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Palaeoenvironmental and ecological interpretation of the trace fossil *Rhizocorallium* based on contained iron framboids (Upper Devonian, South China)

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ABSTRACT

The trace fossil *Rhizocorallium commune* is abundant in shallow-marine deposits of the Upper Devonian (Frasnian) Tuqiaozi Formation in Ganxi, Sichuan Province, South China. It consists of U-shaped spreite burrows developed more or less parallel or slightly inclined to the bedding of marly limestone. Four types of iron framboids (mostly oxygenated from pyrite framboids) were found within the *Rhizocorallium* burrow, including (1) smooth, sheathed spherical, (2) prismatic, (3) octahedral, and (4) pyritohedral submicron crystals. Chemically, the submicron crystals mainly consist of iron, sulphur, oxygen and carbon. The iron framboids represent the stage of evolution of their original pyrite framboids from irregular morphologies and spherical framboids to octahedral and pyritohedral habits due to the activity of sulphate-reducing bacteria. No similar framboids were observed outside *Rhizocorallium*. Therefore, it is likely that sulphate-reducing bacteria colonised the *Rhizocorallium* spreite and marginal tube within a dysoxic environment. With increasing degree of oxygenation of pore water, the pyrite framboids were partly oxygenated into iron framboids and by exceptional circumstances preserved the original morphology of the crystals. Furthermore, it is proposed that the investigated *Rhizocorallium* was constructed by its trace maker for gardening with multifunctional purpose, where different microbial colonies were planted and cultured in the marginal tube and spreite on the mutual basis of food supply and redox conditions. These features indicate that a combined deposit-feeding and gardening model may apply for the construction of *Rhizocorallium commune* from the Devonian of Ganxi. The responsible trace maker probably was a worm-like organism, such as a polychaete.

1. Introduction

The famous ichnogenus *Rhizocorallium* Zenker, 1836 is one of the earliest described and most widespread trace fossils globally, with compositional, developmental and ecological complexities (Knaust, 2013). This distinctive trace fossil ranges from Early Cambrian (Clausen and Vilhjálmsson, 1986) to Holocene (Winn, 2006) in age. It occurs in a wide variety of depositional settings, involving carbonate and siliciclastic rocks and is often used in the characterisation of shallow-marine depositional systems (Fürsich, 1974; Rodríguez-Tovar and Pérez-Valera, 2008; Hofmann et al., 2011; Rodríguez-Tovar et al., 2012; Knaust, 2013). Current controversies are mainly concerned with the morphology, taxonomy, palaeoenvironmental distribution and evolution of the burrow system (Kowal-Linka and Bodzioch, 2011; Schlirf, 2011; Rodríguez-Tovar et al., 2012; Knaust, 2013).

The Late Devonian reveals a series of biotic crises that progressively influenced reef and other tropical, benthic communities (Copper, 2002; Feist et al., 2009; Kazmierczak et al., 2012; Buatois et al., 2013; Feist and McNamara, 2013). The Late Devonian of the Ganxi section (north-eastern Sichuan Province, South China) reveals an abundant and well-developed trace-fossil association which, in the Tuqiaozi Formation (Frasnian), is mainly composed of *Rhizocorallium*. *Rhizocorallium* is a useful environmental indicator, with potential importance in palaeoenvironmental reconstructions, especially in relation with factors such as water energy level, hydrodynamic processes, substrate consistency, and distribution of organic matter (Knaust, 2013).

Here we report several intermediate stages in the evolution of pyrite framboids occurring within the *Rhizocorallium* spreite, interpreted as the pyritised remains of microbial colonies, which were preserved due to reducing bottom conditions and the partly oxygenation of the pyrite framboids into iron framboids. These data provide new evidence pertaining to the behaviour of the *Rhizocorallium* trace maker, depositional and ecological features, and contribute to the understanding of the relationship between trace maker and microbes.

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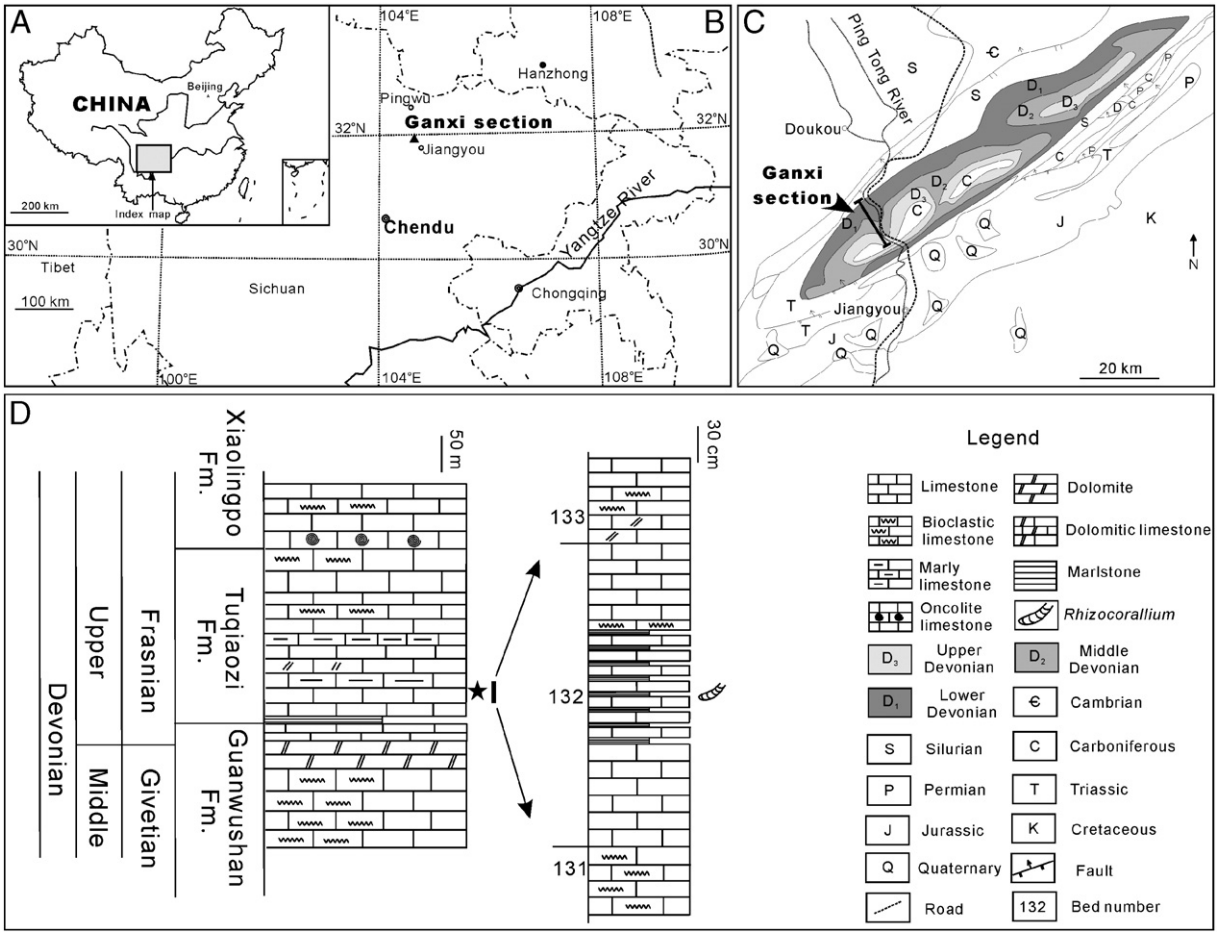

Fig. 1. Location maps and lithostratigraphy of the Ganxi section in the Sichuan Province of South China. A, B. Location of the studied section. C. Geological map of the Devonian Ganxi section (modified after Hou et al., 1988). D. Stratigraphic column of the Middle to Upper Devonian and detailed lithostratigraphy with occurrences of *Rhizocorallium*.

2. Geological setting and methods

Ganxi in Sichuan Province of South China provides excellent outcrops of Late Palaeozoic strata, especially from the Devonian period (Hou et al., 1988). The study area is located in the north-western part of the Upper Yangtze Plate and belongs to the Early Palaeozoic Longmenshan Basin (Fig. 1). The outcrops of Devonian strata are exposed along the Pingtong River on a ca. 15 km long section (Fig. 1). The Devonian strata in this area were deposited along a continental margin without significant tectonic events (Xian et al., 1995). In the Ganxi section, the Upper Devonian strata are up to 1000 m thick and range from the Frasnian to Famennian (Xian et al., 1995). The trace fossils presented in this article were collected from the trace-bearing interval (Bed 132) in the Upper Devonian Tuqiaozi Formation of the Ganxi section (Fig. 1) exposed at 31°54′26″ N, 104°41′22″ E, which consists of limestone beds intercalated with thin-bedded marlstone.

The Tuqiaozi Formation consists of limestone, marly limestone and marlstone with parallel lamination. Body fossils are common and include conodonts, tentaculites and brachiopods in the marlstone and limestone of the lower part, wackestone and packstone with erosion surfaces and graded bedding in the middle part, micrite and bioclastic limestone with abundant dendritic stromatoporoids, brachiopods, tentaculites, ostracodes and *Girvanella* in the upper part (Hou et al., 1988).

The Tuqiaozi Formation conformably overlies the Middle Devonian Guanwushan Formation and underlies the Upper Devonian Xiaolingpo Formation (Fig. 1). The Guanwushan Formation consists of dark-grey, medium- and thick-bedded bioclastic limestone and yellow-white, thin- and medium-bedded dolomite, most likely deposited in open to restricted platform environments (Hou et al., 1988). The Xiaolingpo Formation mainly consists of thick-bedded bioclastic limestone and is distinguished by a thick-bedded oncolite limestone at its base (Fig. 1).

Trace fossils described in this paper occur in the middle part of Bed 132 of the Tuqiaozi Formation, which records a transition from open carbonate platform (lower part of the Tuqiaozi Formation) to storm-affected carbonate ramp environments (middle part of the Tuqiaozi Formation; Hou et al., 1988). On the basis of sedimentological evidence, the depositional environment of the *Rhizocorallium*-bearing interval is interpreted as being in water depths between fair-weather wave base and storm-wave base (Hou et al., 1988).

After the initial ichnological and petrographical work, the freshly broken argillaceous limestone surfaces containing *Rhizocorallium* and fragments of the host strata were selected, cleaned and coated with carbon and gold, respectively. Then they were analysed both petrographically and chemically in a Quanta 250 field emission gun scanning electron microscope (FEI Quanta 250 FEG-SEM) equipped with a Bruker Nano with X-Max 30 mm^2 detector energy dispersive X-ray spectrometer (Bruker Quantax 200 XFlash 6|30 EDS) at the Key Laboratory of Biogenic Traces & Sedimentary Minerals of Henan Province in Jiaozuo, China.

3. Results

3.1. Rhizocorallium

The investigated *Rhizocorallium* specimens occur on the bedding plane of a marly limestone and consist of horizontal and/or slightly inclined U-shaped burrows with a marginal tube enclosing an area