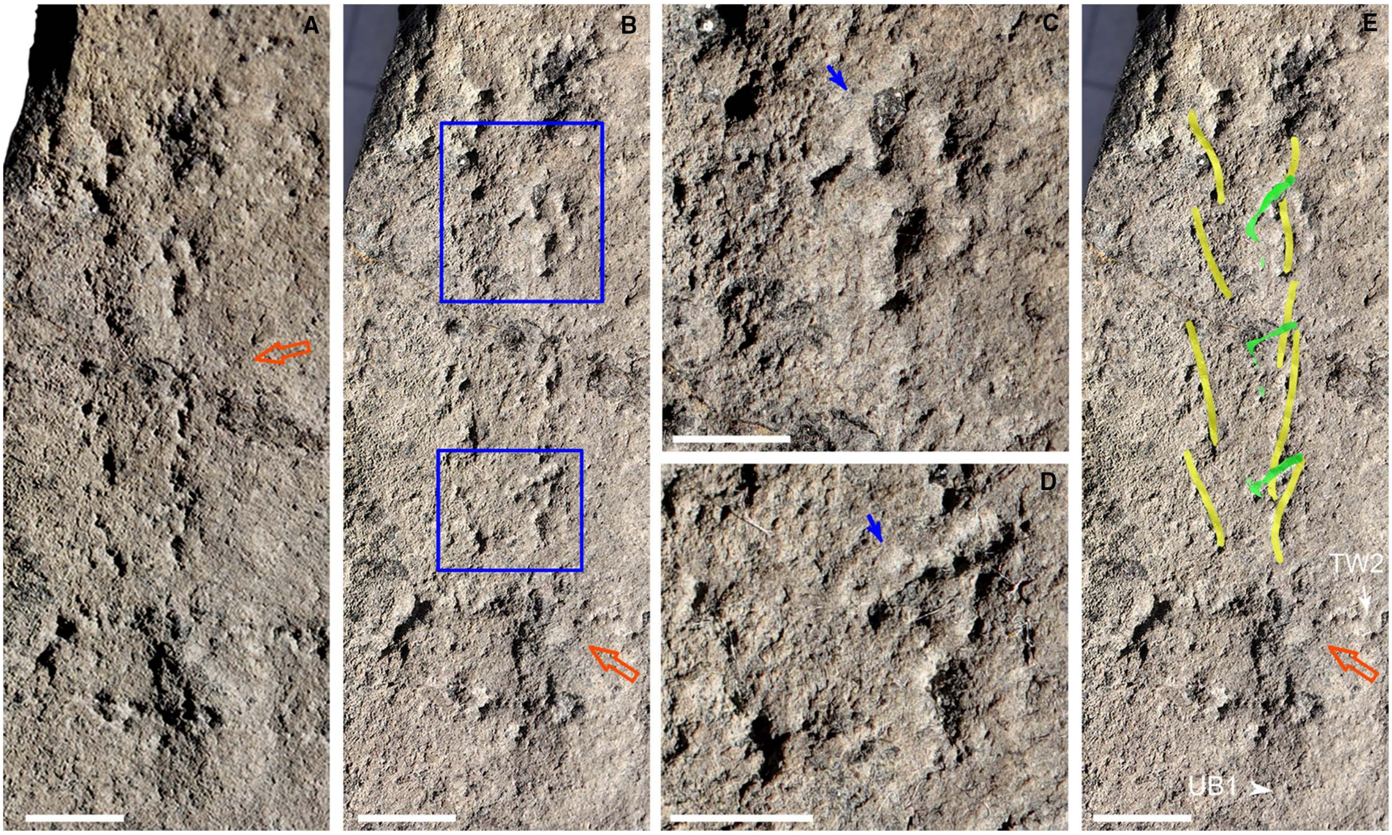

Fig. 3. Trackway TW1 under different lighting directions. (**A** to **E**) All are epireliefs. At least four sets of tracks [yellow lines in (E)] can be vaguely recognized, each consisting of two opposingly facing series that are at an acute angle to the midline. Discontinuous impressions along the midline and oblique scratches on the right side of the trackway are vaguely recognizable in (C) and (D), which are enlargements of top and bottom rectangles in (B), respectively. These faint structures are marked in green color in (E) to assist interpretation. The oblique scratches are marked by blue arrows in (C) and (D). Orange arrows identify lighting directions. Scale bars, 2 cm (A, B, and E); 1 cm (C and D). Figure produced by Z.C. and S.X. using Adobe Photoshop.

example, figure 2E in the study of Meyer *et al.* (*19*)], resulting in positive epirelief or positive hyporelief, respectively. Consistent with other undermat burrows in the Shibantan Member (fig. S1) (*13*, *15*, *19*), UB1 to UB3 are filled with carbonate sediments with a significant amount of calcite cements. This is best seen in UB3 (Fig. 2D), where burrow fills are fractured and exposed to show the dark-colored carbonate, which is distinct from the light-colored clay-rich microbial mat material characterizing the bedding surface [for example, figure 7 in the study of Meyer *et al.* (*15*)].

Possible connections

The trackways and burrows are preserved in close proximity, and there is some evidence that they may be connected. This is best seen in TW2 and UB3, which have similar orientation and width, and seem to be seamlessly connected (Fig. 2D). We note that there may be a slight offset at the junction between TW2 and UB3. Similarly, TW1 seems to be confluent with UB1, both showing the same orientation and the same width. Again, there is a slight offset at the junction.

Other coexisting trace fossils

Specimens of the trace fossil genus *Lamonte* are also present on the same bedding surface where the trackways TW1 and TW2 were found (Fig. 5A). One of the specimens (labeled "Lt" in Fig. 5A; about 6 mm in width) preserves a bilobed burrow that is similar in size and shape to the bilobed burrow (3 to 8 mm in width) of *Lamonte trevallis* specimens (*13*, *15*), which is often connected with a vertical resting trace (*13*, *15*). Two other specimens (labeled "Ls" in Fig. 5A) present on the same slab are much wider, consisting of putative trackways (about 15 to 18 mm in width, with two rows of poorly preserved imprints; arrows in Fig. 5A) that transition into burrows (arrowheads in Fig. 5A). These specimens, here tentatively placed in an open nomenclature (*Lamonte* sp.), may represent a new species of *Lamonte*, because their trackways are more similar to those of *L. trevallis* but are different from the trackways TW1 and TW2 that seem to have discernible groups or series of imprints.

In addition, possible trackways in association with *L. trevallis* have been reported previously from the Shibantan Member (*13*, *15*). One example is shown in Fig. 5B, where the putative trackway is preserved as a negative epirelief (arrows in Fig. 5B), but the burrows are preserved as positive epireliefs (arrowheads in Fig. 5B). Again, there is no evidence for sediment disturbance between the two rows of tracks.

DISCUSSION

Trace maker of trackways

Although the Shibantan trackways consist of recognizable tracks, the track series are somewhat irregularly and variably organized. For example, the track series or groups recognizable in TW1 and TW2 are

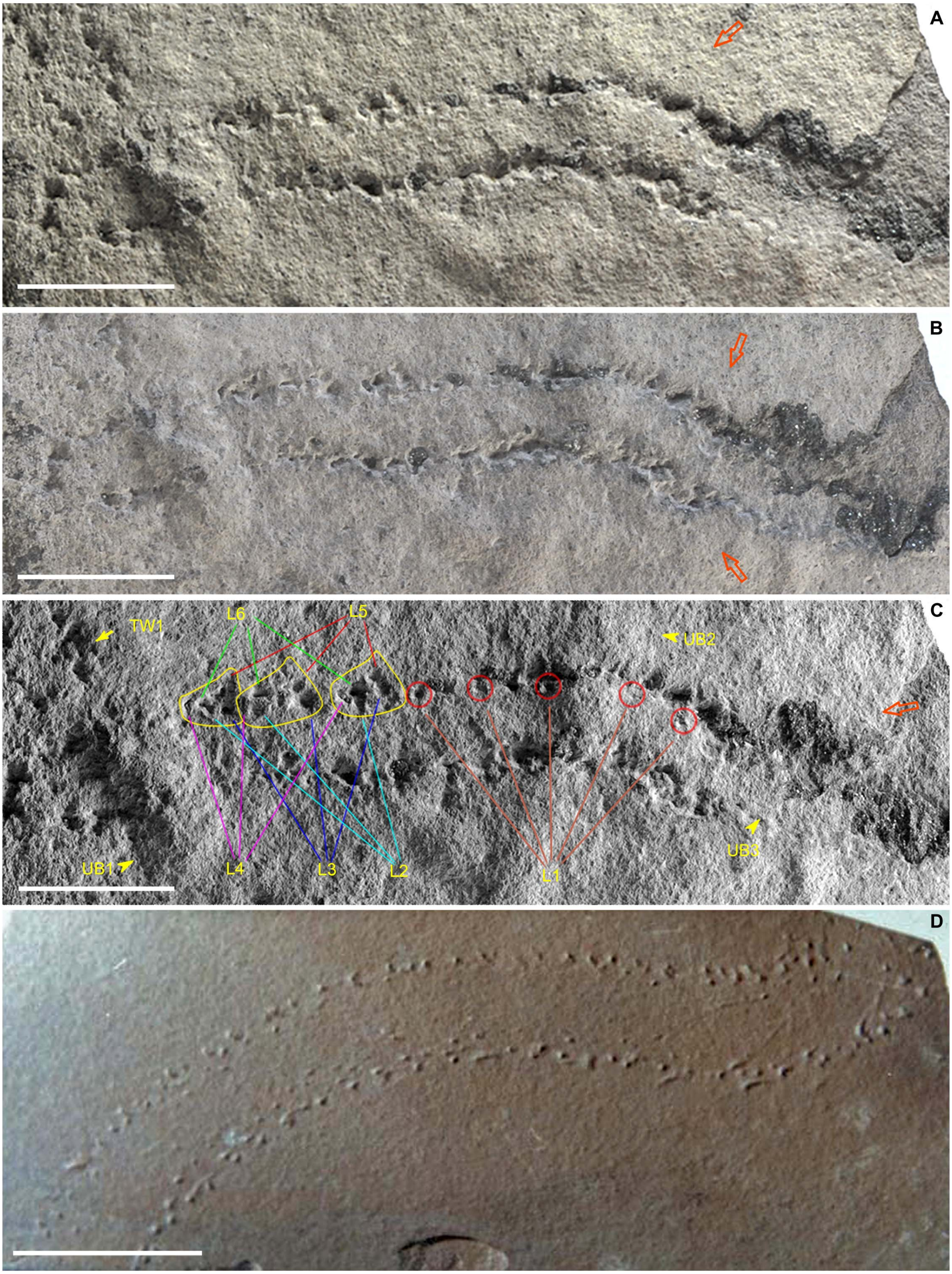

Fig. 4. Comparison between Shibantan and Paleozoic trackways. (**A** to **C**) Epirelief trackway TW2 under different lighting directions. Repeated track groups (yellow lines) and repeated small shallow dimples (red circles) are marked. Labels L1 to L6 denote different imprints or tracks presumably made by different locomotive appendages of the animal. Orange arrows identify lighting directions. (**D**) Early Devonian trackway *Danstairia congesta* from the Old Red Sandstone in Scotland. Courtesy of L. Buatois. Scale bars, 2 cm. Figure produced by Z.C. and S.X. using Adobe Photoshop.

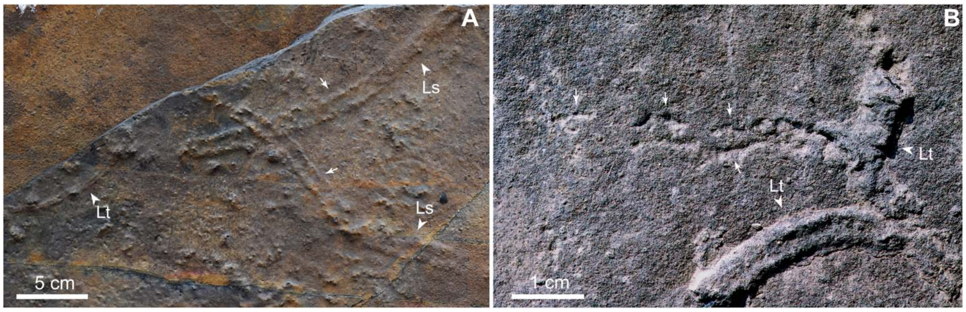

Fig. 5. Possible trackways associated with trace fossils of the genus *Lamonte* from the Shibantan Member. (**A**) Positive hyporelief from the same bedding surface where trackways illustrated in Fig. 2 were found. Two species are recognized on the basis of size: *L. trevallis* (labeled as Lt) is narrower than *Lamonte* sp. (labeled as Ls). Note that *Lamonte* sp. consists of possible trackways (arrows; with poorly preserved imprints) transitioning into burrows (arrowheads). NIGP-166149 (catalog number for the entire slab). (**B**) *L. trevallis* from a different stratigraphic horizon of the Shibantan Member. Note burrows (arrowheads) and possible tracks (arrows) preserved as positive and negative epireliefs, respectively. Also illustrated in the study of Chen *et al.* (*13*). NIGP-154193. Figure produced by Z.C. and S.X. using Adobe Photoshop.

somewhat different. Such differences may, in part, reflect variations in gait, pace, or interactions with the substrate (*24*, *25*). This is particularly true if TW1 and TW2 are undertracks, whose preservation in sediment surface underneath a microbial mat would be obscured (*26*).

The irregular track arrangement in the Shibantan trackways is in notable contrast to modern and Phanerozoic trackways of arthropods or annelids (for example, polychaetes). These younger counterparts, particularly those made by arthropods, are characterized by regularly arranged track series or sets (*23*, *27*, *28*). For example, *Pterichnus*, which has been interpreted as the locomotion traces of myriapods or isopods (*29*), is a trackway consisting of two regularly arranged rows of long and elongated imprints that are obliquely oriented (15° to 20° relative to midline). As another example, *Diplichnites*, which has been interpreted as the walking trackway of homopodous multi-limbed arthropods such as myriapods, euthycarcinoids, and trilobites (*30*–*32*), consists of two regularly arranged rows of small and closely spaced imprints, although there is a great deal of preservational variations.

The Shibantan trackways, however, broadly resemble some Paleozoic trackways with somewhat irregularly arranged tracks. In particular, they are somewhat similar to *Danstairia* from the Lower Devonian Old Red Sandstone in Scotland (Fig. 4D). *Danstairia* consists of two rows of irregularly arranged tracks and lacks distinct series in parts of the trackway (*33*). *Danstairia* has been interpreted as a trackway made by an arthropod (*34*), perhaps in a subaqueous environment (*35*).

Although the exact identity of the trace maker of the Shibantan trackways is difficult to determine in the absence of body remains at the end of the trackways, we suggest that the trace maker was probably a bilaterian animal with paired appendages. The discrete tracks are distinct from trails or burrows made by peristaltic movement of legless worms and indicate that the trace maker instead used paired appendages for locomotion. Both trackways lack a continuous medial drag mark, and TW2 overpasses the burrows UB1 and UB2 without cutting through them, suggesting that the trace maker may have had supporting appendages to elevate the animal body above the sediment surface (if the trace fossils are overtracks) or could pierce a microbial mat (if the trace fossils are undertracks). This style of movement is apparently comparable to arthropod locomotion using jointed appendages. We consider an arthropod-like trace maker possible, although it is not beyond the realm of possibility that the Shibantan trackways may have been made by other animals analogous to modern annelids, onychophorans, or tardigrades, which all have appendages. We emphasize that there is no compelling evidence to phylogenetically place the Shibantan trace maker within the total-group Panarthropoda (or total-group Annelida, for that matter), considering that appendages may have evolved convergently in several groups of bilaterians or may have been present in the last common ancestor of bilaterians (*36*, *37*). The irregular arrangement of tracks in the Shibantan trackways may be taken as evidence that the movement of their trace maker's appendages was poorly coordinated and is distinct from the highly coordinated metachronal rhythm typical of modern arthropods. Thus, modern animals such as arthropods are regarded as interpretive analogs, but not necessarily phylogenetic relatives, of the Shibantan trace maker. All that can be said about the Shibantan trackways maker is that it is probably a bilaterian with paired appendages.

The more tenuous recognition of track series and groups, if confirmed in the future, can inform certain aspects of the Shibantan trace maker. The size of the trackways suggests that the trace maker was probably more than 13.8 mm in width (based on external width of the trackways). Although the detailed characters of its appendages are difficult to reconstruct because of a high degree of overlap among tracks, the trace maker may have had at least four and perhaps as many as five pairs of appendages, given the presence of at least four imprints in each series of TW1 and the possible presence of five imprints in each track group of TW2. However, caveats must be exercised here, because false series or groups of tracks may be generated in some cases (*23*).

Complex behaviors

The intriguing possibility that TW2 may be connected with UB3 and TW1 with UB1 may provide additional information about the complex behavior of the Shibantan trace maker. We note that there is a slight offset at the junction between the trackways and undermat burrows as mentioned above. Considering that the trackways may have been produced by an animal walking atop a microbial mat, whereas the burrows are made within or beneath the mat, the offset could result from a course change during the transition from walking to burrowing, sediment compaction, or postdepositional shearing. If similar connections between trackways and burrows are confirmed with additional examples in the future, it can be inferred that the Shibantan trace maker may have been capable of burrowing beneath and walking atop microbial mats.

This moderately complex behavior is similar to that of the coexisting trace fossil *L. trevallis* (labeled Lt in Fig. 5A), which typically consists of connected burrows, trackways, and vertical resting traces that represent relatively complex behaviors (*13*, *15*). An additional species of *Lamonte* (labeled Ls in Fig. 5A) also seems to have burrows and putative trackways, the latter of which needs to be further investigated, particularly through petrographic examination in thin sections when additional specimens become available to allow destructive analysis. Regardless, the available evidence presented here (Figs. 2 to 5) and elsewhere [for example, figure 5 (A to D) in the study of Chen *et al.* (*13*)] suggests that millimeter-sized bilaterian animals with paired appendages began to play an increasingly important role in the terminal Ediacaran Period to shape the Earth system through their interactions with microbial mats (*13*, *15*).

CONCLUSION

Molecular data suggest that most bilaterian phyla diverged in the Ediacaran Period (*1*). However, only a few late Ediacaran body fossils can be unambiguously interpreted as bilaterian animals. The strongest evidence for Ediacaran bilaterian animals comes instead from trace fossils. Such trace fossils are hitherto represented mostly by burrows. The trackways reported here, from the late Ediacaran Shibantan Member of the Dengying Formation (ca. 551 to ca. 541 Ma ago) in the Yangtze Gorges area of South China, represent the oldest known trackways produced by bilaterian animals with paired appendages. These trackways may be connected with undermat burrows, indicating complex behaviors including epimat walking and undermat mining. Although the phylum-level phylogenetic affinity of the Shibantan trace makers has not been resolved, these trace fossils along with others from the Ediacaran-Cambrian transition (*17*, *38*) complement the body fossil record and provide key insights into the behavioral ecology of early bilaterian animals, particularly their interactions with sedimentary substrates and microbial mats.

MATERIALS AND METHODS

The Shibantan trackways were collected in situ from a stratigraphic horizon about 70 m above the base of the Shibantan Member at Wuhe (Global Positioning System: 30°47′23.1″N, 111°3′22.9″E) in the Yangtze Gorges area (Fig. 1). Abundant trace fossils of the genus *Lamonte* are preserved in the Shibantan Member (*13*, *15*), and some of them were found on the same bedding surface as trackways reported here. Ediacara-type fossils such as *Hiemalora*, *Rangea*, *Aspidella*, *Pteridinium*, and *Wutubus* are preserved in adjacent beds (*39*).

All illustrated Shibantan trace fossils are reposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China. They were photographed using a Nikon D700 camera, under both natural light and low-angle illumination with controlled lighting directions. A latex mold of the hyporelief was made and photographed using the same camera (Fig. 2C).

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at http://advances.sciencemag.org/cgi/content/full/4/6/eaao6691/DC1

Geological setting

fig. S1. Transmitted light microscopic images of petrographic thin sections.

fig. S2. Schematic diagram showing expected differences between preservational variants of burrows and trackways.

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