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Stratigraphic Setting, Methods, and Systematic Paleontology

STRATIGRAPHIC SETTING

The upper Ediacaran Dengying Formation in the Yangtze Gorges area (Fig. 1) is the focus of recent paleobiological and geochemical studies (Chen et al., 2013; Chen et al., 2014; Meyer et al., 2014; Meyer et al., 2017; Chen et al., 2018; Wei et al., 2018; Zhang et al., 2018). It can be subdivided into three lithostratigraphic units: the Hamajing, Shibantan, and Baimatuo members, in ascending order. The Hamajing Member consists of ~30 meters of light gray peritidal dolostone, with tepee structures and karstification features (Meyer et al., 2014). The Shibantan Member consists of 100–150 meters of dark gray, thin-bedded, laminated micritic limestone deposited in subtidal environments (Meyer et al., 2014). It contains a number of soft-bodied Ediacara-type fossils (Chen et al., 2014), animal trails and undermat burrows (Chen et al., 2013; Meyer et al., 2014; Meyer et al., 2017), possible trackways (Chen et al., 2018), problematic macrofossils (Xiao et al., 2005; Shen et al., 2009; Shen et al., 2017), as well as potential biomarkers (Duda et al., 2014). The overlying Baimatuo Member consists of ~100 meter of light gray massive peritidal dolostone, characterized by abundant dissolution vugs and breccia (Meyer et al., 2014). The lightly biomineralized tubular animal fossil *Sinotubulites* have been reported from this member and possibly the uppermost Shibantan Member (Chen et al., 1981).

The Shibantan Member, where *Yichnus levis* was collected, is constrained to be 551–538 Ma in age. The maximum age constraint comes from a ~551 Ma ash bed from the uppermost Miaohu Member (Condon et al., 2005; Schmitz, 2012). The Miaohu Member is regarded as a lithostratigraphic unit in the uppermost Doushantuo Formation, which underlies the Dengying Formation (Xiao et al., 2017; Zhou et al., 2017), although An et al. (2015) correlated the Miaohu

Member with the basal Shibantan Member. Regardless, *Yichnus levis*, which occurs at 20 m and 70 m above the base of the Shibantan Member, is younger than ~551 Ma.

The younger age constraint for the Shibantan Member comes from a recent study showing that the Ediacaran-Cambrian boundary is 538–539 Ma (Linnemann et al., 2019). In the Yangtze Gorges area, the Ediacaran-Cambrian boundary is constrained by biostratigraphic data from the Yanjiahe Formation, which disconformably overlies the Baimatuo Member of the Dengying Formation and consists of limestone, dolostone, phosphatic cherts, and shale. The Yanjiahe Formation contains basal Cambrian small shelly fossils that allow the recognition of three successive assemblage biozones—the *Anabarites trisulcatus*–*Protohertzina anabarica*, the *Purella antiqua*, and the *Aldanella yanjiaheensis* assemblage biozones (Guo et al., 2014). The *Anabarites trisulcatus*–*Protohertzina anabarica* assemblage biozone approximately coincides with the acritarch *Asteridium*–*Heliosphaeridium*–*Comasphaeridium* assemblage biozone and is <5 m above a negative $\delta^{13}\text{C}_{\text{carb}}$ excursion regarded as the basal Cambrian negative carbon isotope excursion (Dong et al., 2009; Jiang et al., 2012; Ahn and Zhu, 2017). Considering that the Shibantan Member contains no Cambrian fossils whereas the Yanjiahe Formation contains basal Cambrian microfossils as well as the basal Cambrian negative carbon isotope excursion, the Ediacaran-Cambrian boundary likely lies somewhere above the Shibantan Member. Given that the Ediacaran-Cambrian boundary is dated at 538–539 Ma in Namibia (Linnemann et al., 2019), the Shibantan Member must be >538 Ma.

A terminal Ediacaran age for the Shibantan Member is also consistent with available radiometric ages from equivalent strata in South China. These include (1) two SHRIMP zircon ^{207}Pb – ^{206}Pb ages of $553.6 \pm 2.7/3.8$ Ma and $546.3 \pm 2.7/3.8$ Ma (first uncertainty is analytical error and second uncertainty is analytical + external reproducibility) from the Jiucheng Member of the

middle Dengying Formation in Yunnan Province, which is regarded equivalent to the Shibantan Member (Yang et al., 2017a), (2) a LA-ICPMS ^{206}Pb - ^{238}U age of 548 ± 8 Ma for the youngest population of detrital zircons from the Gaojiashan Member of the Dengying Formation in Shaanxi Province, which is also regarded equivalent to the Shibantan Member (Cui et al., 2016); and (3) a plethora of recently published new ages from Ediacaran-Cambrian boundary strata in South China (Chen et al., 2015; Yang et al., 2017b).

Specimens of *Yichnus levis* were collected at two horizons ~20 m and 70 m above the base of the terminal Ediacaran (~551–538 Ma) Shibantan Member of the Dengying Formation at two quarries (30°47'19.171"N, 111°03'01.684"E; 30°47'23.097"N, 111°03'21.882"E) near Wuhe, Yangtze Gorges area, South China (Figs. 1, DR1).

MATERIALS AND METHODS

Fossils illustrated in this paper were excavated from bituminous and fetid (sulfide-rich) subtidal limestone about 20 m above the base of the Shibantan Member (ca. 551–ca. 538 Ma) of the Dengying Formation at Wuhe in the Yangtze Gorges area of South China (Figs. 1, DR1). Here, *Yichnus levis* is the only dominant trace fossil, and the only other fossils on the same bedding surface are vendotaenid fragments, although *Arborea* fossils occur about 50 cm above this *Yichnus levis* horizon. Another stratigraphic horizon where *Yichnus levis* occurs is about 70 m above the base of the Shibantan Member at Wuhe. At this horizon, both ichnofossils and body fossils are more diverse, including *Streptichnus narbonnei* and other simple traces, both of which are associated with microbial laminae, as well as body fossils such as *Wutubus*, with adjacent horizons yielding *Aspidella*, *Hiemalora*, *Charnia*, and *Pteridinium* (Chen et al., 2014).

Fossils were excavated with known stratigraphic orientations so that there is no ambiguity about fossil preservation on the top or bottom bedding surfaces (i.e., epireliefs vs. hyporeliefs). Both part and corresponding counterpart slabs were recovered. Trace fossils on the slabs were photographed using a Nikon 700 camera with controlled lighting. Selected specimens were then cut with controlled orientations to make transverse and longitudinal sections of burrow segments as well as gaps between segments. Thin sections were observed and photographed under a Zeiss Axio microscope coupled with an Axiocam 512 digital camera. Submillimeter-thick, crinkled, organic- and clay-rich microlaminae are interpreted as fossilized microbial mats, on the basis of their similarity to modern and fossilized microbial mats (e.g., stromatolites) in carbonate facies (Lee et al., 2000). Bedding-surface MISS (Microbially induced sedimentary structures) such as wrinkles and elephant-skin textures that are common in Ediacaran siliciclastic rocks (Gehling, 1999; Gehling et al., 2005; Bouougri and Porada, 2007; Buatois et al., 2014) are not preserved or easily recognizable in carbonate rocks because of the development of stylolites in carbonate facies.

All illustrated fossils and thin sections are permanently repositied at the Nanjing Institute of Geology and Paleontology (with museum catalog numbers NIGP-169664 and NIGP-169665).

SYSTEMATIC PALEONTOLOGY

Yichnus new ichnogenus

Etymology. Ichnospecies name derived from Yiling (a district of Yichang) where the fossils were found.

Type ichnospecies. *Yichnus levis* new ichnogenus and new ichnospecies

Diagnosis. Same as type ichnospecies by monotypy.

Yichnus levis new ichnogenus and new ichnospecies

(Figs. 2–3)

Etymology. From Latin *levis* (smooth), with reference to the lack of ornaments on the burrow segments.

Holotype. NIGP-169664 (segments #1–6 in Fig. 2), collected from a horizon about 20 m above the base of the Shibantan Member. Reposited at Nanjing Institute of Geology and Palaeontology (NIGP).

Locality and horizon. Specimens were collected at two horizons ~20 m and 70 m above the base of the terminal Ediacaran (~551–538 Ma) Shibantan Member of the Dengying Formation at two quarries (30°47′19.171″N, 111°03′01.684″E; 30°47′23.097″N, 111°03′21.882″E) near Wuhe, Yangtze Gorges area, South China (Fig. 1, DR1).

Diagnosis. *Yichnus levis* consists of disconnected fusiform or spindle-shaped burrow segments that are either isolated or aligned to form a uniserial chain. Burrow segments are straight or gently curved, millimeters in width, and centimeters in length. They are typically preserved as full reliefs and in close association with microbial mats.

Discussion. The simple morphology of *Y. levis* burrow segments—including their cylindrical morphology, structureless burrow fill, and lack of burrow ornamentation or lining—is similar to that of *Planolites*, which is “an unlined burrow infilled with sediments having textural and fabricational characters unlike those of the host rock” and “represents active backfilling of sediment in an ephemeral burrow constructed by a mobile deposit feeder” (Pemberton and Frey, 1982). However, the cylindrical burrows of *Planolites* (e.g., Marengo and Bottjer, 2008) tends to be much longer than the burrow segments of *Y. levis*, and they are not aligned to form chains of

burrows (Geyer and Uchman, 1995). Considering the importance of the in-and-out behavior, *Y. levis* is regarded as an ichnofossil representing a distinct behavior from what is recorded in *Planolites*.

A number of ichnofossils previously described under various ichnogenera—including *Ctenopholeus* Seilacher and Hemleben (1966), *Hormosiroidea* Schaffer (1928), *Saerichnites* Billing (1866), *Treptichnus* Miller (1889), *Tuberculichnus* Książkiewicz (1977), and *Xiangquanheichnus* Yang and Song (1985)—apparently consist of aligned or chained burrows. These genera are closely related and indeed some of them are synonymized (Uchman, 1995; Fürsich et al., 2006; Högström et al., 2013). For example, *Xiangquanheichnus* and *Tuberculichnus* were regarded as junior synonyms of *Saerichnites* (Uchman, 1995), *Tuberculichnus vagans* Książkiewicz (1977) was transferred to *Ptychoplasma vagans* (Uchman et al., 2011) or more recently to *Treptichnus vagans* (Hammersburg et al., 2018), and *Hormosiroidea canadensis* Crimes and Anderson (1985) was synonymized with *Ctenopholeus kutcheri* Seilacher and Hemleben (1966), the type ichnospecies of *Ctenopholeus* (Fürsich et al., 2006). These trace fossils represent complex burrow systems with branching probes or vertical shafts that are preserved as spherical knobs or pits (pearl-string or string of pits) arranged uniserially or biserially on the bedding surface (Uchman, 1995; Fürsich et al., 2006). They are different from *Y. levis* in several important aspects. First, their probes or shafts are preserved as spherical knobs or pits on the bedding surface, rather than elongate spindle-shaped burrows as in *Y. levis*. More importantly, these knobs or pits represent vertical shafts that are connected by horizontal burrows at a lower level (Uchman, 1995; Jensen, 1997; Fürsich et al., 2006), whereas *Y. levis* is characterized by aligned but disjointed burrow segments (Fig. DR2). If the burrow segments of *Y. levis* were connected by horizontal burrows at a lower level, such connections

should have been observed in our thin section analysis. Additionally, some treptichnid burrow segments are bilobed or trilobed (e.g., *Trichophycus tripleurum* Geyer and Uchman, 1995; *Treptichnus triplex* Palić, 1976; *Treptichnus* isp. of Jensen et al., 2000; fig. 4.1–4.2 of Getty et al., 2016), a feature not present in *Y. levis*.

A number of Ediacaran-Cambrian treptichnid fossils superficially resemble *Yichnus levis* in preserving apparently disjointed burrow segments. Short, discontinuous, and aligned burrow segments were sometimes interpreted as various stratinomic variations of *Treptichnus* (Archer and Maples, 1984; Buatois and Mángano, 1993; Uchman, 1995; Jensen et al., 2000; Wilson et al., 2012; Getty et al., 2016). In most cases, this interpretation is warranted, particularly where the discontinuous burrows occur in association with fully exposed specimens of *Treptichnus* and where the connecting horizontal burrow is subtly visible (e.g., *Treptichnus pollardi* in fig. 5A of Höglström et al., 2013 and fig. 5.2 of Geyer and Uchman, 1995). In others (e.g., fig. 4.1–4.2 of Getty et al., 2016), it remains to be verified by thin section or X-ray CT analysis (Meyer et al., 2017) whether the burrow segments are actually connected by unexposed burrows or they were made discontinuous by stratinomic or erosional processes.

Finally, Proterozoic fossils described as *Horodyskia* are characterized by “string of beads” connected by a stolon-like horizontal tube (Yochelson and Fedonkin, 2000; Grey et al., 2002; Dong et al., 2008). These are interpreted as body fossils, rather than trace fossils, and they are characterized by aligned or chained spherical structures connected by a horizontal tubular structure, thus different from the aligned but disjointed spindle-shaped burrow segment of *Yichnus levis*.

Nomenclature note. This publication and the nomenclatural acts it contains have been registered in ZooBank (www.zoobank.org). The ZooBank LSID (Life Science Identifier) for this publication is urn:lsid:zoobank.org:pub:991964F6-DB19-493A-A91D-BFB72973B6B1.



Fig. DR1. Field photographs of excavation sites. Excavation quarry 1 (left: 30°47'19.171"N, 111°03'01.684"E, where *Yichnus levis* occurs ~20 m above the base of the Shibantan Member) and excavation quarry 2 (right; 30°47'23.097"N, 111°03'21.882"E, where *Yichnus levis* occurs ~70 m above the base of the Shibantan Member).

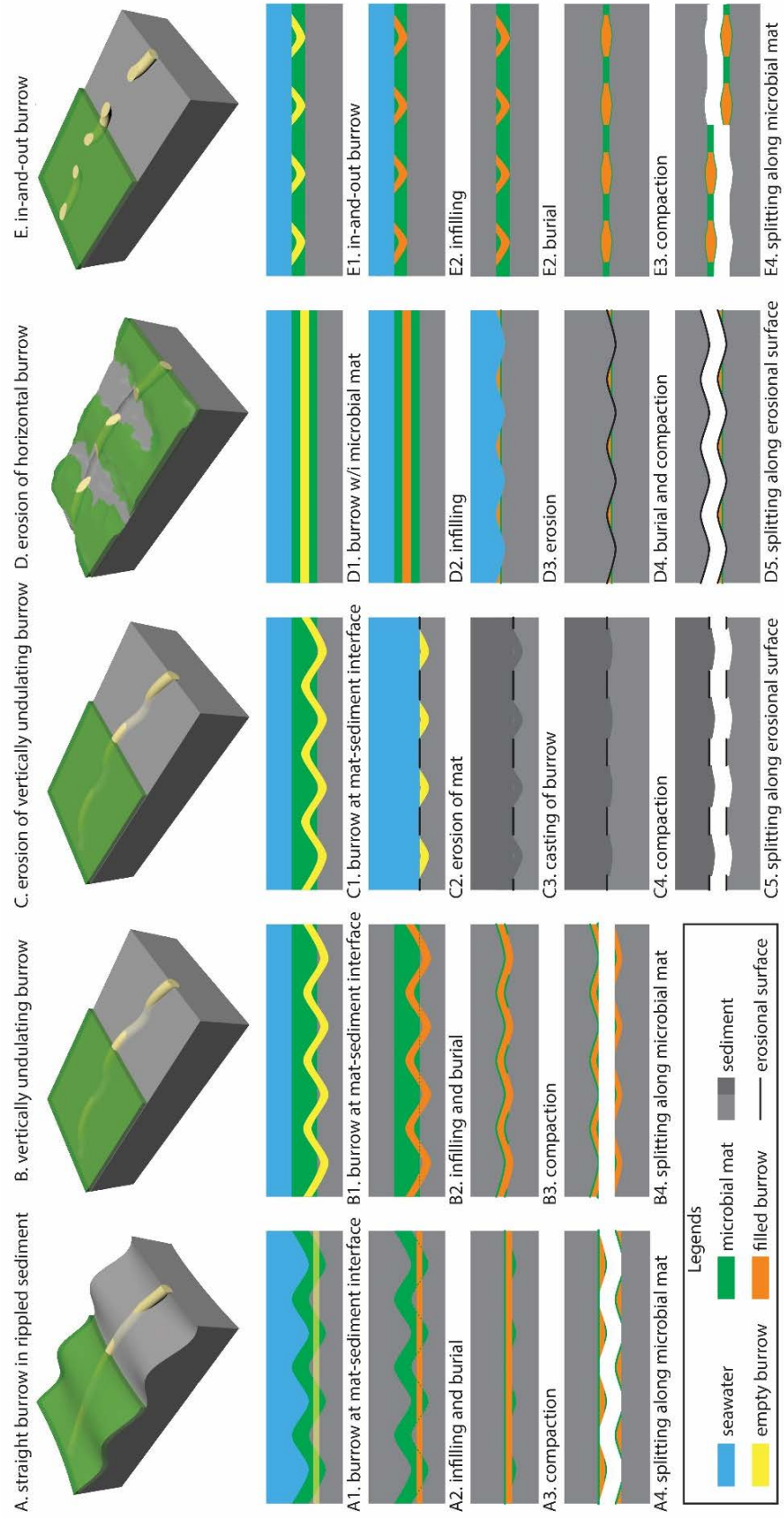


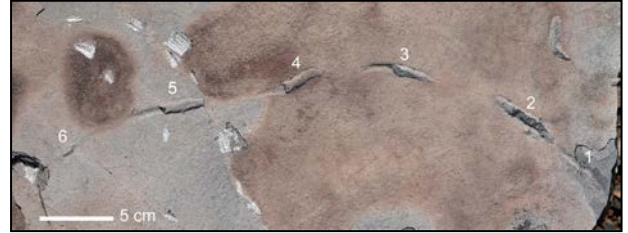
Fig. DR2. Schematic diagrams showing different interpretations of disjointed burrow segments.

Top panels are box diagrams showing burrows in microbial mat or at mat-sediment interface.

Bottom panels are vertical cross-sectional views. **A:** Continuous, shallow, horizontal burrow at the interface between rippled sediment and microbial mat. Note that microbial mat can be above or below burrow. As microbial mat serves as the parting surface, the burrow can be split on the sole or top bedding surface, thus forming apparently disjointed burrow segments on either slab, but the burrow is continuous if both slabs are studied together. **B:** Continuous, shallow, vertically undulating burrow interacting with horizontal sediment and microbial mat. As in (A), burrow can be split on the sole or top bedding surface, thus forming apparently disjointed burrow segments on either slab even though the complete burrow is continuous. **C:** Same as in (B), but the burrow is eroded before it is filled with sediment from overlying layer. As the surviving burrow segments are cast from above, they form convex hyporeliefs (pearl string) and corresponding concave epireliefs (string of pits). Thus, they form semireliefs, rather than full reliefs as in *Yichnus levis*. Crimes and Anderson (1985) proposed a similar model to account for pearl string structures of *Hormosiroidea canadensis*, but others favor the interpretation of *Hormosiroidea canadensis* and related ichnofossils such as *Ctenopholeus kutcheri* as vertical shafts connected by a horizontal burrow at a lower level (Fürsich et al., 2006). **D:** Continuous, shallow, horizontal burrow that is partially eroded. Complete removal of a burrow segment requires erosion of several millimeters of sediment, for which there is no evidence in slabs preserving *Yichnus levis*. **E:** In-and-out behavior, our preferred interpretation to account for the observations of *Yichnus levis*.

Table DR1. Measurement data of *Yichnus levis*.

Segment number	width (mm)	length (mm)	gap to right (mm)
NIGP-169664, segment 1	6.3	56.1	
NIGP-169664, segment 2	6.9	49.4	10.9
NIGP-169664, segment 3	8.2	50.4	38.7
NIGP-169664, segment 4	6.5	44.3	26.1
NIGP-169664, segment 5	7.0	54.7	28.8
NIGP-169664, segment 6	3.4	13.0	32.3
NIGP-169665, segment 1	6.0	34.8	
NIGP-169665, segment 4	8.9	67.1	102.2
NIGP-169665, segment 5	6.3	41.9	29.1
NIGP-169665, segment 6	8.8	43.2	
NIGP-169665, segment 7	5.6	81.7	46.1
NIGP-169665, segment 8	5.7	33.3	
NIGP-169665, segment 9	8.8	44.4	
NIGP-169665, segment 10	8.3	84.0	
NIGP-169665, segment 11	6.5	30.5	100.9
NIGP-169665, segment 12	7.3	48.9	
Max	8.9	84.0	102.2
Min	3.4	13.0	10.9
Mean	6.9	48.6	46.1
Standard Error	0.4	4.4	10.3
Count	16	16	9



Animation DR1. Animation showing a hypothetical animal exhibiting in-and-out behavior and producing a series of disjointed burrow segments that are here described as *Yichnus levis*. Two different video formats are available. The .avi file can be played in most video or animation players. The .swf file can be open in an Adobe Flash player (<https://get.adobe.com/flashplayer/>) or an Adobe Shockwave player (<https://get.adobe.com/shockwave/>).

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