Furongian (upper Cambrian) Guole Konservat-Lagerstätte from South China

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Abstract: The Guole biota contains common shelly fossils and some exceptionally well-preserved soft-bodied fossils. Stratigraphically, it is located in the mudstones and siltstones of the Sandu Formation near Guole Town, Jingxi County, Guangxi, South China. It is the first Furongian (late Cambrian) Burgess Shale-type biota found in the world, thereby filling the gap between middle Cambrian and Lower Ordovician Burgess Shale-type Lagerstätten. Preliminary studies suggest that the Guole biota includes approximately seven metazoan groups as well as algae. These will provide important new evolutionary and ecological information.

Key words: Cambrian, Furongian, Burgess Shale, soft-bodied fossils, South China

1 Introduction

Burgess Shale-type biotas are critically important in understanding the early evolution of the Metazoa (Conway Morris, 1989; Butterfield, 2003; Briggs and Fortey, 2005). The well-known Cambrian Burgess Shale-type biotas, such as the Burgess Shale (Walcott, 1911), Chengjiang (Zhang and Hou, 1985), Sirius Passet (Conway Morris et al., 1987), Emsa Bay Shale (Glassner, 1979), and Kaili (Zhao et al., 1996), are all restricted to the early and middle Cambrian time interval and have not been found in strata younger than the Guzhangan. A major extinction was proposed to explain the absence of a Furongian lagerstätten (Conway Morris, 1989; Bambach et al., 2004), but the recent discovery of Burgess Shale-type biotas in the Lower Ordovician of Morocco suggested a different explanation (Van Roy et al., 2010; Botting et al., 2015; Martin et al., 2015).

In this study, we describe a new group of exceptionally preserved biota, the Guole biota, from the late Cambrian (Furongian) Sandu Formation near Guole Town, Jingxi County, Guangxi Zhuang Autonomous Region, South China. It is the first report of a diversified Burgess Shale-type biota from the late Cambrian. This new Burgess Shale-type assemblage fills a temporal gap between the middle Cambrian and Lower Ordovician stratigraphic record of Burgess Shall-type Lagerstätten (Fig. 1).

2 Geological Setting

The Guole biota was found in late Cambrian strata near Guole Town, Jingxi County, western Guangxi Zhuang Autonomous Region, South China (Fig. 2a). In the Jingxi

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County and its neighboring area, the late Cambrian strata mainly consist of pelitic carbonate rocks. The lower part of the Furongian succession is not usually exposed, and its upper part is overlain unconformably by the dolomites of the Lower Devonian Huangqiongshan Formation. The associated trilobites (Zhu et al., 2007, 2010) indicate that this biota is equivalent to the Probinacunaspis nasalis-Peichiahsanshia humanensis Zone (middle Furongian, Cambrian Stage 9) of northwestern Hunan.

The late Cambrian strata of this area are traditionally assigned to the Sandu Formation because their lithological features and trilobite fauna are similar to those of the eponymous section of the formation, which lies in Sandu County, Guizhou Province (Guangxi Geological Bureau, 1985). The Sandu Formation is richly fossiliferous, with trilobite elements typical of both platform and basin types. In Cambrian times, the Sandu area of eastern Guizhou and the Jingxi area of western Guangxi were both located in the transitional region (Fig. 2b) between the Yangtze Platform and the Jiangnan Basin (Peng, 2000; Zhou et al., 2008).

Han et al. (2000) investigated this area and measured a section of the Sandu Formation near Guole. They argued that the late Cambrian succession in the Jingxi area was different from that of the Sandu area, both in terms of lithology and lithofacies, and proposed a new formation, the Guole Formation, for the upper Cambrian strata of the Jingxi area. However, the description of the section given by Han et al. (2000) is quite different from that documented by the Guangxi Geological Bureau (1985) and our own observation in the field. We therefore prefer to classify this as the Sandu Formation, rather than the Guole Formation until clearer evidence is available.

The interpretation of the lithofacies of the studied area is controversial, from shelf (Han et al., 2000) to basin (Feng et al., 2001). As the strata in this area are very thick (more than 2000 meters) but crop out sparsely, this difference in opinion may simply reflect changes in the lithofacies of the Jingxi area during the late Cambrian. The paleoenvironmental setting is important to the understanding of the Guole biota, but detailed discussion is beyond the scope of this study.

3 Composition of the Guole biota

Preliminary studies of this biota reveal that more than eight major fossil groups have been recognized, including highly diversified trilobites (Han et al., 2000; Zhu, 2005; Zhu et al., 2007, 2010), non-trilobite arthropods (Lerosey-Aubril et al., 2013), brachiopods (Zhan et al., 2010), echinoderms (Han and Chen, 2008; Chen and Han, 2013; Zamora et al., 2013; Zhu et al., 2014), cnidarians, graptolites (Zhan et al., 2010), hyolithids, palaeocoleoids, and algae. The assemblage is dominated by arthropods, echinoderms, and brachiopods, in both abundance and diversity.

3.1 Trilobites and non-trilobite arthropods

Trilobites, comprising at least 25 genera, are the most dominant animal group in the Guole biota in terms of both abundance and diversity (Han et al., 2000; Zhu, 2005). Only four agnostid genera are present: Micagnostus, Neagnostus, Rhaptagnostus, and Lotagnostus. Other trilobites are polymerids belonging to 15 different families, the most common being Sinosaukia, Tamdaspis, Shergoldia, and Guangxiaspis. Most trilobites are preserved with their fully articulated exoskeletons, probably as a result of obstruction events (Zhu et al., 2010). Soft parts of trilobites, such as antennae and appendages, are rarely preserved, with the exception of the eyes of some species (Fig. 3a). This situation is much similar to that in the Kaili biota, in which the antennae and appendages of trilobites are also absent.

To date three aglaspidids, one Mollisonia-like arthropod, and one bivalved-arthropod have been discovered in the Guole biota. Aglaspidids sensu stricto (as defined by Van Roy, 2006) are the most diverse non-trilobite arthropod group in the Guole biota. They include Aglaspella sanduensis (Lerosey-Aubril, Ortega-Hernández, and Zhu, 2013) (Fig. 3b), Glypharthrus? sp. (Fig. 3c), and an unnamed aglaspidid-like arthropod (Fig. 3d). This marks the first time that aglaspidids have been
discovered in the Cambrian strata of China. The presence of *Aglaspella*, the first aglaspidid genus shared by Laurentia and Gondwana, demonstrates that some aglaspidids *sensu stricto* had great dispersal capabilities and were already widely distributed worldwide by the late Cambrian. There is one *Mollisonia*-like specimen among the non-trilobite arthropods (Fig. 3e). The features of its thoracic tergites and tail shield are similar to those of *Mollisonia symmetrica* (Walcott, 1912) and *M. sinica* (Zhang et al., 2002). Bivalved-arthropods are represented by a *Perspicaris*-like form (Fig. 3f) that is the most abundant non-trilobite arthropod found in the Guole biota.
So far, apart from the eyes of some trilobites the only soft parts of arthropods that have been found in the Sandia Formation are two isolated appendages (Fig. 3g). However, as these appendages are detached, they cannot be assigned to any arthropod group.

3.3 Brachiopods

Brachiopods are abundant and diverse in the Guole biota. They comprise six genera, among which one is new, and seven species including three new taxa and two indeterminate species: Oblidae gen. et sp. indet. and Acrotretidae gen. et sp. indet. Identified brachiopods include Billingsella guangxiensis, B. costata sp. nov., Guoleella lata gen. et sp. nov., Palaeostrophia jingxiensis, and Plectotrophia imparicosta sp. nov. (Zhan et al., 2008). Quantitatively, Billingsella guangxiensis, B. costata, and Palaeostrophia jingxiensis are the most abundant brachiopod components. The Guole brachiopod fauna is therefore provisionally termed the Billingsella-Palaeostrophia Fauna. The shells of brachiopods are calcareous, and no soft tissues have been discovered.

3.4 Cnidarians

Tube-shaped Sphenothallus have been recognized in Paleozoic rocks and interpreted as possible cnidarians (Moore and Harrington, 1956; Zhu et al., 2000; Van Iten et al., 2002; Li et al., 2004; Peng et al., 2005), allied with hydrozoans (Price, 1920) or coryphozoa (Kiderlen, 1937; Moore and Harrington, 1956; Bischoff, 1978). Only one specimen and its counterpart were collected in the Guole biota and are questionably assigned to the genus Sphenothallus (Fig. 3h, i), based on the diagnostic features of a mineralized tube with a pair of oppositely situated longitudinal thickenings. Soft tissues are present inside the tube.

3.5 Echinoderms

Echinoderms rank second in terms of both abundance and diversity. Eight different taxa, belonging to four major groups (edrioasteroids, rhombiferans, solutans, and stylophorans) have been identified (Zamora et al., 2013). This assemblage represents the richest and most diverse Furongian echinoderm fauna in the world. Cambroblastus guoensis (Zhu et al., 2014) (Fig. 4a) has a polyplated stalk, highly ornamented thecal plates, and typical disposition of biserial flooring and cover plates. It is the second recorded Cambrian edrioblastoid edrioasteroid, and the first to preserve a complete stem with a distal holdfast attached to a trilobite pygidium. Two different glyptocystitid rhombiferans are found in the Guole biota. The first is a typical primitive glyptocystitid with four circles of plates in the theca and a lateral anal opening (Fig. 4b). The second has a more complex morphology, with a mixture of glyptocystitid-like features (e.g., lateral positioning of the anal pyramid), and other features that are inconsistent with that classification (e.g., absence of a radial circket) (Fig. 4c). These glyptocystitid rhombiferans are morphologically intermediate between the Cambrian coenocrinoids and the typical rhombiferans. Only one species of solutan has been identified from the Guole biota (Fig. 4d). This articulated solutan is the only complete Furongian specimen known to date and represents the oldest solutan from Gondwana. Stylophorans, traditionally subdivided into the two orders Cornuta and Mitatra, are diverse and abundant in the Guole biota. Cornutes clearly dominate the assemblage, comprising two distinct species: "Phylliocystis" jingxiensis (Han and Chen, 2008) (Fig. 4e-f) and a Drepanocarpus-like hanusii (Fig. 4g-h). Mitrates are less common, comprising a few poorly preserved specimens of a basal mitrocystitid (Fig. 4i), as well as a possible lagynocyst similar to Lagynocystis pyramidalis (Barrande, 1887).

3.6 Graptolites

Graptolites are moderately common in the Guole biota. Callograptus sp., Dicytomena sp., and Dendrograptus sp. have been recognized (Zhan et al., 2008). Most specimens are preserved as broken branches, though occasionally complete ones are found.

3.7 Hyoliths

Hyoliths are common in the Guole biota and are represented by at least three taxa. Their specific identification and nomenclature require more work, which is beyond the scope of this paper. One taxon is very abundant and the microstructures of its shell are well preserved (Fig. 3j-k). The gut fillings have been observed in another taxon (Fig. 3i).

3.8 Palaeoscolecids

Palaeoscolecid worms, which are common in Cambrian Burgess Shale-type Lagerstätten (Han et al., 2007; Hu et al., 2008, 2012), are represented in the Guole biota by at least one undetermined new species (Fig. 4j-k). Palaeoscolecids are moderately common in the Guole biota. Along with elongate trunks, cuticularized sclerites, including plates and microplates, can be observed on the trunk surface (Fig. 4k).

3.9 Algae

Complete algae are very rare in the Guole biota, but fragments are common. A possible alga with frequent dichotomous branching has been discovered (Fig. 3m). Its possible alternative interpretation as a colonial metazoan
can be excluded.

4 Discussions

The discovery of the Guole biota extends the geographic and temporal range of the Konservat-

Lagerstätten of South China. A large number of Burgess Shale-type Lagerstätten have been discovered in South China (Steiner et al., 2005; Zhang et al., 2008; Zhu, 2010; Zeng et al., 2014). These are not evenly distributed through the Cambrian but are mainly concentrated in the lower Cambrian, with only the Kaili biota known from the
middle Cambrian, and none being known from the Furongian until the discovery of the Guole biota. The rarity of lagerstätten in the middle to late Cambrian time interval coincides with the reduction of siliciclastic facies in South China after the early Cambrian (Zhang et al., 2008). A late Cambrian regression has been identified in South China (Mei et al., 2007), North China (Mei et al., 2005; Meng and Ge, 2003), and the North American platform (Osguler and Read, 1991) and seems to have been global (Mei et al., 2007). As a result of this regression, South China was mostly covered by carbonate facies (Mei et al., 2007). Siliciclastic facies, in which Burgess Shale-type biota are usually preserved, became very rare and have been reported from only a few localities, such as western Guangxi and southeastern Guizhou. The discovery of the Guole biota suggests that more soft-bodied lagerstätten fossils may be found in these localities.

The Guole biota is a key source for understanding the evolution of early life. The Guole biota represents the first discovery of a late Cambrian Burgess Shale-type biota, filling the gap in the chronological sequence of exceptionally well-preserved biotas. Comparison of the common elements of such lagerstätten provides more insight into their evolution and time succession. For example, the echinoderm assemblage of the Guole biota, which is dominated by rhombiferans and stylophorans (with few edrioasteroids and solutans), appears to be typical of the so-called worldwide classical “rhombiferan-stylophoran” faunas. This type of echinoderm fauna is generally interpreted as being transitional between the “Cambrian Evolutionary Fauna” and the “Paleozoic Evolutionary Fauna” (Sumrall et al., 1997). The echinoderm fauna of the Guole biota therefore plays an important role in understanding the early evolution of echinoderms.

5 Conclusions

The Guole biota is one of the most diverse and informative Burgess Shale-type biotas found in the Yangtze Plate, South China (e.g., Chengjiang fauna, Kaili fauna, and a series of lower and middle Cambrian soft-bodied biotas). Preliminary investigation has identified more than eight major fossil groups, including arthropods, brachiopods, echinoderms, cnidarians, graptolites, hyolithids, palaeoscolecid, and algae, and further exceptionally well-preserved fossils are expected to be found if more intensive excavation is conducted.

The Guole biota is the first late Cambrian Burgess Shale-type Lagerstätten to be discovered in the world. It fills the gap between middle Cambrian and Ordovician fossil lagerstätten and contributes to our understanding of the evolution of early life.

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