

# Palaeoecological Analysis of Trace Fossil *Sinusichnus sinuosus* from the Middle Triassic Guanling Formation in Southwestern China

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**ABSTRACT:** The Luoping Biota discovered from the early Middle Triassic (Anisian) Guanling Formation of southwestern China represents a fully recovered shallow marine ecosystem, marking the end point of Early Triassic biotic recovery following the end-Permian mass extinction. Contemporaneously preserved are prolific trace fossils, which offer good opportunities to understand the palaeoecology of marine invertebrates from a fully recovered shallow marine ecosystem. Here we present a newly discovered sinuous branching burrow from the fossil-bearing unit in Member II of the Guanling Formation. Several features, including the horizontal regular sinuous nature, the branching pattern, typical H-junction, and the small wavelength/amplitude ratio of these sinuous structures within the burrow systems justify assignment of these traces as *Sinusichnus sinuosus*, a trace possibly produced by decapod crustaceans. Close association of *S. sinuosus* with *Rhizocorallium commune* suggests a deposit-feeding strategy of these trace makers. The newly reported Anisian material from the Guanling Formation in Luoping represents first report of *Sinusichnus* from South China. The global record of *Sinusichnus* occurrence suggests that these burrows might have an older history than Early Middle Triassic.

**KEY WORDS:** *Sinusichnus sinuosus*, decapod crustacean, trace fossil, Middle Triassic, Luoping, southwestern China

## 0 INTRODUCTION

The end-Permian mass extinction (EPME) is considered the largest catastrophic event of the Phanerozoic, causing a loss of ~95% of marine species and 81% of terrestrial vertebrate species (Stanley, 2016; Erwin, 2006; Erwin et al., 2002). There has been a consensus that this biotic crisis is closely associated with the devastated palaeoenvironmental conditions triggered by the mass eruption of Siberian Basalt during the Latest Permian (Shen et al., 2011). Due to the long persistence of such stressful environmental conditions in the marine realm, the biotic recovery in the aftermath of the EPME lingered for some 5 Ma (Zhang F F et al., 2018; Tian et al., 2014; Song et al., 2012). It was not until the Early Middle Triassic that fully recovered shallow-marine ecosystems were re-established (Chen and Benton, 2012), which is typically represented by the Luoping Biota of the Middle Triassic Guanling Formation of south-

western China (Chen and Benton, 2012; Hu et al., 2011). Prolific vertebrate and invertebrate fossils from this biota revealed a highly developed shallow marine ecosystem after the EPME (Liu et al., 2014; Benton et al., 2013; Chen and Benton, 2012; Hu et al., 2011). In addition to the abundantly preserved body fossils, trace fossils were also widely distributed in the fossil-bearing units with high diversity and abundance (Luo et al., 2017a, b; Zhang et al., 2014; Benton et al., 2013). A comparison of trace fossil assemblages from the Luoping Biota and those from the Early Triassic suggests that trace makers might well have recovered immediately after the EPME (Luo et al., 2017b). Among the traces produced by decapod crustaceans (e.g. *Rhizocorallium*, *Spongeliomorpha*, and *Thalassinoides*) in Luoping, new trace fossil materials found recently revealed the occurrence of another branching trace with highly regular sinuosity, justifying a reasonable assignment to the crustacean burrow *Sinusichnus sinuosus*, which has not been discovered from South China until recently (Luo et al., 2017b). The aim of this paper is to describe the morphology of this new trace fossil in detail and discuss its palaeoecology. A summary of all reported occurrence of *Sinusichnus* has also been generated, with emphasis on the spatial and temporal distribution of this highly regularly branching trace.

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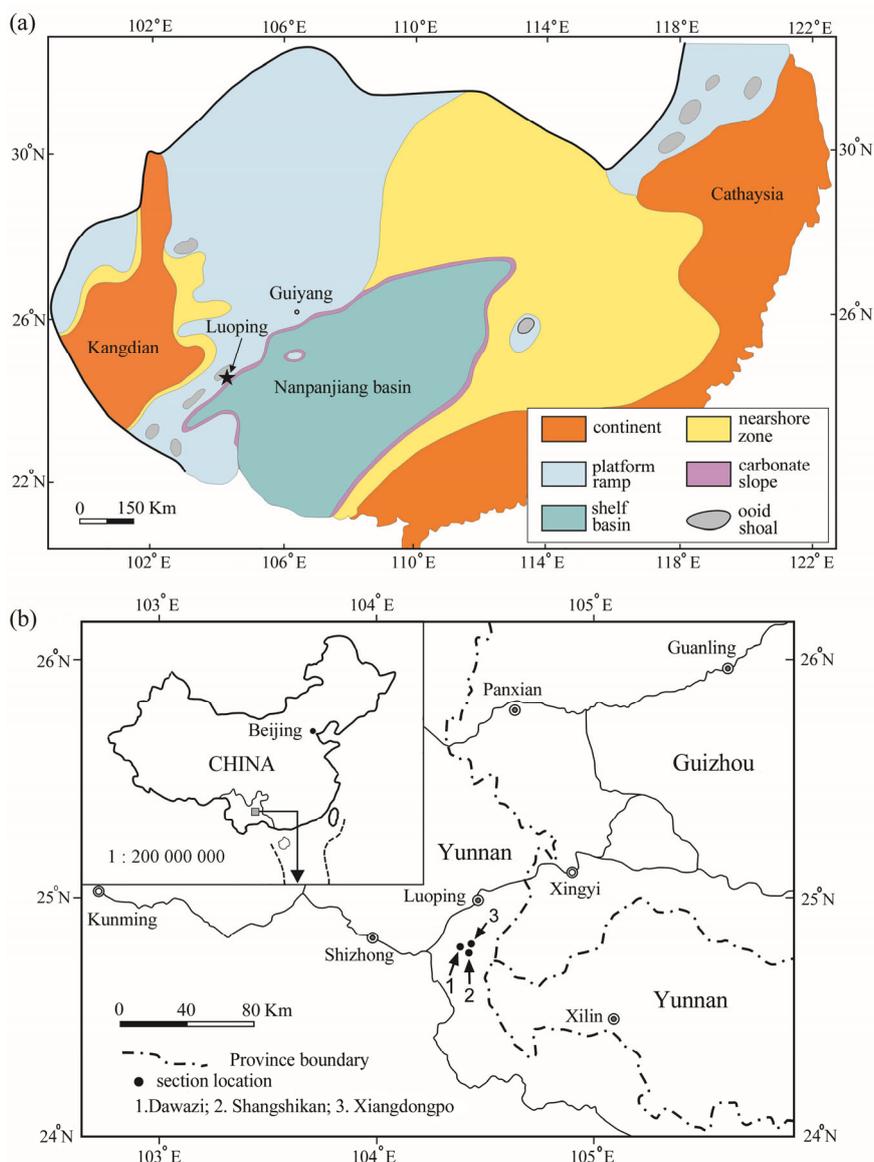
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### 1 GEOLOGICAL SETTING AND STRATIGRAPHY

During the early Middle Triassic, the Luoping area was located on the southwestern part of the Yangtze Block and was separated from the Nanpanjiang Basin by a shoal complex (Enos et al., 2006; Lehrmann et al., 2005; Feng et al., 1997; Fig. 1a). Several spatially and temporally separated intraplateau basins or depressions (e.g., the Panxian, Luoping, Xingyi, and Guanling) have been discovered from the Late Anisian, Late Ladinian and Carnian intervals, respectively, yielding exceptionally preserved reptile fossils (Benton et al., 2013; Hu et al., 2011). The preservation of those fossil Lagerstätten was aided by particular palaeoenvironmental conditions in these basins, such as restricted circulation, density stratification of the water column, and dysoxic to anoxic bottom waters during the burial of the faunas (Benton et al., 2013). In Luoping, abundant marine reptile faunas and invertebrate fossils (including trace fossils) were preserved in dark-colored, micritic limestones

representing the upper part of the Member II of the Guanling Formation (Hu et al., 2011). The Guanling Formation is subdivided into two members. Member I is composed of siliciclastic sediments, representing deposition in subtidal to intertidal environments (Hu et al., 1996). Member II consists of micritic limestones, bioclastic limestones, oncoidal limestones and dolomites in the lower and middle parts, and black muddy limestones, cherty limestones, and grey dolomite in the upper part. The Guanling Formation in the Luoping area, overall, records a deepening upward sequence (Zhang et al., 2008).

Three excavated sections, namely the Dawazi (or Daozi), Shangshikan, and Xiangdongpo revealed the well preservation of the Luoping Biota, which have been studied extensively in terms of the stratigraphy, sedimentology, palaeontology and taphonomy (e.g., Luo et al., 2017a, b, 2013; Feldmann et al., 2015, 2012; Liu et al., 2014; Schweitzer et al., 2014; Zhang et al., 2014; Benton et al., 2013; Huang et al., 2013; Wen et al.,



**Figure 1.** (a) Middle Triassic palaeogeographic map of South China showing the palaeogeographic setting of the Luoping area during that time (base map was modified from Feng et al. (1997)); (b) Location of the studied Xiangdongpo Section in the Luoping County, eastern Yunnan Province, SW China. Location of the other two excavated sections (Dawazi or Daozi, and Shangshikan) with abundant fossils of the Luoping Biota are also shown.

2012a, b; Chen and Benton, 2012; Hu et al., 2011; Zhang et al., 2009, 2008; Fig. 1b). A thickly bedded limestone unit among these three sections aided the correlation among the three sections. The trace fossil studied herein was discovered from the Xiangdongpo Section. Three stratigraphic units were defined in this section, which represent deposition in shallow subtidal to offshore environment (Luo et al., 2017b; Fig. 2).

Biostratigraphical study suggests that the Luoping Biota is of Anisian Age. This is supported by both conodont zonation and bivalve assemblages. The *Nicoraellakockeli* conodont

Zone has been found from the fossil bearing unit at the Dawazi, Shangshikan, and Xiangdongpo sections (Zhang et al., 2014; Bai et al., 2011a, b; Hu et al., 2011; Huang et al., 2009). This conodont zone includes elements such as *Nicoraellagermanicus*, *Nicoraellakockeli* and *Cratognathodus* sp., indicative of a Pelsonian Age of the Middle Anisian (Huang et al., 2009; Zhang et al., 2009). Meanwhile, the underlying Member I of the Guanling Formation yields bivalve assemblages of Anisian Age in South China (Zhang et al., 2008). Further, several clay beds discovered from Member I of the Guanling Formation

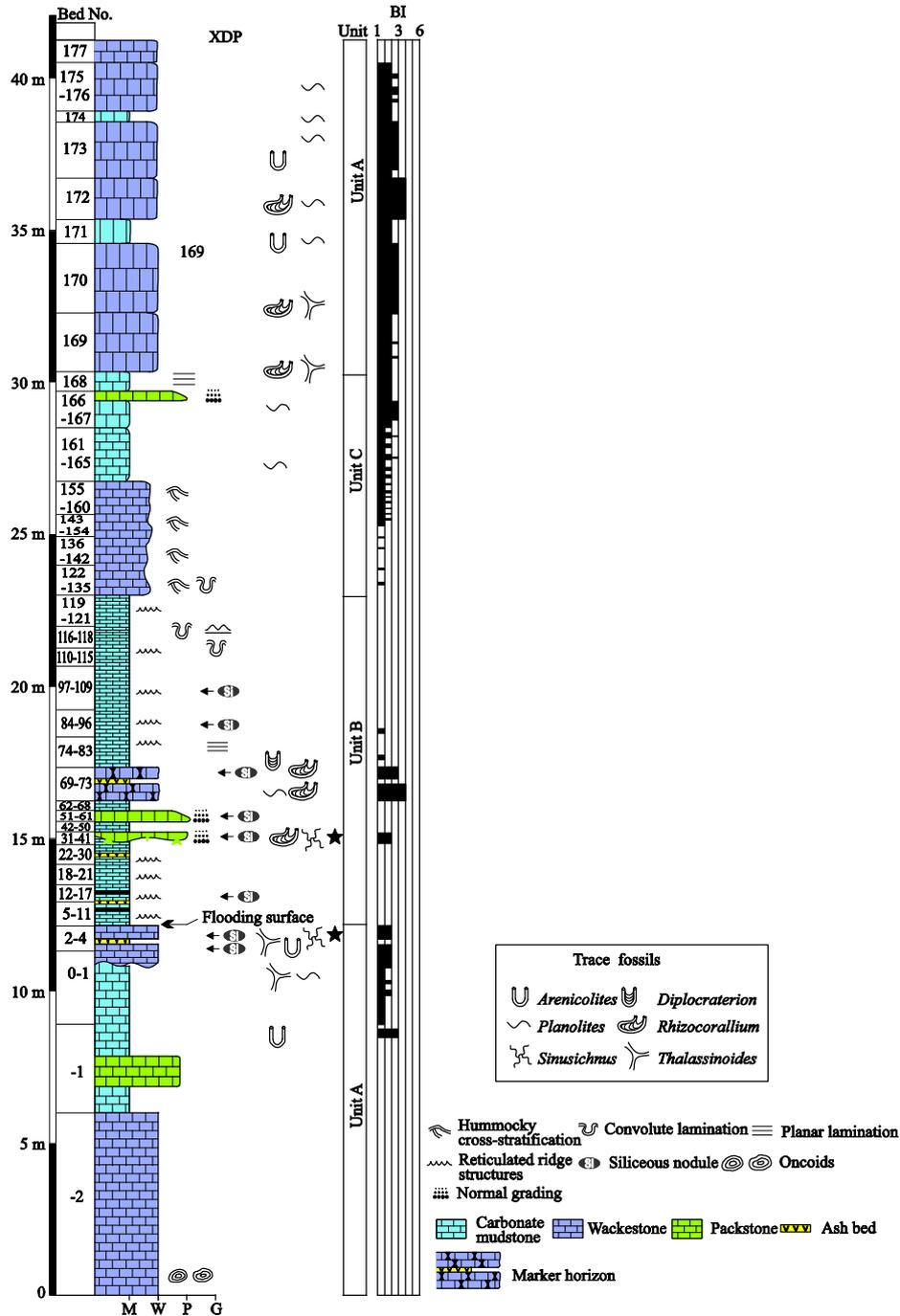
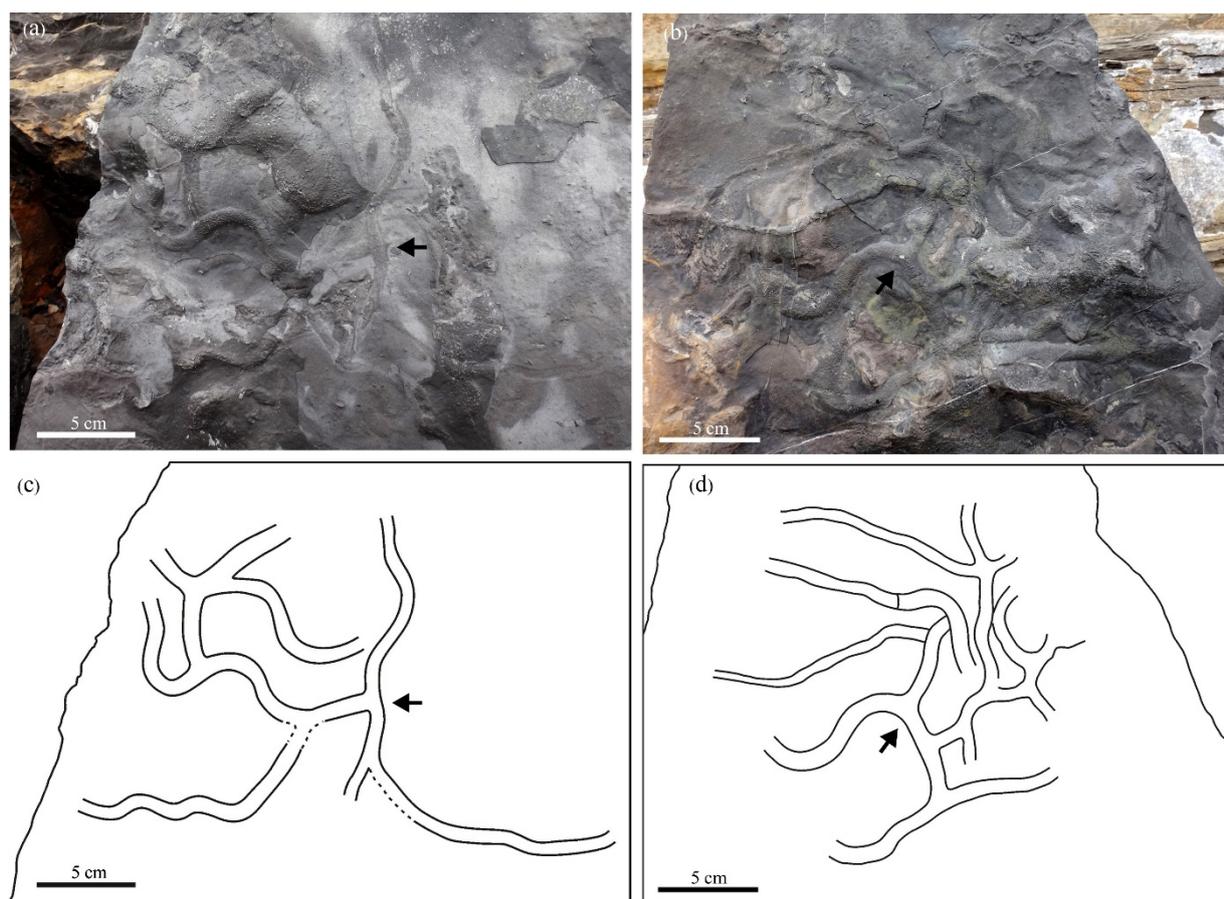


Figure 2. Stratigraphic columns showing the distribution of trace fossils and bioturbation levels of the Xiangdongpo (XDP) Section at Luoping, Yunnan Province (modified from Luo et al., 2017b). Stars indicate horizons with *Simulichnus* occurrences. The bioturbation scheme follows Reineck (1963) and Taylor and Goldring (1993).



**Figure 3.** (a)–(d), Sinuous burrow system of *Sinusichnus sinuosus* preserved as positive hyporelief on soles of wackestones at the Xiangdongpo Section, Luoping County. Note the T-shaped (arrow in (a)) and Y-shaped (arrow in (b)) branching of burrow system. (c) and (d) are the sketches of the burrow systems in (a) and (b) respectively.

were regarded as marker beds of the base of the Anisian in southwestern China (Zhang et al., 2009; Enoset et al., 2006).

## 2 DESCRIPTION OF TRACE FOSSIL MATERIALS

### 2.1 Morphology

*Sinusichnus* occurs at two horizons of the Xiangdongpo Section (Fig. 2). The first horizon shows scarce presence of *Sinusichnus* in association with large sized *Thalassinoides* (Fig. 2). This layer exhibits a nodular appearance on the field exposure. *Sinusichnus* burrows at this horizon are characterized by branched burrow systems, with burrow fillings having a darker color than the host rock. Burrow fillings of *Thalassinoides* are silicified, but fragments of shells and gastropods can be discerned. At the second horizon, *Sinusichnus* are present in the basal part of bioturbated wackestones with silicified nodules (Fig. 2). The well-preserved specimens at this horizon facilitate a detailed examination of trace fossil morphology. Specimens studied were preserved as positive or negative hyporeliefs and can be found at areas spanning several square decimeters. Horizontal burrows are unlined and show regular sinuous tunnels, while less regular to straight tunnels are also observed in the same branching system (Figs. 3a–3d). Burrow width is uniform in a single branching system. Y- or T-shaped branching pattern dominates (Figs. 3a–3b). On some occasions, two closely emplaced triple junctions form an H-like configuration (Fig. 4b).

Branching points with four branches are also observed occasionally (Fig. 4a). The burrowing system penetrates shallowly into the sediments at very shallow depths (no more than 1.5 cm). Burrow surfaces are smooth to knobby. In the vertical profile, retrusive spreiten are not observed. Associated large *Rhizocorallium* are characterized by their long, tongue-shaped burrows, with occasional primary successive branching. These features, combined the dumbbell-like cross-section view justify them as *R. commune* (Knaust, 2013; Rodríguez-Tovar and Pérez-Valera, 2008). U-shaped *R. commune* is more abundant than *Sinusichnus* on the bedding plane. The marginal tubes of *Rhizocorallium* range from 18 to 25 mm in diameter. *Sinusichnus* burrows were locally cross-cut by *Rhizocorallium* or vice versa. There is no distinct color difference between the burrow filling of *Sinusichnus*, *Rhizocorallium*, and their host rocks.

Several mathematical approaches have been applied to the study of geometry and regularity of *Sinusichnus* (e.g., Belaústegui et al., 2014; de Gibert et al., 1999). These approaches include the measurement of wavelength ( $\lambda$ ) and amplitude ( $A$ ) of the sinuous tunnels within *Sinusichnus* burrow system. The diameter ( $d$ ) is also measured (see Fig. 5a for details). Measurements of the former two were plotted in a bivariate diagram to investigate their correlations (Fig. 5b). Data of 18 measurements show a significant correlation between  $\lambda$  and  $A$  ( $R^2=0.7245$ ), which has been observed in other reported *Sinusichnus*



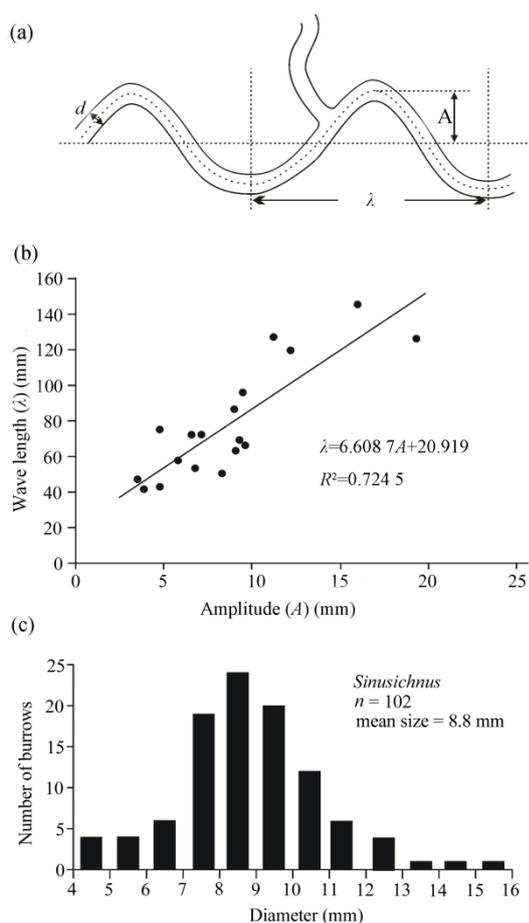
**Figure 4.** Field photos showing the association of *Sinusichnus* (Si) and *Rhizocorallium* (Rh) on soles of wackestones. (a) Tongue-shaped *Rhizocorallium* (Rh), and the small, sinuous and branching *Sinusichnus* (Si). Hammer for scale is 38 cm long. (b) Densely occurred *Sinusichnus* with *Rhizocorallium* at the bottom. Note the characteristic H-shaped morphology of *Sinusichnus*. Note the H-like configuration is composed of two closely emplaced triple junctions (white arrow).

(e.g., Belaústegui et al., 2014; de Gibert et al., 1999). The only difference is the value of slope. De Gibert et al. (1999) reported *S. sinuosus* materials from the Lower Pliocene strata in France and Spain, with a slope value at 5.19. Belaústegui et al. (2014) measured *Sinusichnus* specimens from six localities in Spain and revealed three slope values at around 1.1, 2.5 and 4.05. Diameters of *Sinusichnus* remain identical in each particular burrow system but varied slightly between different specimens. A total measurement of 102 specimens reveals a burrow width ranging from 4 to 16 mm, with an average value at 8.8 mm (Fig. 5c).

### 3 DISCUSSIONS

#### 3.1 Taxonomic Discussion

The newly discovered trace fossil materials are extremely similar to the ichnogenus *Sinusichnus* established by de Gibert (1996). This is revealed by its regular sinuous and branching morphology of horizontal tunnels. Except the type ichnospecies *S. sinuosus* established by de Gibert (1996), Kappel (2003) proposed another ichnospecies *S. priesti* based on trace fossil materials from the Upper Cretaceous strata in Germany. The only feature distinguishing *S. sinuosus* from *S. priesti* is the



**Figure 5.** (a) Schematic figure showing the measurement of the wavelength ( $\lambda$ ), the amplitude ( $A$ ) and diameters ( $d$ ) of sinuous tunnels within *Sinusichnus* specimens from the Middle Triassic Guanling Formation in Luoping, Yunnan Province; (b) correlation plot of wavelength ( $\lambda$ ) versus amplitude ( $A$ ) based on measurements of *Sinusichnus* specimens at Luoping; (c) histogram figure showing the size distribution of *Sinusichnus* burrow diameters.

presence of bioglyphs on the latter. No scratching marks or bioglyphs have been observed in the Luoping specimens, thus allowing a reasonable assignment to *S. sinuosus*. It is noted, however, that the specimens studied here are less regular in some part of the burrow system when compared with *Sinusichnus* from the Pliocene and Miocene strata (e.g., Belaústegui et al., 2014; Buatois et al., 2009). While the positive correlation between wavelength ( $\lambda$ ) and amplitude ( $A$ ) of the Luoping specimens has also been found in typical *S. sinuosus* (de Gibert et al., 1999), further supporting the studied trace fossils are *S. sinuosus*.

Several trace fossils are comparable to *Sinusichnus* in morphology and this has been discussed in detail in previous studies (e.g., Belaústegui et al., 2014; Buatois et al., 2009; de Gibert et al., 1999). These traces include members of the *Thalassinoides* group (e.g., *Thalassinoides*, *Ophiomorpha*; Seilacher, 2007) and the graphoglyptid trace *Protopaleodictyon*. In addition, the similarity between *Sinusichnus* and the horizontal meandering burrows such as *Cochlichnus* and *Cosmorhaphé* has also been mentioned (Belaústegui et al., 2014). The newly discovered specimens from the Middle Triassic Guanling Formation reveal several characteristics that distinguish it from all

the above-mentioned traces. Firstly, it shows the typical Y-shaped branching, which ruled out its possible assignment to the sinuous *Cochlichnus* or *Cosmorhaphé*. The latter two sinuous burrows are both smooth, unbranched grazing traces although the latter occasionally branched (Bordy et al., 2011; de Gibert et al., 1999; McCann and Pickerill, 1988). The regular sinuous morphology in the new specimen (Figs. 3a–3d, 4a–4b) was never present in *Thalassinoides*. Additionally, the absence of pelleted lining in branching tunnels in our specimens distinguishes it from *Ophiomorpha*.

It has also been mentioned that *Sinusichnus* resembles certain graphoglyptid traces, in particular, *Protopaleodictyon* and *Megagraption* (Belaústegui et al., 2014; de Gibert et al., 1999; de Gibert, 1996). However, the found specimen did not display short, blind apical elements or appendages at each undulation typical of *Protopaleodictyon incompositum* (Uchman, 1998). For the latter, the branching burrows of *Megagraption* are instead slightly curved or straight and the branching angles are nearly  $90^\circ$  (Häntzschel, 1975), which morphology is very different from the materials reported herein.

### 3.2 Palaeoecology of *Sinusichnus* from Luoping, Southwestern China

It has been noted that *Sinusichnus* presents morphological similarities with other branching burrows now clustered within the Ophiomorphid traces (e.g. *Thalassinoides*, *Ophiomorpha*, *Spongeliomorpha*, *Pholeus* and *Gyrolithes*, sensu, Seilacher, 2007). These Ophiomorphid traces are currently interpreted as dwelling or feeding traces (Ekdale, 1992), which suggests a similar ethological mode for *Sinusichnus* trace makers. On the other hand, de Gibert et al. (1999) pointed out that the highly regular sinuosity of branches within *Sinusichnus* burrow systems is very characteristic of agrichnial structures, indicating possible farming or trapping strategies. Further, de Gibert et al. (1999) discussed four proposed ethological modes of *Sinusichnus* and favored an ethological change during the ontogeny of the producer from juvenile to adult. For instance, in the Lower Pliocene BaixEbre Basin in Spain, the small and large *Sinusichnus* burrowing systems were preserved together (de Gibert et al., 1999; de Gibert, 1996).

The studied *S. sinuosus* specimens herein might suggest certain deposit-feeding behavior of the trace makers. This is supported by the evidence that the sinuous branching burrow systems are distributed in very shallow tiers. Further, it was found that *S. sinuosus* from the Guanling Formation in Luoping are in close association with *R. commune*. The cross-cutting relationships of these two ichnotaxa show that they most likely belong to the same tier. Thus, they might be produced by organisms sharing similar feeding habits and colonize at the same time. The deposit feeding behavior of trace maker producing *R. commune* has been recognized by several researchers (e.g., Knaust, 2013). The trace makers producing *S. sinuosus* and *R. commune* probably lived at shallow depths to feed on bacteria within sediments. The search for bacteria as food resources of *S. sinuosus* trace makers is further supported not only by the network shaped specimens, but the abundant preservation of reticulated ridge structures in strata (Luo et al., 2013). The latter represent the former presence of microbial mat, implying a

**Table 1** Summary of global occurrences of burrow *Sinuosichnus* from different stratigraphic units all over the world. Note some unpublished data are also included

Ichnospecies	Age	Stratigraphic unit	Locality	Associated ichnotaxa	Palaeoenvironment	References
<i>S. sinuosus</i>	Middle Pliocene	Not described	Var Basin, France	<i>Phycosiphon</i> , <i>Palaeophycus</i> , <i>Teichichnus</i> , <i>Nereites</i>	Submarine fan	de Gibert et al., 1999; de Gibert, 1996
<i>S. sinuosus</i>	Early Pliocene	Not described	BaixLlobregat Basin, Spain	<i>Phycosiphon</i> , <i>Scalartituba</i> , <i>Thalassinoides</i>	Marginal marine	de Gibert et al., 1999; de Gibert, 1996
<i>S. sinuosus</i>	Early Pliocene	Not described	BaixEbre Basin, Spain	<i>Teichichnus</i> , <i>Gyrochorte</i> , <i>Scalartituba</i> , <i>Scolicia</i>	Marginal marine	de Gibert et al., 1999; de Gibert, 1996
<i>S. sinuosus</i>	Late Miocene	Guadaira Formation	Guadalquivir Basin, Spain	<i>Thalassinoides</i> , cf. <i>Bichordites</i>	Fan delta front to slope	Belaustegui et al., 2014
<i>S. sinuosus</i>	Late Miocene	Not described	Dos Hermanas, Spain	<i>Thalassinoides</i> , <i>Teichichnus</i> , cf. <i>Bichordites</i> , <i>Planolites</i>	Shallow marine nearshore	Belaustegui et al., 2014
<i>S. sinuosus</i>	Middle Miocene	Tarragona sequence	El Camp de Tarragona Basin, Spain	No associated traces observed	Shallow marine	Belaustegui et al., 2014
<i>S. sinuosus</i>	Middle Miocene	Socorro Formation	Western Venezuela	<i>Diplocraterion</i> , <i>Ophiomorpha</i>	Prodelta and delta front	Buatois et al., 2009
<i>S. sinuosus</i>	Late Oligocene– Early Miocene	Nartcuál Formation	Eastern Venezuela	<i>Thalassinoides</i> , <i>Didymaulichnus</i> , <i>Teichichnus</i> , <i>Taenidium</i>	Deep-water environment	Buatois et al., 2009
<i>S. sinuosus</i>	Eocene	Vilomara sequence	Ebro Basin, Spain	No associated traces observed	Fan delta front to slope	Belaustegui et al., 2014
<i>S. sinuosus</i>	Late Cretaceous	Hidden Lake Formation	James Ross Island, Antarctica	<i>Thalassinoides</i> , <i>Planolites</i>	Fan delta	Buatois et al., 2009
<i>S. priesti</i>	Late Cretaceous	–	Münster Basin, Germany	–	Not mentioned	Kappel, 2003
<i>S. seilacheri</i>	Middle Triassic	Kersch Member	Germany	<i>Rhizocoralium</i> , <i>Spongeliomorpha</i> , <i>Planolites</i> , <i>Palaeophycus</i>	Shallow marine	Knaust, 2016
<i>S. sinuosus</i>	Middle Triassic	Guangling Formation	Luoping, Yunnan, China	<i>Rhizocoralium</i> , <i>Thalassinoides</i>	Shallow to deep subtidal, offshore	This paper
<i>S. isp.</i>	Early Triassic	Jialingjiang Formation	Sichuan, China	–	Shallow marine	Unpublished data; Zhang L J et al., 2018
<i>S. isp.</i>	Late Devonian	Wutong Formation	Wuhan, China	–	Shallow marine	Unpublished data

prolific distribution of microbes in sediments serving as food resources for the deposit-feeding organisms producing *S. sinuosus* and other deposit feeders.

Several animals have been proposed as the potential trace maker of *Sinusichnus*, which include decapod crustaceans and isopods (Knaust, 2016; Belaústegui et al., 2014; Buatois et al., 2009; de Gibert, 1996). *S. sinuosus* from Luoping might also be produced by decapod crustaceans. In fact, the body fossil record suggested that decapod crustaceans were abundantly preserved in the Luoping Biota, which includes a newly established family and several new species (e.g., Feldmann et al., 2017, 2015, 2012; Huang et al., 2013).

### 3.3 Temporal and Spatial Distribution of *Sinusichnus*

Since de Gibert (1996) established the ichnospecies *Sinusichnus sinuosus* based on Lower–Middle Pliocene specimens from Spain and France, more and more similar structures assigned to *Sinusichnus* have been reported from different localities and stratigraphical ranges (Belaústegui et al., 2014; Buatois et al., 2009; Kappel, 2003). Table 1 summarizes discovered trace fossil *Sinusichnus* from all over the world. These data also include some unpublished data. The oldest known occurrence of reported ichnotaxa could be traced back to the Middle Triassic (Knaust et al., 2016). The study on the ichnology of the Middle Triassic Udelfangen Formation established a new ichnospecies *Sinusichnus seilacheri*, which was probably produced by isopod crustaceans (Knaust et al., 2016; Table 1). Other reported occurrence includes *S. sinuosus* from the Upper Cretaceous Hidden Lake Formation, and several more examples from Miocene and Pliocene (Belaústegui et al., 2014; Buatois et al., 2009; de Gibert et al., 1999; de Gibert, 1996; Table 1). Our reported trace fossil materials from the Middle Triassic strata at Luoping in South China represent the first report from South China, and further supports the long stratigraphic range of *Sinusichnus sinuosus* starting from the Anisian. In addition, recent studies suggest that *Sinusichnus* might have an even longer stratigraphic range dating back to the Late Devonian (Table 1, unpublished data). These occurrences include one occurrence from the Late Devonian Wutong Formation in Wuhan, China, and another one from the Lower Triassic Jialingjiang Formation in Sichuan, China. Whether these older examples are produced by decapod crustaceans or isopod crustaceans remains to be answered.

## 4 CONCLUSION

New Middle Triassic trace fossils were found from the Guanling Formation in Luoping, Yunnan Province. The trace fossil materials were associated with the Luoping Biota assigned to the Anisian in age. Various morphological features suggest that these traces can be tentatively assigned to the decapod trace *Sinusichnus sinuosus*. Thus, these new trace fossil materials represent the first reported *Sinusichnus* from South China, strengthening its early appearance since Anisian. However, the global record of *Sinusichnus* might suggest that these burrows could have an older history back to the Late Devonian.

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## REFERENCES CITED

- Bai, J. K., Yin, F. G., Zhang, Q. Y., 2011a. Microfacies and Enrichment Pattern of Fossils in the Fossiliferous Beds of Luoping Biota, Yunnan Province. *Geology in China*, 38: 393–402 (in Chinese with English Abstract)
- Bai, J. K., Zhang, Q. Y., Huang, J. Y., et al., 2011b. Middle Triassic Sequence Stratigraphy and Sedimentary Facies Analysis at the Shangshikan Section of the Luoping County, Yunnan Province. *Journal of Stratigraphy*, 35: 278–286 (in Chinese with English Abstract)
- Belaústegui, Z., de Gibert, J. M., Lopez-Blanco, M., et al., 2014. Recurrent Constructional Pattern of the Crustacean Burrow *Sinusichnus Sinuosus* from the Paleogene and Neogene of Spain. *Acta Palaeontologica Polonica*, 59: 461–474. <https://doi.org/10.4202/app.2012.0092>
- Benton, M. J., Zhang, Q. Y., Hu, S. X., et al., 2013. Exceptional Vertebrate Biotas from the Triassic of China, and the Expansion of Marine Ecosystems after the Permo-Triassic Mass Extinction. *Earth-Science Reviews*, 125: 199–243. <https://doi.org/10.1016/j.earscirev.2013.05.014>
- Bordy, E. M., Linkermann, S., Prevec, R., 2011. Palaeoecological Aspects of Some Invertebrate Trace Fossils from the Mid- to Upper Permian Middleton Formation (Adelaide Subgroup, Beaufort Group, Karoo Supergroup), Eastern Cape, South Africa. *Journal of African Earth Sciences*, 61(3): 238–244. <https://doi.org/10.1016/j.jafrearsci.2011.06.002>
- Buatois, L. A., Macsotay, O., Quiroz, L. I., 2009. *Sinusichnus*, a Trace Fossil from Antarctica and Venezuela: Expanding the Dataset of Crustacean Burrows. *Lethaia*, 42(4): 511–518. <https://doi.org/10.1111/j.1502-3931.2009.00156.x>
- Chen, Z.-Q., Benton, M. J., 2012. The Timing and Pattern of Biotic Recovery Following the End-Permian Mass Extinction. *Nature Geoscience*, 5(6): 375–383. <https://doi.org/10.1038/ngeo1475>
- De Gibert, J. M., 1996. A New Decapod Burrow System from the NW Mediterranean Pliocene. *Revista Española de Paleontología*, 11: 251–254.
- De Gibert, J. M., Jeong, K., Martinell, J., 1999. Ethologic and Ontogenic Significance of the Pliocene Trace Fossil *Sinusichnus Sinuosus* from the Northwestern Mediterranean. *Lethaia*, 32(1): 31–40. <https://doi.org/10.1111/j.1502-3931.1999.tb00578.x>
- Ekdale, A. A., 1992. Muckraking and Mudslinging: The Joys of Deposit-Feeding. In: Maples, C. G., West, R. R., eds., Trace Fossils. Short Courses in Paleontology. The Paleontological Society, Knoxville, Tenn. 5: 145–171
- Enos, P., Lehrmann, D. J., Wei, J. Y., et al., 2006. Triassic Evolution of the Yangtze Platform in Guizhou Province, People’s Republic of China. *Geological Society of America, Special Paper*, 417: 1–105.
- Erwin, D. H., 2006. Extinction: How Life on Earth Nearly Ended 250 Mil-

- lion Years Ago. Princeton University Press, Princeton. 1–296
- Erwin, D. H., Bowring, S. A., Jin, Y. G., 2002. End-Permian Mass Extinction: A Review. In: Koeberl, C., MacLeod, K. G., eds., *Catastrophic Events and Mass Extinctions: Impacts and Beyond. Geological Society of America, Special Paper*, 256: 353–383
- Feldmann, R. M., Schweitzer, C. E., Hu, S. X., et al., 2012. Macrurous Decapoda from the Luoping Biota (Middle Triassic) of China. *Journal of Paleontology*, 86(3): 425–441. <https://doi.org/10.1666/11-113.1>
- Feldmann, R. M., Schweitzer, C. E., Hu, S. X., et al., 2015. Spatial Distribution of Crustacea and Associated Organisms in the Luoping Biota (Anisian, Middle Triassic), Yunnan Province, China: Evidence of Periodic Mass Kills. *Journal of Paleontology*, 89(6): 1022–1037. <https://doi.org/10.1017/jpa.2015.60>
- Feldmann, R. M., Schweitzer, C. E., Hu, S. X., et al., 2017. A New Middle Triassic (Anisian) Cyclidan Crustacean from the Luoping Biota, Yunnan Province, China: Morphologic and Phylogenetic Insights. *Journal of Crustacean Biology*, 37(4): 406–412. <https://doi.org/10.13039/501100004613>
- Feng, Z. Z., Bao, Z. D., Li, S. W., 1997. Lithofacies Paleogeography of Early and Middle Triassic of South China. Petroleum Industry Press, Beijing. 1–222 (in Chinese)
- Häntzschel, W., 1975. Trace Fossil and Problematica. In: Teichert, C., ed., *Treatise on Invertebrate Paleontology, Part W, Miscellanea, Supplement I. Geological Society of America and University of Kansas Press, Kansas*. 1–269
- Hu, S. L., Li, Y. J., Dai, M., et al., 1996. The Laser Mass-Spectrometer  $^{40}\text{Ar}$ - $^{49}\text{Ar}$  Age of Green Pisolites of Guizhou Province. *Acta Petrologica Sinica*, 12: 409–415 (in Chinese)
- Hu, S. X., Zhang, Q. Y., Chen, Z. Q., et al., 2011. The Luoping Biota: Exceptional Preservation, and New Evidence on the Triassic Recovery from End-Permian Mass Extinction. *Proceedings of the Royal Society B: Biological Sciences*, 278(1716): 2274–2282. <https://doi.org/10.1098/rspb.2010.2235>
- Huang, J. Y., Feldmann, R. M., Schweitzer, C. E., et al., 2013. A New Shrimp (Decapoda, Dendrobranchiata, Penaeoidea) from the Middle Triassic of Yunnan, Southwest China. *Journal of Paleontology*, 87(4): 603–611. <https://doi.org/10.1666/13-024>
- Huang, J. Y., Zhang, K. X., Zhang, Q. Y., et al., 2009. Conodonts Stratigraphy and Sedimentary Environment of the Middle Triassic at Daozi Section of Luoping County, Yunnan Province, South China. *Acta Micropalaeontologica Sinica*, 26: 211–224 (in Chinese with English Abstract)
- Kappel, O., 2003. Ichnofossilien im Campanium des SE-Münsterlan-des. *Münster Fortschritte der Geologie und paläontologie*, 96: 1–195
- Knaust, D., 2013. The Ichnogenus Rhizocorallium: Classification, Trace Makers, Palaeoenvironments and Evolution. *Earth-Science Reviews*, 126: 1–47. <https://doi.org/10.1016/j.earscirev.2013.04.007>
- Knaust, D., Uchman, A., Hagdorn, H., 2016. The Probable Isopod Burrow *Sinusichnus* *Seilacheriisp.* N. from the Middle Triassic of Germany: An Example of Behavioral Convergence. *Ichnos*, 23(1/2): 138–146. <https://doi.org/10.1080/10420940.2015.1132211>
- Lehrmann, D. J., Enos, P., Payne, J. L., et al., 2005. Permian and Triassic Depositional History of the Yangtze Platform and Great Bank of Guizhou in the Nanpanjiang Basin of Guizhou and Guangxi, South China. *Albertiana*, 33: 149–168
- Liu, J., Hu, S. X., Rieppel, O., et al., 2014. A Gigantic Nothosaur (Reptilia: Sauropterygia) from the Middle Triassic of SW China and Its Implication for the Triassic Biotic Recovery. *Scientific Reports*, 4(1): e7142. <https://doi.org/10.1038/srep07142>
- Luo, M., Chen, Z.-Q., Hu, S., et al., 2013. Carbonate Reticulated Ridge Structures from the Lower Middle Triassic of the Luoping Area, Yunnan, Southwestern China: Geobiologic Features and Implications for Exceptional Preservation of the Luoping Biota. *Palaios*, 28(8): 541–551. <https://doi.org/10.2110/palo.2012.p12-122r>
- Luo, M., Hu, S. X., Benton, M. J., et al., 2017a. Taphonomy and Palaeobiology of Early Middle Triassic Coprolites from the Luoping Biota, Southwest China: Implications for Reconstruction of Fossil Food Webs. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 474: 232–246. <https://doi.org/10.1016/j.palaeo.2016.06.001>
- Luo, M., Shi, G. R., Hu, S. X., et al., 2017b. Early Middle Triassic Trace Fossils from the Luoping Biota, Southwestern China: Evidence of Recovery from Mass Extinction. *Palaeogeography, Palaeoclimatology, Palaeoecology*. <https://doi.org/10.1016/j.palaeo.2017.11.028>
- McCann, T., Pickerill, R. K., 1988. Flysch Trace Fossils from the Cretaceous Kodiak Formation of Alaska. *Journal of Paleontology*, 62(3): 330–348. <https://doi.org/10.1017/s0022336000059138>
- Reineck, H. E., 1963. Sedimentgefüge im Bereich der Südliche Nordsee. *Abh. Senckenb. Naturforsch. Ges.*, 505: 1–138
- Rodríguez-Tovar, Pérez-Valera, 2008. Trace Fossil Rhizocorallium from the Middle Triassic of the Betic Cordillera, Southern Spain: Characterization and Environmental Implications. *Palaios*, 23(2): 78–86. <https://doi.org/10.2110/palo.2007.p07-007r>
- Schweitzer, C. E., Feldmann, R. M., Hu, S. X., et al., 2014. Penaeoid Decapoda (Dendrobranchiata) from the Luoping Biota (Middle Triassic) of China: Systematics and Taphonomic Framework. *Journal of Paleontology*, 88(3): 457–474. <https://doi.org/10.1666/13-039>
- Seilacher, A., 2007. Trace Fossil Analysis. Springer-Verlag, Berlin, Germany. 1–226
- Shen, S. Z., Crowley, J. L., Wang, Y., et al., 2011. Calibrating the End-Permian Mass Extinction. *Science*, 334: 1367–1372. <https://doi.org/10.1126/science.1213454>
- Song, H. J., Wignall, P. B., Tong, J. N., et al., 2012. Geochemical Evidence from Bio-Apatite for Multiple Oceanic Anoxic Events during Permian-Triassic Transition and the Link with End-Permian Extinction and Recovery. *Earth and Planetary Science Letters*, 353/354: 12–21. <https://doi.org/10.1016/j.epsl.2012.07.005>
- Stanley, S. M., 2016. Estimates of the Magnitudes of Major Marine Mass Extinctions in Earth History. *Proceedings of the National Academy of Sciences*, 113(42): E6325–E6334. <https://doi.org/10.1073/pnas.1613094113>
- Taylor, A. M., Goldring, R., 1993. Description and Analysis of Bioturbation and Ichnofabric. *Journal of the Geological Society*, 150(1): 141–148. <https://doi.org/10.1144/gsjgs.150.1.0141>
- Tian, L., Tong, J. N., Algeo, T. J., et al., 2014. Reconstruction of Early Triassic Ocean Redox Conditions Based on Framboidal Pyrite from the Nanpanjiang Basin, South China. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 412: 68–79. <https://doi.org/10.13039/100000001>
- Uchman, A., 1998. Taxonomy and Ethology of Flysch Trace Fossils: Revision of the Marian Książkiewicz Collection and Studies of Complementary Material. *Annales Societatis Geologorum Poloniae*, 68: 105–218
- Wen, W., Zhang, Q. Y., Hu, S. X., et al., 2012a. Coelacanths from the Middle Triassic Luoping Biota, Yunnan, South China, with the Earliest Evidence of Ovoviviparity. *Acta Palaeontologica Polonica*, 58(1): 175–193. <https://doi.org/10.4202/app.2011.0066>
- Wen, W., Zhang, Q. Y., Hu, S. X., et al., 2012b. A New Basal Actinoptery-

- gian Fish from the Anisian (Middle Triassic) of Luoping, Yunnan Province, Southwest China. *Acta Palaeontologica Polonica*, 57(1): 149–160. <https://doi.org/10.4202/app.2010.0089>
- Zhang, F. F., Romaniello, S. J., Algeo, T. J., et al., 2018. Multiple Episodes of Extensive Marine Anoxia Linked to Global Warming and Continental Weathering Following the Latest Permian Mass Extinction. *Science Advances*, 4(4): e1602921. <https://doi.org/10.1126/sciadv.1602921>
- Zhang, L. J., Buatois, L. A., Mángano, M. G., et al., 2018. Early Triassic Trace Fossils from South China Marginal-Marine Settings: Implication for Biotic Recovery Following the End-Permian Mass Extinction. *G. S. A. Bulletin*. Submitted
- Zhang, Q. Y., Wen, W., Hu, S. X., et al., 2014. Nothosaur Foraging Tracks from the Middle Triassic of Southwestern China. *Nature Communications*, 5(1): 3973e. <https://doi.org/10.1038/ncomms4973>
- Zhang, Q. Y., Zhou, C. Y., Lu, T., et al., 2008. Discovery and Significance of the Middle Triassic Anisian Biota. *Geology Review*, 54:523–527 (in Chinese with English Abstract)
- Zhang, Q. Y., Zhou, C. Y., Lu, T., et al., 2009. A Conodont-Based Middle Triassic Age Assignment for the Luoping Biota of Yunnan, China. *Science in China Series D: Earth Sciences*, 52(10): 1673–1678. <https://doi.org/10.1007/s11430-009-0114-z>