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A review of Silurian fishes from north-western Hunan, China and related biostratigraphy

WENJIN ZHAO[1-3], MIN ZHU[1-3], ZHIKUN GAI[1,2], ZHAOHUI PAN[1,3], XINDONG CUI[1,3] and JIACHEN CAI[1,3]

[1] *Key Laboratory of Vertebrate Evolution and Human Origins of Chinese Academy of Sciences, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, PO Box 643, Beijing 100044, China. E-mails: zhaowenjin@ivpp.ac.cn, zhumin@ivpp.ac.cn, gaizhikun@ivpp.ac.cn, panzhaohui@ivpp.ac.cn, cuixindong1121@163.com, niudunjianongpao@gmail.com*
[2] *CAS Center for Excellence in Life and Paleoenvironment, Beijing 100044, China*
[3] *College of Earth Science, University of Chinese Academy of Sciences, Beijing 100049, China*

ABSTRACT:

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The Silurian fishes from north-western Hunan, China are characterised by the earliest known galeaspids *Dayongaspis* Pan and Zeng, 1985 and *Konoceraspis* Pan, 1992, and the earliest known antiarch *Shimenolepis* Wang J.-Q., 1991, as well as rich sinacanth fin spines. *Shimenolepis* from Lixian County in north-western Hunan, which was dated as the Telychian (late Llandovery), has long been regarded as the oldest representative of the placoderms in the world. As such, in addition to eastern Yunnan and the Lower Yangtze Region, north-western Hunan represents another important area in South China that yields important fossil material for the research of early vertebrates and related stratigraphy. Here we summarise the Silurian fishes known in north-western Hunan so far, and classify them into three vertebrate assemblages (i.e., the Wentang, Maoshan, and Yangtze assemblages). Based on the updated Silurian vertebrate and stratigraphic databases, the Silurian fish-bearing strata in north-western Hunan can be subdivided into the Rongxi, Huixingshao, and Xiaoxi formations in ascending chronological order, which can be correlated with the Lower Red Beds, the Upper Red Beds, and the Ludlow Red Beds in South China, respectively. A new look at the Silurian strata in Lixian suggests that the age of *Shimenolepis* is late Ludlow rather than late Llandovery as previously suggested. The research on Silurian fishes and biostratigraphy in north-western Hunan not only provides morphological data of early vertebrates, but also offers new palaeoichthyological evidence for the subdivision, correlation, and age assignment of the Silurian marine red beds in South China. The establishment of a related high-precision Silurian stratigraphic framework in north-western Hunan will help to elucidate the temporal and spatial distribution of Silurian fossil fishes, deepen the understanding of the evolution of early vertebrates, and unravel the coevolution between Silurian vertebrates and the palaeoenvironment.

Key words: Early vertebrates; Biostratigraphy; Silurian; North-western Hunan; China.

INTRODUCTION

The Silurian is an important period in the evolution of early vertebrates, characterised by the diversification and endemism of jawless fishes and the advent of jawed vertebrates. Recently, nine vertebrate biogeographical provinces have been recognised for the Silurian (Žigaite and Blieck 2013), and South China Province is mainly defined after its endemic members, characterised by galeaspids (Young 1981, 1993; Pan *et al.* 1996; Zhao and Zhu 2010; Žigaite and Blieck 2013). Apart from those basal taxa, such

as *Hanyangaspis* P'an and Liu in P'an *et al.*, 1975, *Changxingaspis* Wang N.-Z., 1991, and *Dayongaspis* Pan and Zeng, 1985, the Silurian galeaspids mainly comprise the eugaleaspidiform lineage (Zhu and Gai 2006; Zhao and Zhu 2014; Zhu *et al.* 2015). The study of the eugaleaspidiform *Shuyu* Gai, Donoghue, Zhu, Janvier and Stampanoni, 2011 from Zhejiang (Lower Yangtze Region) by means of Synchrotron radiation X-ray tomography has provided new insights into the reorganisation of the vertebrate head before the origin of the jaw (Gai *et al.* 2011; Gai and Zhu 2012). Since 2007, we have conducted a series of extensive field investigations and excavations in the Silurian strata from Qujing, eastern Yunnan, which eventually led to the discovery of a series of exceptionally preserved fossil fishes, such as the oldest articulated osteichthyan *Guiyu* Zhu, Zhao, Jia, Lu, Qiao and Qu, 2009, the maxillate placoderms *Entelognathus* Zhu, Yu, Ahlberg, Choo, Lu, Qiao, Qu, Zhao, Jia, Blom and Zhu, 2013 and *Qilinyu* Zhu, Ahlberg, Pan, Zhu, Qiao, Zhao, Jia and Lu, 2016 (Zhu *et al.* 2009, 2013, 2016). Those fossil fishes have offered insights into the origin and early divergence of osteichthyans and illuminated the jaw evolution (Coates 2009; Friedman and Brazeau 2013; Long 2016). In addition to eastern Yunnan and the Lower Yangtze Region, many Silurian fossil fishes have been found from north-western Hunan since the 1980s, making it another important area in South China for the research of early vertebrates.

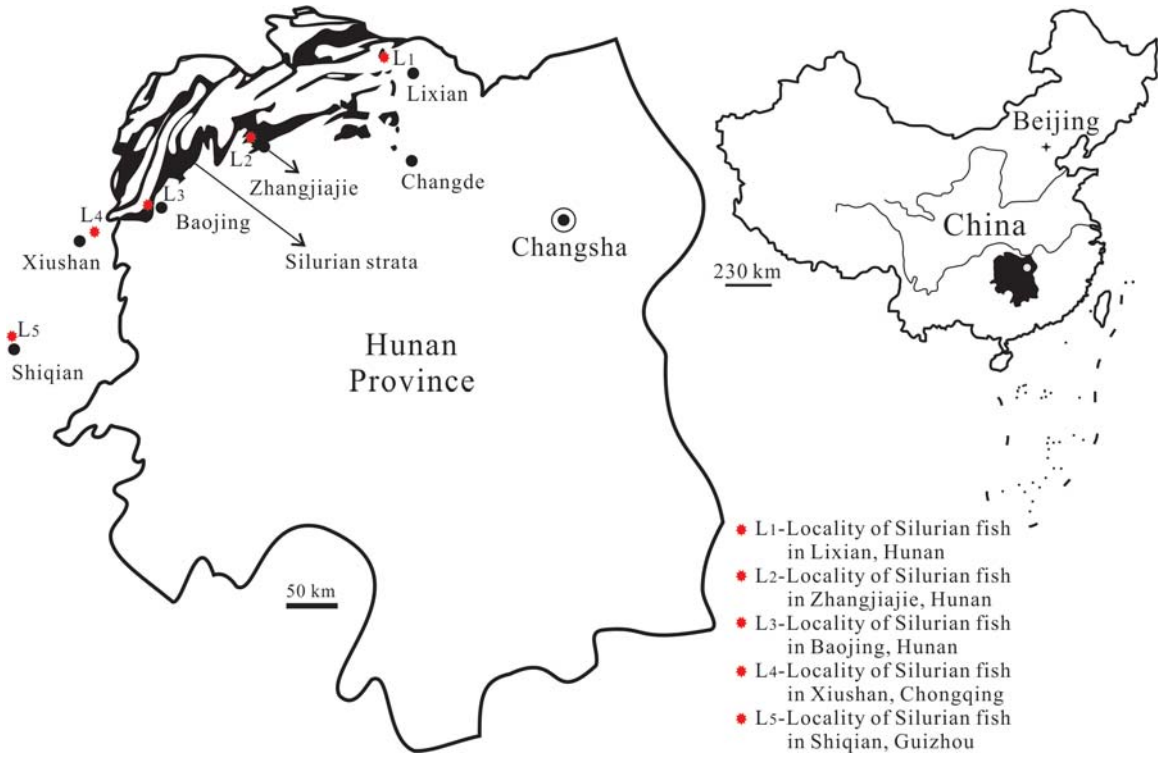
So far, the Silurian fossil fishes from north-western Hunan are mainly dominated by galeaspids, placoderms, and sinacanths, which are most likely referred to the chondrichthyan lineage according to detailed histological studies (Zhu 1998; Sansom *et al.* 2005). The galeaspids are represented by the basal galeaspids from the Rongxi Formation in Zhangjiajie, north-western Hunan, such as *Dayongaspis hunanensis* Pan and Zeng, 1985 and *Konoceraspis grandoculus* Pan, 1992 (Pan and Zeng 1985; Pan 1992). The placoderms include the antiarch *Shimenolepis graniferus* Wang J.-Q., 1991 and an indeterminate taxon of the Chuchinolepidae Chang, 1978 from a fish bed in Lixian, which was originally dated as Telychian (Llandovery Series; Wang J.-Q. 1991). In 1988, Zeng first described some sinacanth fin spines from the Silurian of Wentang, Zhangjiajie. Later, Liu (1997) described additional sinacanth fin spines from the Silurian of Lixian. Based on histological studies, both Zhu (1998) and Sansom *et al.* (2005) suggested that the sinacanth fin spines should be referred to the chondrichthyans, rather than the acanthodians, although further evidence was required both on the general anatomy of sinacanths and on the nature of chondrichthyan synapomorphies. Recent phylogenetic analyses of early gnathostomes consistently assign all acanthodians to the total-group chondrichthyans (Zhu *et al.* 2013, 2016; Long *et al.* 2015; Qiao *et al.* 2016); accordingly, the discrimination between acanthodians and conventionally-defined chondrichthyans turns out to be less crucial. Since 2008, we have conducted a series of extensive field investigations and excavations in the Silurian marine deposits of north-western Hunan. Some new findings of Silurian fishes not only increase our knowledge of Silurian vertebrate diversity, but also provide critical data in the quest for early vertebrate evolution and reliable palaeoichthyological evidence for regional stratigraphic issues, exemplified by the subdivision and correlation of Silurian fish-bearing strata, and the age assignment of Silurian marine red beds in South China.

The main aims of this paper are to: (1) summarise the Silurian fossil fishes thus far known in north-western Hunan, (2) discuss the Silurian vertebrate assemblages and faunas of north-western Hunan, and (3) use the updated Silurian vertebrate database to elucidate some biostratigraphic issues.

SILURIAN FISHES FROM NORTH-WESTERN HUNAN

As early as 1975, the Regional Geological Survey Team of the Bureau of Geology and Mineral Resources of Hunan Province discovered some fish fragments in the Silurian of Hunan. However, these fragments have not been described. Systematic research on the Silurian fishes from north-western Hunan began in 1985, and focused mainly on galeaspids from the Zhangjiajie region (Pan and Zeng 1985). Later reports described some sinacanths and placoderms (Zeng 1988; Wang J.-Q. 1991; Liu 1997; Zhu 1998), which were respectively collected from Zhangjiajie, Baojing and Lixian regions (Text-fig. 1) in north-western Hunan (Zhao *et al.* 2016).

The Silurian galeaspids from north-western Hunan mainly include *Dayongaspis hunanensis* (Text-fig. 2A) and *Konoceraspis grandoculus* (Text-fig. 2B) from the Rongxi Formation in Zhangjiajie (Pan and Zeng 1985; Pan 1992). In addition, there is an undescribed eugaleaspid *Eugaleaspis* cf. *E. xiushanensis* Liu, 1983, collected from the Xiaoxi Formation in Baojing (Pan 1986). Subsequently, the Silurian *E. xiushanensis* and *E.* cf. *E. xiushanensis* have been redefined as *Dunyu xiushanensis* and

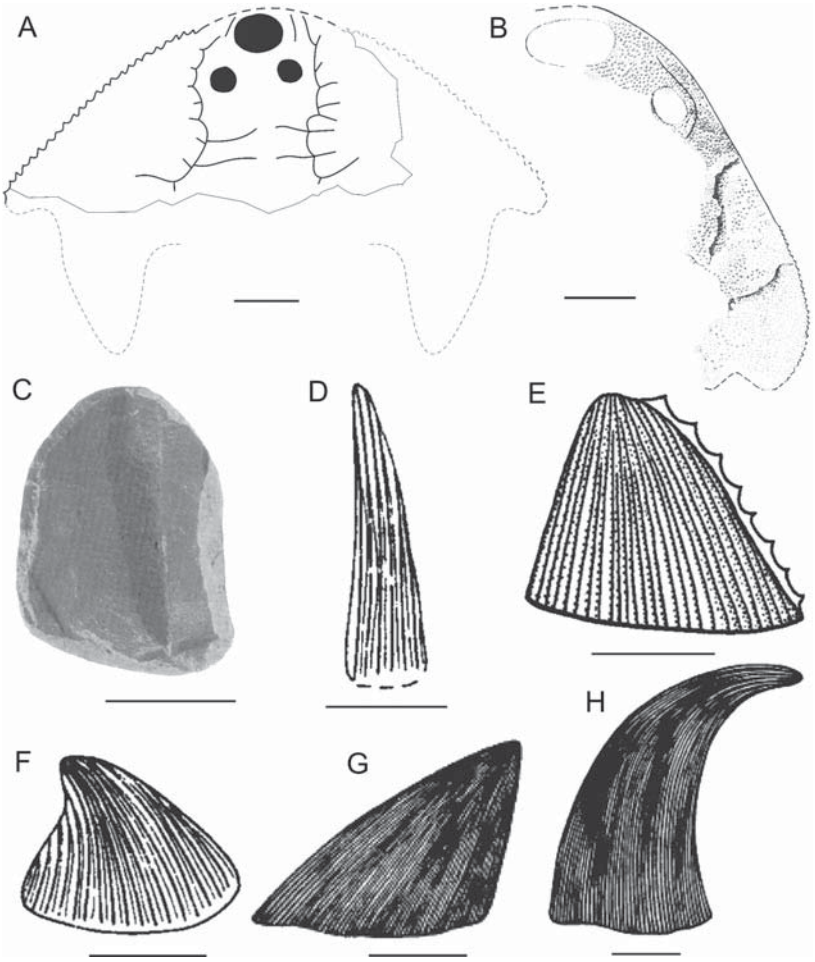


Text-fig. 1. Map showing the outcrop distribution of Silurian strata and the localities of Silurian fossil fishes in north-western Hunan (L_1–L_3) and neighbouring provinces (L_4, L_5), China

D. cf. *D. xiushanensis* because of the presence of posteriorly extending corners, which are absent in the Devonian *Eugaleaspis* spp. (Zhu *et al.* 2012). Galeaspids, a diverse group of jawless vertebrates, first appeared in the Llandovery (early Silurian), flourished in the Early Devonian, and survived until the Late Devonian (Zhu and Gai 2006). Both *D. hunanensis* and *K. grandoculus*, the basal members of the galeaspids (Zhu and Gai 2006), are the oldest galeaspids, dating to the Telychian (late Llandovery).

Pan (1986) reported a basal placoderm (*Wangolepis sinensis* Pan, 1986) from the Xiaoxi Formation in north-western Hunan, but gave no description and thus rendered it a *nomen nudum* (Zhu and Wang 2000). The described Silurian placoderms from north-western Hunan are mainly represented by a few antiarch specimens originally thought to be collected from the Xiushan Formation in Lixian (Wang J.-Q. 1991). They are assigned as *Shimenolepis graniferus* (Text-fig. 2C) and an indeterminate taxon of the Chuchinolepidae. With a Telychian age, *S. graniferus* was regarded as the oldest known placoderm (Wang J.-Q. 1991; Janvier 1996). However, a new look at the Silurian strata in Lixian suggests that *S. graniferus* was collected from the Xiaoxi Formation and its age is late Ludlow rather than late Llandovery as previously suggested (Zhao *et al.* 2016).

The Silurian sinacanth chondrichthyans are mainly characterised by their fin spines. Zeng (1988) first described seven types of fin spines from Wentang, Zhangjiajie region. Based on a detailed histological study, Zhu (1998) assigned these sinacanth fin spines from Zhangjiajie to several genera and species, such as the fin spine 5 to *Sinacanthus wuchangensis* P'an, 1959 (Text-fig. 2D), fin spine 4 to *Sinacanthus* sp., fin spine 2 to *Neosinacanthus planispinatus* P'an and Liu in P'an *et al.*, 1975 (Text-fig. 2E), fin spine 1 to *Neosinacanthus* sp. 1, fin spine 7 to *Neosinacanthus* sp. 2, and fin spine 3 to *Tarimacanthus bachuensis* Zhu, 1998 (Text-fig. 2F). From Lixian, another locality in north-western Hunan, Liu (1997) described four genera and species of sinacanths, including *Eosinacanthus shanmenensis* Liu, 1997 (Text-fig. 2G), *Hunanacanthus lixianensis* Liu, 1997 (Text-fig. 2H), *Neosinacanthus* sp., and *Sinacanthus* sp. These fin spines were mainly collected from the upper part of the Rongxi Formation, whose age is the early Telychian (late Llandovery; Zhao and Zhu 2010,



Text-fig. 2. Fossil fishes from the Silurian of north-western Hunan. **A** – reconstruction of *Dayongaspis hunanensis* Pan and Zeng, 1985. **B** – reconstruction of *Konoceraspis grandoculus* Pan, 1992. **C** – *Shimenolepis graniferus* Wang J.-Q., 1991, an incomplete left posterior plate (internal mould), ventral view. **D** – reconstruction of *Sinacanthus wuchangensis* P'an, 1959 (based on Zeng 1988 and Zhu 1998). **E** – reconstruction of *Neosinacanthus planispinatus* P'an and Liu in P'an *et al.*, 1975 (based on Zeng 1988 and Zhu 1998). **F** – reconstruction of *Tarimacanthus bachuensis* Zhu, 1998 (based on Zeng 1988). **G** – reconstruction of *Eosinacanthus shanmenensis* Liu, 1997. **H** – reconstruction of *Hunanacanthus lixianensis* Liu, 1997. Scale bars = 10 mm

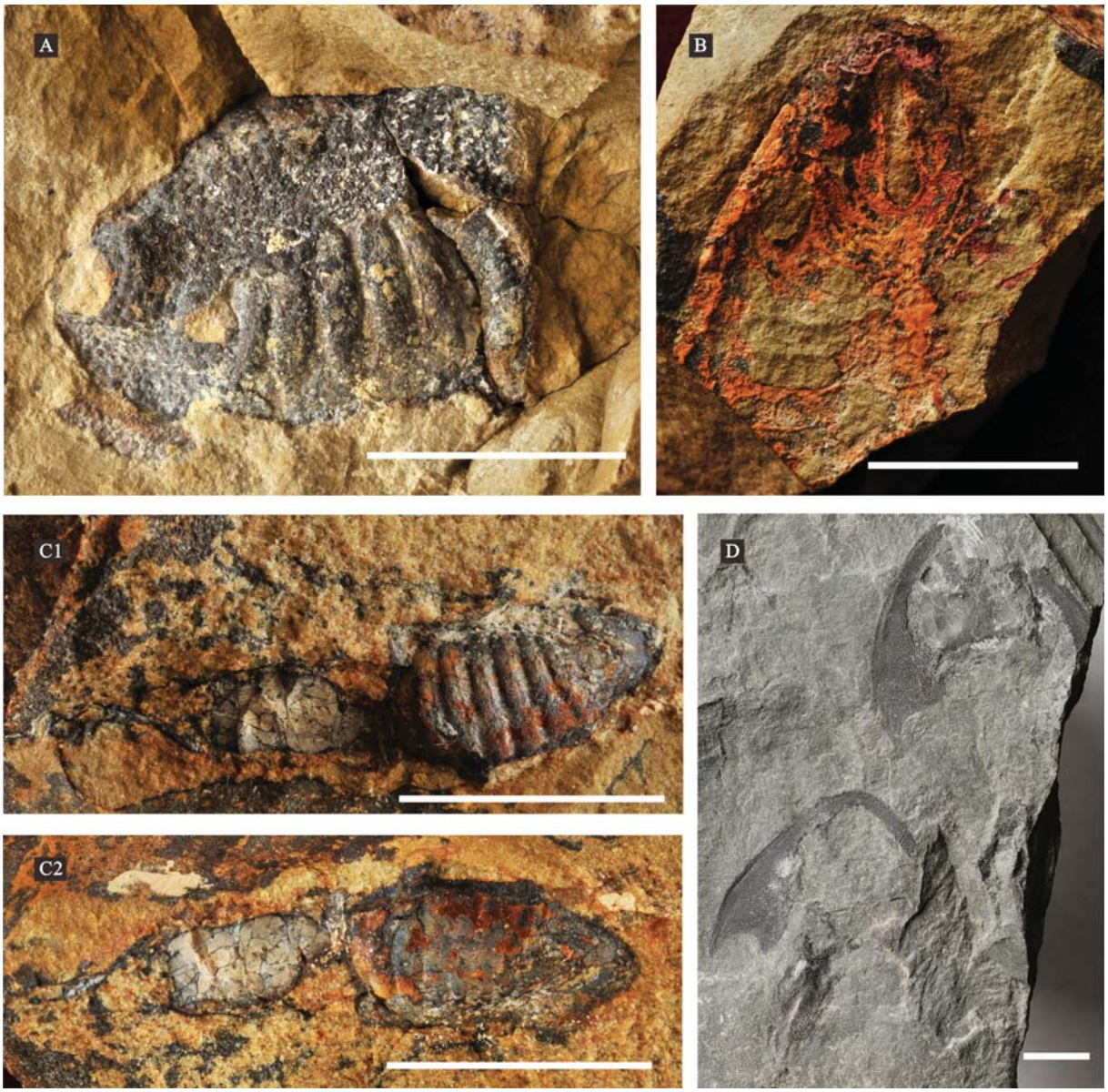
2014; Zhao *et al.* 2016). Despite their fragmentary nature, these fin spines have not only increased the diversity of Silurian fishes, but also provided reliable palaeoichthyological evidence for regional stratigraphic correlation in South China.

During the last five field investigations and excavations since 2008, we found a large amount of fossil fish material (Text-figs 3A–D and 4A–D) in the Silurian strata exposed in north-western Hunan.

This new material includes well-preserved galeaspids (Text-fig. 3A–D), sinacanth fin spines (Text-fig. 4A, B), and maxillate placoderms (Text-fig. 4C, D), from different localities and horizons, including the Rongxi, Huixingshao, and Xiaoxi formations in ascending order (Text-fig. 5; Zhao *et al.* 2016). The new findings of Silurian fishes, together with rich invertebrate remains (Text-fig. 4E, F, e.g., brachiopods, trilobites) and trace fossils (Text-fig. 4G), will make north-western Hunan as another important area in South China for the research of Silurian palaeontology and stratigraphy.

SILURIAN VERTEBRATE ASSEMBLAGES AND FAUNAS IN NORTH-WESTERN HUNAN

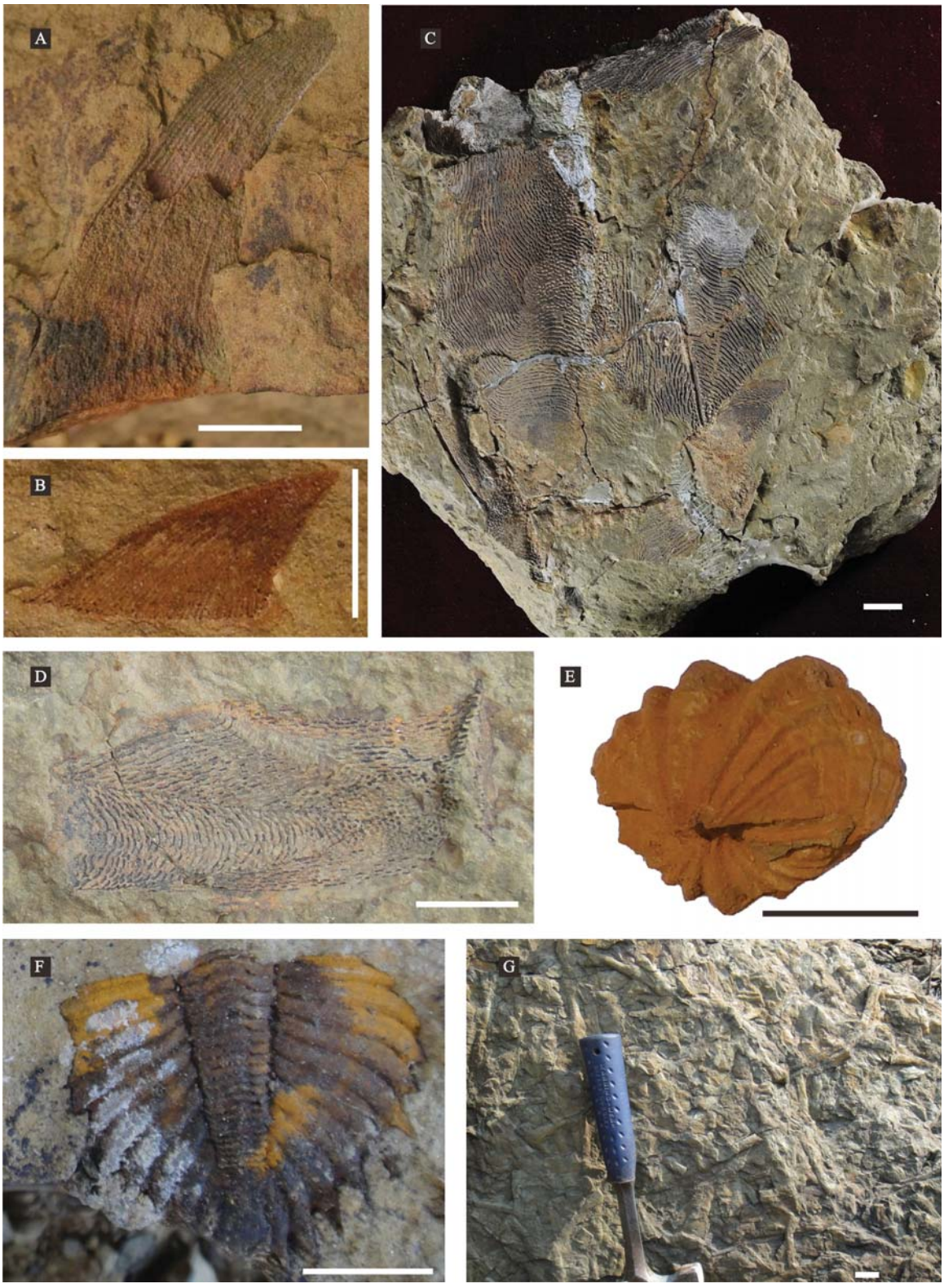
Two vertebrate faunas (Zhangjiajie and Xiaoxiang faunas) and three vertebrate assemblages (Wentang, Maoshan, and Yangtze assemblages) are recognised for the fossil fishes from the Silurian of north-west-



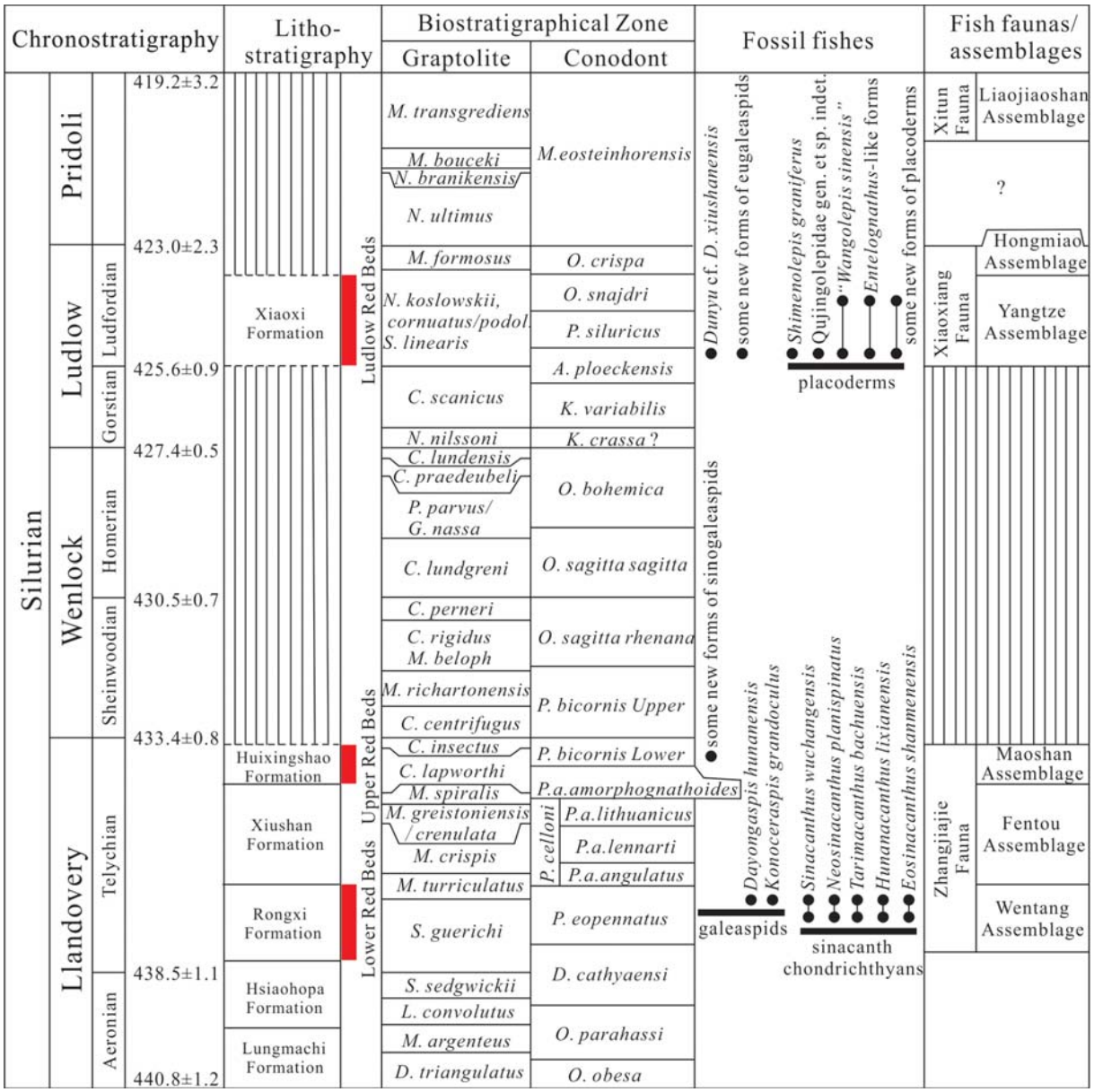
Text-fig. 3. New findings of agnathans from the Silurian of north-western Hunan. A-C – new forms of eugaleaspidiform galeaspids collected from the Huixingshao Formation in Lixian. D – a new eugaleaspidiform galeaspid collected from the Huixingshao Formation in Baojing. Scale bars = 10 mm

ern Hunan (Text-fig. 5; Zhao and Zhu 2010, 2014; Zhao *et al.* 2016).

The Zhangjiajie Vertebrate Fauna was reformulated from the Xiaoxiyu Fauna (Zhao and Zhu 2010) by Zhao and Zhu (2014). It consists of three vertebrate assemblages in South China, i.e., the Wentang, Fentou, and Maoshan assemblages. Only two of these three assemblages (Wentang and Maoshan assemblages) have been identified in north-western Hunan. The missing Fentou assemblage is characterised by some remains of the Mongolepididae Karatajūtė-Talimaa and Novitskaya in Karatajūtė-Talimaa *et al.*, 1990 and Shiqianolepidae Sansom, Aldridge and Smith, 2000 (Chondrichthyes), and mainly distributed in Shiqian of Guizhou Province. More work is needed to identify the Fentou assemblage in north-western Hunan. This fish fauna is characterised mainly by the occurrence of the basal taxa of galeaspids and the flourishing of eugaleaspidiform galeaspids and sinacanths. In age, this



Text-fig. 4. New findings of gnathostomes, invertebrate fossils and trace fossils from the Silurian of north-western Hunan. A, B – sinacanth fin spines from the Rongxi Formation in Lixian. C, D – new forms of placoderms collected from the Xiaoxi Formation in Lixian (C) and Zhangjiajie (D). E, F – invertebrate remains from the Xiushan Formation in Lixian; E – brachiopod; F – trilobite. G – stout tubular trace fossils from the Xiaoxi Formation in Zhangjiajie. Scale bars = 10 mm



Text-fig. 5. Stratigraphical range of Silurian fossil fishes from north-western Hunan. The Silurian fish-bearing beds in north-western Hunan are mainly known from three lithostratigraphic units, the Rongxi, Huixingshao and Xiaoxi formations in ascending order, which can be correlated with the Lower Red Beds, the Upper Red Beds, and the Ludlow Red Beds in South China, respectively. The graptolite and conodont biozones cited here are based on Sadler *et al.* (2009) and Wang (2011), respectively

fauna is restricted to the Telychian (late Llandovery), lasting for about 5 million years.

The Wentang Vertebrate Assemblage, mainly distributed in Zhangjiajie (formerly Dayong) and Lixian, north-western Hunan, is represented by the fish remains from the Rongxi Formation, or the 'Lower Marine Red Beds' (Zhao and Zhu 2010). It is characterised by the appearance of the basal taxa of galeaspids and the flourishing of sinacanths. The assemblage includes the galespids *Dayongaspis hunanensis* (Text-fig. 2A) and *Konoceraspis grandoculus* (Text-fig. 2B) from Wentang, Zhangjiajie, and diversified sincanths from both Zhangjiajie and Lixian (Pan and Zeng 1985; Zeng 1988; Pan 1992; Liu 1997; Zhu 1998), comprising *Sinacanthus wuchangensis* (Text-fig. 2D), *Neosinacanthus planispinatus* (Text-fig. 2E), *Tarimacanthus bachuensis* (Text-fig. 2F), *Eosinacanthus shanmenensis* (Text-fig. 2G), and

Hunanacanthus lixianensis (Text-fig. 2H). Some invertebrate remains, such as brachiopods, trilobites, chitinozoans, and graptolites (Chen and Rong 1996; Holland and Bassett 2002), indicate that the age of the assemblage is early Telychian (late Llandovery, Silurian; Zhao and Zhu 2014).

The Maoshan Vertebrate Assemblage is mainly characterised by the flourishing of xiushuiaspids (basal galeaspids) and sinogaleaspids (eugaleaspidiform galeaspids). The reported fossil fishes from the assemblage were mainly found in the lower part of the Maoshan Formation in the Lower Yangtze Area (Zhao and Zhu 2010, 2014), including the xiushuiaspids *Xiushuiaspis* Pan and Wang, 1983, *Changxingaspis*, and the sinogaleaspids *Shuyu*, *Sinogaleaspis* Pan and Wang, 1980, *Meishanaspis* Wang N.-Z., 1991, and *Anjiaspis* Gai and Zhu, 2005 (Zhu *et al.* 2015). Some well-preserved new forms of sinogaleaspids (Text-fig. 3A–C) were found from the Huixingshao Formation, or the 'Upper Marine Red Beds' in Lixian, and these findings extend the distribution of the fish assemblage to north-western Hunan. According to the age of the underlying upper Xiushan Formation with its index invertebrate fauna, we can place the age of the Maoshan Vertebrate Assemblage in the late Telychian (Zhao and Zhu 2010, 2014).

The Xiaoxiang Vertebrate Fauna was first named by Zhu and Zhao (2009) based on the findings of gnathostomes in the 'Ludlow Marine Red Beds' of Qujing, Yunnan Province. The fauna, including two vertebrate assemblages (Yangtze and Hongmiao assemblages), is characterised by the radiation of placoderms and acanthodians, and the early occurrence and divergence of osteichthyans (Zhao and Zhu 2014, 2015). We can only recognise the Yangtze Vertebrate Assemblage in north-western Hunan. The age of the Xiaoxiang Vertebrate Fauna is restricted to the Ludfordian (late Ludlow), lasting for about 2.6 million years.

The Yangtze Vertebrate Assemblage, from the lower part of the Yuejiashan Formation to the upper part of the Kuanti Formation in Qujing, Yunnan, is mainly represented by the eugaleaspid *Dunyu longiforus* Zhu, Liu, Jia and Gai, 2012, placoderms *Entelognathus primordialis* Zhu, Yu, Ahlberg, Choo, Lu, Qiao, Qu, Zhao, Jia, Blom and Zhu, 2013, *Qilinyu rostrate* Zhu, Ahlberg, Pan, Zhu, Qiao, Zhao, Jia and Lu, 2016, and "*Wangolepis sinensis*" (Pan 1986; Zhu *et al.* 2012, 2013, 2016), and osteichthyans *Guiyu oneiros* Zhu, Zhao, Jia, Lu, Qiao and Qu, 2009, *Megamastax amblyodus* Choo, Zhu, Zhao, Jia and Zhu, 2014 and *Sparalepis tingi* Choo, Zhu, Qu, Yu, Jia and Zhao, 2017 (Zhu *et al.* 2009; Choo *et al.* 2014, 2017). The comparison between *Dunyu* and *Eugaleaspis xiushanensis* suggests that both *E. xiushanensis* from the Xiaoxi Formation in Xiushan, Chongqing and *E.* cf. *E. xiushanensis* from Baojing, north-western Hunan can be reassigned to *Dunyu* (Zhu *et al.* 2012). The high diversity of placoderms and osteichthyans from the Ludlow of Yunnan, suggests that the South China Block might have been an early centre of diversification for early gnathostomes, well before the advent of the Devonian "Age of Fishes" (Choo *et al.* 2017). Although the osteichthyans have not been recorded in the Ludlow strata of north-western Hunan, the basal placoderm "*Wangolepis sinensis*" and the undescribed eugaleaspid *Dunyu* cf. *D. xiushanensis*, together with some new maxillate placoderm materials (Text-fig. 4C, D) from the Xiaoxi Formation in Baojing, Lixian and Zhangjiajie areas of north-western Hunan, clearly assign these fossil fishes to the Yangtze Vertebrate Assemblage. As mentioned above, the antiarchs *Shimenolepis graniferus* (Text-fig. 2C) and an indeterminate taxon of the Chuchinolepidae (Wang J.-Q. 1991) were collected from the Xiaoxi Formation rather than the Xiushan Formation. Based on rich phytodebris microfossils in the Xiaoxi Formation of north-western Hunan (Wang *et al.* 2010) and the Silurian conodont zonation in Qujing (fish beds immediately beneath the first appearance of *Ozarkodina crispa* (Walliser, 1964) in Zhu *et al.* 2009), the Yangtze Assemblage can be assigned to the late Ludlow, probably early to middle Ludfordian (Zhao and Zhu 2014, 2016).

SILURIAN BIOSTRATIGRAPHY OF FISH-BEARING STRATA IN NORTH-WESTERN HUNAN

The Silurian marine strata in north-western Hunan include the Lungmachi, Hsiaohopa, Rongxi, Xiushan, Huixingshao and Xiaoxi formations in ascending chronological order. The fish-bearing strata, including the Rongxi, Huixingshao and Xiaoxi formations, are well exposed in the Shanmen Reservoir of Lixian, Wentang of Zhangjiajie, and Kapeng Reservoir of Baojing (Text-fig. 1; Zhao *et al.* 2016). The same deposits are also distributed in Xiushan of Chongqing Municipality, and Shiqian of Guizhou Province (Text-fig. 1; Chen and Rong 1996; Wang *et al.* 2011; Rong *et al.* 2012). The lower fish-bearing Rongxi Formation, conformably overlain by the Xiushan Formation (Text-fig. 5), is generally thicker (usually 200–500 m) in north-western Hunan, and mainly consists of purple-red and grey-green argillaceous siltstones intercalated with shales. The middle

fish-bearing Huixingshao Formation, conformably overlying the Xiushan Formation (Text-fig. 5), is about 85 to 350 m thick, and commonly dominated by grey-green and purple-red (less) argillaceous siltstones, silty mudstones intercalated with fine sandstones. Abundant tiny tubular trace fossils are well developed in the formation. The upper fish-bearing Xiaoxi Formation, about 97 to 180 m thick, was redefined and reformulated from the Xiaoxiyu Formation (Wang *et al.* 2010; Zhao *et al.* 2016). It is characterised by yellowish-green and few purple-red argillaceous siltstones, silty mudstones intercalated with fine sandstones, yielding abundant stout tubular trace fossils. Both the contact relationships with the underlying Huixingshao Formation and overlying Yuntaiguan Formation (Middle Devonian) are parallel unconformities (Text-fig. 5). Based on the data from our geological investigations since 2008, we suggest that the Silurian fish-bearing strata in north-western Hunan correlate well with the Lower Red Beds, the Upper Red Beds, and the Ludlow Red Beds in South China respectively (Text-fig. 6; Zhao *et al.* 2016). The Rongxi Formation yields mainly sinacanth fin spines and the basal taxa of galeaspids, whereas the Huixingshao Formation yields some sinogaleaspids, and the Xiaoxi Formation yields some *Dunyu*-like eugaleaspids and maxillate placoderms, providing reliable palaeoichthyological evidence for regional stratigraphic correlation in South China.

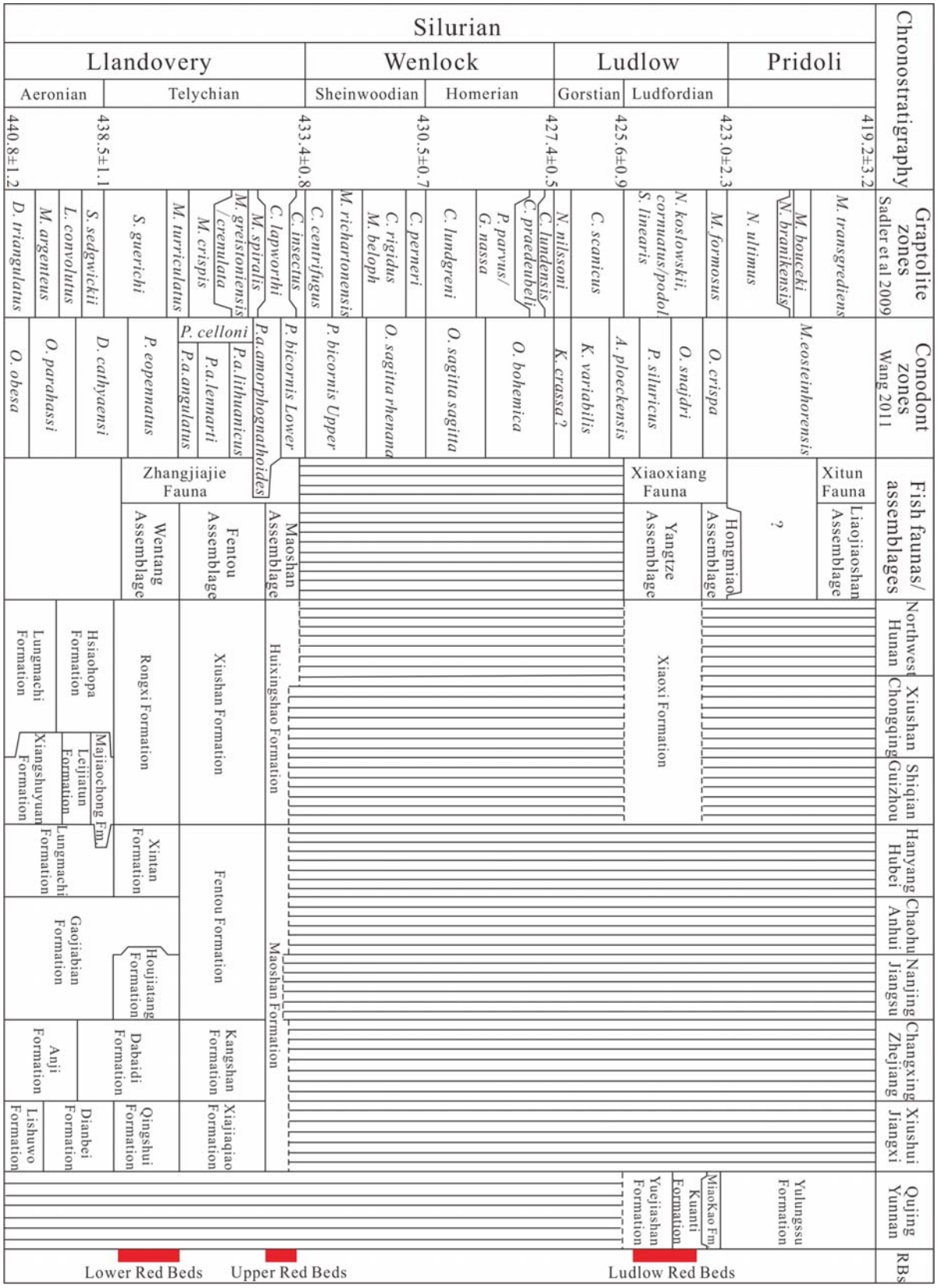
The Silurian marine red beds are known to be distributed widely in China (Rong *et al.* 2012). In South China they generally include three horizons: the Lower Red Beds (e.g., the Rongxi Formation), the Upper Red Beds (e.g., the Huixingshao Formation), and the Ludlow Red Beds (e.g., the Xiaoxi Formation) (Wang *et al.* 2010; Rong *et al.* 2012; Zhao and Zhu 2014, 2015; Zhao *et al.* 2016). They are of inner shelf shallow water origin (Rong *et al.* 2012). During the Silurian period, Xiushan Bay, an important sedimentary basin, developed along the southern coast of the Upper Yangtze Sea. The iron-rich sediments might have been transported by rivers on the Cathaysian hinterland into the Upper Yangtze Sea during different time intervals. The three Silurian marine red beds in South China are usually characterised by a distinct red colour and relatively stable stratigraphic position, making them easily recognisable for regional stratigraphic correlation (Rong *et al.* 2012). This correlation is supported by the updated data of Silurian vertebrate material from South China (Zhao and Zhu 2010, 2014, 2015; Zhao *et al.* 2016). Based on the new data of Silurian fossil fishes in north-western Hunan, together with different kinds of invertebrate fossils and lithostratigraphic changes, the Silurian fish-bearing strata in north-western Hunan correlate well with those exposed in other parts of South China (Zhao and Zhu 2010, 2014, 2015; Zhao *et al.* 2016). For example, the Rongxi Formation can be correlated with the Qingshui Formation in Xiushui, Jiangxi Province, the Huxingshao Formation can be correlated with the Maoshan Formation in Lower Yangtze Region, and the Xiaoxi Formation can be correlated with the Yuejiashan and Kuanti formations in Qujing, Yunnan Province (Text-fig. 6).

Noteworthy here is the horizon and age of *Shimenolepis graniferus*. As the earliest known antiarch, *S. graniferus* was assumed to be collected from the Xiushan Formation, sandwiched between the Rongxi Formation (Lower Red Beds) and the Huixingshao Formation (Upper Red Beds). Due to the lack of detailed stratigraphic works, its exact horizon remained contentious for a long time. Based on the data from our geological investigations since 2008, we have confirmed that *S. graniferus* was collected from the Xiaoxi Formation (Ludlow Red Beds) rather than the Xiushan Formation around the Shanmen Reservoir in Lixian and its age should be late Ludlow rather than late Llandovery as previously suggested (Zhao *et al.* 2016). Nevertheless, *S. graniferus* is still the earliest known antiarch.

CONCLUSIONS

The Silurian strata in north-western Hunan, China yield rich early vertebrate faunas, characterised by the galeaspids *Dayongaspis* and *Konoceraspis*, the sinacanth chondrichthyans *Sinacanthus*, *Neosinacanthus*, *Hunanacanthus*, *Eosinacanthus* and *Tarimacanthus*, the placoderms *Shimenolepis* and "*Wangolepis*", and some new forms waiting for further study. These Silurian fossil fishes make north-western Hunan another important area in South China for providing new data for the study of early vertebrates and related stratigraphy.

The Silurian strata in north-western Hunan include the Lungmachi, Hsiaohopa, Rongxi, Xiushan, Huixingshao and Xiaoxi formations in ascending chronological order. The Silurian fish-bearing strata in north-western Hunan, including the Rongxi, Huxingshao, and Xiaoxi formations, can be correlated with the Lower Red Beds, the Upper Red Beds, and the Ludlow Red Beds in South China respectively. The horizon of *Shimenolepis graniferus* was revised to be the Xiaoxi Formation rather than the Xiushan Formation as previously suggested, and its age is late



Text-fig. 6. Correlation of the Silurian fish-bearing strata in South China

Ludlow rather than late Llandovery. Continued study of Silurian fossil fishes from north-western Hunan and the related stratigraphy can not only provide the critical data in the quest for early vertebrate evolution, but also offer new palaeoichthyological evidence for the subdivision, correlation, and age assignment of Silurian marine red beds in South China.

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