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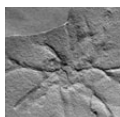
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A diverse ichnofauna from the Cambrian Stage 4 Wulongqing Formation near Kunming (Yunnan Province, South China)

BERND WEBER, SHIXUE HU, MICHAEL STEINER & FANGCHEN ZHAO



A diverse and well-preserved ichnofauna from the Cambrian (Stage 4: Canglangpuan) Wulongqing Formation (Kunming area, Yunnan Province) is reported here for the first time in detail. Early Cambrian ichnoassemblages are common and have been described from many localities worldwide; however, they are rarely associated with a significant body fossil record that enables both a well-defined biostratigraphic calibration of the related ichnofauna and a direct comparison with the possibly related trace originators, as is the case with the Wulongqing Formation. The ichnofauna consists of various simple bedding-plane-parallel and sub-horizontal traces of *Planolites*-type as well as of branching, treptichnid-type burrows, *Phycodes*- and *Teichichnus*-type “spreiten”, star-shaped trace structures associated with short, central and vertical burrow structures, and arthropod traces of the *Diplichnites*-type. Large, star-shaped trace fossils belonging to a new ichnotaxon (*Guanshanichnus glockerichnoides* igen. et isp. nov.) are reported from the Yangtze Platform for the first time and represent the hitherto oldest (equivalent to Botoman regional stage of Siberia) known evidence of this trace type and further global-scale evidence of this trace type from a shallow-water environment. Arthropod traces appear in less abundance in the middle part of the formation. Several arthropod traces display a significant, V-shaped, paired arrangement of scratch marks on the bedding plane; their morphology and size correspond with co-occurring trilobite taxa from the Wulongqing Formation, probably indicating the preservation of trilobite resting traces. The Shitangshan trace fauna as part of the Guanshan Fauna provides new insights into the palaeoecology and taphonomy of Chengjiang-type fossil *Lagerstätten*. • Key words: ichnofossils, Wulongqing Formation, Cambrian Stage 4, Guanshan, Yunnan Province.

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The south-western part of the Yangtze Platform yields the famous Chengjiang fossil *Lagerstätte* which, in addition to diverse skeletal fossils, provides an extraordinary record of soft-body-preserved (Burgess Shale-type) invertebrate fauna (for an overview see *e.g.* Hou *et al.* 2004, Gabbot *et al.* 2004, Luo *et al.* 1999). The Chengjiang Biota is one of the oldest Burgess Shale-type biotas known to date and therefore is crucial in the discussion on the early Cambrian metazoan radiation event (“Cambrian Explosion”). Nevertheless, because of their specific origin the Chengjiang- and Burgess Shale-type fossil *Lagerstätten* contain no – or very rarely a poorly preserved – trace fossil record.

The Guanshan Biota of the Wulongqing Formation (Cambrian Stage 4: upper Canglangpuan regional stage; probably equivalent to the Botoman Stage of Siberia) represents a somewhat younger evolutionary stage and differs in the ecological setting from the older Chengjiang-type *Lagerstätten* on the Yangtze Platform (Qiongzhusian: Yuanshan Member) by its shallower depositional environment incorporating more abundant siltstone and sandstone interbeds within the mudstone sequences. Such interstratified silt beds provide ideal conditions for the preservation of trace fossils. In contrast to the Chengjiang *Lagerstätte*, trace fossils are very abundant in the Wulongqing Formation. Nevertheless, they have never been systematically investigated so far.



Figure 1. The Shitangshan quarry near the village Guangwei, north of Kunming (Yunnan Province) in autumn 2009.

Age and geological setting of the Wulongqing Formation

The Wulongqing Formation is well exposed at Gaoloufang village and in the Shitangshan quarry in the Guanshan area (Fig. 1), close to the village of Guangwei, near Kunming. Outcrops of the Wulongqing Formation are widespread in the Yunnan Province (Kunming-Wuding, Huize, and Malong-Yiliang areas). The localities at Gangtoucun and Gaoloufang near Kunming City are important outcrops, as well as the Sapushan and the Wushishan localities in Wuding County (Fig. 2).

In the Shitangshan quarry, the Wulongqing Formation is about 60 m thick and overlies the fine-grained sandstones of the Hongjingshao Formation (Fig. 2). The contact to the underlying unfossiliferous Hongjingshao Formation is characterized by a several-decimetres-thick basal conglomerate of the lowermost part of the Wulongqing Formation, probably indicating a regional transgression event in SW China (Fig. 3A). The top of the Wulongqing Formation is not preserved in the Shitangshan Quarry. The Wulongqing Formation consists of a monotonous sequence of mudstones with siltstone intercalations (Fig. 2), the lower part of which is mainly composed of mudstone with few thin-bedded silt-sandstone layers. The micaceous siltstone and fine-grained sandstone

beds become more abundant towards the top of the Wulongqing Formation. The mudstone beds display erosive bases and an upward fining. Multiple-graded silt-mud couplets are frequent within the mudstone beds. Sole marks, trace fossils and microbial mat structures (Fig. 3C) are common at the base of the siltstone beds. There are several similarities to lower and middle Cambrian sequences in Baltica: as mentioned in Hu *et al.* (2010; Weber, pers. observation), the sedimentary regime and lithology (as well as several components of the Wulongqing ichnoassemblage) resemble the (middle) Cambrian Åleklinta section of Öland in SE Sweden (*e.g.*, Martinsson 1965, Porada *et al.* 2008).

The age of the Wulongqing Formation is biostratigraphically well constrained by trilobite zonation. The Wulongqing Formation is characterized by the *Palaeolenus* Zone at the base and the *Megapalaeolenus* Zone (= upper Canglangpuan, Stage 4 of the South Chinese regional biostratigraphical zonation) at the top (Fig. 2). According to the South Chinese regional scale (*e.g.* Hu *et al.* 2010), the sequence represents a stratigraphic equivalent to the Balang Formation (Guizhou Province) and the Shipai Formation of the Three Gorges area of Hubei Province, which both contain a similar macrofauna (Luo *et al.* 1994, Pen *et al.* 2005, Zhang & Hua 2005). According to the global Cambrian (ISC) zonation (the Guanshan Fauna belongs to

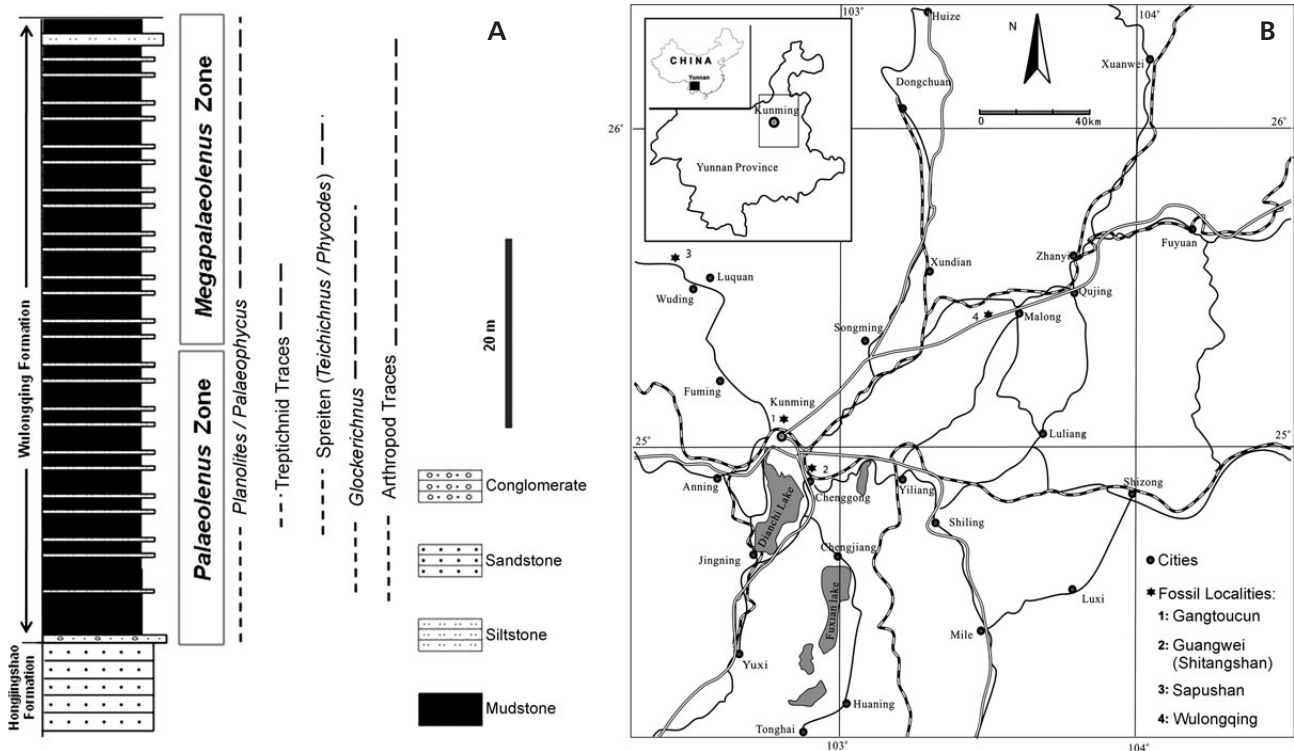


Figure 2. A – the Shitangshan section (Wulongqing Formation) showing approximate stratigraphic distribution of characteristic groups of trilobites (trilobite zones) and trace fossils. • B – a sketch map of the Kunming area showing the most important outcrops of the Wulongqing Formation (Shitangshan quarry is the number 2 near the village Guangwei).

Stage 4, Series II (*ca* 515–510 My). The Wulongqing Fauna can be correlated with the Botoman Stage of Siberia (Sinsk fossil *Lagerstätte*: Ivantsov *et al.* 2005, Ponomarenko 2005) and the Emu Bay fossil *Lagerstätte* in Australia (*e.g.*, Paterson & Brock 2007). A more detailed description of the geological setting, biostratigraphic correlation, taphonomy and macrofossil content of the Wulongqing Formation was published by Hu *et al.* (2010).

Ichnofauna

Luo *et al.* (2008) and Hu *et al.* (2010) briefly reported on the ichnofauna from the Wulongqing Formation. A tentative ichnotaxonomy was given in a checklist of ichnotaxa in Hu *et al.* (2010; partly based on preliminary information from field studies by B.W., personal communication); however, after a careful and more detailed study of the ichnofauna for the present paper, the ichnotaxonomy of the trace assemblage had to be partly revised and in some cases also changed. The Guanshan ichnoassemblage consists of seven groups of trace fossils:

- (i) Simple, horizontally and sub-horizontally inclined or dipping, flat-U-shaped burrows of the *Planolites-Palaeophycus*-type; beds with partly intense bioturbation,
- (ii) *Gordia*- and *Olenichnus*-type traces,

- (iii) Branched *Treptichnus*- and *Thalassionides*-type traces as well as complex *Phycodes*- and *Teichichnus*-type spreiten,
- (iv) Short vertical traces,
- (v) Short, vertical, funnel-shaped burrows, partly associated with star-shaped horizontal structures of *Glockerichnus*-like shape,
- (vi) Arthropod traces,
- (vii) Faecal pellets (coprolites).

(i) Simple, bedding-parallel to shallow-dipping burrows

Mud- and siltstone horizons with intense bioturbation are very common throughout the Wulongqing Formation (Fig. 3B). Along with several non-specific horizontal to sub-horizontal burrows, the trace spectrum contains typical *Planolites*- and *Palaeophycus*-type traces:

Planolites Nicholson, 1873

Figure 3B, D

Description and discussion. – Short, straight or curved, horizontally to somewhat obliquely dipping burrows are

common in the Wulongqing Formation and are attributed to the ichnogenus *Planolites* (Fig. 3D), partly forming sediment beds with intense bioturbation.

Planolites-type traces are mostly unbranched and can vary in shape and width between 3 and 10 mm. The burrows mostly possess smooth walls or may rarely show irregular ornamentation. The burrows are filled with sediment that (in contrast to the related ichnogenus *Palaeophycus*, see below) clearly differs from the surrounding rock matrix. This phenomenon can be explained by the activity of a sediment (deposit) feeder (e.g., Pemberton & Frey 1982, Fillion & Pickerill 1990, Kappel 2002). The characteristic structure of the *Planolites*-type traces was produced by active back-filling of faecal particles or pellets after passing the alimentary canal (“Stopftunnel”) and was caused by an unknown infaunal trace maker. Various ichnospecies have been described on the basis of typical ranges of burrow diameters and surface sculptures (bulges, granulations), e.g., *Planolites beverleyensis* Billings, 1862 (type ichnospecies), maximum burrow diameter about 5–10 mm, and the mostly smaller and shorter *Planolites montanus* Richter, 1937, maximum burrow diameter about 3–7 mm. *Planolites*-type traces are very common during the entire Phanerozoic era and appear already in late Precambrian shallow-water deposits (Häntzschel 1975). Related structures are also known from recent abyssal sediments (e.g., Ekdale *et al.* 1984).

The majority of the *Planolites*-type traces in the Shitangshan ichno-assemblage belong to *Planolites* aff. *beverleyensis*. *Planolites*- and *Palaeophycus*-type traces (compare below) mostly occur in large numbers in certain beds. At least some of them are therefore to be interpreted (after Bromley 1996) as combined domichnia and/or pascichnia of opportunistic deposit feeders consuming nutrient-rich event beds in storm deposits. *Planolites* (and probably also *Palaeophycus*) are therefore involved in the formation of intensively bioturbated horizons of the Shitangshan section as demonstrated in Fig. 3B and D.

***Palaeophycus* Hall, 1847**

Figure 3E

Description and discussion. – Straight or slightly curving bedding-parallel, rarely inclined traces with a smooth (or

irregular, longitudinally sculptured) surface, mostly larger than the *Planolites*-type traces, are also common in the Wulongqing Formation and are here attributed to the ichnogenus *Palaeophycus*.

According to Pemberton & Frey (1982), the ichnogenus *Palaeophycus* can be distinguished from *Planolites* by lined trace walls as well as by an open and secondarily filled domichnial architecture. In contrast to *Planolites*, the sediment fillings of *Palaeophycus*-type traces usually do not differ from the surrounding sediment matrix.

Palaeophycus is mostly unbranched or rarely branched. As with *Planolites*, however, pseudo-branching is often caused by the crossing of different burrow generations. In contrast to the typical network-shaped branching structures of *Thalassinoides* (cf. below), true branching structures in *Palaeophycus*-type traces are always irregular and never show bulges in the branching areas.

Kappel (2002, see also Pemberton & Frey 1982) has emphasized that, along with these ichnotaxonomic dissimilarities, *Planolites* and *Palaeophycus* also display palaeo-ethological differences as *Planolites* represents the feeding burrow of an infaunal and mobile suspension feeder, whereas *Palaeophycus* is an open and passively filled domichnion of an (epifaunal) suspension feeder or a predator.

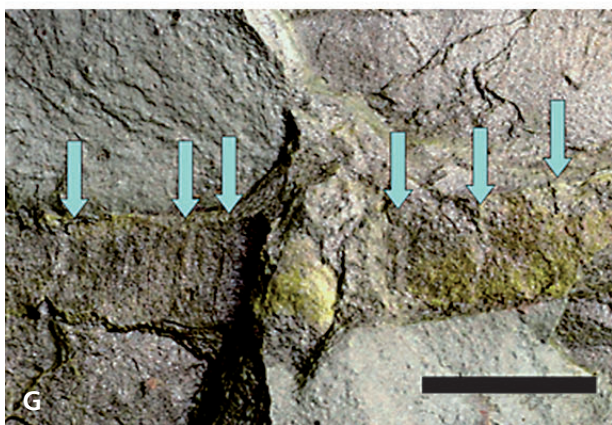
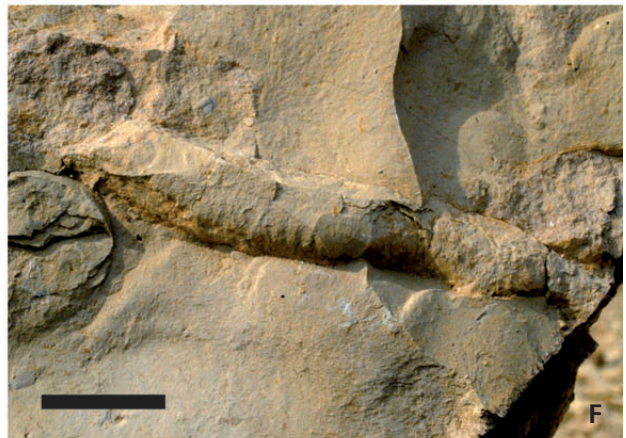
As in the case of *Planolites*-type traces, the ichnotaxonomic differentiation of ichnospecies (distinguished by varying size range and surface ornamentation) of *Palaeophycus* is generally problematic and depends on the trace taphonomy. The specimen of “*Planolites montanus*” Richter, 1937 from the time-equivalent Wushishan Formation (Wuding County) figured by Luo *et al.* (2008, p. 105; pl. 39, fig. 3) displays clearly visible, lined burrow walls and is therefore better assigned to *Palaeophycus tubularis* Hall, 1847. The traces figured here (Fig. 5E) show no true surface ornamentations and are provisionally described as *Palaeophycus* isp.

***Plagiogmus* Roedel, 1929**

Figure 3G

Description and discussion. – The ichnogenus *Plagiogmus* was first reported by Roedel (1929) from glacial erratic boulders of early Cambrian sandstone from southern

Figure 3. A – the conglomerate bed at the base of the Wulongqing Formation (cf. Fig. 2A), hammer head: 20 cm. • B – intense bioturbation in a silt-sandstone bed in the lower–middle part of the Shitangshan section, scale: 5 cm. • C – mud-siltstone surface with wrinkle marks commonly indicating microbial mat structures. • D – numerous *Planolites*-type burrows. The light color of the burrows differs from the darker matrix indicating a different filling of the burrows. • E – hyporeliefs of large *Palaeophycus*-type traces. The colour and composition of the burrow fillings is identical with the surrounding sedimentary matrix indicating an open primary burrow secondarily collapsed and filled with the surrounding sediment. • F – a problematic specimen of *?Psammichnites* showing the fine transversal annulation. A median ridge (or furrow) is only faintly preserved in the left part of the trace. • G – a problematic and unique specimen of *?Plagiogmus*. The left part of the trace displays the typical wide-spaced and relative broad ridges of *Plagiogmus*-type traces (arrows). • H – siltstone slab with numerous *Olenichnus*-type traces. Multiple branching and crossing traces form an irregular net-shaped appearance of this trace fossil. Scales in C–H: 1 cm; coins: 2 cm.



Scandinavia (e.g., Hucke 1967, Häntzschel 1975, Jaeger & Martinsson 1980). The trace was reported from the basal Cambrian of Finnmark (Norway) by Banks (1970), from the early Cambrian of East Greenland (Cowie & Spencer 1970) and from the early Cambrian of central Australia (McIlroy & Heys 1997). *Plagiogmus arcuatus* is characterized by flat, smooth, ribbon-shaped traces (about 1–2 cm wide). They are parallel to the bedding plane, straight or slightly curved and display pronounced transverse ridges (cf. Häntzschel 1975). Zhu (1997) discussed a possible synonymy of *Plagiogmus* and *Psammichnites*; however, comparison with the type material in Roedel's description (1929) shows that *Plagiogmus* clearly differs from *Psammichnites* by its prominent and wide-spaced transversal ridges.

This ichnomorphology is visible especially in the left part of the trace in Fig. 3G (cf. arrows in Fig. 3G). The figured specimen, however, represents a hitherto unique (but not well-preserved) report of this ichnogenus in the Wulongqing Formation. Further material is required to confirm that this represents the first evidence of the ichnogenus *Plagiogmus* in the early Cambrian of China.

***Psammichnites* Torell, 1870**

Figure 3F

Description and discussion. – The ichnogenus *Psammichnites* Torell, 1870 is characterized by large (2–3 cm wide) ribbon-shaped trails with narrow longitudinal ridges or furrows and fine transverse and closely spaced ridges (cf. Häntzschel 1975, W98). The trace type is locally abundant but not a particularly common trace fossil in the basal Cambrian of Baltica, especially in sections of the Hardeberga sandstone in southern Sweden (e.g. Torell 1868, Hadding 1929). *Psammichnites* (especially *Psammichnites gigas* Torell) is also known from Pleistocene erratic boulders in Denmark and northern Germany (e.g. Rohde 2009, figs 1–7). The large and prominent traces were interpreted as repichnia of large (non-shelly) Palaeozoic molluscs (cf. Häntzschel 1975).

The ichnogenus *Psammichnites* has been repeatedly mentioned from basal Cambrian deposits in China: Luo *et al.* (2008) figured new fossil material from the early Cam-

brian Malong Fauna (Jinning area, Yunnan). On the basis of a well-preserved specimens (Luo *et al.* 2008, pl. 40, figs 1, 2), these authors established and described a new ichnospecies of *Psammichnites* (*Psammichnites anningensis* Luo & Zhang, 2008 in Luo *et al.* 2008). Zhu (1997) reported well-preserved specimens of *Psammichnites* from the Shiyantou Formation of Meishucun (Yunnan). Finally, Hu *et al.* (2010) only mentioned *Qipanshanichnus gyrus* Luo *et al.*, 1994 from the Guanshan Biota which is probably related to *Psammichnites* and probably to several other Pc-C *Taphrhelminthopsis*-like trace types (for discussion see Jensen 2003).

The specimen described herein (Fig. 3F) displays a faint transverse (narrow-spaced) annulation. A longitudinal ridge (or furrow), however, is also faintly preserved and absent in several parts of the trace. For that reason, we attribute this single specimen in Fig. 3F from the Shitangshan section only tentatively to the ichnogenus *Psammichnites*.

?*Olenichnid* traces

Figure 3H

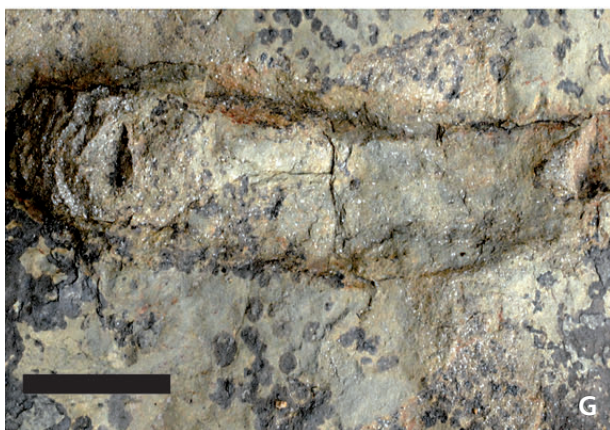
Description and discussion. – The fine straight or partly curved, bedding-parallel traces in Fig. 3H represent a single specimen and are here provisionally attributed to *Olenichnus* Fedonkin, 1985. The traces are mainly horizontal, with minor vertical inclination, and a few specimens display a faint, irregular, transversal annulation. They are multiple-branched and cross each other, forming an irregular, net-shaped structure. Numerous small knobs on the figured slab represent cross-cut vertical components of the burrow system. *Olenichnus* was also reported and described from the early Cambrian Mickwitzia sandstone, south-central Sweden, by Jensen (1997).

***Gordia* Emmons, 1844**

Figure 4A

Description and discussion. – According to Häntzschel (1975), the ichnogenus *Gordia* is characterized by long and slender worm-like traces. They are of uniform thickness,

Figure 4. A – *Gordia* cf. *marina* Emmons on a mudstone-siltstone slab. The specimen displays the typical looping horizontal burrows of the ichnotaxon *Gordia*. • B – large (uncollectable) slab with hyporeliefs of *Thalassinoides*-type traces from the middle part of the Shitangshan section showing the typical T- or Y-shaped branching and the resulting net-shaped trace architecture of *Thalassinoides*. • C – typical “broom-shaped” spreite of *Phycodes*-type from the middle part of the Shitangshan section. • D–F – two different ichnotaphonomic preservations of *Treptichnus pedom* from the lower-middle part of the Shitangshan section. • F – *Teichichnus* isp., a part of an exichnium of a *Teichichnus* spreite showing the stacked gutters forming a flat U-shaped spreite. • G – the characteristic image of a lateral cross-cutted *Teichichnus* spreite. • H – exichnial preservation of a knob-shaped structure representing a circular central area of a *Guanshanichnus* specimen. On the right edge of the circular structure, some of the ray-shaped ridges are preserved. The specimen demonstrates that at least a part of the knob-shaped structures are (exichnial) preservations of the short vertical burrow structures of *Guanshanichnus* (cf. Fig. 5B–F).



mostly irregularly winding and curved, sometimes looping and crossing, but never meandering. Häntzschel (1975) synonymized *Gordia* with the also common ichnogenus *Helminthoidichnites* Fitch, 1850. Hofmann & Patel (1989), however, maintained these as separate ichnotaxa as *Gordia* typically displays self-crossings of the same burrow, whereas *Helminthoidichnites* never shows crossings (for a more detailed discussion see Jensen 1997). *Gordia*-type traces are very common worldwide and known from Ediacaran (e.g. Hofmann 1981) up to Cenozoic times. Yue *et al.* (2009) investigated *Gordia marina* in the (early middle) Cambrian Kaili Biota (Guizhou, South China) and their probably trophic interaction with *Pararotadiscus* carcasses. The trace originators are thought to be priapulids that fed on *Pararotadiscus* and several arthropod carcasses. The single slab in Fig. 4A collected from the Shitangshan quarry shows a looping trace on the left side, which displays a crossing of the same burrow in its upper part. Following Hofmann & Patel (1989), we attribute the trace to the ichnogenus *Gordia* (very likely *Gordia marina* Emmons, 1844; see also Peel 2010).

(ii) Branched burrows and “spreiten”

In contrast to the ubiquitous *Planolites*- and *Palaeophycus*-type traces, branched burrows and “spreiten” are generally more rare and seem to be restricted to the middle part of the Shitangshan section (see Fig. 2A).

?*Thalassinoides* Ehrenberg, 1944

Figure 4B

Description and discussion. – The ichnogenus was established by Ehrenberg (1944) and later emended by Kennedy (1967). *Thalassinoides* is characterized by three-dimensional and open burrow systems. Burrows are branching into Y- or T-shaped bifurcations forming horizontal (bedding plane parallel) networks that are connected to surface by vertical shafts (which were never observed in the Shitangshan specimens described here). The burrows are typically 10–15 mm wide and display swellings (usually up to 30 mm) at the branching points (cf. Häntzschel 1975). *Thalassinoides* is mainly known from Late Palaeozoic to Cenozoic occurrences. Myrow (1995) described a smaller type from the (middle) Cambrian to Lower Ordovician Peerless and Manitou formations in central Colorado as *Thalassinoides horizontalis*.

In the middle part of the Shitangshan section, beds with relatively thick bedding-parallel, T- and Y-shaped branching burrows are common. Similar traces were reported from an equivalent section near Wushishan (Wuding County), northwest of Kunming area (see Fig. 2) by Luo *et*

al. (2008, p. 106, pl. 40/5) as *Thalassinoides xiaoluoguiensis* Luo, 1994. Zhu (1997) reported *Thalassinoides*-like traces from the Upper Yuanshan Formation (Haikou, Yunnan) which, however, only faintly display the Y-shaped network structure, with no swellings and no vertical shafts. Dornbos (2004) interpreted similar structures from the Meishucun section as *Thalassinoides*.

Thalassinoides xiaoluoguiensis Luo *et al.*, 2008 is represented only by a unique specimen of a Y-shaped branching horizontal burrow. The specimens from the Wulongqing Formation figured here (Fig. 4B) represent a more typical *Thalassinoides*-type trace as they display the typical network of multiple Y- and T-shaped branching burrows with swellings at the branching points. Both remain questionable because of the lack of vertical shaft structures.

Phycodes Richter, 1850

Figure 4C

Description and discussion. – According to Häntzschel (1975, W93–94), traces of the ichnogenus *Phycodes* consist of bundled unbranched and horizontal tunnels forming a “broomlike” pattern. The trace is characterized by a proximal unbranched tunnel, whereas the traces are branching distally into several free cylindrical burrows that display a delicate annulation beneath a smooth “bark”. The “broom-shaped” trace architecture of the single specimen in Fig. 4C strongly resembles that of *Phycodes palmatum* Hall, 1847 from the lower Cambrian of the Salt Range in Pakistan (Seilacher 1955; cf. also Häntzschel 1975, W94, Fig. 59-2e) but lacks the “delicate annulation”.

Treptichnus pedum (Seilacher, 1955)

Figure 4D, E

Description and discussion. – The ichnotaxon *Treptichnus pedum* (syn. *Phycodes pedum*, *Trichophycus pedum*) is used as an index fossil for the base of the Fortunian Stage and thus as a global indicator of the earliest Cambrian. The ichnogenus *Treptichnus* was first reported by Miller (1889) and later mentioned as “featherstich trail” by Wilson (1948) who describes the characteristic ichnomorphology of a treptichnid trace in which a “...straight or curved row of short individual burrows of equal length...” and which “... are arranged alternating to right and left resulting in a featherstich pattern” (*cit.* from Häntzschel 1975, W117).

A couple of specimens of treptichnid traces were collected in the lower and middle parts of the Shitangshan section (lower Wulongqing Formation). The specimen in Fig. 4D displays a short row of elongated knob-shaped burrows (in positive hyporeliefs) in which these individual

burrows join each other at low angles as short projections. This arrangement is characteristic of *Treptichnus pedum* (cf. Jensen 1997, Fig. 62B). The relation of *Treptichnus pedum* to the originally described (zigzag-shaped) ichnospecies *Treptichnus bifurcus* Miller, 1889 and also to *Plangtichnus erraticus* Miller, 1889 (cf. Archer & Maples 1984) has been discussed by Jensen (1997). For a more detailed discussion of treptichnid traces and related synonymy see Jensen (1997). The row of circular knob-shaped (hypichnically preserved) burrows in Fig. 4E apparently represents a certain type of lower-plane preservation of *Treptichnus pedum* cut off at another bedding plane level.

Jensen (1997) interpreted them as a series of dwelling tubes (domichnia), which possibly were inhabited by a suspension feeder *sensu* Bromley (1990). Recently, Vannier *et al.* (2010) showed that the trace architecture of the Palaeozoic *Treptichnus pedum* resembles the infaunal traces of recent priapulids. This aspect is of great interest for the interpretation of the ichnoassemblages and palaeoecology of the early Cambrian Chengjiang-type *Lagerstätten* because a large variety of priapulid worms were reported from the Chengjiang and the Guanshan biotas of Yunnan. Luo *et al.* (2008) described two taxa of priapulids (*Guanduscolex minor* Hu, Luo & Fu, 2008 and *Palaeoscolex* sp.) from the Guanshan Biota. Further taxa (*Sicyphorus*, *Wudingscolex*, *Yunnanoscolex* and *Paramaotianshania*) were recently reported from related sections by Hu *et al.* (2012). Some of them correspond in terms of their body size with the treptichnid traces from the middle Wulongqing Formation in the Shitangshan section.

***Teichichnus* Seilacher, 1955**

Figure 4F, G

Description and discussion. – *Teichichnus*-type spreiten are common in the middle and upper parts of the Shitangshan section. They resemble *Teichichnus* from the (middle) Cambrian beds of Öland (south-eastern Sweden, Martinsson 1965) and the early Cambrian Mickwitzia sandstone (southern-central Sweden, Jensen 1997). The ichnogenus has been characterized by Häntzschel (1975, W114) as “a series of long horizontal burrows stacked vertical to bedding...”. They represent wall-shaped laminar bodies of about 10 to 50 cm length, consisting of flat U-shaped gutters. The traces are generally not branching. Martinsson (1965) reported specimens up to 135 cm in length from the (middle) Cambrian of Öland (southern Sweden). This material was re-described by Schlirf & Bromley (2007) as a new ichnotaxon (*Teichichnus duplex*). The type species (*Teichichnus rectus* Seilacher, 1955) was originally described as a “retrusive, tightly guided spreite”. The only given differential feature of the second ichnospecies erected by

Legg (1985). *Teichichnus ovillus* Legg, 1985 is the existence of both retrusive and protrusive parts of spreiten. A protrusive or a retrusive spreiten architecture, however, may be simply caused by the reaction of a certain infaunal trace originator to a varying sedimentary regime (higher sedimentation rates or erosive phases, *i.e.* probably the same behavioural pattern in response to different environmental signals, and should be therefore avoided as an ichnotaxobase (see Fürsich 1974). According to Jensen (1997), the basic ichnomorphology of “teichichnia” (*sensu* Martinsson 1965) are “...flat U- or L-shaped burrows that were shifted upwards and in direction of burrow length, as a consequence of sediment influx”.

The specimens from the Shitangshan section collected so far are relatively small (*ca* 10–20 cm length of the spreiten), *e.g.* in relation to the (middle) Cambrian specimens from Öland. The short fragments (Fig. 4F) and the cross-cut spreite (Fig. 4G) represent the basic morphology of *Teichichnus* but do not provide sufficient taxonomic features for an ichnospecies determination.

(iii) Short vertical burrows

Figures 4H, 5A–F

Description and discussion. – The middle part of the Wulongqing Formation in the Shitangshan quarry contains numerous, large, knob-shaped, vertical burrows of unknown origin. Jensen (1997) described and figured very similar structures from Baltica (early Cambrian Mickwitzia sandstone, Sweden). The burrows are sub-circular, mostly elongated to ellipsoid hyporeliefs, which frequently show a central pore or a short knob-shaped structure as a positive hyporelief in a shallow depression (Figs 4H, 5B–D). The ichnotaxonomic attribution of these burrows remains an open question; however, some of these specimens display remains of radially arranged rays (Fig. 4H). Thus, some of them could represent vertical burrows (*e.g.* Figs 4H, 5D, E) of nearby completely destroyed specimens of large star-shaped vertical burrows (see below) that have been eroded by bottom-current activity. Parting lineation around some of these structures (Fig. 5E, F) may support this interpretation.

(iv) Star-shaped traces

Description and discussion. – The Guanshan ichnoassemblage contains large (up to some decimetres in diameter), star-shaped traces, which show several taxonomic similarities to the ichnogenus *Glockerichnus* Pickerill, 1982 (formerly “*Glockeria*” Książkiewicz, 1968; see also Häntzschel 1975 and Uchmann 1998). Because some of the star-shaped traces from the Wulongqing Formation display unusual and

hitherto unknown taxonomic features, we present here a more detailed ichnotaxonomic study of these traces.

***Glockerichnus* Pickerill, 1982**

Description and discussion. – Various ichnospecies of the ichnogenus *Glockerichnus* were originally described from Mesozoic and early Cenozoic (Cretaceous: Senonian to early Palaeogene) sequences in Europe by Książkiewicz (1968, 1970 and 1977): *Glockerichnus glockeri* Książkiewicz, 1968, *Glockerichnus sparsicostata* Książkiewicz, 1968 and *Glockerichnus parvula* Książkiewicz, 1970 (*nomen nudum*). Other related ichnotaxa are “*Glockeria*” *disordinata* Książkiewicz, 1977, “*Glockeria*” *dichotoma* Seilacher, 1977, and *Glockerichnus alata* (Seilacher, 1977).

The specimens of *Glockerichnus glockeri* described by Książkiewicz (1968, 1970, 1971) from the Polish Carpathian flysch are characterized by rosetted traces, consisting of numerous longer and shorter, straight and distally tapering rays (or “ribs”, Książkiewicz 1970), which run radially from a diffuse central field (see sketch in Fig. 8A). The distal parts of some of the larger main ribs show a characteristic dichotomous branching, which was originally not mentioned by Książkiewicz (1970), but was assigned by Uchman (1998) as a distinct taxonomic feature of the ichnogenus *Glockerichnus*. The Carpathian specimens of *Glockerichnus glockeri* are up to 15 cm in diameter (after Książkiewicz 1970). The two other ichnospecies described by Książkiewicz (1968, 1970) are smaller, but largely similar to the ichnomorphology of *Glockerichnus glockeri*, and were also reported from the Polish flysch. The specimens of *Glockerichnus sparsicostata* and *Glockerichnus parvula* figured by Książkiewicz (1968, 1970, 1971) display no convincing features of true ichnotaxabases. They could be poorly preserved specimens of the type species *Glockerichnus glockeri*. The much smaller (2–3 cm in diameter) “*Glockeria*” *parvula* (*nomen nudum*) was only tentatively attributed to “*Glockeria*” by Książkiewicz (1968, 1970) and may simply represent smaller and poorly preserved specimens of *Glockerichnus glockeri* or, probably, the central areas of larger specimens of *Glockerichnus*. The type material of the Książkiewicz collection was restudied and revised by Uchman (1998).

Palaeoethology. – The ichnogenus *Glockerichnus* represents a distinct, star-shaped radiating (graphoglyptid) trace fossil (Pickerill 1982). *Glockerichnus*-type traces vary in size from 2–3 cm up to 20–30 cm. The ethological classification of *Glockerichnus* was first given by Seilacher (1953) as a star-shaped *fodinichnion* (Seilacher 1955, 1959; Uchmann 1998). *Glockerichnus* may represent a combined domichnid-fodinichnid trace of an unknown infaunal trace originator which was stated again by Uchman

(1998). Recent examples of star-shaped ichnia of similar shape and size are known, for example, from the Pacific ocean floor (Ewing & Davis 1967), figured in Häntzschel 1970 (pl. 1, fig. a).

(v) The star-shaped trace fossils from the Wulongqing Formation

In comparison to the type-ichnospecies *Glockerichnus glockeri* from the Mesozoic-Cenozoic flysch of Poland, the star-shaped traces from the Wulongqing Formation show several similarities, but also a variety of different ichnotaxonomic features. We therefore suggest establishing a separate ichnotaxon.

***Guanshanichnus glockerichnoides* igen. et isp. nov.**

Figures 6A, B, 7A–E, 9A–C

Derivation of name. – Ichnogenus derived from the geographical name of the type area (Guanshan) as well as from the name of the fossil *Lagerstätte* and the related biota described from there (Guanshan Fauna). The ichnospecies name refers to the ichnomorphological similarities to *Glockerichnus glockeri*.

Holotype. – Specimen in Fig. 6A (NIGPAS collection, Nanjing Institute of Palaeontology, Nanjing, China (no collection number available so far).

Type locality and stratigraphy. – The trace fossil material described here was collected and photographed in the Shitangshan quarry close to the village of Guangwei, near Kunming, Yunnan Province, South China (Figs 1, 2). South Chinese regional biostratigraphical zonation: Wulongqing Formation [*Palaeolenus* Zone at the base and the *Megapalaeolenus* Zone (= Canglangpuan Stage)] at the top. Global biostratigraphic zonation of the Cambrian system: Stage 4, Series II (ca 515–510 My). The Wulongqing Fauna can be correlated about with the Botoman of Siberia.

Material. – About 20 specimens, in different stages of preservation, partly in fragments. Some further specimens in large uncollectable slabs were measured and photographed in the field (e.g. Fig. 7A).

Diagnosis. – Short vertical burrows with a circular central structure. Starting from a broader proximal base, numerous ray-shaped, distally tapering and partly dichotomously branching ribs are arranged around the circular central field, forming a star-like structure on the sediment surface about 2 to 30 cm in diameter. The short vertical burrows



Figure 5. A – very large exichnial bell-shaped burrow structure which probably belongs to a large specimen of *Guanshanichnus*. • B–F – examples of varying preservations of large circular and short vertical burrows from the middle part of the Shitangshan section. • A–D showing the central depressions or knob-shaped elevations indicating a central vertical burrow. B and D show sub-circular elongation (ellipsoid shape) and E, F are associated with parting lineation structures indicating bottom currents and erosional processes. Scales in F: 1 cm, A, C, D and coins: 2 cm.

display a more or less cone- or bell-shaped (in cross-section funnel-shaped) structure.

Differential diagnosis. – (1) In contrast to the Mesozoic and Cenozoic specimens from Europe that all show relatively thick, spindle-shaped and transversally wrinkled ribs (e.g., Książkiewicz 1970, figs 7a–c; Książkiewicz 1977, pl. 8, figs 1–3; Uchman 1998, pp. 141–143; see also sketch in Fig. 8A herein), the star-shaped traces from the Guan-

shan area (Wulongqing Formation) are characterized by many relatively thin (sometimes very thin), ray-shaped, partly dichotomously branching ribs, which show no transversal wrinkling and (starting from a broader proximal base at a circular central field) taper more or less continuously in a distal direction. (2) In contrast to *Glockerichnus glockeri* Książkiewicz, 1968 and the related ichnotaxa (“*Glockeria*” *sparsicostata* Książkiewicz, 1968; “*Glockeria*” *parvula* Książkiewicz, 1970, “*Glockeria*” *disordinata*

Książkiewicz, 1977; “*Glockeria*” *dichotoma* Seilacher, 1977a; *Glockerichnus alata* Seilacher, 1977a), the new ichnotaxon *Guanshanichnus glockerichnoides* igen. et isp. nov. is characterized by a broad and prominent, circular, central area from which a large number of the distally tapering and partly dichotomously branching, ray-shaped structures radiate (type specimen: Fig. 6A, further specimens in Figs 6B, 7A–E), some preserved in large slabs (Figs 6B, 7A) and therefore partly not collectable. The star-shaped traces display a more or less completely circular radial structure and no evidence of a bilateral arrangement as reported for *Glockerichnus glockeri* by Uchmann (1998).

The *Guanshanichnus* structures are frequently associated with knob- or bell-shaped structures of approximately similar size ranges, commonly 1–3 cm, in some cases up to more than 5 cm in diameter (Fig. 5A). Part of them could represent strongly weathered casts of the vertical burrows of *Guanshanichnus*. As some of them are additionally associated with parting lineation structures, bottom currents could have completely destroyed the primary radial surface structures and left the casts of the vertical burrow structures in the sediment body (see text above).

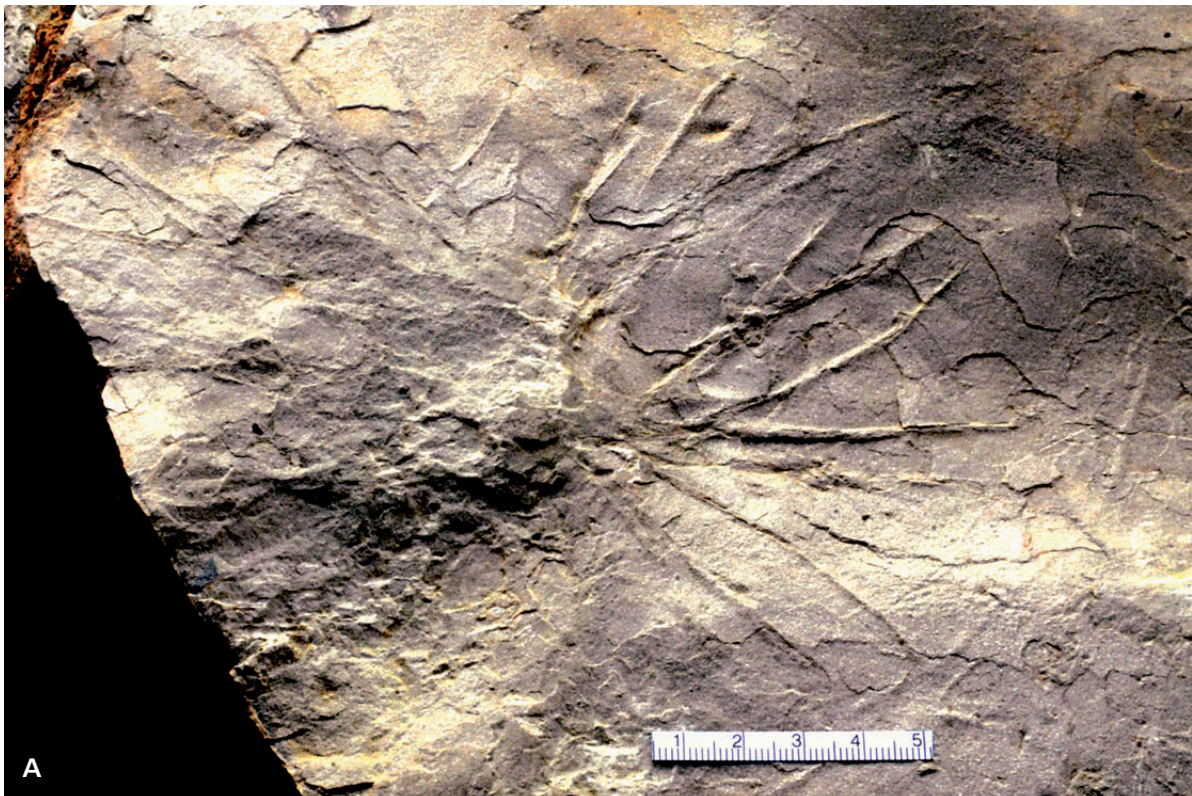
Stratigraphic range. – The stratigraphic range of the hitherto described occurrences of the similar and probably related ichnotaxon *Glockerichnus glockeri* ranges from the Ordovician of Chrustenice and Beroun in Bohemia (Richter 1927, Prantl 1946, Mikuláš 1998) and from the Early Ordovician Klabava Formation in Bohemia (Mikuláš 1992) to the Lower Cretaceous–Palaeogene of various European localities (Häntzschel 1970, pp. 211, 212), and may further range into Holocene and recent deep sea occurrences (Häntzschel 1970). The specimens from the Early Ordovician of Bohemia (Mikuláš 1992; esp. the specimen in pl. IV, fig. 2) show strong similarities to the specimens from the early Cambrian Guanshan Formation (see above). Thus, *Guanshanichnus glockerichnoides* igen. et isp. nov. represents an Early Palaeozoic occurrence (basal Cambrian) of this type of star-shaped (“*Glockerichnus*-like”) vertical burrows.

Description and discussion. – The Wulongqing specimens of *Guanshanichnus glockerichnoides* igen. et isp. nov. range in size from about 2–8 cm up to 20–30 cm in diameter (Fig. 6A, B) and show a dichotomous branching of the radial and distally tapering rays similar to that of *Glockerichnus glockeri*; however, in contrast to *Glockerichnus*, the large and well-preserved specimens of *Guanshanichnus glockerichnoides* igen. et isp. nov. from the Wulong-

qing Formation display a circular star-shaped structure consisting of thin, ray-shaped burrows, which are arranged in large numbers around a prominent circular central area (Figs 6A, B, 7A–E). The basic morphology (*i.e.*, the dichotomously branching rays), is identical with that of *Glockerichnus glockeri*; however, the numerous ray-shaped burrows are relatively thin in relation to *Glockerichnus glockeri*. In some cases (Figs 6B, 7A–C), they resemble very thin and multiple-branching rays, whereas the radial burrows in *Glockerichnus glockeri* and related ichnotaxa are generally thicker and mostly spindle-shaped (see re-drawn sketch from Książkiewicz 1968, Fig. 8A). This is clearly a differential feature in relation to the type species of *Guanshanichnus glockerichnoides* igen. et isp. nov. and cannot be explained by any diagenetic or preservational phenomena. On the other hand, the newly described ichnotaxon displays a broad variety of different preservational forms (Figs 6A, B, 7A–E) and sizes (about 2–8 up to 30 cm). Smaller and poorly preserved specimens were only mentioned (not figured), and tentatively attributed by Hu *et al.* (2010) to *Astropolichnus cf. hispanicus*.

Along with the different shape and higher number of ribs, the second characteristic differential feature of *Guanshanichnus glockerichnoides* igen. et isp. nov. is the mostly well-visible, circular central area in the star-shaped traces, whose diameter can vary significantly in different specimens (see above). In some specimens, the circular central area displays a very prominent, broad circular structure (Figs 6A, B, 7D). In weathered specimens (Fig. 9C), the centre of the star-shaped structure appears more diffuse or may show only a smaller and rather faintly preserved central vertical burrow (Fig. 7B). Larger specimens can display small central circles (*cf.* 6A, 7A, C), whereas relatively small specimens can possess a relatively large circular structure (Figs 7D, E, 9B). This phenomenon can be explained (1) by different qualities of preservation of the traces and (2) by representing different horizontal planes through the short vertical (funnel-shaped) central burrows (sketch in Fig. 8B). Therefore, it may not inevitably indicate the occurrence of different trace types (*i.e.*, different ichnospecies of *Guanshanichnus*) in the Shitangshan ichnoassemblage but could represent simply a preservational phenomenon. Häntzschel (1970) figured a specimen (pl. 1, fig. b) as a “star-like trace” from the Kimmeridgian–Lower Tithonian flysch of Bielsko, Polish Carpathians. This specimen displays a small, circular, central burrow that was not mentioned in the taxonomic description of “*Glockeria*” by Książkiewicz (1968); however, the specimen displays relatively thick spindle-like

Figure 6. A – holotype specimen of *Guanshanichnus glockerichnoides* igen. et isp. nov. from the upper Shitangshan section. • B – another large specimen of *Guanshanichnus glockerichnoides* that also displays the relative large circular central field and the numerous and very thin distally branching rays (specimen belongs to slab in Fig. 7A), scale: 2 cm.



rays and therefore could instead represent a specimen of *Glockerichnus glockeri*. Mikuláš (1992) figured an early Ordovician specimen from Bohemia that displays similarities with *Guanshanichnus glockerichnoides* gen. et isp. nov. as it shows a faint circular central field and numerous thin and distally tapering ray-shaped, radially arranged burrows similar to those in the Shitangshan specimens. Finally, the *Glockerichnus* isp. from siliceous marls (Turonian, Carpathian Mts: Książkiewicz collection material) which was re-figured in Uchmann (1998, figs 47A, B) displays numerous thin rays (but a diffusely preserved central area), and may be attributed to *Guanshanichnus*. Finally, Zhu (1997, figs 5A, B) figured a specimen of an unnamed star-shaped trace from the Shiyantou Formation of Meishucun that displays a relative large circular central field and short, distally tapering, partly branching rays. This ichnomorphology matches perfectly those of the smaller specimens of *Guanshanichnus glockerichnoides* (Fig. 7D).

Uchman (1998) emphasized that *Glockerichnus* always occurs in flysch deposits between the Ordovician and Miocene. The flysch deposits represent deep water environments (upper slope to deep sea facies). During the Mesozoic and Cenozoic eras, these environments are commonly characterized by typical deep-water ichnotaxa such as *Lorenzina*, *Paleodictyon*, etc. The occurrence of the (“*Glockerichnus*-like”) star-shaped traces of the *Guanshanichnus* type in the Botoman Shitangshan ichnoassemblage, however, is characterized by a different palaeoenvironment, belonging to a near-shore shallow water regime. The associated diverse ichnoassemblage contains fodinichnid, domichnid and repichnid ichnotaxa (e.g., *Planolites*, *Teichichnus*, (?) *Thalassinoides* and arthropod repichnia (such as *Diplichnites*, *Merostomichnites*), which all represent characteristic members of the shallow-marine *Cruziana* ichnofacies. On the basis of this ichnofacies data, the depositional environment of the host sediments of the Guanshan Biota can therefore be characterized as shallow marine softgrounds which were deposited between fair-weather and storm-wave bases, resulting in a sequence of mudstone and sandstone beds. The Ordovician finds of *Glockerichnus* reported by Mikuláš (1992, 1998) also clearly belong to shallow seas, outside flysch/turbidite sedimentation areas.

The unknown trace makers of the early Palaeozoic *Guanshanichnus* traces were obviously still adapted to shallow water conditions, whereas later Phanerozoic representatives of this trace type gradually moved into deeper shelf and deep sea habitats during Late Palaeozoic to Cenozoic times. On the other hand, combined star-shaped domichnia and fodinichnia represent a common type of trophic strategies in benthic (infaunal and epifaunal) organisms and therefore could have been produced by taxonomically very different invertebrate trace makers in both shallow marine and deep water environments (i.e., during early Palaeozoic and younger deposits, respectively).

Other problematic star-shaped structures

Several problematic stellate structures were found in the middle part of the Wulongqing section (Figs 9D, E, 10E). They consist of five to six radially arranged, pear-shaped (convex) lobes or lobate depressions and are preserved as three-dimensional casts (hyporeliefs) or as flat impressions whose surfaces are covered by yellowish-red iron oxides. Well-preserved specimens show a central plug (probably the end part of a short vertical burrow), have a constant diameter of 5–7 mm and (if preserved as a positive hyporelief) are 2–3 mm high. Similar problematic structures have been reported from the early Cambrian of the Arumbera section (Amadeus Basin, central Australia) by Walter *et al.* (1989). These authors compared the Amadeus basin specimens with *Asterichnus* isp.; however, the former lack the characteristic features of a retrusive spreite that are evident in *Asterichnus*. The problematic stellate structures from the Wulongqing Formation are smaller than the Australian specimens. The specimens from the Shitangshan quarry display similarities in their shape (but not in their size range) to the problematic star-like fossils “*Palaeosemaestoma*” from the Lower Jurassic of Germany (Sehnde, Lower Saxony) as figured by Häntzschel (1970, p. 207, pl. 2, fig. b). Finally, the traces resemble the ichnogenus *Gyrophyllites* Glocker, 1841 (Häntzschel 1975, W66, 2a, b) from the European Flysch (Upper Cretaceous); however, an arrangement of the radiating leaf-shaped spreiten in different levels as described in *Gyrophyllites* (Häntzschel 1975, W65) is not preserved in the Shitangshan specimens. Thus, the trace fossil assignment and origin of the structures here described (Figs 9D, E, 10E) remain unclear.

(vi) Arthropod traces

In comparison with the high number of other invertebrate traces, arthropod traces are rarely occurring in the whole Wulongqing Formation so far and are mainly restricted to the middle part of the section (Fig. 2A). Along with non-specific series of arthropod scratch marks, short trackways of *Diplichnites*-type traces consisting of two paired rows of scratches were found (Fig. 9G, H) as well as a typical *Merostomichnites* (Fig. 10C).

Diplichnites Dawson, 1873

Figures 9G, H, 10A

Description and discussion. – The traces commonly consist of two series of short (straight or gently curved) ridges, each 3–5 mm in length. Some specimens from the Wulongqing section are large (10–20 mm in width) and up to 10 cm in

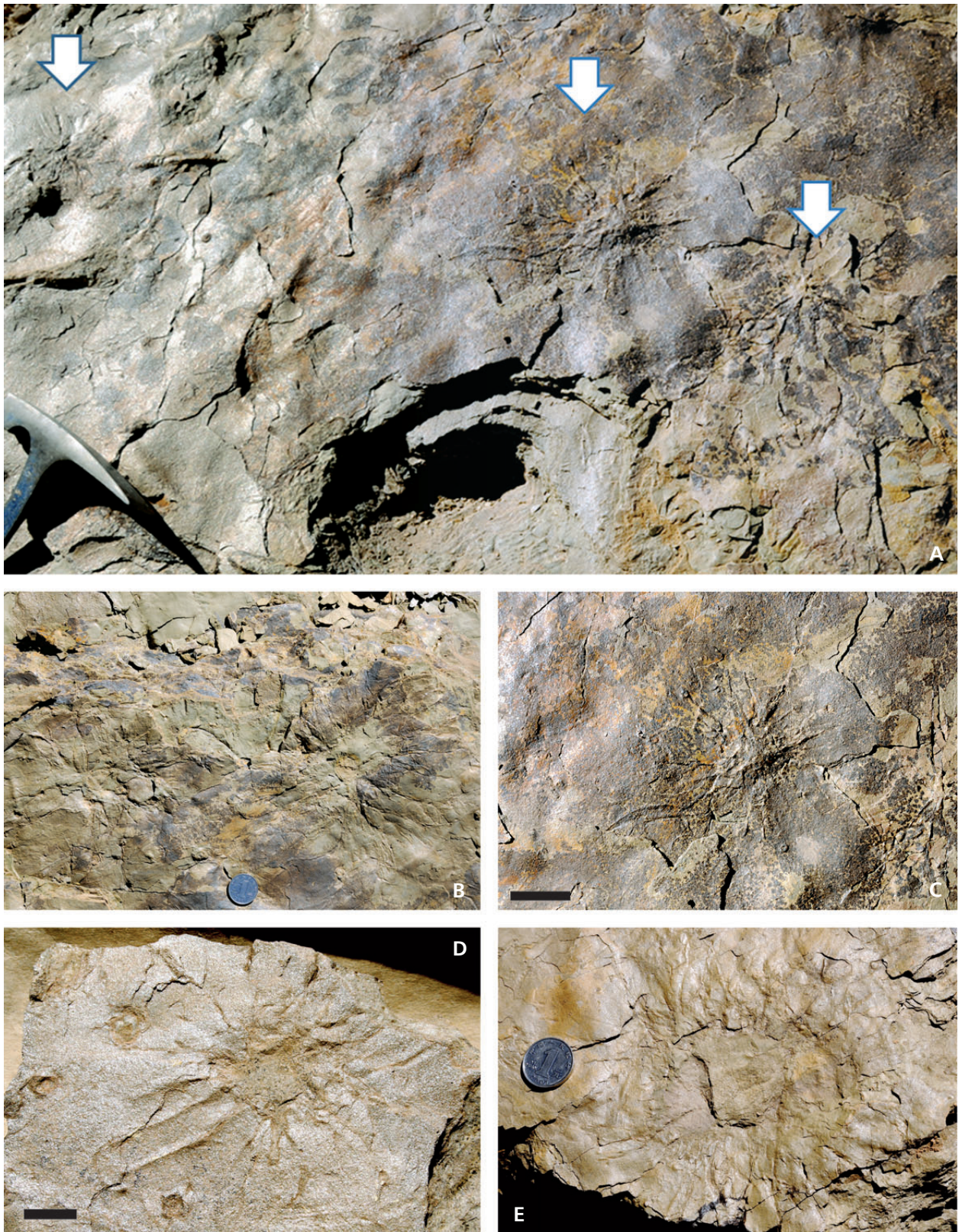


Figure 7. A – an uncollectable slab (*in situ*) with numerous specimens of *Guanshanichnus glockerichnoides* (arrows), hammer head: about 20 cm.
• B–E – examples of different preservations of *Guanshanichnus* in the Shitangshan section (see discussion), collections of the FUB Berlin. Scales in 7C, D: 1 cm, coins: 2 cm.

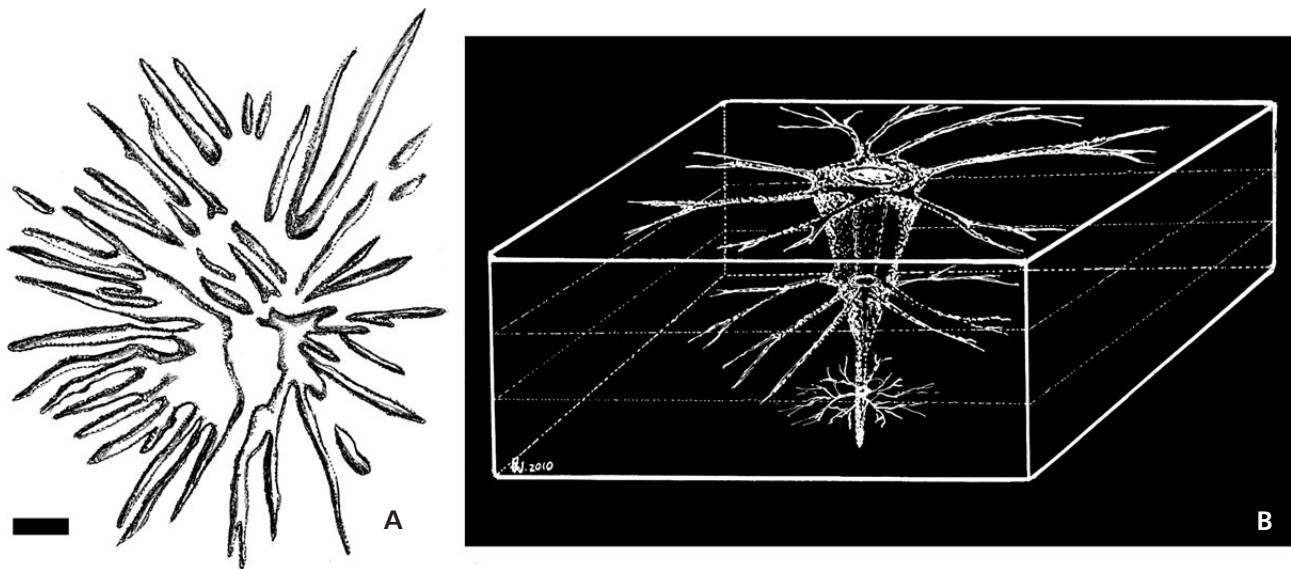


Figure 8. A – re-drawing of a sketch of *Glockerichnus glockeri* (from Kziaskiewicz 1970, fig. 7a) which displays the characteristic elongate spindle-shape of the rays in *G. glockeri*. • B – reconstruction of *Guanshanichnus glockerichnoides* igen. et isp. nov. showing the (probably retrusive) development of the funnel-shaped vertical burrows with radially arranged and branching rays (probes) in different levels of development of the trace structure which may have caused the variability of the trace type by preservation of different developmental stages.

length. Series of bulbous hyporeliefs may represent faint undertrack preservations of *Diplichnites* (Fig. 9H).

The *Diplichnites*-type traces represent repichnia of epibenthic arthropods, in many cases those of trilobites. The ichnogenus *Diplichnites* occurs in several other Cambrian shallow marine environments, e.g., in Australia (Walter *et al.* 1983), Pakistan (Seilacher 1955), Canada (Young 1972), Spain (Crimes *et al.* 1977) and in the Nomtsas Formation, Namibia (Crimes & Germs 1982). The youngest occurrence of *Diplichnites* is in the lower Permian (Walter *et al.* 1989).

***Merostomichnites* Packard, 1900**

Figure 10C

Description and discussion. – The trace in Fig. 10C represents a unique but well-preserved specimen of *Merostomichnites*. This arthropod trace type is characterized by two (or more) parallel rows (at approx. 1 cm intervals) of single spindle- or bow-shaped impressions, partly ornamented with oblique transverse ring-shaped structures. *Merostomichnites* is known from Cambrian to lower Triassic occurrences in Europe and North America. The youngest

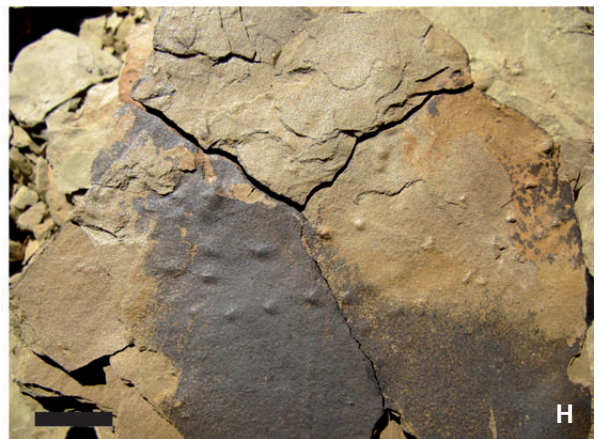
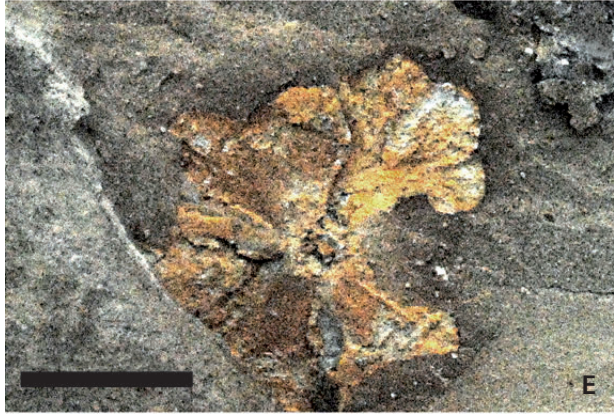
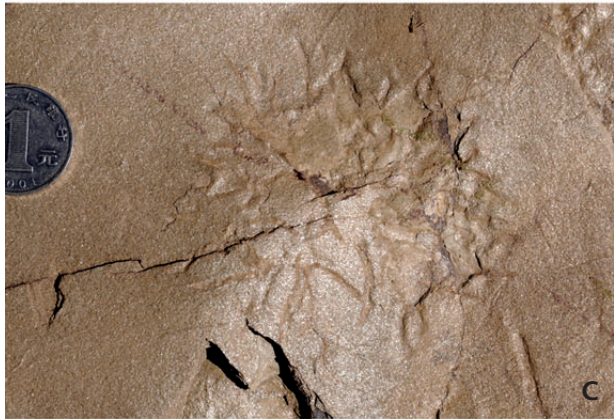
evidence of a *Diplichnites*-like trace was reported by Kim *et al.* (2005) from the Cretaceous. The Palaeozoic traces were attributed to trilobites and eurypterids, whereas the Mesozoic specimens may belong to phyllocarids (Häntzschel 1975) or other benthic crustaceans.

The unique specimen from the Wulongqing Formation in Fig. 10C represents the first evidence of *Merostomichnites*-type traces from the early Cambrian of China. They were most probably produced by several redlichid trilobite taxa, which are commonly preserved as body fossils in the intercalated mudstone beds of the Wulongqing Formation (Fig. 10B).

Trilobite resting traces

The specimen in Fig. 10A displays a V-shaped arrangement of obliquely orientated bifid ridges. This arrangement agrees in shape and size with the morphology (thorax and abdominal parts) of several trilobite taxa from the Guanshan Fauna and for that reason can be interpreted as a resting trace of a trilobite. The specimen in Fig. 10A therefore may be interpreted as a rarely preserved transitional form of *Diplichnites*-type repichnia and a *Rusophycus*-type resting

Figure 9. A – close-up photo of a branching ray (probe) from the holotype specimen (6A) showing the thin and continuously tapering rays in *Guanshanichnus glockerichnoides* igen. et isp. nov. • B, C – examples of small (probably early developmental stages) and partly weathered or eroded specimens demonstrating the preservational variability of the ichnotaxon. • D, E – problematic small star-like trace fossils from the upper Shitangshan section. The traces display a rosette-like shape of radially arranged lobes (partly 3D-preserved – 9D). • F – example of similar rosette-shaped vertical traces in a recent shallow marine environment (South-China Sea) which are produced by small crustaceans (photo: Hu Shixue). • G, H – examples of hyporelief-preservations of *Diplichnites* from the lower–middle part of the Shitangshan section. Scales in A, B and coins: 1 cm, D, E: 0.5 cm, F, H: 1 cm.



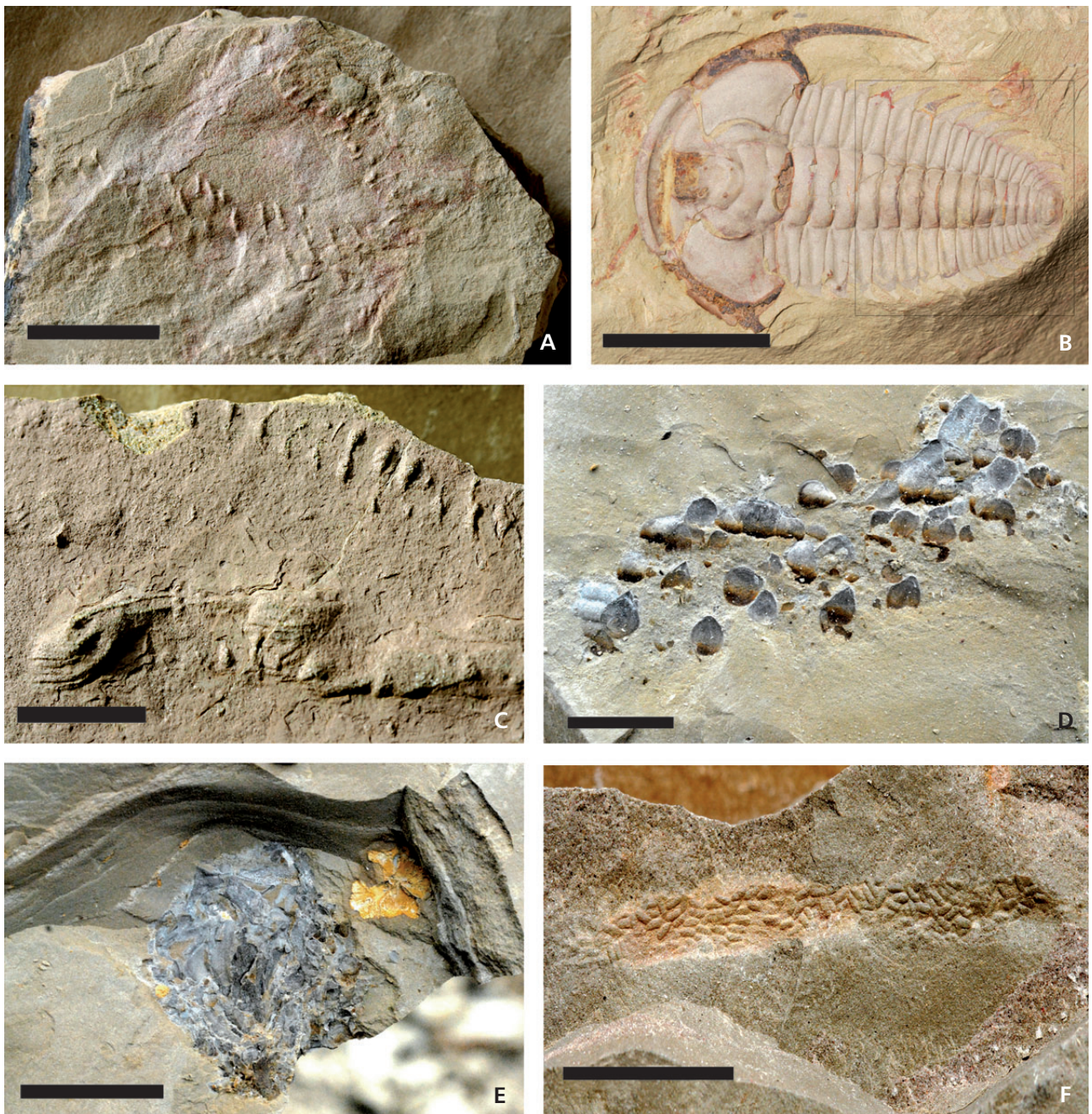


Figure 10. A, B – U-shaped arrangement of single impressions of *Diplichnites*-type arthropod traces (A) correlate in their shape and size range with coinciding typical redlichide trilobite taxa (*Redlichia mansuyi* Resser & Endo, 1937, fig. 10B). They therefore may be interpreted as transitional forms of *Diplichnites*-type repichnia and *Rusophycus*-type digging/resting traces of trilobites. • C – *Merostomichnites* isp. is known by a single specimen from the Shitangshan section. The single impressions in the Shitangshan specimen display the characteristic oblique annulation of *Merostomichnites*-type arthropod traces. • D – accumulation of intact shells of lingulid brachiopods. Such accumulations may be interpreted both as coprolites of a specialized predator and as result of current-related transport of shells and their subsequent allochthonous embedding (e.g. in microbial mucus). • E – example of a frequently found coprolite type consisting of shredded and fragmented parts of arthropod (probably trilobite) carapaces indicating the presence of larger predators (e.g. predatory arthropods as anomalocarids) in the Guanshan Biota. • F – the problematic ichnogenus *Tomaculum* Groom, 1902 was repeatedly found in the Shitangshan section. The here figured example of a long, hose-like structure filled with ellipsoid fecal pellets strongly resembles *Tomaculum problematicum* from the Palaeozoic of Europe. Scales in A, B, E: 2 cm, D–F: 1 cm.

trace. Regarding the average size and morphology, the co-occurring trilobite *Redlichia mansuyi* Resser & Endo, 1937 (Fig. 10B) from the Shitangshan quarry may represent a possible originator of this unique resting trace.

(vii) Faecal pellets (coprolites)

Figures 10D–F

Faecal pellets and coprolites are considered to be trace fossils as they represent the result of a physiological process as well as the behaviour of a living organism. In exceptionally well-preserved cases, coprolites enable the reconstruction of specific ecological interactions (*e.g.* between prey and predator: food chains) within a fossil ecosystem.

Tomaculum Groom, 1902

Figure 10F

Several specimens of long and bedding-parallel (*Planolites*-like), mostly flattened sausage-shaped structures or longer tubes filled with numerous ellipsoid faecal pellets (Fig. 10F) were found in the Shitangshan section.

A similar structure from an approximately time-equivalent outcrop in Wushishan (Wuding County, Yunnan) was described and figured by Luo *et al.* (2008, p. 133, pl. 39, fig. 4) as *Tomaculum problematicum* Groom, 1902. The ichnospecies has been earlier reported, *e.g.* by Volk (1941) from the Ordovician of Thuringia (Germany), and was recently revised and critically discussed in terms of the problematic taxonomy and interpretation of *Tomaculum* by Eiserhardt *et al.* (2001).

Other non-specific faecal pellets

Figure 10 D, E

Various ball- or sausage-shaped accumulations consisting of shells of lingulid brachiopods (Fig. 10D) and/or of fragmented arthropod (mainly trilobite) carapaces (Fig. 10E) are relatively common in the Wulongqing Formation and may represent faecal lumps of predators. The relatively large pellets of shredded arthropod carapaces (Fig. 10E) may indicate the hunting and feeding activity of the largest Chengjiang predators *Anomalocaris* Whiteaves, 1892 and *Amplectobelua* Hou, Bergström & Ahlberg, 1995 which both are characteristic elements of the Chengjiang-type biotas. The identification of the sausage-shaped accumulation of intact lingulid shells (Fig. 10D) as coprolites, however, remains problematic. Such shelly accumulations could also be caused by short-distance transportation of the shells by a weak bottom current and their final trapping by a microbially caused mucus production (microbial mats mentioned above, Fig. 3C).

Discussion and conclusions – Palaeoenvironment and composition of the ichnofauna

The depositional regime of the Wulongqing Formation has been reconstructed by Hu *et al.* (2010) as a storm-dominated subtidal to offshore transitional palaeoenvironment. Sedimentary structures of the mudstone-siltstone sequence of the Wulongqing Formation indicate sedimentation in a shallow marine palaeoenvironment between fair-weather and storm-wave bases. The related ichnoassemblage described above (*Cruziana* ichnofacies) is consistent with this interpretation.

The horizons with Chengjiang-type softpart preservation indicate rapid autochthonous deposition shortly after storm events, whereas the silty beds with fragmented trilobite carapaces and brachiopod shells point to a parautochthonous depositional regime in which carcasses of shelly invertebrates were transported locally by bottom currents (see parting lineation, see Fig. 5E, F) or by storm waves over short distances to their burial sites. Alternating horizons with intense bioturbation (*e.g.*, beds with simple *Planolites*-type trace fossils) could indicate a more ephemeral feeding activity and mass propagation of opportunistic infaunal consumers appearing in the nutrient-rich beds deposited after storm events. Other beds with various vertical burrows, star-shaped traces and arthropod repichnia and cubichnia may be interpreted as the more regular infaunal and epifaunal activity of invertebrates occupying the sea floor between the storm events. The frequent ripple marks and especially the common occurrence of characteristic wrinkle marks (Fig. 3C) in the mudstone-siltstone beds demonstrates the abundance of microbial mats in the Wulongqing sequence and additionally indicates their deposition under shallow marine conditions within the photic zone. The proximal setting and the co-occurrence of beds with Chengjiang-type soft-part preservation of invertebrates (early Cambrian fossil *Lagerstätte*, Hu *et al.* 2010) and beds with episodic high levels of bioturbation (Fig. 3B) within the Wulongqing sequence extend our knowledge about the possible variety of palaeoecology and the related faunal inventory of Chengjiang-type fossil *Lagerstätten* (Hu *et al.* 2010).

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