Lower Devonian trace fossils and their paleoenvironmental significance from the western Yangtze Plate, South China

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Abstract: Abundant and diverse trace fossils occur in the littoral-neritic sediments recording an Early Devonian transgression in South China. The well-exposed Ganxi section is located in the Longmen Mountain 100 km northwest of Chendu, Sichuan. The Lower Devonian strata are dominated by sandstones, siltstones, muddy shales, limestones, bioclastic limestones, and muddy limestones. About thirteen ichnogenera were systematically described, including *Arenicolites*, ?*Balanoglossites*, *Chondrites*, *Cylindrichnus*, *Diplocraterion*, *Planolites*, *Palaeophycus*, *Phycodes*, *Rhizocorallium*, *Rusophycus*, *Skolithos*, *Thalassinoides*, and *Zoophycos*. Six trace fossil associations under different sedimentary environments have been recognized as follows: the *Skolithos* and *Diplocraterion-Skolithos* associations mainly consist of domichnia derived from a high-energy zone of the foreshore to upper shoreface; the *Rusophycus-Phycodes* association is characterized by fodinichnia and cubichnia generated in a lower-energy zone of the upper shoreface; the *Chondrites-Palaeophycus* association mainly consists of domichnia, chemichnia, and fodinichnia as indicators of the lower-energy and suboxic conditions of a coastal lagoon; the *Rhizocorallium* association includes feeding and dwelling burrows formed in a lower-energy zone of the upper offshore enriched with food; and the *Zoophycos* association is characterized by fodinichnia and pascichnia as indicators of the lower offshore frequently influenced by storm waves. The entire sequence shows several transgressive-regressive cycles from the Lochkovian to Pragian and much storm influence in the Emsian.

Key words: Trace fossil association, ichnofacies, Lower Devonian, Ganxi, South China

1. Introduction

Trace fossils are known to be good indicators of sedimentary environments (Knaust and Bromley, 2012). The type, morphology, and diversity of trace fossils are now known to be a proxy to paleoenvironmental factors, including energy level, substrate stability, salinity variations, and oxygenation levels (Curran, 1985; Ekdale, 1988; Knaust and Bromley, 2012). The most significant advantage of trace fossils is that they are autochthonous indicators of paleoecological conditions (Bromley, 1996). In most cases, trace fossil data contribute to a better understanding of the sediments from the perspective of organism–substrate interactions (Uchman et al., 2004).

The Lower Devonian sediments of the western Yangtze Plate are divided into the Pingyipu, Ganxi, Ertaizi, and Yangmaba formations, known for their well-exposed and complete stratigraphic record and long history of investigations (Hou et al., 1988). Several aspects of the sedimentology, paleontology, sequence stratigraphy, and isotope geochemistry of the mentioned formations in

the Ganxi section (Figures 1a and 1b) were studied over the last fifty years (e.g., Xian et al., 1995; Zheng and Liu, 1997; Liao and Ma, 2007). Lower Devonian trace fossils of the region are poorly known. Lin et al. (1986) mentioned the presence of *Diplocraterion* and *Thalassinoides* in the Pingyipu Formation. Yang et al. (1988) listed some trace fossils from the studied units, including *Arenicolites*, *Chondrites*, *Cruziana*, *Dimorphichnus*, *Helminthopsis*, *Phycodes*, *Planolites*, *Skolithos*, *Thalassinoides*, and *Zoophycos*. Moreover, in recent years, a variety of well-preserved trace fossils have been found and recorded in the Lower Devonian of the Ganxi section. The aim of the present paper is to provide a detailed ichnological and sedimentological analysis of the Ganxi section.

2. Geological setting

The studied area is located in the northwestern part of the Upper Yangtze Plate and belongs to the Lower Paleozoic Longmenshan Basin (Figures 1c and 1d). The Devonian strata in this region were deposited on a continental margin

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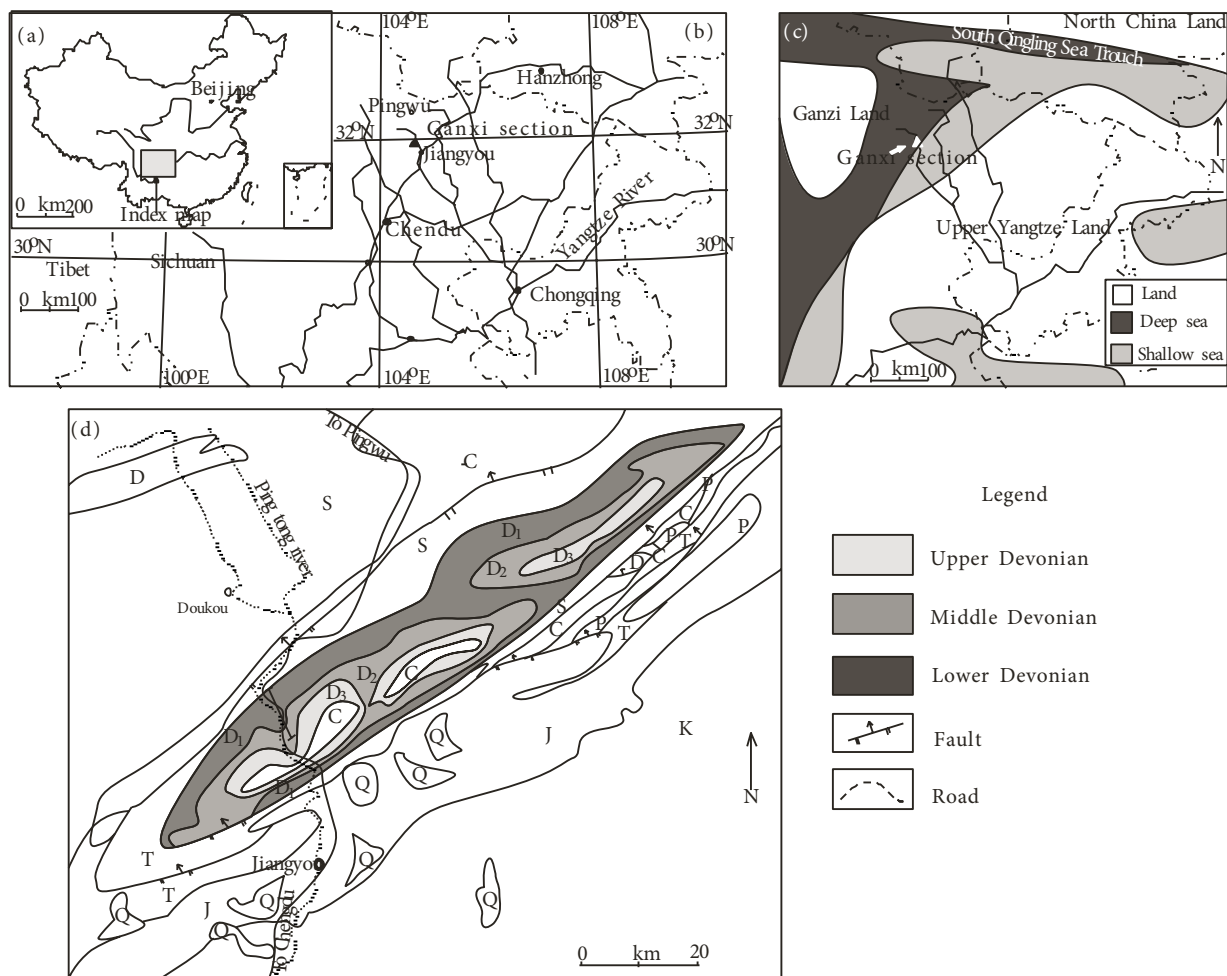
Figure 1. Location, paleogeography and geological map of the Ganxi section in Sichuan Province, South China. (**a–b**) Location of the studied section. (**c**) Devonian paleogeographical map of the Ganxi section and its adjacent regions. (**d**) Geological map of the Devonian in the Ganxi section (modified after Hou et al., 1988).

(Figure 1c) where no significant tectonic events occurred throughout Devonian time (Hou et al., 1988; Xian et al., 1995). The biostratigraphy and chronostratigraphy of the studied area were established by Xian et al. (1995). In the Ganxi section, the Lower Devonian strata are up to 2000 m thick and range from the Lochkovian to Emsian (Figure 2) (Xian et al., 1995). Our field investigation started at the Guixi petrol station (31°58′37.22′′N, 104°3834.46′E) and ended at the west gate of the Jiuhuangshan Mountain scenic spot (31°5542.20′N, 104°4018.73′E). The Lower Devonian of this section comprises four lithostratigraphic units: in ascending order, the Pingyipu, Ganxi, Ertaizi, and Yangmaba formations (Figure 2). The Lower Devonian strata unconformably overlie gray-green thin-bedded phyllitic shale of the Middle Silurian.

The basal Devonian unit, the Pingyipu Formation, consists of fine-grained sandstones, siltstones, and muddy shales with abundant trace fossils and scarce macrofossils (Figure 2). It is approximately 1200 m thick and considered as clastic coastal deposits (Hou et al., 1988). The primary sedimentary structures in the sandstones and siltstone include large- and small-scale cross-bedding, parallel and horizontal lamination, ripple lamination, and interference ripples (Figures 3a–3d). Its lower part is mainly characterized by the relatively abundant trace fossils, whereas the middle part contains abundant plant debris and benthic invertebrate fossils (Figures 4a–4c), mainly brachiopods and crinoids, which are indicative of marine influences.

The Ganxi Formation, overlying the Pingyipu Formation, mainly consists of siltstones, shales, and limestones, including bioclastic limestones. The thickness of the Ganxi Formation is approximately 400 m. This formation is essentially a mixed clastic and carbonate
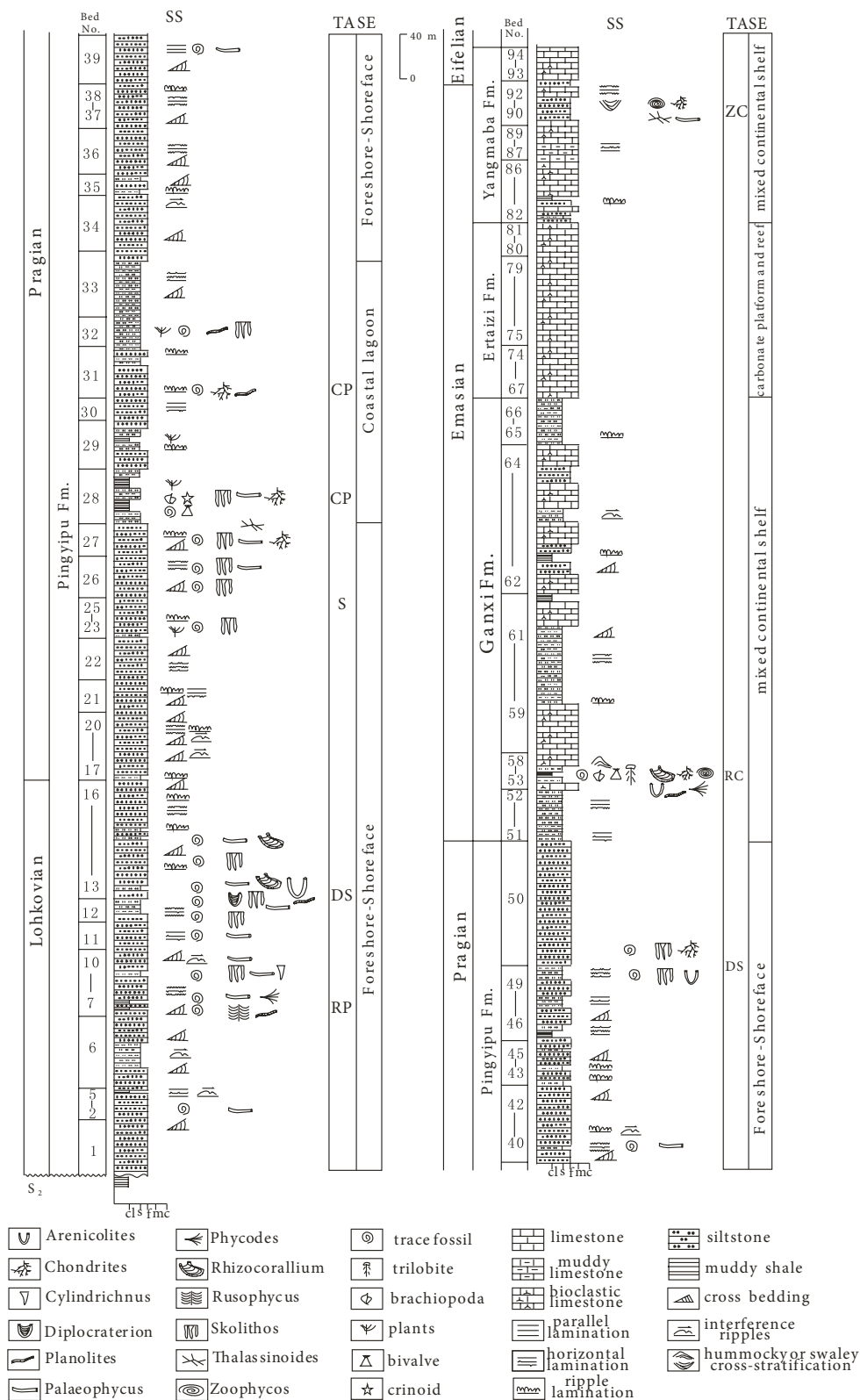
Figure 2. Stratigraphic column of the Lower Devonian showing the distribution of trace fossils in the Ganxi section. TA and SE mean trace fossil association and sedimentary environment, respectively. SS means sedimentary structures.

Figure 3. Sedimentary structures from the Lower Devonian strata in the Ganxi section. (**a**) Cross-bedding, Pingyipu Formation. (**b**) Horizontal lamination, Pingyipu Formation. (**c**) Ripple lamination, Pingyipu Formation. (**d**) Interference ripples, Pingyipu Formation.

sequence, generally accepted as a mixed continental shelf deposit (Hou et al., 1988; Zheng et al., 2010). The primary sedimentary structures in the siltstones include hummocky cross-stratification (Figure 4d), horizontal lamination, ripple lamination, low angle cross-bedding, and interference ripples. Its lower part contains abundant trace fossils and body fossils, mainly brachiopods (Figure 4e), bivalves, crinoids, and trilobites. Its middle and upper parts are characterized by the relative abundance of brachiopods and corals.

The Ertaizi Formation, approximately 200 m thick, consists of gray medium-thick bedded limestones and bioclastic limestones. This formation is an essentially carbonate sequence and contains abundant corals, brachiopods, and stromatoporoids (Figure 4f) typical of the carbonate platform and reef environments (Hou et al., 1988).

The topmost unit of the Lower Devonian, the Yangmaba Formation, is composed of limestones, including bioclastic limestones, muddy limestones (Figure 4g), sandstones, and shales. It is approximately 200 m thick, essentially a mixed clastic and carbonate sequence, deposited on a continental shelf with mixed origins (Hou et al., 1988). The primary sedimentary structures in the sandstones include swaley cross-stratifications (Figure 4h), erosion surfaces,

and ripple and horizontal laminations. Its upper part is characterized by the abundance of trace fossils.

The described invertebrate trace fossils mainly occur in the fine-grained sandstones and siltstones from the lower and middle part of the section (Figure 2).

3. Materials and methods

The Ganxi section was studied during several field surveys from 2009 to 2014. Thirteen ichnogenera were recognized on bedding and vertical surfaces in the field (Table; Figures 5–7). Part of the illustrated material is housed in the collection of the Earth Science Museum of Henan Polytechnic University, China, while the remaining documentation is based on field observations. Some specimens in the field were weathered and mossy. In order to examine the detailed morphology, the specimens were cleaned with brush and distilled water. After that, the specimens were photographed in the field and/or in the laboratory.

4. Description of trace fossils

Ichnogenus *Arenicolites* Salter, 1857
   Arenicolites isp.
   (Figure 5a)
   Description: Simple subvertical U-shaped burrows,

Figure 4. Body fossils, sedimentary structures and lithology from the Lower Devonian strata in the Ganxi section. (**a–b**) Plant fragments, Pingyipu Formation. (**c**) Body fossil assemblages, including brachiopods (B) and crinoids (C), Pingyipu Formation. (**d**) Hummocky cross-stratification, Ganxi Formation. (**e**) Brachiopods assemblages, Ganxi Formation. (**f**) Large coral reef, Ertaizi Formation. (**g**) Muddy limestone, Yangmaba Formation. (**h**) Erosion surface and swaley cross-stratification, Yangmaba Formation.

Table. Overview showing the distribution of trace fossils of the Early Devonian in the Ganxi section, South China.

	Early Devonian		
	Pingyipu Formation	Ganxi Formation	Yangmaba Formation
Arenicolites isp.	+	+	
?*Balanoglossites* isp.			++
Chondrites targionii (Brongniart, 1828)	++	++	
Chondrites ?intricatus (Brongniart, 1823)		++	
Cylindrichnus concentricus Howard, 1966	+		
Diplocraterion parallelum Torell, 1870	++		
Diplocraterion helmerseni (Öpik, 1929)	+		
Palaeophycus tubularis Hall, 1847	+++	+++	+++
Palaeophycus heberti (Saporta, 1872)	++		
Palaeophycus striatus Hall, 1852	+		
Phycodes isp.	+		
Planolites beverleyensis Billing, 1862	++		
Rhizocorallium commune Schmid, 1876	+++	+++	
Rusophycus lungmenshanensis Yang, 1988	++		
Skolithos linearis Haldemann, 1840	+++		
Thalassinoides isp.	++		+
Zoophycos isp. type A		++	
Zoophycos isp. type B			++
Zoophycos isp. type C			++

Note: +, rare; ++, common; +++, abundant.

with parallel limbs, preserved in convex full relief of siltstone and filled with silty clay. The tubes are about 5.0 mm in diameter. The burrow depth is about 4.3 cm and the limbs are 2.1–2.7 cm apart.

Occurrence: Ganxi Formation. Rare.

Discussion: Burrow morphology is consistent with the ichnogenus *Arenicolites*, which is distinguished from the morphologically similar *Diplocraterion* by the absence of spreite (Bromley, 1996). *Arenicolites* was interpreted as the dwelling traces of either infaunal amphipods or vermiforms (Bromley, 1996; Yang et al., 2004). The *Arenicolites* samples with thinly-lined walls indicate that the trace-maker could secrete substances to support the burrow.

Ichnogenus *Balanoglossites* Mägdefrau, 1932
? *Balanoglossites* isp.
(Figure 5b)

Description: Slightly to moderately curved, horizontal, Y-shaped branched, essentially cylindrical, hypichnial burrows, with delicate longitudinal striations. The main gallery is 2.1 cm wide, while side branches are 1.2 cm wide.

Occurrence: Yangmaba Formation. Common.

Discussion: The constrictions and narrower blind branches are the main differences from *Thalassinoides*

(Knaust, 2008; Jaglarz and Uchman, 2010). ?*Balanoglossites* cooccurs with *Zoophycos*, *Chondrites*, and *Palaeophycus* in the fine-grained sandstones (Bed 91) of the Yangmaba Formation and is considered to be formed in a relatively quiet offshore environment near a storm-wave base after several storm events in the Early Devonian (Zhang, 2014).

Ichnogenus *Chondrites* Sternberg, 1833
Chondrites targionii (Brongniart, 1828)
(Figures 5c and 5d)

Description: Tree-like, slightly curved, branched, flattened tunnels, with two orders of branches. Second-order branches dominate. The angle of branching ranges from 25° to 45°. The diameter of burrows in the Pingyipu and Ganxi formations is about 0.8 mm (Figure 5c) and 2.2 mm (Figure 5d), respectively. The overall burrow system is more than 2 cm wide. The traces are preserved in concave or convex epirelief.

Occurrence: Pingyipu and Ganxi formations. Common.

Discussion: *Chondrites* was revised by Fu (1991), who distinguished only four distinct ichnospecies (*C. targionii*, *C. intricatus*, *C. patulus*, and *C. recurvus*). Not all *Chondrites* can be synonymized with them (Uchman, 1999; Uchman

Figure 5. (**a**) *Arenicolites* isp., convex epirelief, Ganxi Formation. (**b**) ?*Balanoglossites* isp., convex hyporelief, Yangmaba Formation. (**c**) *Chondrites targionii*, concave epirelief, Pingyipu Formation, collection number: D-GX-1. (**d**) *Chondrites targionii*, convex epirelief, Ganxi Formation. (**e**) *Chondrites* ?*intricatus*, convex epirelief, Ganxi Formation. (**f**) Small (*C.* ?*intricatus*, white arrow) and large (*C. targionii*, black arrow) *Chondrites* together, convex epirelief, Ganxi Formation. (**g**) *Cylindrichnus concentricus*, vertical section view, Pingyipu Formation, collection number: D-PYP-1. (**h**–**i**) *Diplocraterion parallelum*, vertical section view, full relief, Pingyipu Formation. (**j**) *D. helmerseni*, vertical section view, full relief, Pingyipu Formation. (**k**) *Palaeophycus tubularis*, convex hyporelief, Pingyipu Formation. (**l**) *Palaeophycus tubularis*, convex epirelief, Ganxi Formation. (**m**) *Palaeophycus tubularis*, convex hyporelief, Yangmaba Formation. (**n**) *Palaeophycus heberti*, convex hyporelief, Pingyipu Formation. (**o**) *Palaeophycus striatus*, convex epirelief, Pingyipu Formation.
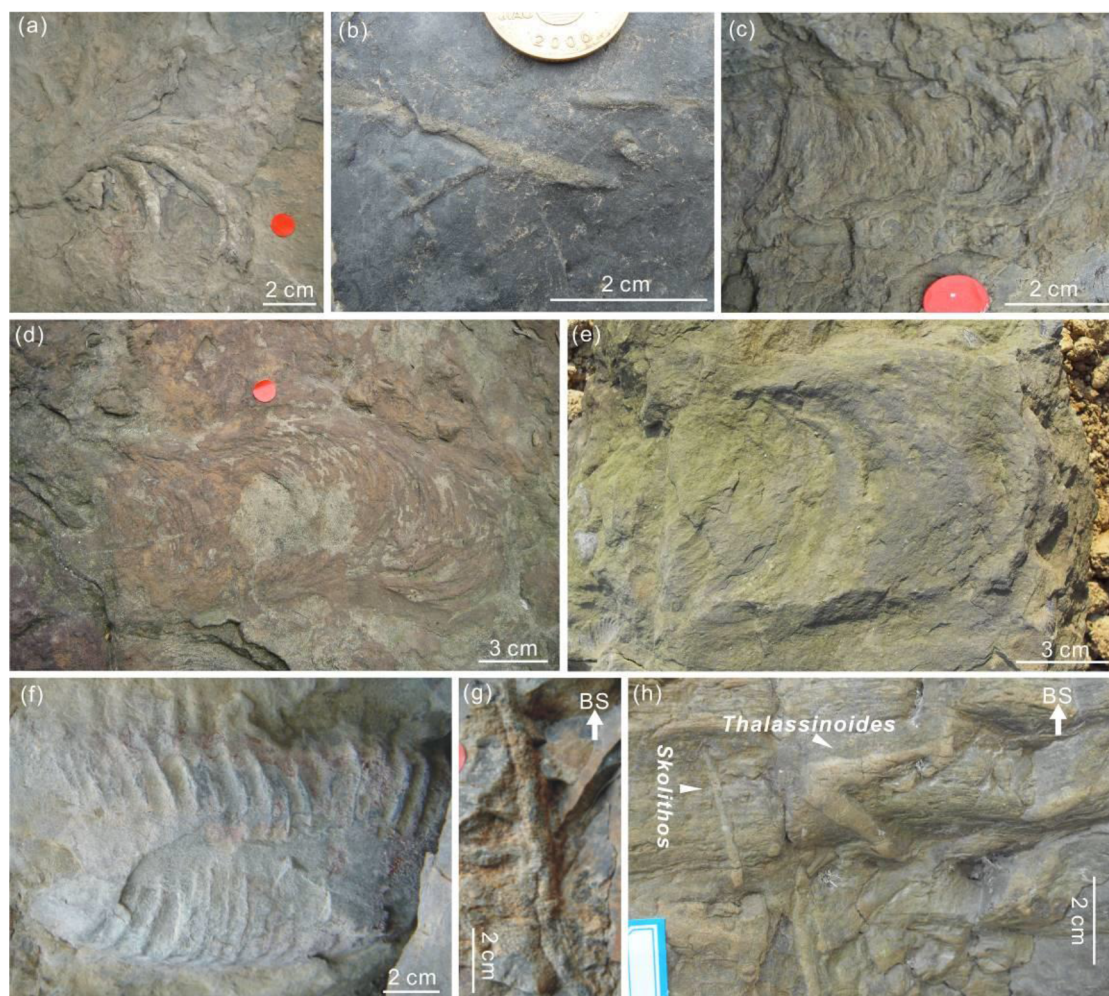
Figure 6. (**a**) *Phycodes* isp., convex epirelief, Pingyipu Formation. (**b**) *Planolites beverleyensis*, convex epirelief, Pingyipu Formation, collection number: D-PYP-2. (**c**) *Rhizocorallium commune*, convex epirelief, Pingyipu Formation. (**d–e**) *Rhizocorallium commune*, convex epirelief, Ganxi Formation, collection number: D-GX-3, D-GX-4, D-GX-5. (**f**) *Rusophycus lungmenshanensis*, convex hyporelief, Pingyipu Formation, collection number: D-GX-8. (**g**) *Skolithos linearis*, vertical section view, full relief, Pingyipu Formation. (**h**) *Thalassinoides* isp. and *Skolithos* isp., vertical section view, semirelief, Pingyipu Formation.

and Wetzel, 1999; Uchman et al., 2012). Apart from the general morphology, morphometric parameters can be used as complementary diagnostic criteria for *Chondrites* ichnospecies (Uchman, 1999). The burrows here showing primary successive branching, slightly curved tunnels, and mostly sharp angles of branching are diagnostic of *C. targionii* (Fu, 1991; Uchman, 1999).

Chondrites is a feeding system of unknown trace-makers related to infaunal deposit-feeders such as annelids or sipunculoids (Osgood, 1970) and might be able to live at the aerobic/anoxic interface hosting chemosymbiotic organisms (Bromley and Ekdale, 1984; Fu, 1991). The specimens described here occur in the argillaceous

mudstone that might have been deposited in a dysoxic environment.

Chondrites ?*intricatus* (Brongniart, 1823)
(Figures 5e and 5f)

Description: Small, tree-like branching, downward radiating, straight and short hypichnial burrows. Branches form sharp angles (30°–40°). The diameter of burrows is about 0.9 mm. The tunnels are slightly but distinctly concentrated and show crossovers. The tunnels are filled with similar materials as the host rock.

Occurrence: Ganxi Formation. Common.

Discussion: *C.* ?*intricatus* and *C. targionii* cooccur in the same bed of the Ganxi Formation (Figure 5f). The
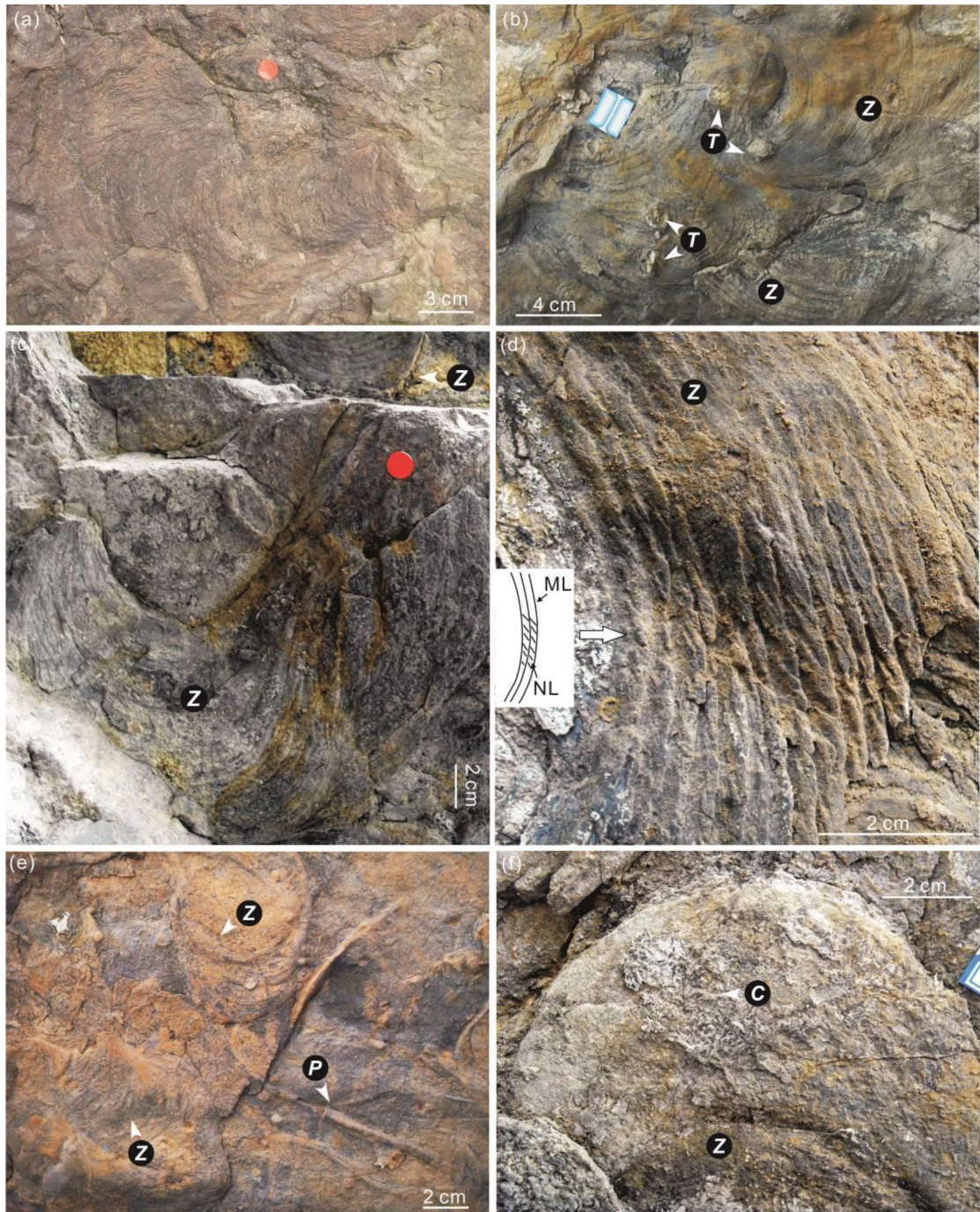
Figure 7. (**a**) *Zoophycos* isp. type A, convex epirelief, Ganxi Formation. (**b–d**) *Zoophycos* isp. type B, J-shaped form with clear primary lamellae (ML) and secondary lamellae (NL), *Thalassinoides* (T) cross-cutting the *Zoophcyos* spreiten (Z), convex hyporelief, Yangmaba Formation. (**e, f**) *Zoophycos* isp. type C, arcuate U-shaped form, cooccurring with *Palaeophycus* (P) and *Chondrites* (C), Yangmaba Formation.

larger form (*C. targionii*) cross-cut the smaller form (*C. ?intricatus*). The differently sized *Chondrites* forms might be produced in sediments of different dissolved oxygen levels.

Ichnogenus *Cylindrichnus* Toots in Howard, 1966
Cylindrichnus concentricus Toots in Howard, 1966
(Figure 5g)

Description: Vertical subcylindrical to subconical, straight to slightly curved burrows, slightly tapered over their length of several centimeters. The tubes are concentrically laminated in transverse section. Diameter and depth of the burrows ranges from 3 to 10 mm and 5.2 to 6.4 cm. Full relief preservation and the burrows were filled with materials similar to the host rock.

Occurrence: Pingyipu Formation. Rare.

Discussion: *Cylindrichnus* is considered as a permanent dwelling structure of suspension-feeding organisms (Vossler and Pemberton, 1989; Frey and Howard, 1990; Yang et al., 2004). *Cylindrichnus* is different from *Skolithos* by the bow-shaped traces (Belaústegui and Gibert, 2013). The burrow diameter of *Skolithos* is uniform throughout its length while *Cylindrichnus* is slightly tapering at the lower end of the burrow. Another difference is that the tube of *Skolithos* is not concentrically laminated in the transverse section. *Cylindrichnus* is common in shoreface to offshore environments as a component of the *Skolithos* and *Cruziana* ichnofacies (Frey and Howard, 1985; Vossler and Pemberton, 1989).

Ichnogenus *Diplocraterion* Torell, 1870
Diplocraterion parallelum Torell, 1870
(Figures 5h and 5i)

Description: Vertical, spreite-bearing U-shaped retrusive (Figure 5h) or protrusive (Figure 5i) burrows, with parallel limbs, which show rough surfaces and back-fills of the same lithology as the host rocks. Full relief preservation.

Occurrence: Pingyipu Formation. Common.

Discussion: The *D. parallelum* in Bed 13 of the Pingyipu Formation (Figure 5h) was well exposed (tubes 2.7 mm in diameter; traces 5.6 cm in depth). Limbs 2.7 cm apart. It represents a typical retrusive U-shaped burrow.

Another *D. parallelum* is poorly preserved in Bed 49 of the Pingyipu Formation due to weathering and denudation (Figure 5i). The casts of the U-shaped spreiten burrows were carefully observed. The tube imprint shows the clear upward convex lunate back-fill menisci, which indicate the downward movement of the trace-maker in the substrate (Zonneveld et al., 2012). The *D. parallelum* in Bed 49 was about 82.0 mm in depth, and the limbs are 20.0 mm apart and 3.2 mm in diameter.

The morphology here meets the diagnosis of *D. parallelum* (see Fürsich, 1974). It is a dwelling structure of suspension-feeding organisms. *Diplocraterion* is a characteristic component of shallow-marine, high-energy environments (Gaillard and Racheboeuf, 2006), but it has also been reported from freshwater environments (Morrissey et al., 2012).

Diplocraterion helmerseni (Öpik, 1929)
(Figure 5j)

Description: Simple U-shaped, spreiten burrow perpendicular to bedding plane. The burrow has an expanded, arc-shaped base. The tubes are not well preserved and about 8.0 mm in diameter. The limbs are 3.0–6.3 cm apart.

Occurrence: Pingyipu Formation. Rare.

Discussion: Fürsich (1974) recognized *Diplocraterion parallelum*, *D. helmerseni*, *D. biclavatum*, *D. habichi*, and *D. polyupsilon*. *D. helmerseni* was first described as *Corophioides helmerseni* (Öpik, 1929). Osgood (1970) distinguished *Corophioides cincinnatiensis* from *D. helmerseni* by its greater regularity of the spreiten and more abrupt basal expansion. Fürsich (1974) synonymized both ichnospecies under *Diplocraterion helmerseni* (Öpik, 1929).

Ichnogenus *Palaeophycus* Hall, 1847
Palaeophycus tubularis Hall, 1847
(Figures 5k–5m)

Description: Straight or slightly curved, cylindrical, horizontal, more or less smooth, conspicuous thinly-lined epichnia (Figure 5l) or hypichnia (Figures 5k and 5m). True branching is comparatively rare and cross-overs are common. The diameter ranges from 6.0 to 7.0 mm and the burrows are at least 18 cm long. The burrow fills are structureless and similar to the host sediments.

Occurrence: Pingyipu, Ganxi, and Yangmaba formations. Abundant.

Discussion: *Palaeophycus* ichnospecies are distinguished primarily by wall lining and ornamentation (Pemberton and Frey, 1982). *P. heberti* is thick-walled while *P. tubularis* is thin-walled, and both of them are bounded by smooth surfaces. *P. striatus* is characterized by continuous parallel striae, *P. sulcatus* shows irregularly anastomosing striae, and *P. alternatus* displays an alternation of striae and annulation (Pemberton and Frey, 1982). *Palaeophycus* is interpreted as dwelling structures (domichnia), a facies-crossing form in various freshwater and marine environments, probably produced by polychaetes and many other invertebrates (Häntzschel, 1975; Pemberton and Frey, 1982).

Palaeophycus heberti (Saporta, 1872)
(Figure 5n)

Description: Straight or slightly curved, cylindrical, unbranched, smooth, thick-lined hypichnial burrows. The traces show cross-overs. The diameter of burrows is 5.0–6.0 mm and the length ranges from 6.0 to 8.5 cm.

Occurrence: Pingyipu Formation. Common.

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Palaeophycus striatus Hall, 1852

(Figure 5o)

Description: Horizontal, cylindrical, unbranched, straight to slightly curved, epichnial burrow, with longitudinal parallel striae, about 1.5 cm in diameter and about 9.5 cm in length. The striae are 1.0 to 1.5 mm wide.

Occurrence: Pingyipu Formation. Rare.

Ichnogenus *Phycodes* Richter, 1850

Phycodes isp.

(Figure 6a)

Description: A bundle (five or six) of epichnial horizontal tubes, 0.9–1.1 mm in diameter. They originate from a thick, single stem, which is inclined 20° to 30° to the bedding plane and 7–10 cm long. The tubes are relatively short and display a short, flabellate pattern. Burrows are filled with sandstone similar to the host rocks.

Occurrence: Pingyipu Formation. Rare.

Discussion: *Phycodes* is a relatively common and widely reported ichnotaxon from Phanerozoic shallow and, less commonly, deep-marine and nonmarine environments (Seilacher, 1955; Osgood, 1970; Han and Pickerill, 1994). It is characterized by essentially horizontal bundled structures forming typically flabellate or broom-like burrows that are developed from a single or a few initial tunnels. Until now, many additional ichnospecies of *Phycodes* have been named and/or described in the literature, such as *P. circinatus* (Richter, 1853) and *P. templus* (Han and Pickerill, 1994). Our specimen displays arc-shaped branches and shows the flabellate pattern, but closer determination is impossible due to the poor preservation.

Phycodes is generally interpreted as a structure produced by a deposit-feeding organism (e.g., annelids, see Häntzschel, 1975), which repeatedly make tunnels from their permanent dwelling to actively exploit the food resources within the sediment (Muñiz, 1998; Mayoral et al., 2013). *Phycodes* is recorded mainly in shallow-marine environments, being a component of the *Cruziana* ichnofacies.

Ichnogenus *Planolites* Nicholson, 1873

Planolites beverleyensis Billing, 1862

(Figure 6b)

Description: Horizontal, unbranched, cylindrical, smooth-walled, unlined, straight to slightly curved epichnial burrows, 2–4 mm in diameter and about 1.1–3.2 cm long. The fill is structureless, differing in lithology from the host rock.

Occurrence: Pingyipu Formation. Common.

Discussion: *Planolites* and *Palaeophycus* are commonly compared. *Planolites* is actively filled and unlined while *Palaeophycus* is passively filled and lined (Pemberton and Frey, 1982). *Planolites montanus* is characterized by relatively small, curved to snake-like burrow and the

filling materials tend to consist of cleaner, better-sorted sediment than the host rocks (Pemberton and Frey, 1982). *P. beverleyensis* is characterized by relatively large, smooth, straight to slightly curved burrow whose fill is different from the lithology of host sediments. *P. beverleyensis* is distinguished from *P. montanus* primarily by the larger size and less tortuous course (Billings, 1862; Pemberton and Frey, 1982). *P. annularius* is characterized by distinctly annulated, subcylindrical burrows (Pemberton and Frey, 1982). Using the first criterion, the specimen described may be assigned to *P. beverleyensis*. *Planolites* is a feeding burrow produced by vagile endobenthic deposit feeders, e.g., polychaetes (Alpert, 1975; Pemberton and Frey, 1982).

Ichnogenus *Rhizocorallium* Zenker, 1836

Rhizocorallium commune Schmid, 1876

(Figures 6c–6e)

Description: Horizontal to oblique tongue-like epichnial structures with spreites enclosed by a tubular marginal tube with parallel limbs. No scratches or fecal pellets are found in the spreiten or the marginal tube. The limbs are 2.1–4.5 cm apart. The diameter of the marginal tube is 5.0 to 8.0 mm. The length of burrow ranges from 6.4 to 13.2 cm.

Occurrence: Pingyipu and Ganxi formations. Abundant.

Discussion: *Rhizocorallium* was systematically revised to comprise only two ichnospecies, *R. jenense* and *R. commune* (Knaust, 2013). *R. jenense* (Triassic to Holocene) is a comparatively small, inclined and heavily scratched firm-ground burrow with passively filled spreiten material, while *R. commune* (Early Cambrian to Holocene) consists of extensive, more or less horizontal burrows with occasionally scratch-marked marginal tubes and spreites between the tubes (Knaust, 2013). Paleozoic marine *Rhizocorallium commune* is interpreted as a structure produced by suspension-feeding or deposit-feeding organisms, probably polychaetes, and was restricted to the *Cruziana* ichnofacies of shallow-marine environments (Knaust, 2013).

R. commune is quite abundant in the Ganxi Formation (Figures 6d–6f) and distributed along the muddy siltstone bedding surfaces, together with brachiopods and other trace fossils such as *Zoophycos*, *Chondrites*, and *Palaeophycus*. It indicates a quiet, low-energy, food-rich, upper offshore environment.

Ichnogenus *Rusophycus* Hall, 1852

Rusophycus lungmenshanensis Yang, 1988

(Figure 6f)

Description: Small ovate, bilobate, and almost symmetrical hypichnial mound, 4.0 cm wide, 12.0 cm long, and 3 mm high (maximum values), separated into two lobes by a median furrow. The external margins of the lobe are gently arcuate. The lobes are entirely covered with

fine (less than 1 mm wide) straight or slightly bent ridges running obliquely from the margins to the median furrow at an angle of 70°–80°.

Occurrence: Pingyipu Formation. Common.

Discussion: The type material of *Rusophycus lungmenshanensis* derives from the Guixi Member of the Pingyipu Formation in the Longmenshan Mountain area (Yang et al., 1988). Paleozoic *Rusophycus* samples are interpreted as arthropod, mostly trilobite resting traces (Crimes and Herdman, 1970; Osgood and Drennen, 1975). *Rusophycus* commonly occurs in shoreface to offshore environments and is a component of the *Cruziana* ichnofacies (Uchman et al., 2004; Pandey et al., 2014).

Ichnogenus *Skolithos* Haldemann, 1840
Skolithos linearis Haldemann, 1840
(Figure 6g)

Description: Simple, perfectly straight and vertical to slightly curved or inclined, cylindrical or subcylindrical burrows, about 8.0 mm in diameter and 10.3 cm in length, with rough surfaces. The passive fills in the burrow are similar to the host rocks.

Occurrence: Pingyipu Formation. Abundant.

Discussion: *Skolithos* is interpreted as dwelling structures of annelids or phoronids (Alpert, 1974) and it occurs in various shallow-marine environments from the Late Precambrian to Recent.

Ichnogenus *Thalassinoides* Ehrenberg, 1944
Thalassinoides isp.
(Figure 6h)

Description: Three-dimensional endichnial burrow systems made of predominantly horizontal galleries and vertical shafts, burrow limbs straight to slightly curved. Cylindrical tunnels are 2.0–5.1 mm in diameter and show smooth and sharp margins. Branches are T-shaped, enlarged at points of bifurcation. The whole burrow system is about 8.2 cm in depth.

Occurrence: Pingyipu Formation. Common.

Discussion: *Thalassinoides* is considered to be a dwelling and feeding structure of decapod crustaceans and mostly occurs in shallow-marine environments (Myrow, 1995; Carvalho et al., 2007). The specimen described here is preserved in the pipe rocks of Bed 27 in the Pingyipu Formation and cooccurs with *Skolithos*. *Thalassinoides* superimposes *Skolithos* or vice versa, which altogether indicates a high-energy coastal shoreface environment.

Ichnogenus *Zoophycos* Massalongo, 1855
Zoophycos isp. type A
(Figure 7a)

Description: Epichnial, horizontal to inclined, extended U-shaped spiraling spreites, with poorly preserved marginal tube. The structure is 12–14 cm wide and graduates from tight (U-shaped) to broadly arcuate. Primary and secondary lamellae are distinguishable.

Occurrence: Ganxi Formation. Common.

Discussion: *Zoophycos* is a complex and still enigmatic trace fossil because its various morphologies, evolution, and taxonomy remain unsolved (Uchman and Demírcan, 1999; Chamberlain, 2000; Olivero, 2003; Knaust, 2009). Due to the variety of morphological forms, *Zoophycos* can contain only *Rhizocorallium*-like elements, as the lateral shift and progressive deepening of individual *Rhizocorallium*-like burrows might gradually lead to the development of a tongue-like *Zoophycos* spreite system (Vanuxem, 1842; Bradley, 1973; Miller, 1991; Uchman and Demírcan, 1999; Bromley and Hanken, 2003; Carvalho and Rodriguez, 2003; Pervesler and Uchman, 2004). *Zoophycos* is sometimes known as a rare component of a compound burrow system most likely produced by the same organism as *Rhizocorallium commune* (Knaust, 2004, 2013). The specimen described here is probably a transitional form between *Rhizocorallium* and *Zoophycos*, belonging to a morphological group quite common in the Devonian (Vanuxem, 1842; Seilacher, 1983; Miller, 1991; Gaillard and Racheboeuf, 2006).

Zoophycos is usually considered as a feeding burrow of worm-like deposit feeders, such as sipunculids (Wetzel and Werner, 1981; Olivero, 2003), echiurans (Kotake, 1992), and polychaetes (Knaust, 2009). *Zoophycos* occurs in shallow marine deposits in the Paleozoic and both shelf and deep-sea deposits in the Mesozoic and Cenozoic (Bottjer et al., 1988; Carvalho and Rodriguez, 2003; Knaust, 2004). The specimen observed here cooccurs with *Rhizocorallium*, *Palaeophycus*, and *Chondrites* and brachiopods, indicating a relatively quiet upper offshore environment rich in food.

Zoophycos isp. type B
(Figures 7b–7d)

Description: Horizontal, spiraling or helicoidal, hypichnial J-shaped spreiten. The outline is cock-tail shape and the marginal tube is not very distinct. The lamina are arranged and spiraled concentrically around a central point. The primary and secondary lamellae are clearly distinguished and equally spaced. The primary lamellae are about 3.0–4.0 mm apart. The whole trace fossil is 11 cm in the widest and 14 cm in the longest points.

Occurrence: Yangmaba Formation. Common.

Discussion: Wetzel and Werner (1981) summarized and proposed two basic morphological forms with J-shaped and U-shaped spreiten, which are quite commonly used to describe *Zoophycos* (Löwemark et al., 2004; Knaust, 2009; Zhang, 2014). The specimens observed here display J-shaped form and cooccur with *Thalassinoides*.

Zoophycos isp. type C
(Figures 7e and 7f)

Description: Hypichnial, horizontal, flat, arcuate U-shaped spreites with visible marginal tube. The primary

and secondary lamellae are not easily distinguishable. The maximum width is about 4.6 cm. The marginal tube is about 8 mm wide.

Occurrence: Yangmaba Formation. Common.

Discussion: The specimen described here should be referred to U-shaped *Zoophycos*. *Zoophycos* is quite abundant on the sole surfaces of fine-grained sandstone (Bed 91) from the Yangmaba Formation and cooccurs with small *Chondrites*, *Palaeophycus*, and *Thalassinoides*, indicating that the trace makers of *Zoophycos* and *Chondrites* were opportunistic organisms (r-strategists) and enjoyed a relative quiet, nutrient-rich, offshore environment near a storm-wave base after several storm events in the Lower Devonian (Zhang, 2014).

5. Discussion
5.1. Trace fossil associations
Several trace fossil associations, each identified by the most abundant and common ichnotaxon, can be recognized. Ichnocoenosis means all the traces produced by organisms simultaneously occupying a certain substrate, following Bromley (1996). Concerning our materials in the Ganxi section, we prefer to use "association" because the constitutive traces were often not formed simultaneously in the same bed. Moreover, the different ichnotaxa of the same association are not necessarily present in the same bed. They only characterize a specific group of beds that probably correspond to relatively similar environmental conditions.

In the Ganxi section, six trace fossil associations were recognized within the studied Lower Devonian sequence (Figure 2). Four of these associations were very clearly found in the Pingyipu Formation, one in the lower part of the Ganxi Formation, and the last in the upper part of the Yangmaba Formation.

Skolithos association: The *Skolithos* association consists of two recognized ichnotaxa (in decreasing order of abundance): *Skolithos linearis* and *Palaeophycus tubularis*. The two ichnogenera occasionally cooccur on the sole surface of the same beds. *Skolithos* is relatively frequent and dominant in the association. The burrow totally penetrates medium to thick fine-grained sandstone beds (20–60 cm). They represent dense monospecific populations (pipe rock) of supposed endobenthic worms (domichnia). The pipe rock is always intercalated with unbioturbated beds with cross-bedding and ripple lamination, which indicate a high-energy environment. *Palaeophycus tubularis* is rarely observed, and it occurs only in fine-grained sandstone, indicating calmer environments.

Rusophycus-Phycodes association: Three ichnotaxa characterize this association: *Rusophycus lungmenshanensis*, *Phycodes* isp., and *Planolites beverleyensis*. *Rusophycus lungmenshanensis* and *Phycodes* isp. are the most abundant

traces and *Rusophycus* is dominant. All of them are preserved in hyporelief and/or epirelief and mainly occur in dark, thin-bedded siltstone. Concerning the enclosing sediment, cross-bedding, horizontal lamination, and ripple lamination occur in the underlying and overlying thick-bedded sandstone. The main trace makers of the association are arthropods. *Rusophycus* is a resting trace while *Phycodes* and *Planolites* are deposit feeding structures. This association might indicate a relatively lower-energy, nutrient-rich, upper shoreface environment between the mean low tidal level and normal wave base.

Diplocraterion-Skolithos association: This rich association is characterized by eight trace fossils: *Diplocraterion parallelum*, *Skolithos linearis*, *Palaeophycus tubularis*, *Palaeophycus heberti*, *Diplocraterion helmerseni*, *Palaeophycus striatus*, *Cylindrichnus concentricus*, and *Rhizocorallium commune*. *D. parallelum* and *Skolithos linearis* are the most abundant traces and *D. parallelum* is dominant. The association mainly consists of deep vertical burrows, which totally penetrate fine-sandstone beds 20–30 cm thick. Specially, *D. parallelum* is exclusively protrusive and represents dense monospecific populations (pipe rock) of suspension-feeding organisms (dwelling structures). Other traces are not common and are fragmentarily expressed in the intercalated thinner beds.

Chondrites-Palaeophycus association: Six ichnospecies comprise this association: *Chondrites targionii*, *Palaeophycus tubularis*, *Palaeophycus heberti*, *Planolites* isp., *Skolithos* isp., and *Thalassinoides* isp. Most of these trace fossils are surficial and visible on bedding surfaces. They characterize a low-density association. *Chondrites targionii* and *Palaeophycus tubularis* might be abundant. Deep burrows are rare. The association is mainly preserved in gray-dark thin-bedded muddy siltstones and siltstones. They alternate with thinner sandy or silty levels frequently showing intense bioturbation. Some tempestites occur at the base of the association. The association also cooccurs with body fossils, mainly brachiopods, crinoids, and plant fragments (Figures 4a and 4c). The diameter of *Chondrites* burrows is only 1.0–1.2 mm.

Rhizocorallium association: The *Rhizocorallium* association comprises six recognizable trace fossils: *Rhizocorallium commune*, *Zoophycos* isp. type A, *Palaeophycus tubularis*, *Chondrites* ?*intricatus*, *Chondrites targionii*, and *Arenicolites* isp. These ichnotaxa cooccurred in the same bed of the Ganxi Formation. The epichnial burrows mainly occur on the bedding surfaces of muddy siltstones. They characterize a high-density association and most of the ichnotaxa belong to fodinichnia. *Rhizocorallium commune* is the most common in this association. This trace fossil bed is overlain by medium-bedded sandstones hosting hummocky cross-stratification (Figure 4d). Body fossils, such as brachiopods and

trilobites, are commonly concentrated in the same bed of the *Rhizocorallium* association.

Zoophycos association: This association is characterized by seven recognized ichnospecies: *Zoophycos* isp. type B, *Zoophycos* isp. type C, ?*Balanoglossites* isp., *Chondrites* isp., *Thalassinoides* isp., *Palaeophycus tubularis*, and *Palaeophycus* isp., and a few undetermined burrows. In contrast to more recent *Zoophycos*, the burrow outlines in our specimens are always simple without lobes. *Zoophycos* is dominant and displays J-shaped and U-shaped forms. Trace fossils in this association are clearly visible on the sole surface of gray-white thin-bedded fine-grained sandstone beds from the upper part of the Yangmaba Formation. *Zoophycos* also cooccurs with *Chondrites* and is often cross-cut by *Thalassinoides* (Figure 7). Swaley cross-stratification, erosion surface (Figure 4h), and horizontal lamination often occur in the underlying and overlying gray medium-bedded fine-grained sandstone. The association often occurs in the intervals of storm beds (Zhang, 2014).

5.2. Paleoenvironmental significance and evolution
Devonian marine shelves (as presented in this study) were broad, with extensive clastic sedimentation (Goldring and Langenstrassen, 1979), which were significantly different from modern shelves in many parts of the world (Seilacher, 1983; Miller, 1991; Gaillard and Racheboeuf, 2006).

The Pingyipu Formation is mainly a continental marginal sea deposit (Hou et al., 1988). Its lower part at the Ganxi section probably corresponds to a foreshore to shoreface environments. Marine influences were evident in the burrowing activities of benthic organisms. It was in the relatively quiet, stable intervals between storm or coarse sedimentation that the benthic organisms were able to exercise and make traces, and the deposit feeding (*Phycodes*) and resting traces (*Rusophycus*) are dominant in such conditions. In the unstable environment, clean, well-sorted clastic sediments were usually abruptly deposited and subject to continuous penecontemporaneous erosion. Only rapid and ephemeral colonization by opportunistic organisms was possible under such circumstances. Dense pipe rocks formed by deep burrowing worms dominating the thick-bedded fine-grained sandstone beds (*Diplocraterion-Skolithos*) can be referred to this strategy. The opportunistic ecology of *Skolithos* and *Diplocraterion* is well known, and these dwelling burrows commonly occur in high-energy foreshore to shoreface clastic environments (Alpert, 1975; Heinberg and Birkelund, 1984; Vossler and Pemberton, 1989; Gaillard and Racheboeuf, 2006). *Cylindrichnus* and *Arenicolites* are commonly found in low diversity ichnoassemblages, typically in shallow-marine environments (Frey and Howard, 1985; Vossler and Pemberton, 1989; Frey and Howard, 1990; Bromley, 1996). Rare occurrences of *Chondrites* and *Rhizocorallium*

commune probably indicate calmer periods with deposition of fine-grained sediment and organic matter. Following the above discussion, the *Diplocraterion-Skolithos* association probably indicated a lower foreshore to upper shoreface environment.

In the middle part of the Pingyipu Formation, two associations were observed, i.e. the *Skolithos* and *Chondrites-Palaeophycus* associations. In the *Skolithos* association, *Skolithos linearis* (dominant) and *Palaeophycus tubularis* were produced in more stable conditions with less sandy input. *Palaeophycus* occurs on the sole surfaces of pipe rocks (*Skolithos* is dominant). Thus, a lower foreshore to upper shoreface environment is assigned.

The low-density *Chondrites-Palaeophycus* association results from a relatively diversified surficial benthic fauna and attests to hospitable shallow-marine conditions. *Chondrites* and *Palaeophycus* dominated, but rare occurrences of *Planolites*, *Thalassinoides*, and *Skolithos* were also present. *Palaeophycus tubularis* commonly occurs in the overlying beds of the *Chondrites*-bearing buried bed. Dwelling burrows are decreased in size and abundance and the fodinichnia *Palaeophycus* are common. Plant fragments and brachiopods, crinoids, and bivalves cooccur with *Palaeophycus* in the same beds. In the underlying siltstone beds with bioturbational structures (bioturbation index BI = 4) (Droser and Bottjer, 1989) and ripple laminations are distinguished. These observations point toward a quiet, food-rich, dysoxic shallow marine environment, such as a coastal lagoon.

The *Rhizocorallium* association was distinguished in the lower part of the Ganxi Formation. It includes *Rhizocorallium commune*, *Zoophycos* isp. type A, *Palaeophycus tubularis*, *Chondrites* ?*intricatus*, *Chondrites targionii*, and *Arenicolites* isp. This relatively high ichnodiversity association dominated by *Rhizocorallium commune* characterizes a more stable environment. Suspension-feeding (*Rhizocorallium*) and deposit-feeding (*Chondrites*) burrows are abundant. No cross-cutting relationships are found between these trace fossils. *R. commune* and *Zoophycos* isp. type A are all typical shallow marine trace fossils. Dwelling burrows (*Arenicolites*) are rare. *Chondrites* and *Palaeophycus* are often associated with *Rhizocorallium*. In the same bed containing the *Rhizocorallium* association, branchiopods were concentrated in the lower bedding surface of muddy siltstone. Finer, muddy siltstones have a better preservation potential for organic matter, which was exploited by the worm-like suspension or deposit feeder. In the overlying sandstone beds, hummocky cross-stratification was observed (Figure 4d). Here, a quiet, nutrient-rich, upper offshore near storm wave base is probable.

The *Zoophycos* association, characterizing fine-grained deposits, corresponds to some larger environmental

changes, probably a significant deepening of water (Gaillard and Racheboeuf, 2006). The *Zoophycos* ichnofacies was first established and often referred to continental slopes below storm wave base level, in calm conditions (Seilacher, 1967). Over the past twenty years, the importance of *Zoophycos* as a paleoecological index trace fossil has been better recognized (Bottjer et al., 1988; Carvalho and Rodriguez, 2003; Olivero, 2003; Knaust, 2009). In the Paleozoic, *Zoophycos* occurred in both shallow and deep water deposits, but from the Mesozoic onwards it has been restricted to continental slope and basinal deposits (Olivero, 2003; Knaust, 2009). The *Zoophycos* association here was observed in the upper part of the Yangmaba Formation, where *Zoophycos* was the dominant trace fossil, with J-shaped and arcuate U-shaped forms. High-density *Zoophycos* is preserved as convex hyporelief in the fine-grained sandstone. Small *Chondrites* and *Palaeophycus* cooccur with *Zoophycos*. *Thalassinoides* is a ubiquitous trace, which frequently cross-cuts the *Zoophycos* spreites. In the adjacent beds, swaley cross-stratification, horizontal lamination, and erosion surface were observed. *Zoophycos* and *Chondrites* were the dominant traces in the fine-grained sediments of the wave scour hollows. This indicates a temporary dysoxic-anoxic environment after storm events. Trace-makers of *Zoophycos* and *Chondrites* were the first colonizers of sediments after storm events (Zhang, 2014). The last to appear in the burrowing sequence is *Thalassinoides*, whose progenitor took advantage of the sediment already reworked by the *Zoophycos* producers. Here, a lower offshore near storm wave base environment is probable.

The observed trace fossil succession clearly evokes the classical ichnofacies succession proposed by Seilacher (1967): *Skolithos* ichnofacies (represented by *Skolithos* and *Diplocraterion-Skolithos* associations), *Cruziana* ichnofacies (*Rusophycus-Phycodes*, *Chondrites-Palaeophycus*, and *Rhizocorallium* associations) and *Zoophycos* ichnofacies (*Zoophycos* association). However, the succession clearly does not illustrate an evolution from the shore to abyssal depths as suggested by the initial model. Rather, it represents a narrower bathymetric range, as has been proposed for the Devonian (Goldring and Langenstrassen, 1979; Gaillard and Racheboeuf, 2006).

In the Ganxi section, all the trace fossil associations suggest a fully shallow marine environment. The following succession of trace fossil associations of the Lower Devonian is observed (Figure 2). At the base, unbioturbated cross-bedded sandstones are followed by the *Rusophycus-Phycodes* association in siltstones, the *Diplocraterion-Skolithos* association in sandstones, the *Skolithos* association in sandstones, the *Chondrites-Palaeophycus* association in muddy siltstones, the *Diplocraterion-Skolithos* association in sandstones, the

Rusophycus association in muddy siltstones, and eventually the *Zoophycos* association in marlstones and sandstones. The following paleoenvironmental succession may be envisaged.

The lowermost, Lochkovian part records the succession from a probably high-energy lower foreshore (cross-bedded sandstones) to upper shoreface environments. Such a succession is coincident with the transgressive-regressive cycle reconstructed by Zhang and Gong (2013). The sudden appearance of the *Chondrites-Palaeophycus* association (*Cruziana* ichnofacies) indicates a rapid rise of relative sea level during the early Pragian and places the area studied in a coastal lagoon. The succeeding *Diplocraterion-Skolithos* association appears in the late Pragian and indicates a foreshore to upper shoreface environment. The appearance of the *Rusophycus* association, which occurs in the muddy siltstones intercalated in the limestone with abundant body fossils from the lower part of the Ganxi Formation (Emsian), indicates a quiet, food-rich, upper offshore setting. Sparse sandstone interbeds in the upper part of the Yangmaba Formation, hosting the *Zoophycos* association, demonstrated a generally continuous influx of coarser materials onto the carbonate platform influenced by episodic storms, indicating a lower offshore setting close to the storm wave base.

In summary, as is well known among ichnologists, the Seilacherian ichnofacies model must not be applied blindly (Ekdale and Bromley, 1984; Ekdale, 1988; Frey and Howard, 1990; Bromley, 1996; Miller and D'Alberto, 2001; Gaillard and Racheboeuf, 2006) in order to fully realize its potential in illustrating significant ecological trends through the frequently recorded succession of trace fossil associations. This succession (from the *Skolithos* and *Cruziana* to *Zoophycos* associations) clearly occurs in the Lower Devonian series of the western Yangtze Plate continental margin, as with the Lower Devonian strata in Bolivia (Gaillard and Racheboeuf, 2006).

6. Conclusions

The Lower Devonian strata, which are well exposed in the Ganxi section of South China, yield pertinent data for studying marine benthic fauna during the Lower Devonian transgression. Altogether 13 ichnogenera have been described, including *Arenicolites*, ?*Balanoglossites*, *Chondrites*, *Cylindrichnus*, *Diplocraterion*, *Planolites*, *Palaeophycus*, *Phycodes*, *Rhizocorallium*, *Rusophycus*, *Skolithos*, *Thalassinoides*, and *Zoophycos*. Most of the trace fossils are presented in sandstones and few in muddy siltstones and marlstones.

Six trace fossil associations have been recognized: *Rusophycus-Phycodes*, *Diplocraterion-Skolithos*, *Skolithos*, *Chondrites-Palaeophycus*, *Rhizocorallium*, and *Zoophycos* associations. They are interpreted to follow a foreshore

to offshore environmental gradient. The *Skolithos* and *Diplocraterion-Skolithos* associations belong to the *Skolithos* ichnofacies, indicating a well-oxygenated and high-energy setting within the foreshore to shoreface zone. The *Rusophycus-Phycodes* association, occurring in the siltstone intervals of cross-bedded sandstone, probably indicates a more proximal *Cruziana* ichnofacies within the upper shoreface zone. The *Chondrites-Palaeophycus* association, present in the muddy siltstone together with rich body fossil assemblages (including abundant plant fragments), marks the distal *Cruziana* ichnofacies within the coastal lagoon environment. The *Rhizocorallium* association reflects a quiet, food-rich, upper offshore setting, belonging to the *Cruziana* ichnofacies. The *Zoophycos* association (*Zoophycos* ichnofacies) probably indicates a lower offshore zone characterized by frequent storm influences.

The trace fossil associations and the ichnofacies succession suggest that the Lower Devonian strata of the Ganxi section represents several transgressive-regressive cycles and were often influenced by storm events in the Pragian and Emsian.

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